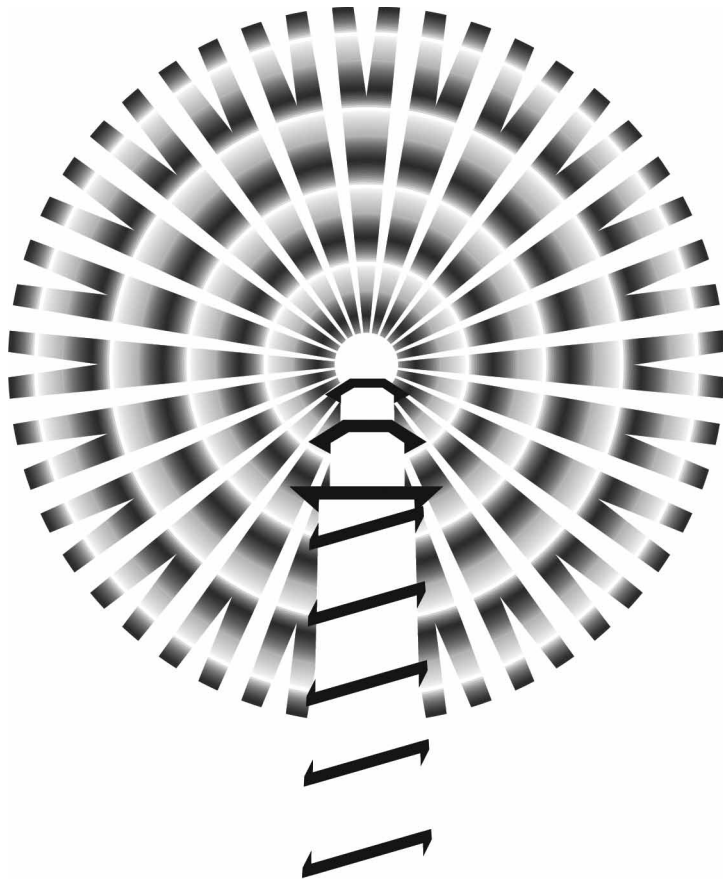


PERCEPTION

VOLUME 34

SUPPLEMENT



XXVIII

Annual Meeting

EUROPEAN
CONFERENCE
ON VISUAL
PERCEPTION

A Coruña - Spain

2005

Abstracts

Twenty-eighth European Conference on Visual Perception

A Coruña, Spain

22 – 26 August 2005

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Acknowledgements

ECVP2005 logo by Diego Uribe (winner of the ECVP2005 Logo Contest, sponsored by SR Research Ltd).
ECVP2005 website by Thomas Dyar.

Administrative assistance by Shannon Bentz and Elizabeth Do, and Carolina Martínez-Conde-García.

Special thanks to the following organisations for their support of ECVP2005:

ConferenceSoft.com, Congrega S.L., PALEXCO, and Pion Ltd.

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ECVP '05 Abstracts

MONDAY

SYMPOSIUM

VISUAL CIRCUITS AND PERCEPTION SINCE RAMON Y CAJAL

◆ Specificity of feedforward connections within the visual pathway

J-M Alonso, C-I Yeh, C Weng, J Jin (SUNY College of Optometry, Department of Biological Sciences, 33 West 42 Street, New York, NY 10036, USA; e-mail: jalonso@sunyopt.edu)

Humans can judge whether a line is located to the left or right of a point of reference with a precision of 5 s of arc. This exceedingly high spatial resolution requires not only a large number of small and densely packed photoreceptors but also a precise wiring of the visual pathway. This exquisite wiring is a main characteristic of retinogeniculate and geniculocortical connections. In the cat, each divergent retinal afferent makes connection with just a few neurons (~20) within the lateral geniculate nucleus (LGN) and the strongest connections are reserved for neurons that have very similar response properties (eg two on-centre cells with nearly identical receptive field positions and sign). In addition to the strong connections, each geniculate neuron receives weaker inputs from other retinal afferents that contribute to enhancing the diversity of receptive field sizes that represent each point of visual space in LGN. The specificity of the retinogeniculate pathway is replicated at the next processing stage in the thalamocortical pathway. Each neuron within layer 4 of primary visual cortex receives input from a selected group of geniculate afferents that share certain response properties in common (eg two on-centre cells with adjacent receptive fields). It is usually assumed that 1000 geniculate afferents converge at the same cortical point, and that each layer 4 cortical cell 'chooses' 30 of these afferents as input. However, recent measurements of the synaptic currents generated by single geniculate afferents in the cortex indicate that number of 'choices' available to a layer 4 cell may be more reduced than previously thought. In that sense, the thalamocortical pathway could be specific by two counts—by providing a selected group of afferents to each cortical point and by selecting a subgroup of these afferents to feed a common cortical cell.

[Supported by NIH-EY05253 and SUNY Research Foundation.]

◆ Parallel geniculocortical pathways and local circuits in primary visual cortex

E M Callaway (Systems Neurobiology Laboratories, The Salk Institute for Biological Studies, 10010 North Torrey Pines Road, La Jolla, CA 92037, USA; e-mail: callaway@salk.edu)

The functional properties of LGN input to various layers in primate V1 were investigated by recording from the terminal arbors of LGN afferents within V1, following muscimol inactivation of V1 neurons. Of particular interest was the identification of the functional properties of LGN input to superficial layers and elucidation of the pathways that carry red/green versus blue/yellow colour-opponent input to V1. Red/green colour-opponent afferents were found exclusively in the parvocellular-recipient layer 4C β , while blue/yellow opponency was found only in afferents terminating above layer 4C, in layers 4A and 2/3. Furthermore, within the blue/yellow opponent populations, 'blue-ON' and 'blue-OFF' inputs were segregated. Blue-OFF inputs were found in layer 4A and blue-ON extended from layer 4A into layer 3. Achromatic afferents were found, as expected, in the magnocellular-recipient layer 4C α . These observations indicate that blue-ON, blue-OFF, and red/green opponent LGN neurons are anatomically distinct neuronal populations that provide parallel input to V1. Red/green opponency appears to be carried exclusively by the parvocellular pathway, while blue-ON input comprises part of the koniocellular pathway. Blue-OFF input most likely arises from a subset of parvocellular neurons that targets layer 4A, but may instead be part of the koniocellular pathway. A variety of anatomical and physiological methods in brain slices was used to study local circuitry within V1, downstream of the afferent magno-, parvo- and koniocellular pathways. These local circuits provide substrates for extensive mixing of inputs within V1, such that the V1 outputs represent novel, resynthesised pathways and not a simple continuation or elaboration of the retino-geniculocortical pathways.

[Supported by NIH/NEI.]

Monday

◆ **Patterns of connectivity of interneurons expressing calcium-binding proteins in visual areas of the occipital and temporal lobes of the primate**

J DeFelipe (Cajal Institute, CSIC, Avenida Doctor Arce 37, E 28002 Madrid, Spain; e-mail: defelipe@cajal.csic.es)

Cytoarchitectonics, myeloarchitectonics, and patterns of long-range connections have been the main basis for subdividing the neocortex into distinct areas and for trying to correlate anatomical characteristics with the functional subdivisions of the cortex. However, relatively little is known about differences in the microcircuitry involving pyramidal cells with interneurons or between interneurons. The majority of interneurons are GABAergic and specific subpopulations of these neurons are immunoreactive for the calcium-binding proteins calbindin (CB), calretinin (CR), and parvalbumin (PV). Among the most characteristic morphological types of neurons immunoreactive (ir) for CB are double bouquet cells, whereas for PV they are chandelier cells and large basket cells, and for CR, bipolar cells and double bouquet cells. We have studied the distribution of double bouquet cells and chandelier cells in three well-differentiated cytoarchitectonic areas of the so-called ventral (occipitotemporal) visual pathway of the macaque monkey: the first and second visual areas (V1 and V2) in the occipital lobe and area TE of the inferior temporal cortex. Furthermore, we used double immunocytochemical methods to explore the connections between CB-ir, CR-ir, and PV-ir neurons. We found that the same morphological types of interneurons were identified in all cortical areas examined, but the number and distribution of particular types differed between areas. In addition, the number and frequency of CB-ir, CR-ir, and PV-ir terminals, which were observed in contact with the cell somata and proximal dendrites of CB-ir, CR-ir, and PV-ir interneurons, varied depending on the chemical type of interneuron, but the patterns of these connections were similar in the different cortical areas studied. Thus, certain characteristics of intracortical circuits remain similar, whereas others clearly differ in the various areas of the occipitotemporal visual pathway, which might represent regional specialisations related to the differential processing of visual stimuli in these areas.

◆ **Linking neural circuits to perception: The case of visual attention**

M Carrasco (Department of Psychology and Center for Neural Science, New York University, 6 Washington Place, New York, NY 10003, USA; e-mail: marisa.carrasco@nyu.edu)

What mechanisms are involved in visual attention and where are they localised in the brain? I discuss how relating psychophysics to electrophysiology and neuroimaging has advanced our understanding of brain function, and in particular of attention. Covert attention enhances performance on a variety of perceptual tasks carried out by early visual cortex. In this talk, I concentrate on the effect of attention on contrast sensitivity, and discuss evidence from psychophysical, electrophysiological, and neuroimaging studies indicating that attention increases contrast gain. First, I illustrate how psychophysical studies allow us to probe the human visual system. Specifically, I discuss studies showing that attention enhances contrast sensitivity, and how these studies allow us to characterise the underlying mechanisms, namely external noise reduction and signal enhancement. Then, I relate these findings to single-unit recording studies, which show that attention can reduce external noise by diminishing the influence of unattended stimuli and that it can also boost the signal by increasing the effective stimulus contrast. Current neuroimaging techniques can be used to link human performance to non-human primate electrophysiology by providing an intermediate level of analysis. Human electrophysiological studies have provided evidence that attention can increase sensory gain, and neuroimaging studies have shown attentional modulation of neural activity in early visual cortex. For instance, the effect of transient (exogenous) attention on stimulus representations in early visual areas has been documented with the use of rapid event-related fMRI. Attention improves performance and the concomitant stimulus-evoked activity in early visual areas. These results provide evidence regarding the retinotopically specific neural correlate for the effects of attention on early vision. Combining psychophysical and fMRI studies helps bridge the gap between single-unit physiology and human psychophysics, and advance our understanding of attention, in particular, and of brain function, in general.

[Supported by the Beatrice and Samuel A Seaver Foundation.]

THE PERCEPTION LECTURE◆ **Brain and visual perception**

D H Hubel (Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115, USA;
e-mail: dhubel@hms.harvard.edu)

I begin by describing the state of visual neurophysiology in the mid-1950s, when methods for recording from single cortical cells were just being developed. I describe how Torsten Wiesel and I got started, in the fall of 1958, how much we owed to the examples of Stephen Kuffler, Vernon Mountcastle, and anatomists such as Welle Nauta. I discuss the part played by luck and dogged persistence, in our discovery of orientation selectivity. I discuss the functions of the lateral geniculate body and the striate cortex, in transforming the information they receive from the structures that feed into them. Finally I show how our knowledge of the physiology can help explain some common visual phenomena, including the filling in of contours, colour afterimages, the waterfall illusion, and the MacKay illusion.

Tuesday

TUESDAY

SYMPOSIA

ADAPTATION, BRIGHTNESS, AND CONTRAST

- ◆ **Cortical mechanisms of contrast adaptation and contrast-induced receptive field plasticity**
M V Sanchez-Vives, L G Nowak¶, D A McCormick§ (Instituto de Neurociencias de Alicante, Universidad Miguel Hernández-CSIC, San Juan de Alicante, Spain; ¶ Centre de Recherche de Cerveau et Cognition, CNRS, Université Paul Sabatier, Unité Mixte de Recherche 5549, 133 route de Narbonne, F 31062 Toulouse Cedex, France; § Department of Neurobiology and the Kavli Institute for Neuroscience, Yale University School of Medicine, New Haven, CT 06510, USA; e-mail: mavi.sanchez@umh.es)

Contrast adaptation is a well known psychophysical phenomenon (Blakemore and Campbell, 1969 *Journal of Physiology* **203** 237–260) characterised, among other things, by a decrease in contrast sensitivity following an exposure to a high-contrast stimulus. The neuronal correlate of this phenomenon was found in the primary visual cortex, where the time course of changes in neuronal activity closely paralleled those observed psychophysically (Maffei et al, 1973 *Science* **182** 1036–1038). Underlying neuronal adaptation to high contrast, there is a slow hyperpolarisation of the membrane potential (Carandini and Ferster, 1997 *Science* **276** 949–952) which is due neither to inhibition nor to a decreased stimulus-modulated (F1) synaptic activity. Intracellular recordings in the primary visual cortex of anesthetized cats confirmed that contrast adaptation is due at least in part to the activation of slow after-hyperpolarising currents (Sanchez-Vives et al, 2000 *Journal of Neuroscience* **20** 4267–4285). The involvement of intrinsic properties was demonstrated by showing that a similar decrease in the response to low contrast could be evoked either by previous stimulation with high contrast or by neuronal firing induced with intracellular current injection. The finding in these neurons of a Na⁺-dependent K⁺ current with a slow time course, similar to that observed during contrast adaptation (Sanchez-Vives et al, 2000 *Journal of Neuroscience* **20** 4286–4299), suggested that it could underlie this phenomenon at least partially. Gain and size of the receptive fields of neurons in cat area 17 also vary with time depending on their previous history of firing (Nowak et al, 2005 *Journal of Neuroscience* **25** 1866–1880). In this presentation we evaluate the plasticity of visual responses induced by the preceding contrast stimulation and we discuss the role of intrinsic membrane properties and synaptic mechanisms as neuronal basis of this plasticity.

[Supported by the Human Frontiers Science Program Organization, PRESENCIA (EU) and Ministerio de Educación y Ciencia Español to MVS, Centre National de la Recherche Scientifique to LGN, and NIH to DAM.]

- ◆ **Perceptual filling-in: More than meets the eye**
P De Weerd (University of Maastricht, Faculty of Psychology, Neurocognition Group, Postbus 616, NL 6200 MD Maastricht, The Netherlands;
e-mail: P.deweerd@psychology.unimaas.nl)

When a gray figure is surrounded by a background of dynamic texture, fixating away from the figure for several seconds will result in an illusory replacement of the figure by its background. This visual illusion is referred to as perceptual filling-in. The study of filling-in is important, because the underlying neural processes compensate for imperfections in our visual system (eg the blind spot) and contribute to normal surface perception. A long-standing question has been whether perceptual filling-in results from symbolic tagging of surface regions in higher-order cortex (ignoring the absence of information), or from active neural interpolation (active filling-in of information). Psychophysical research has revealed a pattern of data that is most compatible with the latter hypothesis. In particular, the finding that the fixation time required to perceive filling-in increases with the cortical representation size of the figure in retinotopic cortex is not compatible with the symbolic-tagging hypothesis. The data suggest that the time before filling-in reflects an adaptation of boundary detectors and other figure–ground segregation mechanisms, after which fast filling-in of the figure takes place by its background. Physiological recording studies in rhesus monkeys have added evidence in favour of the active interpolation hypothesis. In these studies, V2 and V3 neurons with receptive fields placed over a gray figure increased their activity during perceptual filling-in of the figure, in the absence of any physical change in the stimulus. Recent data suggest that perceptual filling-in is facilitated by attention. This counter-intuitive finding suggests that attention directly strengthens interpolation processes that produce filling-in, instead of strengthening figure–ground segregation. The contribution of attention to filling-in raises the question whether filling-in can be learned. Given the similarities of processes underlying perceptual filling-in and processes facilitating cortical plasticity, this hypothesis is worth exploring.

◆ **Neural responses and perception during visual fixation**

S Martínez-Conde (Barrow Neurological Institute, 350 W Thomas Road, Phoenix, AZ 85013, USA; e-mail: smart@neuralcorrelate.com)

Aspects of the neural code that relate to our visual perception are of great interest. One of the ways this can be addressed is by correlating the eye movements that occur during visual fixation with the spike trains that they provoke in single neurons. Since visual images fade when eye movements are absent, it stands to reason that the patterns of neural firing that correlate best with fixational eye movements are important to conveying the visibility of a stimulus. Fine examination of responses shows that the visibility of stimuli is dependent on either movement of the eyes, or movement of the world. Visibility is, moreover, encoded better neurally by transient bursts of spikes than by firing rate or the overall density of spiking activity. By using psychophysics and physiology methods, these studies identify the mechanisms and levels of the brain in which visibility and brightness may begin to be processed.

[Supported by the Barrow Neurological Foundation.]

◆ **The visual phantom illusion: A perceptual product of surface completion depending on the mechanism of perceptual transparency**

A Kitaoka, J Gyoba ¶, K Sakurai § (Department of Psychology, Ritsumeikan University, 56-1 Toji-in Kitamachi, Kita-ku, Kyoto 603-8577, Japan; ¶ Department of Psychology, Graduate School of Arts and Letters, Tohoku University, Kawauchi 27-1, Aoba-ku, Sendai 980-8576, Japan; § Department of Psychology, Tohoku Gakuin University, 2-1-1 Tenjinzawa, Izumi-ku, Sendai 981-3193, Japan; e-mail: akitaoka@lt.ritsumei.ac.jp)

The visual phantom illusion was first discovered by Rosenbach (1902 *Zeitschrift für Psychologie* **29** 434–448) and named ‘moving phantoms’ by Tynan and Sekuler (1975 *Science* **188** 951–952) because of its strong dependence on motion. Genter and Weisstein (1981 *Vision Research* **21** 963–966) and Gyoba (1983 *Vision Research* **23** 205–211) later revealed that phantoms can be generated by flickering the grating (flickering phantoms) or by low-luminance stationary gratings under dark adaptation (stationary phantoms). Although phantoms are much more visible at scotopic or mesopic adaptation levels (scotopic phantoms) than at photopic levels, Kitaoka et al (1999 *Perception* **28** 825–834) proposed a new phantom illusion which is fully visible in photopic vision (photopic phantoms). Kitaoka et al (2001 *Perception* **30** 959–968) finally revealed that the visual phantom illusion is a higher-order perceptual construct or a Gestalt, which depends on the mechanism of perceptual transparency. Perceptual transparency is known as a perceptual product that depends on brightness and contrast. Kitaoka et al (2001 *Vision Research* **41** 2347–2354; 2001 *Perception* **30** 519–522) furthermore demonstrated the shared mechanisms between visual phantoms and neon colour spreading or between visual phantoms and the Petter effect. In our latest studies, the visual phantom illusion can be seen with a stimulus of contrast-modulated, envelope gratings. We assume that this effect also depends on perceptual transparency induced by contrast modulation. Further, we found that the Craik–O’Brien–Cornsweet effect and other lightness illusions can generate the visual phantom illusion. In these new displays, the phenomenal appearance looks like that of photopic phantoms. In sum, we conclude that the visual phantom illusion can be explained in terms of surface completion, which is given by perceptual transparency.

RECENT DISCOVERIES ON RECEPTIVE FIELD STRUCTURE

◆ **Neural circuits and synaptic mechanisms underlying the emergence of visual cortical receptive fields**

L M Martínez, J-M Alonso ¶, J A Hirsch § (Departamento de Medicina, Facultad de Ciencias da Saúde, Universidade da Coruña, Campus de Oza, E 15006 A Coruña, Spain; ¶ SUNY College of Optometry, Department of Biological Sciences, 33 West 42 Street, New York, NY 10036, USA; § Department of Biological Sciences, University of Southern California, 3641 Watt Way, Los Angeles, CA 90089, USA; e-mail: lmo@neuralcorrelate.com)

Unlike cells in the lateral geniculate nucleus of the thalamus that supply them, neurons in the primary visual cortex show a great variety of receptive-field structures. This functional diversity emerges from the specific computations performed by a widespread and distributed network of synaptic connections which includes both thalamocortical and corticocortical projections. Yet, after 40 years of intense study, the precise organisation of the circuits that generate each cortical receptive-field type, and even their specific roles in visual processing, are still a matter of intense debate. To learn how neural circuits generate receptive-field structure and other functional response properties, we combined the techniques of multiple extracellular and whole-cell recordings in vivo with intracellular labeling and quantitative receptive-field mapping. Our recent studies show that cells with simple receptive fields, ie those comprising antagonistic subregions where stimuli of the reverse contrast evoke responses of the opposite sign, are an exclusive feature of the input layers of the cortex. Complex cells, on the other hand, populate other cortical layers and

Tuesday

the precise structure of the complex receptive field changes significantly according to laminar location (Martinez et al, 2005 *Nature Neuroscience* **8** 372–379). In addition, we have demonstrated that the receptive fields of most layers 2 + 3 complex cells are generated by a mechanism that requires simple cell inputs (Martinez and Alonso, 2001 *Neuron* **32** 515–525). Therefore, our results strongly suggest that simple cells and complex cells represent successive stages of receptive field construction along the early visual pathway. First, simple receptive fields emerge as the most direct approach to build orientation detectors from geniculate cells with circular receptive fields. In a second step, complex cells originate from the need to build orientation detectors that are independent of the contrast polarity and position of the stimulus within the receptive field.

[Supported by NIH and HFSP]

◆ **Representing multiple stimulus features in functional maps: Insights from ferret visual cortex**
 D Fitzpatrick (Department of Neurobiology, Duke University Medical Center, Box 3209, Durham, NC 27710, USA; e-mail: fitzpat@neuro.duke.edu)

Viewed in the plane of the cortical surface, cortical columns are arranged in an orderly fashion forming overlapping maps that are thought to represent stimulus features such as edge orientation, direction of motion, and spatial frequency. We have recently argued that patterns of activity in visual cortex are better explained in the framework of a single map that incorporates the spatiotemporal tuning functions of cortical receptive fields (orientation in space-time) (Basole et al, 2003 *Nature* **423** 986–990). Questions remain, however, about the existence of a separate map of spatial frequency. To further explore this issue, intrinsic signal imaging techniques were used to examine the patterns of activity evoked by sine-wave gratings in ferret visual cortex. Changes in spatial frequency were accompanied by systematic shifts in the distribution of activity that accord with the mapping of visual space. For example, changing stimulus spatial frequency from low to high resulted in a progressive restriction of neural activity to the cortical representation of the area centralis. In addition, a finer scale modular activation pattern was evident within the representation of central visual space; interdigitated patches of neurons respond preferentially to high and low spatial frequencies, consistent with previous reports of a modular mapping of spatial frequency. However, comparison of this modular pattern with the mapping of preferred orientation revealed a striking correlation: regions responding to the highest spatial frequencies were restricted to sites that responded preferentially to cardinal orientations (mostly horizontal). A cardinal bias in the response of cortical neurons to high spatial frequencies is consistent with the perceptual oblique effect and natural scene statistics. These results challenge the view that spatial frequency is mapped independently of other stimulus features, and offer further evidence that a single map of orientation in space-time accounts for the spatial distribution of population activity in visual cortex.

[Supported by NEI grant EY 11488.]

◆ **The contribution of feedforward, lateral, and feedback connections to the classical receptive field centre and extra-classical receptive field surround of primate V1 neurons**

A Angelucci (Department of Ophthalmology, Moran Eye Center, University of Utah, 50 North Medical Drive, Salt Lake City, UT 84132, USA; e-mail: alessandra.angelucci@hsc.utah.edu)

What circuits generate the response properties of V1 neurons? V1 cells respond best to oriented stimuli of optimal size within their receptive field (RF). This size tuning is contrast-dependent, ie the optimal stimulus size of a neuron is larger at low contrast. Stimuli involving the extra-classical surround suppress the RF centre's response. Surround suppression is fast and long range, extending well beyond the low-contrast spatial summation region of V1 cells (lsRF). To determine the contribution of feedforward, lateral, and inter-areal feedback connections to V1 to the RF centre and surround of V1 neurons, we have quantitatively compared the spatial extent of these connections with the size of the RF centre and surround of V1 neurons. FF afferents to V1 are coextensive with the size of the high-contrast spatial summation field of V1 cells and can, thus, integrate signals within this RF region. V1 lateral connections are commensurate with the size of the lsRF and may, thus, underlie contrast-dependent changes in spatial summation, and lateral facilitation effects from the 'near' surround. Contrary to common beliefs, the spatial and temporal properties of lateral connections cannot fully account for the dimensions and onset latency of surround suppression. Inter-areal feedback connections to V1, instead, are commensurate with the full spatial range of centre–surround interactions. Feedback connections terminate in a patchy fashion in V1, and show modular and orientation specificity, and spatial anisotropy collinear with the orientation preference of their cells of origin. Thus, the spatial and functional organisation of feedback connections is consistent with their role in orientation-specific centre–surround interactions. A biologically-based recurrent network model of centre–surround interactions in V1

is presented, which is based on integration of inputs from feedforward, lateral, and feedback connections. Physiological data are provided in support of the predictions of the model, revealing that modulation from the 'far' surround is not always suppressive.

[Supported by NSF IBN 0344569, NIH EY 015262, RPB, University of Utah Research Foundation, and Wellcome Trust 061113.]

◆ **Receptive fields as prediction devices: A comparison of cell tuning to single images and to natural image sequences in temporal cortex**

D I Perrett, D Xiao, N E Barraclough, M W Oram, C Keyser[¶] (School of Psychology, University of St Andrews, St Andrews KY16 9JP [[¶] KY16 9JU], Scotland, UK; e-mail: dp@st-andrews.ac.uk)

We experience the world as a continuous stream of events where the previous scenes help us anticipate and interpret the current scene. Visual studies, however, typically focus on the processing of individual images presented without context. To understand how processing of isolated images relates to processing of continuously changing scenes, we compared cell responses in the macaque temporal cortex to single images (of faces and hands) with responses to the same images occurring in pairs or sequences during actions. We found two phenomena affecting the responses to image pairs and sequences: (a) temporal summation, whereby responses to inputs from successive images add together, and (b) 'forward masking', where the response to one image diminishes the response to subsequent images. Masking was maximal with visually similar images and decayed over 500 ms. Masking reflects interactions between cells rather than adaptation of individual cells following heightened activity. A cell's 'receptive field' can be defined by tuning to isolated stimuli that vary along one dimension (eg position or head view). Typically, this is a bell-shaped curve. When stimuli change continuously over time (eg head rotation through different views), summation and masking skew the tuning. The first detectable response to view sequences occurs 25 ms earlier than for corresponding isolated views. Moreover, the responses to sequences peak before the most effective solitary image: the peak shift is $\sim 1/2$ the bandwidth of tuning to isolated stimuli. These changes result in activity across cells tuned to different views of the head that 'anticipate' future views in the sequence: at any moment the maximum activity is found in those cells tuned to images that are about to occur. We note that, when sensory inputs change along any dimension, summation and masking transform classical receptive field properties of cells tuned to that dimension such that they predict imminent sensations.

ORAL PRESENTATIONS

ATTENTION, DECISION, AND COGNITION

◆ **Developmental dyslexia: Evidence for an attentional cortical deficit**

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Developmental dyslexics show impaired phonological processing, correlated with reduced activity in the left temporo-parietal cortex, and also deficits in processing rapidly changing auditory information, correlated with a disturbance in the left inferior prefrontal cortex. Our aim was to investigate the performance of dyslexic children on tasks requiring spatial attention. In a first experiment, the subjects (dyslexic and control children, aged between 8 and 12 years, non-dyslexic adults; $N = 10$ subjects/group) were asked to indicate which of the sides of a pre-bisected line was perceived as longer. In a second experiment, the subjects ($N = 27$ subjects/group) searched for a discrepant target amidst an array of distractors, in tasks involving a single feature (orientation or shape) or a conjunction of features (orientation and shape). The third experiment included pop-out tasks (texture segmentation, visual feature search; $N = 19$ subjects/group). All subjects were right-handed and had normal or corrected-to-normal vision. Dyslexic children did not show the overestimation of the left visual field (pseudoneglect) characteristic of normal observers, but a highly significant left 'minineglect'. They showed shorter reaction times and an increased error rate in visual conjunction, but not in visual feature tasks, indicative of a deficit in executive functions. These deficits decreased with increasing age. Basic visual functions (visual acuity, contrast sensitivity) were not affected. In addition to their known left-cortical deficits, developmental dyslexics show impairments in the cortical network responsible for the deployment of selective, goal-directed spatial attention, known to involve structures in the posterior parietal and the dorsolateral prefrontal cortex on the right side of the brain (Corbetta and Shulman,

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2002 *Nature Reviews Neuroscience* **3** 201–215). We conclude that developmental dyslexia involves subtle deficits in an extended, bilateral cortical network.

[Supported by Deutsche Forschungsgemeinschaft (Si 344/16-1,2) and Evangelische Studienstiftung, Villigst, eV.]

◆ **Dog or animal? What comes first in vision?**

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Object recognition experiments using picture naming or word priming have shown that object categorisation is faster at the basic level (eg dog) than at the superordinate level (eg animal) (Rosch et al, 1976 *Cognitive Psychology* **8** 382–439). However, ultra-rapid go/no-go visual categorisation revealed that humans categorise natural scenes very rapidly and accurately at the superordinate level (animal/non-animal), and we recently showed that basic level categorisation is more time consuming in this particular task (Macé et al, 2003 *Acta Neurobiologiae Experimentalis* **63** Supplement, 24). In the present study, we designed a dog/non-dog experiment in which we varied the proportion of non-dog animals in the pool of distractor images (0%–50%–100%). The intermediate (50%) condition was identical to our last experiment and gave similar results: compared to the superordinate (animal) task, accuracy was 2.1% lower and mean RT was increased by 63 ms for basic (dog) categorisation. The effect was even more pronounced (accuracy decrease: 3.9%, mean RT increase: 82 ms) when the distractors were 100% non-dog animal pictures. On the other hand, when the distractors did not contain any animal pictures, performance in the dog task was similar to the animal task and even slightly better (accuracy increase: 2%; mean RT decrease: 5 ms). Task-associated EEG recordings showed that the ERP difference between target and distractor trials developed at the same latency regardless of the distractors but was strongly reduced in amplitude when all distractors were non-dog animals. Such data suggest that the entry category in visual categorisation is at the superordinate level and that further visual processing is needed for categorisation at the basic level. This shows that ultra-rapid visual processing cannot be used for basic-level categories except when the distance from distractors in terms of visual features is increased by suppressing all images belonging to the same superordinate category.

◆ **Innovation in design and aesthetics: How attributes of innovation influence attractiveness in the long run**

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Innovativeness is defined as ‘originality by virtue of introducing new ideas’. Thus, innovative designs often break common visual habits and are evaluated as relatively unattractive at first sight (Leder and Carbon, 2005 *Applied Cognitive Psychology* in press). In most empirical studies, attractiveness is measured only once. These measures do not capture the dynamic aspects of innovation. However, as demonstrated by Carbon and Leder (loco cit.) the validity of attractiveness evaluations can be improved by the so-called ‘repeated evaluation technique’ (RET). RET simulates time and exposure effects of everyday life. Using RET, we investigated the appreciation of different car designs and art pictures varying in innovativeness (uncommon for portraits). While the exposure theory on its own (Zajonc, 1968 *Journal of Personality and Social Psychology* **9** 1–27) would predict a general increase of liking on increasing exposure, RET revealed dissociate effects depending on innovativeness. Only innovative material showed an increase in attractiveness. Low innovative designs and art objects were rated as being relatively attractive at the beginning, but did not profit from elaboration due to RET.

◆ **MEGaVis: Perceptual decisions in the face of explicit costs and perceptual variability**

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In motor tasks with explicit rewards and penalties, humans choose movement strategies that maximise expected gain (Trommershäuser et al, 2003 *Journal of the Optical Society of America A* **20** 1419–1433). We used an analogous perceptual task. A stimulus was briefly presented (1 s), followed by a test display. The stimulus consisted of 32 randomly placed line segments (0.7 deg in length) in a circular window (4.6 deg diameter). Segment orientations were drawn from a von Mises distribution whose mean and standard deviations were varied from trial to trial. Subjects then saw a test display containing two green arcs (the reward region) at opposite sides of the circular window and two red arcs (the penalty region) also at opposite sides. All arcs were 22°, and the penalty region either overlapped half of the reward region or abutted it. Subjects rotated this display

by key presses until satisfied. If the mean texture orientation fell within the reward region (ie if the subject's setting was within $\pm 11^\circ$ of the correct value), the subject won 100 points. If the mean orientation fell within the penalty region, the subject lost a fixed number of points (0, 100, or 500). We compared each subject's performance across conditions to a decision strategy that maximises expected gain (MEGaVis: Maximize Expected Gain in a Visual task). MEGaVis predicts subjects will shift settings away from the penalty more for (i) larger penalties, (ii) closer penalty regions, and (iii) larger stimulus variability. With blocked variability conditions, subjects generally compensated for their variability and the reward/penalty structure; they made settings in a nearly optimal fashion. If, instead, stimulus variability was drawn from a continuous distribution across trials, this required subjects to estimate stimulus variability on a trial-by-trial basis. Under these conditions, performance was poor and there was a variety of subject strategies.
[Supported by NIH EY08266.]

◆ **Norm-based coding of face identity**

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Faces all share the same basic configuration, and yet we can identify thousands of them. An efficient way to individuate faces would be to code how each face deviates from this common configuration or norm. Support for norm-based coding comes from evidence that caricatures, which exaggerate how a face differs from the norm (average) face, are recognised more readily than undistorted images. However, it is difficult to rule out exemplar accounts based on reduced exemplar density further from the norm. Here, we present new evidence for norm-based coding. We show that faces and their antiface, which lie opposite the norm in face space, are coded as perceptual opposites. This result supports norm-based coding because faces and their antifaces are only opposite in relation to the norm. Initial support comes from the face identity aftereffect (FIAE), in which exposure to a face biases perception towards the opposite identity (Leopold et al, 2001 *Nature Neuroscience* 4 89–94). We show that this FIAE occurs only for opposite, and not for equally dissimilar but non-opposite, adapt–test pairs. An important characteristic of perceptual opposites is that they cannot be perceived simultaneously. One cannot perceive reddish–green or up–down motion in the same object. Therefore, if faces and their antifaces are coded as opposites, it should not be possible to see Danish–AntiDans. We asked people to judge the similarity of face–antiface pair blends and non-opposite pair blends to their respective component faces. As predicted, similarity ratings were substantially lower for face–antiface blends. Taken together, these results suggest that faces and antifaces are coded as perceptual opposites, which supports norm-based coding.

◆ **Number of distractors and distractor spacing differentially affect attention and saccade tasks**

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Targets are harder to identify when surrounded by similar objects. One possible explanation for this visual crowding is a limitation in attentional resolution: a crowded target cannot be resolved because the 'attentional spotlight' into which it falls includes other objects (Tripathy and Cavanagh, 2002 *Vision Research* 42 2357–2369). A tight link between attention and eye movements has been posited. If visual crowding results from limits on attentional resolution, this suggests that saccade accuracy will be affected by the same variables that lead to crowding. Here we tested two: number of distractors and spacing. Stimuli were Landolt squares with the target defined by colour. Targets were either presented alone or flanked by one or two differently coloured distractors on each side. Spacing between stimuli was either 'close' or 'wide'. The stimuli appeared on both sides of fixation and differed only in the presence of the target colour. In separate blocks, ten observers either identified the gap location or made a single saccade to the target. Eye position was monitored with a dual-Purkinje-image eye tracker. Observers showed nearly perfect accuracy in both the gap identification (94% correct) and saccade tasks (error in eye position 0.12 deg) with no distractors. Number of distractors had little effect in the gap task (60% correct with one distractor, 58% with two), but a significant effect on eye position (0.23 and 0.34 deg for one and two distractors, respectively). The opposite was true of spacing. For the gap task performance was worse with close (33%) than wide (60%) spacing, while there was no difference in saccade accuracy (both 0.28 deg error). The dissociation between variables that affect gap detection and saccade accuracy suggests that the underlying link between attention and eye movements may not be as tight as previously thought.
[Supported by NIH/NIMH MH067793 to CMM.]

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◆ **Rapid scene categorisation and RSVP paradigms**

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Human observers are very good at deciding whether a briefly flashed natural scene contains an animal or a face and previous backward-masking experiments have shown that animal detection accuracy is already close to optimal with disrupting delay as short as 40 ms (Bacon-Macé et al, 2005 *Vision Research* **45** 1459–1469). Here we used a rapid serial visual presentation (RSVP) paradigm to further analyse the nature of masking mechanisms in a categorisation task. Twenty pictures were flashed with a fixed display time (6.25 ms), but at rates corresponding to SOAs ranging from 6.25 to 119 ms. Performance at detecting an animal in a RSVP sequence was surprisingly low compared to the original masking experiment, since an interval between frames of 119 ms is necessary to achieve 90% correct. One explanation for this difficulty is that RSVP presentations produce both forward and backward masking. But other factors are also important. By varying the nature of the other images in the sequence (noise patterns, other natural images, or scrambled photographs) we found that other meaningful images were particularly disruptive, suggesting a form of higher-level masking mechanism. Finally, we noted that when the target category was a famous human face, detection in RSVP conditions was much easier, with 90% as soon as 44 ms of SOA. We conclude that the nature of masking processing in RSVP tasks involves several interference mechanisms, and that the categories of both targets and masks are critical in determining whether the stimulus will be detected.

◆ **When beauty is in the eye of the beholder: Individual differences dominate preferences for abstract images, but not real-world scenes**

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Previous studies of preference for real-world scenes found a high degree of agreement for ratings across subjects [Vessel and Biederman, 2002 *Journal of Vision* **2** 492a; Vessel and Biederman, 2001 *9th Annual Workshop on Object Perception and Memory (OPAM), Orlando, FL, 15 November*]. Individual preference ratings were correlated with the group average of the other subjects at levels of 0.55 to 0.68 ('mean-minus-one' correlation), with up to 66% of the variance in group preference ratings predictable from descriptive factors, such as naturalness. How much of this agreement is attributable to familiarity with the themes and/or semantic content of the images? To address this question, we created a large set of abstract, novel colour images and measured subjects' visual preferences. There were six categories of images: pseudocoloured microscopic images, fractals, artificially generated kaleidoscopic images, cropped satellite imagery, textured novel 3-D objects, and an 'other' category containing an assortment of abstract renderings and patterns. Image selection spanned a wide spectrum of attractiveness, and debriefing indicated that image origin was generally not apparent to the naive observer. The images were serially presented for 1 s each, and subjects performed forced-choice, 'one-back' paired comparisons between images. We estimated preference values for the full stimulus set from these paired comparisons (a sorting algorithm guided presentation order to optimise the estimation procedure). Unlike for real-world scenes, preference was quite variable between subjects (mean-minus-one $r = 0.35$), though individual subject's preferences showed robust reproducibility (correlation of 0.66 between first and second half of the experiment). Subjects' preferences were highly variable both within and across image categories (0.17, 0.09, respectively). These results demonstrate that preferences for abstract images are less predictable than preferences for real-world scenes, which may be heavily dependent on semantic associations. This abstract stimulus set will allow us to separately study visual and semantic contributions to the neural basis of visual preference.

[Supported by NEI T32 EY07158-03.]

MOTION PERCEPTION

◆ **Underactivation of the sensory system and overaction of the complementary cognitive system during motion perception in schizophrenia**

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Visual motion perception is normally supported by neural processing of the sensory system. Indeed, focal damage to motion-sensitive areas such as the middle temporal area (MT) induces an acute motion-perception impairment that may recover gradually over time. It is unclear how distributed

cortical damage affects motion perception and its neural correlates. Schizophrenia, compared with neurological disorders, shows (i) few signs of gross organic changes in any single cortical area, but (ii) a variety of functional abnormalities including motion perception. This mental disorder may thus provide a model for understanding the roles of cortical network in motion processing. Here, we studied the pattern of cortical activations, measured by functional magnetic resonance imaging (fMRI), during motion as well as non-motion discrimination in schizophrenia patients ($N = 10$) and normal people ($N = 8$). Psychophysical thresholds of three visual tasks, direction discrimination, velocity discrimination (both motion), and contrast discrimination (non-motion), were measured first. For fMRI, task difficulty conditions were set (a) at easy levels (70% of motion coherence for direction discrimination, 50% difference in velocity for velocity discrimination, 80% difference in contrast for contrast discrimination; performance: 90% correct or better) and (b) at difficult levels (two times perceptual thresholds of individual subjects; performance: 70% correct or better). Compared with normal controls, cortical response in patients was shifted from occipital to frontal regions during direction and velocity discrimination but not during contrast discrimination. The fMRI BOLD signals to motion discrimination in schizophrenia were significantly reduced in MT and significantly increased in the left inferior convexity of the prefrontal cortex (ICPFC), which is normally involved in high-level cognitive processing, such as visual object representation. This shift in neural processing suggests a recruitment of the complementary cognitive system to compensate for the deficient sensory system for motion perception in schizophrenia.

[Supported by NIH, NARSAD, and the Milton Fund of Harvard University.]

◆ **Investigating phase-specific interactions between different varieties of motion with a motion-cancellation paradigm**

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A wealth of empirical evidence suggests that first-order and second-order motion are processed separately, at least initially, in human vision. However, the vast majority of studies of second-order motion perception are focused almost exclusively on one class of patterns, those defined by modulations of image contrast. This practice relies heavily on the assumption that different varieties of second-order motion are likely to be processed in an homogenous manner, although there is little evidence that this is actually the case. To investigate this issue, we used a novel, psychophysical, motion-cancellation paradigm to measure whether phase-specific interactions occur between first-order (luminance modulation) and second-order (modulations of either the contrast, flicker rate, or spatial length of noise carrier elements) sinusoidal motion patterns at an early stage in visual processing. The rationale was that, if two spatially superimposed patterns (of comparable suprathreshold visibility when presented in isolation) drifting in the same direction interact in a phase-specific manner, such that the ability to identify the direction of motion is impaired, it is likely that they are encoded by the same mechanism. However, if they fail to interact perceptually, this would provide strong evidence that they are processed independently. Results showed that first-order (luminance-defined) motion patterns did not interact with any of the second-order motion patterns tested (contrast, flicker, and spatial length). For second-order motion phase-specific interactions occurred between contrast-modulated and flicker-modulated images, although no interaction was apparent between contrast-modulated and length-modulated stimuli. The findings clearly reinforce the notion that first-order and second-order motion are encoded separately in human vision. Moreover, they demonstrate that although some second-order patterns are processed by a common mechanism, this is not true of all types of second-order stimuli. As such, when considered in terms of their perceptual properties, second-order motion patterns are not necessarily an homogenous class of visual stimuli.

[Supported by a BBSRC Responsive Research Grant to TL.]

◆ **Extra-retinal adaptation of cortical motion sensors**

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Repetitive eye movement leads to a compelling motion aftereffect (MAE). One contributing factor is thought to be an extra-retinal motion signal generated after adaptation, possibly related to the suppression of post-adaptation afternystagmus. However, extra-retinal signals are also generated during pursuit. They modulate activity within cortical motion area MST and so suggest an alternative means of inducing the MAE. To differentiate between these two mechanisms we examined storage of the MAE across a period of darkness. Afternystagmus dissipates in the dark, so MAE mediated by afternystagmus suppression should not store. However, if extra-retinal pursuit signals contribute, storage should be evident because cortical motion areas are known to mediate the storage effect. Observers viewed a large random-dot pattern moving upwards in the dark,

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confining their eye movements to a vertical central blank region. In the nystagmus condition, they stared at the blank region, producing rapid reflexive eye movement. In the pursuit condition, they were instructed to actively pursue the motion. After 60 s, the stimulus was replaced by a stationary test spot and MAE duration recorded. The MAE lasted for approximately 16 s in both conditions. With a delay of 40 s inserted between adaptation and test, the MAE virtually disappeared in the nystagmus condition (~ 4 s duration) but was almost completely stored following pursuit (15 s). Eye movements were more accurate during pursuit (gain of 0.84 versus 0.58), arguing against explanations based on adaptation by retinal slip. The results suggest pursuit can adapt cortical motion areas whereas nystagmus cannot. Less clear is whether cortical mechanisms are the sole determinant of pursuit-induced MAE. Following oblique pursuit, we found the MAE changes direction from oblique to vertical. This suggests involvement of a subcortical mechanism as well, one based on the relative recovery rate of horizontal and vertical eye-movement processes that are recruited during oblique pursuit. [Supported by the Wellcome Trust.]

◆ **Perception of phase wave motion**

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We describe a new class of motion stimulus, containing phase wave motion. The stimulus consists of a 2-D array of pattern elements. Each element oscillates in position over the same distance. When all elements oscillate in-phase, the pattern moves rigidly back and forth. When the relative phase of oscillation varies progressively across the pattern, a travelling wave of oscillation can be created that has the appearance of a fabric blowing in a breeze. Observers readily perceive the direction and speed of the phase wave, even though it contains no motion energy that can be detected by low-level motion processes, other than the local element oscillation. We present some initial psychophysical data and review possible explanatory models based on texture processing and second-order motion processing. [Supported by the Engineering and Physical Sciences Research Council, UK.]

◆ **Tracking deviations in multiple trajectories: The influence of magnitude of deviation**

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The ability of human observers to detect deviations in multiple straight-line trajectories is severely compromised when a threshold paradigm is employed; observers are unable to process more than a single trajectory accurately (Tripathy and Barrett, 2004 *Journal of Vision* 4 1020–1043). Here we investigate the ‘effective’ number of trajectories that can be attended simultaneously when detecting deviations that are substantially suprathreshold. In the first experiment, the stimuli were linear, non-parallel, left-to-right trajectories all moving at the same speed (4 deg s^{-1}). One of the trajectories deviated clockwise/anticlockwise at the vertical mid-line of the screen. The number of trajectories (N) was varied between 1 and 10. The angle of deviation was fixed at $\pm 76^\circ$, $\pm 38^\circ$, or $\pm 19^\circ$. The proportion of trials in which the direction of deviation was correctly identified was determined for each N and the ‘effective’ number of attended trajectories was estimated. Observers ‘effectively’ attend to 3–4 trajectories when detecting deviations of $\pm 76^\circ$, 2–3 trajectories for $\pm 38^\circ$ deviations, and 1–2 trajectories when attending to deviations of $\pm 19^\circ$. In the second experiment, N was fixed at 10 and the number of deviating trajectories (D) was varied between 1 and 10. The angle of deviation was fixed at $\pm 76^\circ$, $\pm 38^\circ$, or $\pm 19^\circ$. The proportion of trials in which the direction of deviation was correctly identified was determined for each D and the ‘effective’ number of attended trajectories was estimated. This ‘effective’ number ranged from 4–5 trajectories for deviations of $\pm 76^\circ$ to only 1–2 trajectories for deviations of $\pm 19^\circ$. When the deviations are much greater than threshold ($\pm 76^\circ$), our results are consistent with previous findings that observers can track up to 4–5 identical objects with nearly 85% accuracy [Pylyshyn and Storm, 1988 *Spatial Vision* 3 179–197; Scholl et al, 1999 *Investigative Ophthalmology & Visual Science* 40(4) S4195].

◆ **A second-order barber-pole illusion unrelated to veridical motion signals**

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The ability to detect motion direction is locally constrained by the so-called ‘aperture problem’: a one-dimensional luminance profile (such as a line or contour) can move in various directions while generating the same response in a local-motion detector. Only at singularities where luminance

changes in both dimensions, such as the line endings ('terminators'), the veridical direction of line displacement can be detected. When a grating is moving behind an elongated aperture, it seems to move along the longer aperture border, giving rise to the barber-pole illusion. Whereas this illusion is traditionally attributed to a larger number of terminators moving along one border (cf Wallach, 1935 *Psychologische Forschung* **20** 325–380), some recent work (eg Fisher and Zanker, 2001 *Perception* **30** 1321–1336) suggests that the illusion is better described by the integration of local-motion signals arising from central and border regions of the aperture. We present here a new way to manipulate the features of the barber pole by using second-order patterns, in which either no first-order motion signal is available, or it is conflicting with the perceived motion direction. This condition can be achieved by generating second-order contours defined by flicker, orientation, or phase shifts, such as in abutting gratings known as 'illusory contours' (von der Heydt et al, 1984 *Science* **224** 1260–1262). Perceived direction of motion was measured by asking observers to adjust a line after the stimulus presentation, using various stimulus geometries. For a range of second-order contours and apertures, our observers reported motion directions perpendicular to the moving contour, or along the longer border of an elongated aperture. Taken together, our exploratory study demonstrates that perceived direction is not exclusively determined by local, luminance-defined, motion signals, but can follow second-order motion signals, and most importantly can be inconsistent with the physical movement of line endings.

◆ **Trans-saccadic integration of motion signals in human MT+ revealed by fMRI**

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Previous psychophysical studies have shown that motion signals are integrated spatiotopically across saccades (Melcher and Morrone, 2003 *Nature Neuroscience* **6** 877–881). Here we report a study of the neural substrate of trans-saccadic motion integration with fMRI. Dynamic random-dot patterns were displayed within a central square, while subjects fixated either to the left or the right of the square, or saccaded between the fixation dots. Three conditions were used: random noise only; random noise with one brief interval of coherent motion; and random noise with two brief intervals of coherent motion, separated by an interval of 1 s. In some conditions, subjects made a saccade between the two motion intervals, in others they maintained fixation. Subjects were required to discriminate the direction of motion while event-related BOLD responses were acquired. Area MT+ was identified on the basis of statistical maps and selectivity to flow motion, and further subdivided into a retinotopic and a non-retinotopic portion on the basis of the BOLD response to contralateral and ipsilateral visual stimuli in a passive viewing condition. The results show that the response in cortical area MT+ is higher for the two intervals of motion than for one interval, implying integration. The integration occurred mainly in conditions with an intervening saccade. It was strong and reliable for both the retinotopic and non-retinotopic portion of MT, and occurred across hemispheres. These results indicate that human MT may have a specialisation for the construction of spatiotopic receptive fields and the capability to integrate visual motion over a time scale of seconds.

◆ **Interactions of Glass patterns and random-dot kinematograms**

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We have measured the apparent direction of motion of random-dot kinematograms (RDKs) and investigated the influence of translational Glass patterns of varying orientation on the results. If the dots in each frame of the RDKs themselves form a Glass pattern, and if the axis of this Glass pattern is close to the RDK motion direction, then the apparent direction of motion of the RDK is strongly deviated towards this axis. This agrees with the neurophysiological result of Krekelberg et al (2003 *Nature* **424** 674–677) and also supports the hypothesis of Geisler (1999 *Nature* **300** 323–325), Burr (2000 *Current Biology* **10** R440–R443), Burr and Ross (2002 *Journal of Neuroscience* **22** 8661–8664), and Olshausen and Barlow (2004 *Journal of Vision* **4** 415–426). This postulates that Glass figures mimic the effects of motion blur, and that motion blur is used to establish the local axis of motion, especially in the patterns that result from optic flow. Further experiments probed this hypothesis with patterns in which the dots in the RDKs had a united lifetime of two frames, and those in the Glass figures were independently generated so that they were not coherently related in position to the RDK dots. Paired dots of the same polarity could also be replaced by anti-pairs of opposite polarity, since anti-pairs have been shown to counteract the perceptual appearance of Glass pairs.

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LEARNING AND MEMORY◆ **I thought you were looking at me: Directional aftereffects in gaze perception**

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Eye gaze is an important social signal in humans and other primates. Converging evidence from neurophysiological and neuroscientific studies has identified specialised gaze-processing circuitry in regions of the superior temporal sulcus. We report a series of adaptation experiments that examine the functional organisation of gaze perception in humans. We found that adaptation to consistent leftward versus rightward gaze gave rise to a compelling illusion that virtually eliminated observers' perception of gaze in the adapted direction; gaze to the adapted side was seen as pointing straight ahead, though detection of gaze to the opposite side was unimpaired. This striking aftereffect persisted even when retinotopic mapping between adaptation and test stimuli was disrupted by rescaling or reorientation of the adaptation stimuli, indicating that our findings do not reflect adaptation to low-level visual properties of the stimuli. Moreover, adaptation to averted gaze did not affect performance on the 'landmark' task of line bisection, illustrating that our findings do not reflect a change in spatial bias more generally. We interpret our findings as evidence for distinct populations of human neurons that are selectively responsive to particular directions of seen gaze.

[Supported by the Medical Research Council.]

◆ **Morphing visual memories through gradual associations**

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The perceptual memory system encodes stimuli and objects together with the associations and relations between them. It is not clear how these associations are captured by the brain and whether representations of related memories interact with each other. Computational models of associative memory suggest that memories are stored in cortical networks as overlapping patterns of synaptic connections, implying that related memories stored in the same network will interact with each other. Here, we investigated how exposure to face stimuli that are associated with a previously memorised face influences the long-term memory of the stored face. To study this, we performed the following psychophysical protocol: subjects were trained to recognise a set of faces. After the memories of the faces were confirmed by an identification task, subjects repeated the identification task on various faces, including a sequence of stimuli gradually transforming between a pair of faces—from one memorised face to another initially distinguishable face (morph sequence). For each subject, this task was repeated in multiple daily sessions on the same pair of faces. This protocol led to a gradual change in identification of the morph sequence by more than half of the subjects, eventually resulting in wrongly remembering the two pair faces as the same one and in an increase in their perceived similarity. A critical parameter for this effect to take place was the initial discriminability between the pair faces. A similar procedure, with the exception that at every session the morph sequence was presented in a random order, did not yield any significant change in identification, recognition, or similarity. These experimental results provide evidence that network mechanisms underlying long-term memory of objects entail interactions between encodings of related memories. Our experimental work is complemented with an associative-memory model that captures these findings.

◆ **Perceptual learning via recursive prior updating**

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Behavioural work [Gibson and Pick, 2000 *An Ecological Approach to Perceptual Learning and Development* (Oxford: Oxford University Press)], cell physiology (Crist et al, 1997 *Journal of Neurophysiology* **78** 2889–2894), and neuroimaging studies have suggested that some perceptual learning is mediated by top-down attentional processes. The optimal learning paradigm (OPL) allows researchers to compare how well humans learn with respect to an ideal Bayesian learner. This framework assumes that the human observer, like the ideal observer, updates the weighting (priors) of different sources of information as he/she learns which sources are relevant and which are irrelevant (Eckstein et al, 2002 *Journal of Vision* **4** 1006–1019). Here, we test whether the learning is mediated by the prior updating by using the classification image technique (Ahumada and Lovell, 1971 *Journal of the Acoustical Society of America* **49** 1751–1756). In the current OPL paradigm, a learning block consisted of 4 trials. On each trial a contrast increment might appear (50% probability) on one of four Gaussian pedestals (at equidistant locations from fixation) with added contrast noise. The possible location of the increment was randomly chosen for each learning block and was fixed throughout the 4 learning trials. The task was to correctly decide

whether the increment was present or absent and was followed by feedback about signal presence/absence. Performance based on 20 learning blocks for three observers increased significantly from the 1st to the 4th learning trials (average hit rate increased 3.58%; false alarm rate decreased 9%). The classification values across false alarm trials significantly increased for the target-relevant location as learning trials progressed while those of the three remaining irrelevant locations decreased. The results suggest that this type of human learning is mediated by a systematic increase in the weighting of relevant sources of information and a decrease in the weighting of irrelevant sources of information (ie recursive prior updating).
[Supported by the National Institute of Health.]

◆ **Repetition priming effects at the border**

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Current psychophysical and neuroimaging work strives to uncover neurobiological mechanisms of repetition priming using chiefly well-discernible stimuli (eg Henson, 2003 *Progress in Neurobiology* 70 53–81). In these studies, the frequently repeated stimuli typically yield shorter response times (RTs) and lower error rates than the rarely presented stimuli. Some, however, report a reverse repetition effect. Here, we ask whether repetition priming occurs with barely distinguishable stimuli and how, if at all, these effects depend on the presentation order of stimuli. Participants had to accomplish a visual binary classification task without practice and feedback, assigning two gray disks (size difference, 5%) into either 'small' or 'large' categories by pressing a respective key. In a 2 × 2 design, we varied the frequency of small and large disks in the sets (3:1 or vice versa) and the serial order of their presentation (either small or large ones were more likely to occur at the series outset). The results indicate that, with an average percentage of correct responses of 69%, the stimuli were only barely distinguishable. Unlike usual repetition priming effects, (i) for RT, repetition priming was highly stimulus- and experimental-set-specific, occurring with the small disks in the concordant sets (with frequent stimuli presented mainly at the series outset), and with the large disks in the discordant sets (with mainly infrequent stimuli occurring at the outset). With the large disks in concordant series and small disks in discordant series, RT repetition priming was reversed. (ii) Similarly, the reverse priming effects were found for the error rate, with frequently repeated—both small and large—disks giving rise to higher error rates. We conclude that, in comparison to the findings obtained with well-discernible stimuli, barely distinct stimuli produce reverse repetition priming effects. Repetition priming is likely to engage multiple neural mechanisms.

◆ **Slow and fast processes in visual 'one-shot' learning**

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A striking example of active vision is when it takes a while to realise what is hidden in a seemingly ambiguous bilevel quantised image. Famous examples such as 'the Dalmatian' and 'Dallenbach's cow' are visual teasers in which naive subjects find it difficult to see what is in the figure. Once the subjects realise what is in the picture, there is a one-shot perceptual learning, and recognition of what is in the image is possible after the passage of a considerable amount of time. These visual 'aha!' experiences or 'one-shot' learning processes are interesting for several reasons. First, the combination of low-level spatial integration and top-down processes involved provides important clues to the general neural mechanism of active vision (Kovačs et al, 2004 *Journal of Vision* 4 35a). Second, the temporal factors involved in this process, such as the brief synchronisation of neural activities (Rodríguez et al, 1999 *Nature* 397 430–433), provide crucial contexts for the integration of sensory information. Here, we report a series of experiments where the temporal factors involved in one-shot visual learning are studied. The subjects were presented with several bilevel quantised images, and were asked to report what was in the image. We measured the time required in delivering the correct answer. We found that there are at least two distinct cognitive processes involved. In the 'fast' process, the subjects almost immediately realise what is in the image, with the report time distribution decaying in an exponential manner. In the 'slow' process, the realisation occurred in a quasi-Poisson process, with the moment of realisation evenly distributed over time. Thus, the visual system seems to employ at least two

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different strategies in deciphering an ambiguous bilevel quantised image. We discuss the implications of our result for the neural mechanisms of dynamic cognition in general.

- ◆ **Visual learning of complex movements: Investigation of neural plasticity mechanisms**
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The ability to recognise complex movements and actions is critical for the survival of many species. In a series of psychophysical and functional imaging studies, we have investigated the role of learning for the recognition of complex motion stimuli. We trained human observers to discriminate between very similar human movement stimuli as well as between artificial movements. Our psychophysical results indicate no difference in the learning process for the two stimulus groups. Additionally, follow-up event-related fMRI adaptation experiments show an emerging sensitivity for the differences between the discriminated stimuli in lower-level motion-related areas (hMT+/V5 and KO/V3B). This effect was consistent for both stimulus groups. However, differences in brain activity between natural and artificial movements were obtained in higher-level areas (STSp and FFA). While sensitivity for artificial stimuli emerged only after training in these areas, sensitivity for natural movements was already present before training, and was enhanced after training. By extending a hierarchical physiologically inspired neural model for biological motion recognition (Giese and Poggio, 2003 *Nature Reviews Neuroscience* 4 179–192), we tried to model the BOLD signal changes during discrimination learning. The learning of novel templates for complex movement patterns was implemented by a combination of time-dependent and competitive hebbian learning, exploiting mechanisms that are physiologically plausible. The model accounts for the emerging sensitivity for novel movement patterns observed in fMRI. Learning of biological-motion patterns might thus be explained by a combination of several well-known neural principles in visual cortex. [Supported by DFG, Volkswagen Foundation, HFSP, and the Max Planck Society.]

VISUOMOTOR CONTROL

- ◆ **Planning sequences of arm – hand movements to maximise expected gain**
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We examined how subjects plan movement sequences in a ‘foraging’ task involving three disks that appeared simultaneously at a small number of possible locations on a touch-screen monitor. Subjects received monetary rewards for the disks they touched within 1.6 s. Disk colour signaled the value. The subjects could choose to attempt three disks in any order and could choose to attempt fewer than three disks. The dependent variable was the estimated probability of hitting each disk (p_A, p_B, p_C) as a function of sequence. It might be (0.9, 0.6, 0.5) for sequence ABC but (0.9, 0, 0.9) for sequence AC (no attempt to hit B). The sequence ABC offers the higher probability of hitting all three disks but, if A and C are made valuable enough, the sequence AC has higher expected gain. We tested whether subjects planned movement sequences that maximised expected gain. The experiment consisted of three sessions. In the first session, ten naive subjects were trained until their performance was stable. In the second session, we measured how accurately each subject could execute each of the 12 possible sequences of length 2 or 3 on three disks of equal value. In the last session, the values of the disks were altered by amounts that varied between blocks of trials. Subjects were told the values of the colour-coded disks before each block and were free to choose any sequence. On the basis of second-session performance we could predict the strategy each subject should adopt on each trial in order to maximise expected value for each assignment of values to disks. Subjects did change strategies in the expected direction but typically favoured strategies that maximised probability of hitting three disks over the maximum expected gain strategy. [Supported by Grant EY08266 from the National Institute of Health.]

- ◆ **Visual detection and eye – hand coordination under free-viewing and gaze-locked pixelised conditions: Implications for prosthetic vision**
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Our objective was to determine the need for eye-position feedback in the design of retinal and cortical visual prostheses with external image acquisition. Electrodes in such devices are stationary

relative to the tissue substrate, hence there will be a perceived image shift in response to an eye movement, unless a built-in eye-tracking signal is used to produce a compensatory image shift. Normally-sighted subjects performed two tasks using a 6×10 (12 deg \times 20 deg) pixelisation filter of Gaussian profile dots ($\sigma = 1$ deg) generated in real-time and viewed monocularly in a video headset. Up to 30% of the dots were missing, and dynamic noise with 100% SNR could be added. In a virtual mobility task, subjects used cursor keys to manoeuvre through 10 rooms in a computer-generated variable floor plan. In a checkerboard test, subjects used live input from a camera mounted on the headset to first count, and subsequently place black checkers on, 1–16 randomly located white fields in an 8×8 black checkerboard. Gaze-locked and free-viewing trials were alternated, while drop-outs and dynamic noise were introduced once performance stabilised. Performance was scored in terms of accuracy (% correct) and response time. We found that subjects reach stable performance in any condition after several hours of practice. Gaze-locked response times and error rates are 1.5–3 times those in the free-viewing condition, becoming more similar over time. Learning effects were similar across tests and conditions. Increased difficulty caused performance to drop temporarily, then stabilise close to the previous level. Subjects varied substantially in response time, accuracy, and rate/degree of learning; some performance differences could be attributed to speed–accuracy tradeoff. These results demonstrate visual task performance under highly adverse conditions, as can be expected for visual prostheses. We are expanding this series of experiments and including subjects with severe low vision. [Supported by NIH R01 EY12843, Foundation Fighting Blindness.]

◆ **How fast do we react to moving obstacles?**

M P Aivar, E Brenner, J B J Smeets (Department of Neuroscience, Erasmus MC, Postbus 1738, NL 3000 DR Rotterdam, The Netherlands.; e-mail: p.aivar@erasmusmc.nl)

Previous results have shown that people react within about 120 ms if the target that they are moving to suddenly starts to move (Brenner and Smeets, 1997 *Journal of Motor Behavior* 29 297–310). In daily life, movements are executed in environments that are clustered with many different objects. In the present study, we examined whether people can respond as quickly when one of these objects suddenly starts to move in a direction that will make it cross the path of the hand. Subjects moved a stylus across a digitising tablet. Each trial started with the simultaneous presentation of a target and an obstacle. Subjects were instructed to move to the target as quickly as possible without hitting the obstacle. The obstacle was always near the target, and was either slightly above or slightly below a straight path between the starting position and the target. In most of the trials the obstacle was static, but in some trials the obstacle started to move across the straight path between the starting position and the target as soon as the subject's hand started to move. We found that hand trajectories always curved away from the initial obstacle position. In trials in which the obstacle unexpectedly started to move, most subjects moved their hand further away from a straight path. By comparing the trajectories on trials in which the obstacle started moving with trajectories on trials in which it appeared at the same position and stayed there, we estimated that it took our subjects about 250 ms to respond to the obstacle starting to move. This result shows that reactions to changes in the target of the movement are faster than reactions to changes in other objects in the surrounding. [Supported by European grant HPRN-CT-2002-00226.]

◆ **Making goal-directed movements with 'relocated eyes'**

A Brouwer, R Kanai¶, Q V Vuong (Max Planck Institute for Biological Cybernetics, PO Box 2169, D 72012 Tübingen, Germany; ¶Psychonomics Division, Helmholtz Research Institute, Utrecht University, Heidelberglaan 2, NL 3584 CS Utrecht, The Netherlands; e-mail: anne-marie.brouwer@tuebingen.mpg.de)

We investigated the effect of various viewpoints on remapping visuo-motor space. Subjects tapped targets on a touch monitor that was placed horizontally in front of them. The targets appeared at one of seven positions at a fixed distance from the starting position of the hand. Subjects viewed the monitor and their hand through video glasses attached to a camera that was placed at a fixed radius from the centre of the monitor and elevated 45°. On each trial, the camera was randomly positioned at one of seven azimuths (-90° to $+90^\circ$ in 30° steps). We recorded tapping errors and movement times. Both errors and movement times were described by a U-shaped curve when plotted as a function of camera position: performance progressively decreased with larger azimuths. However, the minimum of the curve was shifted to the right of the central camera position. In a second experiment, we found that this bias of camera position depended on the hand that subjects used to tap the targets rather than on handedness: if subjects used their left hand, the bias shifted towards the left of the central camera position.

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In order to perform the task, subjects could use 'static information', consisting of the lay-out of the scene with the monitor and the hand. In principle, this information specified the camera position and the location of the target in space. In addition, subjects could use 'dynamic information' which involves the visual feedback of moving the hand in a certain direction. Subjects could use this information to adjust their movements online to reach the target. We hypothesise that the U-shaped curve and bias are caused by the dependence of these strategies on camera position.

[Supported by the European Commission (Grant HPRN-CT-2002-00226).]

- ◆ **The role of the ground plane in the maintenance of balance: Are we 'hooked like puppets'?**
B J Rogers, H J Richards (Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, UK; e-mail: bjr@psy.ox.ac.uk)

Lee and Lishman (1975 *Journal of Human Movement Studies* 1 87–95) first reported that vision plays an important role in the maintenance of balance. Using their 'swinging room', they reported that observers swayed in synchrony with the room, as if 'hooked like puppets'. However, the ground plane beneath the observers was always stationary; the sidewalls of their 'room' were very close—less than 80 cm on either side; and the closest part of the room in front was only 30 cm away. We investigated whether the movements of a ground plane surface or the sidewalls of a swinging room with more normal room dimensions would be equally effective in inducing sway. Observers stood on either a firm platform or a compliant foam pad within a suspended room whose floor and/or sidewalls could be made visible with a dense array of self-luminous patches. The floor and/or walls were moved sinusoidally with an amplitude of ± 3 cm at frequencies of either 0.02 Hz (50 s period) or 0.05 Hz (20 s period). Observer sway was monitored with a ceiling-mounted video camera. The gain and phase of each observer's movements at the frequency of the room oscillation were derived from these traces. Like Lee and Lishman, we found that sway was much larger when observers stood on a compliant surface—emphasising the importance of ankle-foot proprioception in normal balance. Movements of the walls or walls + floor produced in-phase oscillations with gains of around 0.6 for the faster oscillation frequency and compliant surface and significantly less (0.25) for the slower oscillation frequency. Movements of the floor alone produced low gains of between 0.1 and 0.2. While the visual flow from very close objects and surfaces plays a role in the maintenance of balance, ground plane optic flow appears to be relatively unimportant.

- ◆ **Visual information is used throughout a reach to control endpoint precision**
A Ma-Wyatt, S P McKee (Smith-Kettlewell Eye Research Institute, 2318 Fillmore Street, San Francisco, CA 94115, USA; e-mail: anna@ski.org)

Goal-oriented reaches necessarily rely on visual information: to localise the position of the object in space and to plan the movement. Previously, we found that visual error limited pointing error for a target location beyond 4 deg eccentricity. It was previously believed that rapid movements were not under visual control, but recent work has shown that visual feedback can be used to correct a trajectory for both fast and slow reaches. We investigated whether visual information is used throughout the reach to control endpoint precision for a rapid point. Subjects fixated a central fixation point and pressed a key to initiate a trial. The target was a high-contrast dot subtending 0.5 deg, presented for 110 ms at one of eight locations on an isoeccentric circle. The radius of this circle (target eccentricity) was 8 deg. Subjects were instructed to point as quickly as possible. Pointing times were ~ 400 ms. Negative feedback was given if the subject was too spatially inaccurate or too slow. Photographic shutters closed off the subject's view 50 ms, 180 ms, or 250 ms into the movement. If the observer is chiefly using visual information (the brief target) to formulate a motor plan before reaching, then closing off the shutters should have a minimal effect on pointing precision. If, however, the subject is using visual information throughout the reach to guide the movement, then closing off visual information during the reach should lead to a degradation of performance. Precision was compromised if the view of the hand was restricted during the reach. Precision decreased the most for conditions in which the shutter closed 50 ms into the reach. Our results show that visual information is used to guide the hand throughout a reach, and this visual information has a significant impact on endpoint precision.

[Supported by a Rachel C Atkinson Fellowship to AMW and NEI EY006644 to SPM.]

WEDNESDAY

SYMPOSIA

THE NEURAL BASES OF VISUAL AWARENESS

- ◆ **Bilateral frontal leucotomy does not alter perceptual alternation during binocular rivalry**
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When binocular fusion is impossible, perception spontaneously oscillates between the possible patterns. It has been proposed, based on functional MRI (fMRI) studies, that a right frontoparietal network controls these perceptual alternations. fMRI results, however, are correlational in nature and lesion studies are needed to assess the causal role of the identified frontoparietal network. We studied one patient whose subcortical connections between prefrontal cortex and the rest of the brain were severely damaged by a bilateral leucotomy. Despite these lesions, the patient showed perceptual oscillations indistinguishable from normal observers. Together with previous studies on patients with parietal damage and split-brain patients, our findings cast doubts on the causal role of the right frontoparietal network in binocular rivalry.

[Supported by the Spanish Ministry of Education.]

- ◆ **Learning blindsight**
P Stoerig (Institute of Experimental Psychology II, Heinrich-Heine-University, Universitätsstrasse 1, D 40225 Düsseldorf, Germany; e-mail: stoerig@uni-duesseldorf.de)

Fields of dense cortical blindness result from destruction or denervation of primary visual cortex. Although the patients do not (consciously) see visual stimuli which are confined to the blind field, reflexive (pupil light reflex, blinking, OKN) as well as non-reflexive (indirect or forced-choice) responses may still be elicited. The variability both in prevalence (0–100%) and performance (chance level to 100% correct) of blindsight is large, and likely to depend on lesion and patient factors as well as on the function tested. Among these, the amount of experience with responding to blind-field stimuli has received little attention, although early observations on monkeys with striate cortical ablation indicate that blindsight does not kick-in automatically when conscious vision is lost. As monkeys, unlike patients, commonly receive extensive training before they are formally tested, and more consistently show high levels of performance, we have studied human blindsight as a function of time. Patients underwent manual localisation training with feedback provided upon each response. Results on this as well as a number of other functions including detection, discrimination of orientation, motion, and wavelength show that (i) blindsight can be learned, (ii) different functions differ in difficulty, and (iii) patients profit from learning blindsight in their daily life, as predicted from the visually guided behaviour of blindsight-experienced cortically blind monkeys. Changes in performance were found to correlate with changes in BOLD activation patterns evoked by stimulation of the blind field, and may invoke changes in the visual field defect with regard to its density and/or its extent. As such changes are observed even when no evidence for activity within the lesioned or denervated striate cortex is revealed with fMRI, not only blindsight but even the recovery of some conscious vision may be possible without V1.

[Supported by the Deutsche Forschungsgemeinschaft (SFB 194/A15).]

- ◆ **Visual masking approaches to visual awareness**
S L Macknik (Barrow Neurological Institute, 350 W Thomas Road, Phoenix, AZ 85013, USA; e-mail: macknik@neuralcorrelate.com)

The most fundamental goal of the visual system is to determine whether a stimulus is visible, or not. Yet it remains unknown how the visual system accomplishes this basic task. Part of the problem is that the question ‘What does it mean for something to be visible?’ is itself difficult to approach. In order to address this general question, I have broken it up into several, more specific parts: (i) What are the physical aspects of stimuli that are more visible than others? (ii) What types of neural activity encode visible signals? (iii) What brain areas must be activated for the stimulus to be consciously visible? (iv) What specific circuits, when activated, produce the feeling of visibility? All of these questions must be answered in order to understand the visual system at its most basic level. I present results from psychophysical, physiological, and optical/magnetic imaging experiments that have begun to address all of these questions. I have used visual masking and other illusions of invisibility to render visual targets invisible, despite the fact that they are unchanged physically on the retina. By comparing the responses to visible versus invisible targets, I have begun to determine the physical and physiological basis of visibility.

[Supported by the Barrow Neurological Foundation.]

Wednesday

◆ **Top – down attentional control of synchronised neural activity in visual cortex**

R Desimone (McGovern Institute for Brain Research, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA 02139, USA; e-mail: desimone@mit.edu)

A complex visual scene will typically contain many different objects, few of which are currently relevant to behaviour. Thus, attentional mechanisms are needed to select the relevant objects from the scene and to reject the irrelevant ones. Brain imaging studies in humans as well as neurophysiological studies in monkeys have identified some of the neural mechanisms of attentional selection within the ventral, 'object recognition', stream of the cortex. The results support a 'biased competition' model of attention, according to which multiple stimuli in the visual field activate their corresponding neural representations throughout the cortical areas of the ventral stream. These representations engage in mutually suppressive interactions, which are strongest for stimuli occupying the same receptive field. The suppressive interactions are then biased in favour of one of the competing populations by 'top-down' signals specifying the properties of the relevant stimulus in a given behavioural context. This top-down bias may originate in parietal and prefrontal cortex, and it is expressed in visual cortex, at least in part through an increase in high-frequency (gamma) synchronisation of neurons carrying critical information about the location or features of the behaviourally relevant stimulus. Conversely, low-frequency (beta) synchronisation of neural activity may be relevant for suppressing distractors. High-frequency and low-frequency synchronisation appears to be differentially present in superficial versus deep layers of the cortex, respectively, in visual areas V1 through V4, suggesting that they play different roles in feedforward and feedback connections in the cortex.

[Supported by NIMH IPR and McGovern Institute at MIT]

FORM, OBJECT, AND SHAPE PERCEPTION

◆ **The role of contour curvature in form-based motion processing**

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The visual system is more sensitive to the presence of local maxima of positive contour curvature than it is to relatively uncurved segments of contour. Several theories imply that local maxima of positive curvature along a contour are particularly revealing about 3-D shape and motion. The goal of the present series of experiments was to specify the role of regions of relatively high contour curvature in form and motion processing. Five types of stimuli were used for MRI experiments, consisting of two half ellipses joined along their common major axis. The sharpness of curvature discontinuities varied across these stimuli. In different experiments, stimuli either had the same area, the same radius, or the same objective or the same subjective speed of rotation. In order to guarantee that they were maintaining fixation, observers carried out a simple task at the fixation point that was not directly related to issues of curvature processing (press button when fixation point blinks). Between fifteen and twenty-seven subjects were run in standard fMRI block-design experiments, GE 1.5T, one-shot EPI, FA 90°, epochs 20 s, TR = 2.5 s, 25 axial slices. Areas of the brain where the BOLD signal varied parametrically with the strength of contour curvature discontinuities included human MT+. Several extrastriate visual areas, including V2, also varied parametrically with curvature sharpness. Human psychophysics also demonstrates that perceived motion speed tracks parametrically with curvature abruptness, even when all stimuli rotate at the same objective speed. In particular, ellipses rotating at a constant angular velocity appear to rotate more quickly with increasing aspect ratio. These data suggest that contour curvature information is processed in extrastriate visual cortex and MT+, where it is used to generate information about motion on the basis of form-defined trackable features.

◆ **Bayesian inference of form and shape**

P Mamassian (CNRS and Université de Paris 5, 71 avenue Édouard Vaillant, F 92774 Boulogne-Billancourt Cedex, France; e-mail: pascal.mamassian@univ-paris5.fr)

The perception of 2-D form and 3-D shape involves both objective and subjective aspects. Objective aspects include the information contained in the curvature and contrast of contours, while subjective aspects include preferred lighting and viewing positions. The Bayesian statistical framework offers a natural way to combine these two aspects by referring to the likelihood function and the prior probabilities. The likelihood represents knowledge about image formation, such as Koenderink's rule that a concave contour in the image corresponds to a saddle-shape surface patch (Koenderink, 1984 *Perception* 13 321–330). Priors represent preferences on scene characteristics such as the Gestalt laws of perceptual groupings (Feldman, 2001 *Perception & Psychophysics* 63 1171–1182). In this presentation, I attempt to summarise the recent efforts to apply the framework of Bayesian inference to the perception of form and shape. Examples are

drawn from illusory contours for form and shape, motion perception, and 3-D shape from texture, motion, and binocular disparities. Some outstanding issues for future research are provided. [Supported by the Chaire d'Excellence from the French Ministry of Research.]

◆ **Neural basis of shape representation in the primate brain**

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Visual shape recognition—the ability to recognise a wide variety of shapes regardless of their size, position, view, clutter, and ambient lighting—is a remarkable ability essential for complex behaviour. In the primate brain, this depends on information processing in a multi-stage pathway running from primary visual cortex (V1), where cells encode local orientation and spatial-frequency information, to the inferotemporal cortex (IT), where cells respond selectively to complex shapes. A fundamental question yet to be answered is how the local orientation signals (in V1) are transformed into selectivity for complex shapes (in IT). To gain insights into the underlying mechanisms we investigated the neural basis of shape representation in area V4, an intermediate stage in this processing hierarchy. Theoretical considerations and psychophysical evidence suggest that contour features, ie angles and curves along an object contour, may serve as intermediate-level primitives in the processing of shape. We tested this hypothesis in area V4 using single-unit studies in primates. We first demonstrated that V4 neurons show strong systematic tuning for the orientation and acuteness of angles and curves when presented in isolation within the cells' receptive field. Next, we found that responses to complex shapes were dictated by the curvature at a specific boundary location within the shape. Finally, using basis function decoding, we demonstrated that an ensemble of V4 neurons could successfully encode complete shapes as aggregates of boundary fragments. These findings identify curvature as one basis of shape representation in area V4 and provide insights into the neurophysiological basis for the salience of curves in shape perception.

◆ **Shape perception for object recognition and face categorisation**

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Even though shape is the basis of object recognition, there is still an on-going debate about how it is perceived and represented in the brain. An important question is how various visual cues, like disparity and texture, are integrated into a unique shape percept. Different visual information has also been shown to play an ancillary role in shape perception. For example, cast shadows can help disambiguate shape perception (Kersten et al, 1996 *Nature* **379** 31), while 2-D retinal motion information can help organise dots into meaningful shapes despite incongruent depth information (Bühlhoff et al, 1998 *Nature Neuroscience* **1** 254–257). Shape perception is also important for object categorisation. For example, faces varying in shape and texture may be perceptually grouped into different categories (a phenomenon known as categorical perception). Previous studies have shown that faces varying in expressions, identity, or race are perceived categorically (eg Levin and Angelone, 2002 *Perception* **31** 567–578). We did not find a similar effect for faces varying in masculinity/femininity (Bühlhoff and Newell, 2004 *Visual Cognition* **11** 823–855). This difference in perception for sex and identity is supported by new studies showing a lack of sensitivity to sex changes in familiar faces, while changes in identity are easily noticed. These results have implications for the nature of shape representations of faces in the brain.

ORAL PRESENTATIONS

LIGHTNESS, BRIGHTNESS, AND CONTRAST

◆ **Predicting the contrast response functions of LGN and V1 neurons from the contrast of natural images**

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Histogram equalisation showed that the respective contrast response functions (CRFs) of fly large monopolar cells, cat X and Y cells, and macaque M cells are all optimal for the representation of the contrast range these neurons encounter in natural images (Laughlin, 1981 *Zeitschrift für Naturforschung* **36** 910–912; Tadmor and Tolhurst, 2000 *Vision Research* **40** 3145–3157). Additionally, cat V1 neurons are optimised for signalling contrast in natural images according to a similar

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principle (Clatworthy et al, 2003 *Vision Research* **43** 1983–2001). However, experimentally measured CRFs show that macaque P cells and V1 neurons are less sensitive to contrast than predicted by histogram equalisation of the contrasts in natural scenes. We have recalculated the distribution of contrasts encountered by retinal, geniculate, and V1 neurons in natural scenes. Banks of 70 difference-of-Gaussian and 80 Gabor contrast operators, both biologically plausible and representative of the range of macaque neurons, sampled the contrasts at more than 40 million positions in monochromatic natural scenes (van Hateren and van der Schaaf, 1998 *Proceedings of the Royal Society of London, Series B* **265** 359–366). As an alternative approach, contrast was also sampled at 16 000 positions fixated by human observers during free viewing of these images (Martin and Tadmor, 2004 *Perception* **33** Supplement, 145). The results of fixation sampling show that increased contrast at fixated positions is not sufficient to account for the greater contrast insensitivity of macaque P and V1 cells. On the other hand, histogram equalisation of the contrast outputs of only the most responsive model neurons at each image location provides very good matches of experimentally measured CRFs of macaque P and V1 neurons. Our analysis suggests that macaque P and V1 neurons employ a contrast coding strategy intrinsically different from M cells and cat visual neurons, which is related to the contrast of spatially optimal features.

◆ **Amplifying the effective perceptual contrast of a grating**

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Consider a horizontal slice of a vertically oriented test grating with a contrast so low that it cannot be distinguished either from a uniform field or from its negative—the same grating shifted by 180°. We embed a test grating in a higher-contrast surround, the amplifier grating. The amplifier itself consists of slices of a higher-contrast vertical grating, shifted 90° from the test grating. We find that the combination of these two gratings gives rise to a perception of slant. The perceived slant is mirror-opposite for the test and for the negative test. Thereby, a grating that is itself completely invisible reliably induces opposite slant perceptions depending on its phase. Equivalently, we superimpose a slant-neutral checkerboard stimulus on slanted gratings. (A priori, this would be an uninformative masking stimulus.) Actually, it functions as an amplifier, enabling discrimination between two oppositely slanted gratings at contrasts of as little as 1/5 to 1/8 the contrast at which the unamplified (‘unmasked’) gratings can be discriminated. These amplification phenomena for static slanted gratings are analogous to motion phenomena in which the discrimination of the direction of motion of translating vertical gratings is greatly facilitated by the addition of a stationary flickering grating. The amount of amplification is quantitatively predicted by direct application of the motion theory formulated in x, t (van Santen and Sperling, 1984 *Journal of the Optical Society of America A* **1** 451–473) to slant in x, y . We experimentally confirmed contrast amplification for a variety of first-order (luminance modulation) gratings and second-order (texture-contrast modulation) gratings. Among the uses of this sensitive assay method is the efficient complete removal of luminance cues from texture stimuli (cf Lu and Sperling, 2001 *Vision Research* **41** 2355–2374).

[Supported by the US Air Force Office of Scientific Research, Life Sciences.]

◆ **Probe disks reveal framework effects within multi-illuminant scenes**

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When identical gray disks are pasted into photos of real scenes depicting regions of different illumination, disks in the shadowed region appear much lighter than those in the sunlit region. In condition 1, using a Munsell chart, observers matched such probe disks for lightness at 13 locations in the photo. In condition 2, disks were altered in shape/size to conform to slant/distance of depicted walls. In condition 3, some blur was added to disk edges to match the graininess of the photo. On average, disks in the shadowed framework appeared 3 Munsell steps lighter than those in the sunlit framework. Disks within a region of illumination appeared roughly equal in lightness, while a lightness step-function occurred at illumination boundaries. This suggests that regions of illumination function as frames of reference. The illusion was significantly greater when the size and shape of the disks conformed to the depicted location, and significantly greater still with blurred disks. We conclude that illusion size depends on the degree to which the disks appear to belong to the framework of illumination on which they are pasted. In a further experiment, probe disks were added to Adelson’s checkered-shadow display, to test the

framework effect against a local contrast effect. Disks in different frameworks, but with equal local contrast, differed on average by over 2 Munsell steps, while disks of very different local contrast, but within a single framework of illumination, differed by little or nothing. Frameworks rock! [Supported by National Science Foundation BCS-0236701 and Public Health Service GM 60826-02.]

◆ **The phantom contrast effect**

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Agostini and Galmonte (1997 *Investigative Ophthalmology & Visual Science* **38** S895; 2002 *Psychonomic Bulletin & Review* **9** 264–269) showed that a linear luminance gradient can largely modify the lightness of a target region. In the present work, a version of the gradient configuration is offered where the luminance range has been drastically reduced. In this condition, the gradient is almost unnoticeable. Comparing the lightness of a gray target placed at the centre of this gradient with that of an identical target surrounded by a surface having a homogenous luminance value equal to the highest luminance of the gradient, they appear quite different even though their backgrounds appear the same. This perceptual paradox is remarkable because it suggests that smooth changes in luminance, even when difficult to detect, can affect lightness perception. This paradox could be due to the local contrast between the target and its closest surrounding luminance. But, by narrowing the spatial distribution of an identical reduced-range luminance gradient, the direction of the effect is reversed. It is not possible to account for this result by considering only the local contrast between the last luminance of the gradient and that of the target. This suggests that the visual system computes surface colours taking into account the global spatial distribution of luminance gradients.

◆ **fMRI correlates of corner-based illusions show that BOLD activation varies gradually with corner angle**

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The Alternating Brightness Star (ABS) is a novel visual illusion which shows that perception of corner brightness varies gradually with the angle of the corner. Recent psychophysical studies of this illusion (Troncoso et al, 2005 *Perception* **34** 409–420) have shown a linear relationship between corner brightness and corner angle, with sharp angles leading to stronger illusory percepts and shallow angles leading to weak percepts. Here we explore the BOLD correlates of the ABS illusion in the human cortex. We presented normal volunteers with ABSs of five different angles: 15° (sharp corner), 45°, 75°, 105°, and 180° (no corner). The results show that BOLD signal varies parametrically with corner angle throughout the visual cortex, matching previous psychophysical data and offering the first neurophysiological correlates of the ABS illusion. These results may have important consequences for our understanding of corner and angle processing and perception in the human brain.

[Supported by the Barrow Neurological Foundation, UCL Graduate School.]

◆ **Multi-dimensional scaling analysis of Adelson's snake lightness illusion**

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Using a novel dissimilarity scaling method, Logvinenko and Maloney recently demonstrated that the manifold of achromatic colours of an object has two dimensions—lightness and surface brightness (*Perception & Psychophysics* in press). The following question then arises: which of these two dimensions—lightness or surface brightness—is involved in simultaneous lightness contrast? Since Adelson's snake pattern invokes a strong lightness (or surface brightness?) illusion, we chose it for study. We measured the dissimilarity between different targets embedded in adjacent horizontal strips of the snake pattern, and then applied the scaling algorithm of Logvinenko and Maloney to the resulting data. The output configuration was found to be one-dimensional, indicating that our observers experienced an illusory shift in only one of two dimensions—most likely lightness. This result is in line with the hypothesis that simultaneous lightness contrast is a pictorial illusion (Logvinenko et al, 2002 *Perception* **31** 73–82).

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- ◆ **Adaptation to skewed image statistics alters the perception of glossiness and lightness**
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The human visual system has a striking ability to estimate the surface qualities of natural objects. How does the brain do this job? We recently found that the apparent glossiness and lightness of natural surface images is influenced by the 2-D image statistics of the luminance histogram (Adelson et al, 2004 *Journal of Vision* 4 123a; Motoyoshi et al, 2005 *Journal of Vision* in press). As the luminance histogram was skewed more positively (negatively), the surface looks more glossy and darker (more matte and lighter). We here introduce a novel effect of adaptation on perceived surface properties. After adapting to a textured image whose luminance histogram was positively (negatively) skewed, a test surface image looked more matte and lighter (more glossy and darker). The aftereffect was robustly observed not only when the adapting images were of natural surfaces, but also when they were random-dot patterns with skewed statistics, which, by themselves, look neither matte or glossy. Although the adapting stimuli have skewed statistics in the luminance domain, the critical issue may be the way the statistics are skewed in the sub-band domain. Stimuli with positive (negative) skew will preferentially stimulate on-centre (off-centre) cells, and thus the adaptation should produce a bias in the sensitivity of on and off channels. This bias could explain the change in the gloss and lightness, since the relative response of the channels is correlated with the skew of the image statistics, and is also correlated with the reflective properties of complex surfaces. We also found a parallel simultaneous-contrast effect: a surface surrounded by images with skewed histogram looked more matte or glossy. Both the aftereffect and the simultaneous-contrast effect support the importance of image statistics in the perception of surface properties.

- ◆ **Discounting luminance contrast produced by an illumination edge depends on its shape**
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A luminance ratio produced by a reflectance edge was found to be overestimated as compared to an objectively equal luminance ratio produced by an illumination edge (Logvinenko, 2004 *Perception* 33 Supplement, 54). It was also found that the visual system was more likely to interpret a straight luminance edge as an illumination border than a curved luminance edge (Logvinenko et al, in press *Perception & Psychophysics*). We ascertained the effect of the illumination edge shape (straight versus circular) on the 'illumination edge discounting'. Thirty observers were presented with a piece of grey paper crossed by a straight illumination edge. Luminance of the shadowed and illuminated fields was 8.4 cd m^{-2} and 84 cd m^{-2} . Twenty test squares of different shade of greyness were painted on each field. They constituted a series of reflectance edges (incremental on the shadowed field and decremental on the lit field) the luminance contrast of which varied from 1.1 to 5.0. The observers were asked to point out which of the test squares had the same luminance contrast as the illumination edge. On average, they judged the luminance contrast produced by the reflectance edge as apparently equal to 3.7 times the luminance contrast produced by the illumination edge. In other words, luminance contrast produced by an illumination edge was discounted by a factor of 3.7. However, when the illumination edge had a circular shape, it was discounted by only a factor of 1.1. This result confirms that straightness of a luminance edge is an important cue for its interpretation as an illumination edge.

COLOUR

- ◆ **Articulation and chromatic characteristics determine colour naming in normal and colour-blind observers**

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Two colour-naming experiments were carried out to compare the use of basic colour categories in normal and colour-blind observers (protanopes and deuteranopes). In experiment 1, using a sample of 102 simultaneously presented stimuli, observers were required to perform two searching tasks. In some trials, they had to point to 'the best example of a category' (prototype searching task). In other trials, subjects had to point to 'all the stimuli that could be named with a category' (compatible stimuli searching). High concordance levels were observed between normal subjects and dichromats in the prototype searching task (they pointed frequently to the same stimulus) but not in the searching task for compatible stimuli. In both tasks, performance was influenced by the specific category considered. For example, there was no difference between

normal subjects and dichromats in the prototype searching task for the yellow category (all the observers pointed to the same stimulus!), though differences appeared for brown and purple. In experiment 2, we evaluated lightness and articulation effects in the use of basic colour categories. Chromatic co-ordinates of the eleven prototypes of Spanish basic colour categories were used to create two sets of stimuli. The first set ('standard prototypes') incorporated luminance levels similar to those in experiment 1 (consequently, this parameter changed with chromatic category). On the other hand, the same luminance was used to create the stimuli included in the second set ('equated prototypes'). Each stimulus of the two sets was individually presented in two different ways: with ('Mondrian condition') and without ('Gelb condition') an articulated background. As expected, the performance of normal and of dichromats was similar to experiment 1 when the standard prototypes were presented in the Mondrian condition. On the other hand, important differences appeared when stimulus type (equated prototypes) or background (Gelb condition) was changed. It can be concluded that background articulation influences lightness perception of the target stimulus and the use of basic colour categories, specially for colour-blind observers.

◆ **Influence of saturation on colour preference and colour naming**

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Young children typically prefer less, and acquire later, the colour terms brown and grey relative to those of the other nine basic colours (Pitchford and Mullen, 2005 *Journal of Experimental Child Psychology* **90** 275–302). As brown and grey are desaturated relative to the other basic colours, saturation may be a factor in determining colour preferences and emerging colour cognition. We tested this hypothesis using two experimental tasks (preference and naming) given to a group of young children ($N = 27$, mean age = 4 years 9 months) and adults ($N = 30$, mean age = 28.5 years). Both tasks used the same stimuli, which were seven pairs of Munsell chips drawn from different category boundaries. Each colour pair was matched for hue and luminance, but one chip was saturated (eg 7.5 BG 6/8) and the other was relatively desaturated (eg 7.5 BG 6/2). A non-basic colour term (eg teal) was assigned to each of the 14 chips. A colour preference task measured the rank preference order across the 14 chips, then the non-basic colour terms were taught in a task whereby each colour chip was presented on 10 occasions for learning and naming. Results showed that children preferred and learned to name significantly more saturated than desaturated colours and a significant correlation was found between preference and naming across the 14 chips. Adults also learned significantly more saturated than desaturated terms although the difference in preference for saturated and desaturated colours was not significant, and neither was the correlation between preference and naming. Children's and adults' colour naming correlated significantly however, indicating that for both groups the ease of learning new colour terms was similar across colours. This suggests that saturation influences colour preference and colour naming, especially in childhood, but that preferences may be modified over time.

◆ **Selective processing of colour categories and other stimulus attributes in the cortex: Evidence from clinical studies**

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Polarity-sensitive signals can code for the four distinct 'cardinal directions' in colour space, both in the retina and in the lateral geniculate nucleus. Psychophysical findings show that S-cone signal increments and decrements can lead to the perception of 'blue' and 'yellow' colours, respectively, whilst positive and negative L–M cone contrast signals of equal magnitude lead to the perception of 'red' and 'green', in the absence of S-cone signal changes. The processing of opponent-colour signals and the generation of perceived primary colours in extrastriate areas of the cortex is less well understood. Studies in subjects with diseases of the retina and the optic nerve tend to produce symmetric loss of red–green (rg) or/and yellow–blue (yb) chromatic sensitivity. In this study, we have examined twenty subjects with damage to extrastriate areas of the cortex and looked specifically for loss of contrast acuity, motion perception, and rg and yb colour discrimination. The stimuli were presented at the fovea and in each of the four quadrants (~6 deg eccentricity). The results reveal a number of interesting findings suggesting that damage to neural substrates in the cortex can cause selective loss of colour, contrast acuity, and/or motion sensitivity. Ten subjects showed severe loss of rg with almost normal yb chromatic sensitivity.

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Two subjects showed significantly greater loss of 'red' than 'green' sensitivity. Four subjects showed significantly greater loss of sensitivity for 'yellow', but not for 'blue' stimuli. Chromatic sensitivity was spared selectively in two subjects that exhibited massive loss of contrast acuity and motion sensitivity at the same location in the visual field. The loss of sensitivity for processing a specific stimulus attribute was often location-specific. These findings suggest that the concept of 'functional specialisation' in the cortex should be extended to colour categories and other stimulus features.

◆ **A novel grating stimulus for segregating PC and MC pathway function**

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We have measured cell responses and psychophysical thresholds to a compound grating stimulus with red and green bars alternated with dark areas (ie, red–black–green–black). Responses to such gratings were compared to responses to standard luminance and red–green chromatic gratings at a variety of spatial and temporal frequencies and contrasts. MC cells gave very similar responses to the luminance and compound gratings, and little or no response to the chromatic grating. PC cells responded vigorously to the compound and chromatic gratings, and weakly to the luminance grating. Their response to the compound grating was at half the temporal (and spatial) frequency of that of MC cells, ie a red on-center cell responded only to the red bars. Modeling of cell responses indicated that PC cell responses should show some higher-harmonic distortions to the compound grating. Such distortions were present but minor, especially at low contrast. The three grating types are easily discriminable by observers. We measured detection and discrimination thresholds for the three gratings. Detection of the compound grating followed the envelope of detection of chromatic and luminance gratings. Discrimination of the different gratings was possible very close to detection threshold, even at the highest spatial frequencies. This can be possible only if both MC and PC pathways contribute to discrimination. This points to a nuanced view of the roles of MC and PC pathways in fine spatial vision. To elucidate the fine spatial and chromatic structure of objects, both pathways must be implicated. This novel stimulus provides a unique signature for MC and PC pathway activity, and may be useful for identifying their inputs to central sites.

[Supported by EY 13112.]

◆ **Activation of human visual cortex during local and relational judgments of surface colour and brightness**

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Psychophysical studies of human brightness and colour constancy provide evidence of low-level adaptation mechanisms that partially discount illumination changes and higher-level mechanisms for judging the relations between colours in a scene. We performed an fMRI experiment to assess whether human visual cortex responds differentially to achromatic and chromatic stimuli during tasks requiring judgments of (a) local surface colour (or brightness) irrespective of surrounding surfaces, and (b) the relationship between colours (or brightnesses) across surfaces in the scene. Subjects viewed sequentially presented pairs of radial Mondrian patterns with a simulated change in illumination. In the local task, subjects judged whether the appearance of a patch at a constant spatial location changed over the illumination interval. In the relational task, subjects judged whether the appearance of the patch changed in a fashion consistent with the illumination change. The position of surround patches in the second Mondrian was randomised with regards to the first to prevent subjects from using local contrast information during the relational task. A letter-recognition task, incorporating the Mondrian patterns as backgrounds, served to control for attentional effects. Brain regions selected to respond more vigorously to chromatic patterns than to achromatic patterns, regardless of the task, were situated in ventral-occipital visual cortex. These regions were more active during appearance tasks than during the letter-recognition tasks. For both chromatic and achromatic stimuli, we found no differential activation during the two tasks involving appearance judgments. We conclude that the identified colour sensitive region in ventral-occipital cortex is associated with the judgment of surface colour and brightness, be it local or relational.

[Supported by Grant 051.02.080 from the Cognition Program of the Netherlands Organization for Scientific Research (NWO).]

◆ **Comparison of colours within and between hemifields**

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When a subject makes a psychophysical discrimination between two stimulus attributes, what neural mechanism underlies the actual process of comparison? It is possible to imagine dedicated comparator neurons that draw inputs of opposite sign from the primary analysers in the two local regions where the stimuli lie. However, such hard-wired connections are unlikely to subserve the comparison of well-separated objects, for an enormous bulk of long connections would be required to link every possible pair of local feature-detectors (Danilova and Mollon, 2003 *Perception* 32 395–414). If comparisons do depend on hard-wired comparators, we might expect discrimination to deteriorate with separation, since connections in the visual cortex are known to become sparser with distance. In the case of spatial frequency, we have shown that, in fact, discrimination thresholds are constant as the separation of stimuli increases up to 10 deg. In the case of colour, discrimination is optimum at a separation of 2–3 deg, but even at a separation of 10 deg the threshold is only of the order of 6% for the tritan axis of colour space (Danilova and Mollon, 2004 *Perception* 33 Supplement, 47). To understand further the comparison of separated colours, we asked if discrimination deteriorates when the two stimuli fall in different hemifields rather than the same hemifield. In the former case, the comparison requires transmission of information across the corpus callosum. The stimuli were presented for 100 ms at random positions on an imaginary circle of 5 deg radius centred on the fixation point. No significant differences were found according to whether stimuli fell in the same or different hemifields. Furthermore, when both stimuli fell within one hemisphere, there was no significant advantage for stimuli delivered to the left hemifield, although a left-hemifield advantage for chromatic discrimination has previously been reported (Davidoff, 1976 *Quarterly Journal of Experimental Psychology* 28 387–396).

[Supported by the Wellcome Trust 072684/Z/03/Z.]

◆ **Human chromatic-discrimination ability of natural objects**

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Discrimination of different chromatic hues is a fundamental visual capability. Traditional measurements of colour discrimination have used patches of a single homogeneous colour. Everyday colour vision, however, is based on natural objects which contain a distribution of different chromatic hues. We studied chromatic discrimination using photographs of various natural fruit objects. In a 4AFC experiment, four stimuli were briefly presented on a CRT monitor in a 2 × 2 arrangement. Three of the stimuli were identical (test stimuli) and the fourth one (comparison stimulus) differed. The stimuli were either homogeneous patches of light, or digital photographs of fruit objects (banana, orange, etc), and were displayed on top of a homogeneous background whose chromaticity was also systematically varied. The mean colour of the comparison stimulus was varied along 8 different directions in colour space relative to the test stimulus. Discrimination thresholds were measured along these 8 directions and ellipses were fitted to the resulting threshold contours. In agreement with earlier studies, we found that discriminability was best when the test stimuli had the same average colour as the adapting background. However, when fruit objects were used as stimuli, thresholds were elevated and threshold contours were elongated in a way that reflected the distribution of hues in the image. For test stimuli that had an average colour different from the background, threshold contours for fruit objects and homogeneous patches were identical. We conclude that the distribution of hues within natural objects can have a profound effect on colour discrimination and needs to be taken into account when predicting discriminability.

[Supported by DFG grant Ge 879/5.]

◆ **The fMRI response of the LGN and V1 to cardinal red – green, blue – yellow, and achromatic visual stimuli**

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We compared the responsiveness of the LGN and the early retinotopic cortical areas to stimulation of the two cone-opponent systems (red–green and blue–yellow) and the achromatic system. This was done at two contrast levels to control for any effect of contrast. MR images

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were acquired on seven subjects with a 4T Bruker MedSpec scanner. The early visual cortical areas were localised by phase encoded retinotopic mapping with a volumetric analysis (Dumoulin et al, 2003 *NeuroImage* **18** 576–587). We initially located the LGN in four subjects by using flickering stimuli in a separate scanning session, but subsequently identified it using the experimental stimuli. Experimental stimuli were sine-wave counterphasing rings (2 Hz, 0.5 cycle deg⁻¹), cardinal for the selective activation of the L/M cone-opponent (RG), S cone-opponent (BY), and achromatic (Ach) systems. A region of interest analysis was performed. When presented at equivalent absolute contrasts (cone contrast = 5%–6%), the BOLD response of the LGN is strongest to isoluminant red–green stimuli and weakest to blue–yellow stimuli, with the achromatic response falling in between. Area V1, on the other hand, responds best to both chromatic stimuli, with the achromatic response falling below. The key change from the LGN to V1 is a dramatic boost in the relative blue–yellow response, which occurred at both contrast levels used. This greatly enhanced cortical response to blue–yellow relative to the red–green and achromatic responses may be due to an increase in cell number and/or cell response between the LGN and V1. We speculate that the effect might reflect the operation of contrast constancy across colour mechanisms at the cortical level.

BIOLOGICAL MOTION AND TEMPORARY VISION

◆ **Body-view specificity in peripheral biological motion**

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Biological motion (BM) perception is the ability to see an action from just white dots that mark locations on an invisible body. We showed that BM is perceived just as well in the visual periphery as in the fovea. This was only the case when the walker was oriented away from the fovea. In contrast, eccentric walkers oriented towards the fovea were hardly recognised as walkers at all. In a series of experiments, we show that this advantage for outwards-oriented BM has not been caused by the stimulus-response correspondence. Instead, it was specific for human movement and independent of the kind of locomotion (walking, crawling). To explain this effect, we conducted an event-related fMRI experiment. Among the usual areas, biological motion activated the ventral premotor cortex (vPMC) and the secondary somatosensory cortex (S1). Increased contralateral activity from outwards-oriented walkers over inwards-oriented walkers was only present in the vPMC and S1. None of the other known areas responding to biological motion showed any difference between outwards-oriented and inwards-oriented walkers. The vPMC and the S1 are known to be involved in perceiving and understanding the actions of others. These areas are also known to be involved in action execution in the own contralateral side of the body. We conclude that the contralateral representation is also valid for action observation. Intriguingly, this means that the vPMC and the S1 represent the own contralateral side of the body, but just as well as the contralateral side of the body of others.

◆ **Flash-lag in depth is induced by stereomotion but not looming: Distorted size and position perception**

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The apparent spatial offset of a flash behind a moving object, called the flash-lag effect (eg Nijhawan, 1994 *Nature* **370** 256–257), has been extensively investigated. Here we compare the flash-lag effect from motion-in-depth simulated by stereomotion and looming. Motion-in-depth evoked by looming can be nullified by stereomotion, which suggests that both cues converge onto a common motion-in-depth stage (Regan and Beverley, 1979 *Vision Research* **19** 1331–1342). We provide evidence that the flash-lag-in-depth effect occurs before any common stage. The stimulus was a stereogram containing a frontoparallel square (4.63 deg × 4.63 deg) defined by randomly placed dots. The perception of motion-in-depth (towards or away from the observer) was generated by the opposed motion of the stereoscopic images (stereomotion), by the radial motion of the dots (looming), or by both cues in combination. A Gaussian blob (SD = 22 min of arc) was flashed (1 frame) in a hole in the centre of the square half-way through each motion sequence. Observers adjusted the disparity of the blob until its perceived position in depth matched that of the square. All observers perceived a strong apparent offset in depth (0.22 cm at 12.54 cm s⁻¹) of the flashed blob only when stereomotion was present. The flash-lag effect was speed-dependent,

and was accompanied by an apparent change in the blob size depending on the direction of motion. This size illusion was quantified (3% at 12.54 cm s^{-1}) by requiring observers to adjust the size of the blob in one direction of motion until its perceived size matched that of another blob in the opposite direction. Looming had negligible influence on both the position and size settings of the blob. Our results suggest that the mechanisms responsible for stereomotion and looming are both independent and have qualitatively different outputs.

[Supported by Grant HKU7149/02H from the Research Grants Council of Hong Kong.]

◆ **Statistically optimal integration of synergies in the visual perception of emotion from gait**

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When recognising complex shapes, humans probably integrate information from the analysis of simpler components. Biological-motion recognition might also be based on an integration of simpler movement components. This hypothesis seems consistent with results from motor control, showing that the control of multi-joint movements is based on simpler components, called synergies, which encompass a limited number of joints. We tested whether subgroups of joints, as perceptual analogues of synergies, define meaningful components for the perception of biological motion. Extending an existing motion-morphing technique (Giese and Poggio, 2000 *International Journal of Computer Vision* **38** 59–73), we simulated point-light walkers with two different synergies (including the joints of the upper body and the lower body) by morphing between neutral walking and walks with different emotional styles (sad, angry, fearful). We separately varied the amount of information about the emotion conveyed by the two synergies. The percept of emotions was assessed by an expressiveness rating, and by a yes–no task requiring subjects to distinguish neutral and emotional walks (eg ‘neutral or sad?’). Subjects’ responses were fitted and predicted by using Bayesian ideal-observer models that treated the contributions from the two synergies as independent information sources. The morphed stimuli looked very natural, even if only one synergy provided information about the emotion. As expected, ease of emotion recognition increases with the contribution of the emotional prototype to the morph. The contributions of the synergies to the overall perceptual judgment vary between emotions. Quantitative modelling shows that in most cases the emotion-recognition performance of the subjects can be predicted accurately by Bayesian ideal-observer models that integrate the emotion information provided by the two synergies in a statistically optimal way. We conclude that biological-motion recognition might be based on spatiotemporal components with limited complexity, and integrated in a statistically optimal fashion.

[Supported by Human Frontier Science Program, Volkswagen Foundation, and Hermann and Lilly Schilling Foundation.]

◆ **The time course of estimating time-to-contact**

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Perception of motion-in-depth needs integration time, as do the mechanisms for estimating the time that an object will take to contact an observer. Because the different sources of information that feed these mechanisms take different times to provide a reliable signal [eg optical size (θ) is available before higher-motion areas can obtain a reliable estimate of its rate of expansion ($\dot{\theta}$)], one would expect systematic bias in the observer’s responses for different times of stimulus exposure. On the other hand, the same mechanisms should account for the ability to respond equally to different object sizes once the different sources of information have been integrated. In one experiment, observers judged whether simulated objects had arrived at the point of observation before or after a reference beep (1.2 s). Five different exposure times in the range 0.1–0.9 s were used. On average, observers produced more accurate responses for small objects before 0.5 s. From this time on, trained observers showed size-invariance, while less trained ones reversed the pattern (more accuracy with large objects). The whole pattern of results across time is well accounted for by a nonlinear combination of θ and $\dot{\theta}$: $\dot{\theta} \exp(-\alpha\theta)$, where α determines how θ and $\dot{\theta}$ are weighted (Hatsopoulos et al, 1995 *Science* **270** 1000–1003). Unlike in previous studies, however, the best account is achieved by modulating α with time so that θ is taken more into account at the beginning of the trajectory (larger α) while $\dot{\theta}$ is largely considered after 0.5 s (smaller α). This modulation is consistent with studies on temporal integration of radial motion.

[Supported by grant TIN2004-04363-C03-02 from the Spanish Ministry of Education.]

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◆ **Visual motion expands perceived time**

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It has been proposed that perceived duration is based on the total number of events experienced by observers. In the present study, we investigated how visual motion—a form of change in the visual modality—affects perceived duration. For a target stimulus, we used a square moving with a variable speed (0 to 48 deg s⁻¹) for a variable duration (0.2 to 1.0 s). We found that the perceived duration of motion increased with increasing speed; at high speeds, magnitude of the effect increased up to an overestimation by 250 ms and then saturated. However, the overestimation of duration was not determined by the speed alone; it also depended on stimulus duration. With longer presentation times, time dilation was attenuated. Next, we examined whether the magnitude of time dilation depends on perceived or physical speed. In order to dissociate perceived and physical speeds, we ran an experiment using low-contrast and isoluminant stimuli and compared the results with those obtained with high-contrast stimuli. Both types of stimuli tested are generally perceived to move slower than high-contrast stimuli. We found that time dilation for perceptually slow-moving stimuli shows the same speed-duration dependence as that for high-contrast stimuli. This indicates that time dilation is determined by the physical aspects of the stimulus and not by its perceived speed. In sum, we show that perceived duration of visual motion depends on both its speed and duration. Fast speeds appear to last longer than slow speeds. Also, time dilation is larger when physical presentation of motion is short than when it is longer. In conclusion, time dilation is independent of perceived speed, which makes it tempting to suggest that there are separate processes for time and speed perception. [Supported by the Netherlands Organisation for Scientific Research.]

◆ **Coding change: Brain systems sensitive to the arrow of time**

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Although we cannot reverse the flow of time, motion pictures technology allows us to render temporal events in reverse. Often, such reversals are immediately detectable: natural laws, from gravitational forces to the physiology of locomotion, imbue dynamic scenes with an easily detectable directionality. Other reversals, such as the order of events in a developing plot, may require analysis at longer time scales. What are the brain mechanisms involved in the analysis of temporal relationships, and do they differ for these different cases? This research is based on previous findings of voxel-wise correlations to repeated presentations of movies, which was effective for revealing brain areas that exhibit consistency in their response to external stimuli (Hasson et al, 2004 *Science* **303** 1634–1640). Here we presented observers with two repeated presentations of original ('forward', F) and time-reversed ('backward', B) movie clips while collecting whole-brain fMRI activity. There were three movie categories: 'inanimate' (eg collapsing buildings), 'animate' (eg people moving), and 'plot' clips taken from silent classic movies. Time-courses obtained from each backward clip were reversed (rB), corrected for hemodynamic delay, and then correlated (C) with those obtained from the forward clip (CrB, F). Results were compared with those obtained by correlating two forward presentations (CF1, F2). Posterior temporal and occipital cortices exhibited comparable CrB, F and CF1, F2 maps, suggesting that activity in these areas depends primarily on the content of individual frames. Sensitivity to the arrow of time in the 'inanimate' and 'animate' clips was revealed in the intraparietal sulcus, where CrB, F values were significantly lower than CF1, F2 values. For the 'plot' clips, time sensitivity was also revealed in the left temporal-parietal junction (TPJ). Our results reveal distinct cortical areas sensitive to different temporal grains, ranging from individual frames to discrete motion clips to longer plot-related events.

[Supported by the Human Frontier Science Program (HFSP).]

BINOCULAR VISION

◆ **Amblyopic suppression: all-or-none or graded?**

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We have shown previously that if the fellow fixing eye (FFE) is closed, amblyopic eye (AME) can integrate spatial orientation information similar to normal. Here, we investigate the neural nature of suppression in amblyopic subjects by evaluating spatial integration under conditions

of binocular stimulation. Five amblyopic observers were tested. Squints and refractions were corrected before data collection. We used a task in which subjects had to judge the mean orientation of an array of oriented Gabors. The Gabor orientations were samples from a Gaussian orientation distribution of variable bandwidth and mean that was left or right of vertical. The internal noise and number of samples were estimated from fitting a standard equivalent noise model to the data. Different numbers of orientation samples were either presented to FFE, AME, or both, under dichoptic viewing. In some cases, Gabor elements with random orientations (termed noise) were added to the signal orientations in one or other of the above conditions. When the same number of stimuli is presented to both eyes simultaneously, FFE suppresses the AME, whether it has signal or noise. Increasing the number of elements presented to the AME enhances its contribution to the overall performance. Specific ratio of the number of elements presented to AME and FFE (average 64 : 4) leads to equal influence of the either eye on the overall performance. Our results suggest that the AME suppression is not an all-or-none event but rather a process with stimulus-dependent weights that can be modulated.

[Supported by the Canadian Institute of Health Research grant (CIHR 108-18) to RFH.]

◆ **Binocular rivalry produced by temporal-frequency differences**

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Do differences in temporal frequency alone produce binocular rivalry? 100 frames (64 × 64 pixels) from a random dynamic noise animation were stacked and filtered in three dimensions in the frequency domain (stack height being the time dimension). Spatially (x, y), each frame was filtered to a low-frequency pass-band (0.7–1.4 cycles deg⁻¹). In the third dimension (t), varying the pass-band produced various temporal frequencies when the frames played in animation. We used eighth-octave pass-bands centred on 0.9, 1.8, 3.5, 7, or 14 Hz. The stack was duplicated and different temporal-frequency pairs were dichoptically presented. Because the temporal frequencies came from the same stack of noise frames, spatial content was matched. Frequency matching was used to test for temporal-frequency rivalry: following short presentations of random duration, subjects matched the final perceived frequency to one of thirteen comparison modulations. Bimodally distributed matches would indicate rivalry between the two modulation rates. A control experiment was performed to test whether phase differences alone between matched modulation rates could generate rivalry. Matching data were bimodal when frequencies differed by at least 2 octaves (eg 1.8 and 7 Hz). Monitoring rivalry alternations over long periods revealed that dominance durations for temporal-frequency rivalry adhered to the conventional gamma distribution. The control data rule out an explanation due to phase differences. Spatially matched patterns differing in temporal modulation rate cause binocular rivalry. This shows that rivalry can arise in the magno pathway. Rivalry therefore is not limited to spatial conflicts arising in the parvo pathway, as recently claimed. The relatively large temporal-frequency difference (≥ 2 octaves) required to elicit rivalry agrees with data on temporal channels, revealing the existence of just 2 or 3 rather broad channels. Small temporal-frequency differences would therefore drive the same channel (not producing rivalry), just as it occurs for small spatial-frequency differences.

◆ **Configural cues combine with disparity in depth perception**

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From viewing geometry, one can show that binocular disparity provides metric depth information, and that configural cues, such as familiarity and convexity, provide ordinal depth information. Because the cues specify different types of information, it is not clear how they can be combined. However, a statistical relationship exists between depth in the scene and physical cue values. Thus, for a given depth, a range of likely disparity and configural cue values are specified (by likelihood functions). This statistical information could be combined in Bayesian fashion to estimate the most likely depth. Are configural cues combined with disparity information? Our experiment used bipartite, random-dot-stereograms with central luminance edges shaped like either a human face in profile or a sine wave. Disparity specified that the edge and dots on one side were closer than the dots on the other side. Configural cues suggested that the familiar, face-shaped region was closer than the unfamiliar side or provided no information when the sine-wave contour was used. Observers indicated which of two sequential presentations contained more relative depth. When the disparity and configural cues indicated that the same side was in front, observers perceived more depth for a given amount of disparity than when configural cues provided

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no information (sine wave). When the cues indicated opposite sides in front, observers perceived less depth than when configural cues provided no information. More importantly, the just-discriminable change in depth was smaller when configural cues provided information (face profiles) than when they did not (sine wave). This striking result shows that configuration (which from the geometry provides only ordinal depth information) can be combined with disparity (which provides metric information) to increase the precision of depth perception. The results are best understood in a Bayesian framework in which the statistical relationship between observed cues and scene depth allow for combination.

[Supported by NIH Training Grant in Vision Science T32 EY07043 to JB, NIH National Eye Institute Grant R01-EY12851 to MSB, and NSF Grant BCS 0425650 to MAP.]

◆ **Do people compensate for incorrect viewing position when looking at stereograms?**

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A conventional picture viewed from its centre of projection (CoP) produces the same retinal image as the original depicted scene. When viewed from another position, the retinal image specifies a different scene, but people typically perceive the original depicted scene, not the one specified by the retinal image. Thus, they compensate for incorrect viewing position. Compensation is based on a measurement of the slant of the picture surface, and the primary cue for the measurement is binocular disparity. Using disparity works because disparity signals the slant of the picture surface and is unaffected by the depicted 3-D contents of the picture. In stereograms, the disparity signals both the 3-D contents of the depicted scene and the slant of the picture surface. Here, we ask if observers compensate for incorrect viewing position with stereograms in a fashion similar to the compensation with conventional pictures. We conducted a series of experiments in which observers varied the dihedral angle of a stereoscopic hinge stimulus. Observers indicated whether the dihedral angle was greater or less than 90°. The stimulus was presented on a computer display, which could be rotated about the vertical axis to vary obliqueness of viewing position. We compared the perceived right angle to that predicted if observers did or did not compensate for oblique viewing angle. We also manipulated the information the observer had about viewing position from minimal (isolated hinge stimulus, display frame invisible) to maximal (hinge stimulus embedded in conventional picture, display frame visible). We observed little evidence for compensation in all conditions. This suggests that the compensation mechanism for incorrect viewing position that is used with conventional pictures is not used with a disparity-specified scene in stereograms.

[Supported by DOE CSGF.]

◆ **Role of attention in binocular integration**

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The level of integration or rivalry between images seen through the two eyes is examined. Is this interaction one of direct competition, with one ultimately suppressing the other? Alternatively, do the two images live side by side, in harmony, with only top-level attentional mechanisms choosing between them? Several specific cases are discussed that provide evidence that attention may indeed be the key. As one special case of binocular images, the 'eyes-wide-shut' illusion is discussed, and a more detailed review of its physiological basis than may be provided at the new illusion presentations at the A Coruña Science Museum is given.

[Supported by Israel Science Foundation Center of Excellence and US–Israel Bi-National Science Foundation grant.]

◆ **The effect of binocular misalignment on cyclopean visual evoked potentials**

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Visual evoked potentials (VEPs) to dynamic random-dot correlograms (RDCs) are a well-established method of assessing cortical binocularity, particularly in infants (eg Braddick et al, 1980 *Nature* **228** 363–365). The RDC stimulus alternates between a correlated state, with identical patterns in each eye, and an anticorrelated state, in which each eye sees the negative of the other eye's pattern. An absence of a response to this alternation is generally regarded as indicating a lack of cortical binocularity. However, it could instead be a result of inaccurate vergence: if the two eyes' images are sufficiently misaligned, both alternation states will be binocularly uncorrelated and they will be indistinguishable. We have examined the effect of binocular misalignment on adults' VEP responses to RDCs, and to the cyclopean stimulus of Ohzawa and Freeman (1988 *Vision Research*

28 1167–1170). In the latter, gratings drifting in opposite directions are presented to each eye. Binocular summation produces a counterphase grating which generates a VEP. The temporal phase of the counterphase grating, and thus of the VEP, will be altered by binocular misalignment, but the presence and amplitude of the VEP should be unaffected. For both stimuli, binocular misalignment was produced by changing the disparity of a fixation marker. As expected, with RDCs the amplitude of the VEP decreased with increasing misalignment; beyond about 1 deg, no VEP could be detected. With the grating stimulus, VEP amplitude was not affected by misalignment, but phase varied as predicted. These results suggest that the VEP in response to RDCs is likely to be a rather unreliable measure of cortical binocularity in subjects, such as young infants, who have poor control of vergence, whereas the grating stimulus VEP is more robust. Future experiments will compare VEPs to the two stimuli in infants.

[Supported by Medical Research Council programme grant G790850.]

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THURSDAY

SYMPOSIA

EYE MOVEMENTS IN VISUAL PERCEPTION

◆ **A cholinergic mechanism underlies persistent neural activity necessary for eye fixation**

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Where and how does the brain produce the sustained neural activity necessary for eye positions of fixation? The generation of the neural activity responsible for eye fixation after spontaneous eye movements was studied *in vitro* and *in vivo*. Rat sagittal brainstem slices taking in the prepositus hypoglossi (PH) nucleus and the rostral paramedian pontine reticular formation (PPRF) were used for the intracellular recording of PH neurons and their synaptic activation from PPRF neurons. Single electrical pulses applied to the PPRF showed a monosynaptic projection on PH neurons. This synapse was found to be glutamatergic in nature, acting on AMPA-kainate receptors. Train stimulation (100 ms, 50–200 Hz) of the PPRF area evoked a sustained depolarisation of PH neurons exceeding (by hundreds of ms) stimulus duration. Both duration and amplitude of this sustained depolarisation were linearly related to train frequency. The train-evoked sustained depolarisation was demonstrated to be the result of the additional activation of cholinergic fibres projecting onto PH neurons, because it was prevented by slice superfusion with atropine and pirenzepine (two cholinergic antagonists), and mimicked by carbachol (a cholinergic agonist). Carbachol also evoked a depression of glutamate release by a presynaptic action on PPRF neuron terminals on PH neurons. As expected, microinjections of pirenzepine in the PH nucleus of alert behaving cats evoked an ipsilateral gaze-holding deficit consisting of an exponential-like, centripetal eye movement following each saccade directed toward the injected side. These findings strongly suggest that persistent activity characteristic of PH neurons carrying eye-position signals is the result of the combined action of eye-velocity signals originated in PPRF neurons and the facilitative role of cholinergic terminals of reticular origin.

[Supported by grant BFI2000-00936 from Spanish MECED.]

◆ **The physiology and psychophysics of visual search in monkeys free to move their eyes**

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Most studies of eye movements in awake, behaving monkeys demand that the animal make specific eye movements. We have developed a new paradigm in which the monkey performs a visual search for an upright or inverted T among 7, 11, or 15 cross distractors, and reports the orientation of the distractor with a hand movement. The search array is radially symmetric around a fixation point, but once the array appears, the monkey is free to move its eyes. The monkey's performance in this task resembles that of humans in similar tasks (Treisman and Gelade, 1980 *Cognitive Psychology* 12 97–136): manual reaction time shows a set size effect for difficult searches (the crosses resemble the Ts) but not for easy searches (the T pops out). Saccades are made almost exclusively to objects in the array, and not to intermediate positions, but fewer than half of the initial saccades are made to the T. We recorded from neurons in the lateral intraparietal area (LIP) while the monkey performed the search. LIP neurons distinguish the saccade goal at an average of 86 ms after the appearance of the array. The time at which neurons distinguish saccade direction correlates with the monkey's saccadic reaction time, suggesting that most of the jitter in reaction time for free eye movements comes from the discrimination process reflected in LIP. They distinguish the T from a distractor on an average of 111 ms after the appearance of the array, suggesting that LIP has access to cognitive information about the target, independent of the saccade choice. These data show that LIP has access to three different signals: an undifferentiated visual signal reporting light in the RF; a cognitive visual signal; and a saccade-related signal. [Supported by the National Eye Institute, Whitehall Foundation, W M Keck Foundation, James S MacDonnell Foundation.]

◆ **Statistics of fixational eye movements and oculomotor control**

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During visual fixation, our eyes perform miniature eye movements involuntarily and unconsciously. Using a random-walk analysis, we found a transition from persistent to anti-persistent

correlations as a function of the time scale considered (Engbert and Kliegl, 2004 *Psychological Science* **15** 431–436). This finding suggests functional dissociations (i) of the role of fixational eye movements on short and long time scales, and (ii) between drift and microsaccades. Here we propose a mathematical model for the control of fixational eye movement based on the concept of time-delayed random-walks (Ohira and Milton, 1995 *Physical Review E* **52** 3277–3280). On the basis of results obtained from numerical simulations we estimate time delays within the brainstem circuitry underlying the control of fixational eye movements and microsaccades.

[Supported by Deutsche Forschungsgemeinschaft (DFG, grant 955/3) and Promotionskolleg “Computational Neuroscience of Behavioral and Cognitive Dynamics” (University of Potsdam).]

◆ **Fixational eye movements and motion perception**

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Small eye movements maintain visibility of static objects, and at the same time randomly oscillate their retinal images. The visual system must compensate for such motions to yield a stable visual world. According to the theory of visual stabilisation based on retinal motion signals, objects are perceived to move only if their retinal images make spatially differential motions with respect to some baseline movement, probably due to eye movements. Several kinds of motion illusions favouring this theory are demonstrated: with noise adaptation or flicker stimulation, which is considered to decrease motion sensitivity in restricted regions, image motions due to eye movements are actually perceived as random ‘jitter’. This indicates that the same amplitudes of such image motions are normally invisible as all regions are sensitive enough to register uniform motions as being uniform. As such, image oscillations originating in fixational eye movements may go unnoticed perceptually, but this does not mean that the oscillations have been filtered out from the brain; they can still exist in early motion processing and can influence various aspects of motion-detection performance. Lower threshold of uniform motion, for example, has been found to correlate positively with fixation instability, indicating that image oscillations are, though unnoticed, working as a limiting factor of motion detection. Also, the compelling motion illusion that appears in static figures (Kitaoka and Ashida, 2002 *Perception* **31** Supplement, 162), sometimes referred to as the ‘rotating snake’, also positively correlates with fixation instability, such that poorer fixation makes the illusion greater. As a possible account, an interaction between image oscillations due to small eye movements and a low-level motion detection circuit is argued. Finally, the dependence of motion detection on the occurrence of fixational eye movements is analysed in finer detail, with some mention of separate effects of the two subtypes: fixational saccades and fixational drifts.

FROM PERCEPTIVE FIELDS TO GESTALT. IN HONOUR OF LOTHAR SPILLMANN

◆ **In honour of Lothar Spillmann—filling in, emptying out, adaptation, and aftereffects**

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During prolonged strict fixation, visual properties appear to become weaker over time. Colours become less saturated, contrast is reduced, and (we find) wiggly lines appear to become straighter, and an irregular lattice of dots appears to become gradually more regular. Also, a peripherally viewed gray patch on a red surround, or embedded in twinkling dynamic noise, seems to disappear from view after some seconds. When the adapting field is replaced by a uniform gray test field, the patch now appears to be filled-in with the red colour, or with the dynamic texture, of the surround. The short-term visual plasticity produced by this tangled mass of adaptation, aftereffects, spatial and temporal induction, and filling-in is examined. Is the filling-in during the aftereffect analogous to filling-in of the natural blind spot? Lothar Spillmann has cast much light on these topics during his highly productive career, but I shall restore the status quo.

[Supported by a UCSD Senate Grant.]

◆ **Lightness, filling-in, and the fundamental role of context**

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Visual perception is defined by the unique spatial interactions that distinguish it from the point-to-point precision of a photometer. The perceptual properties of spatial interactions and more generally the importance of visual context for neuronal responses and perception have been explored. Investigations into the spatiotemporal dynamics of lightness provide insight into underlying mechanisms. For example, backward-masking and luminance-modulation experiments suggest that the representation of a uniformly luminous object develops first at the borders and the centre

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fills-in. The temporal dynamics of lightness induction are also consistent with a filling-in process. There is a slow cutoff temporal frequency above which surround luminance modulation will not elicit perceptual induction of a central area. The larger the central area, the lower the cutoff frequency for induction, perhaps indicating that an edge-based process requires more time to 'complete' the larger area. In recordings from primary visual cortex, it is found that neurons respond in a manner surprisingly consistent with lightness perception and the spatial and temporal properties of induction. For example, the activity of V1 neurons can be modulated by light outside the receptive field and, as the modulation rate is increased, response modulation falls off more rapidly for large uniform areas than smaller areas. The conclusion drawn from these experiments is that lightness appears to be computed slowly based on edge and context information. A possible role for the spatial interactions is lightness constancy which is thought to depend on extensive spatial integration. V1 neurons are not only strongly context-dependent, but this dependence makes V1 lightness constant on average. The dependence of constancy on surround interactions underscores the fundamental role that context plays in perception. In more recent studies, further support has been found for the importance of context in experiments using natural-scene stimuli. [Supported by the USA National Eye Institute and the National Science Foundation.]

◆ **Beyond a relay nucleus: New views on the human LGN**

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The LGN is the thalamic station in the projection of the visual pathway from retina to visual cortex and has been traditionally viewed as a gateway for sensory information. Its topographic organisation and neuronal response properties have been extensively studied in nonhuman primates, but are poorly understood in humans. I report on a series of studies aimed at elucidating functional roles of the human LGN in perception and cognition using fMRI. Functional LGN topography was studied by presenting periodic flickering checkerboard stimuli that evoked a traveling wave of activity. The contralateral visual hemifield was found to be represented with the lower field in the medial-superior portion and the upper field in the lateral inferior portion of each LGN. The fovea was represented in posterior and superior portions, with increasing eccentricities represented more anteriorly. This topography is strikingly similar to that of the macaque. Selective attention has been shown to modulate neural activity in both extrastriate and striate cortex. The poorly understood role of earlier, subcortical structures in attentional processing was studied. Attention was found to modulate neural responses in the LGN in several ways: it enhanced neural responses to attended stimuli, attenuated responses to ignored stimuli and increased baseline activity in the absence of visual stimulation, suggesting a role as a gatekeeper in controlling attentional response gain. Most recently, the level at which competing inputs to the eyes, as perceived in binocular rivalry, can be resolved started to be investigated. Similar neural correlates of binocular rivalry were found in the LGN and V1, suggesting a mechanism by which LGN layers that process the input from one particular eye are selectively enhanced or suppressed.

◆ **From perceptive fields to Gestalt**

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I discuss select studies on visual psychophysics and perception that were done in the Freiburg laboratories during the last 35 years. Many of these were inspired by single-cell neurophysiology in the cat. The aim was to correlate the phenomena and effects under consideration to the possibly underlying mechanisms from retina to cortex. To this extent, I deal with light and dark adaptation (photochromatic interval, rod monochromacy, Ganzfeld), colour vision (spectral sensitivity, latency differences, colour assimilation), perceptive field organisation (Hermann grid illusion, Westheimer paradigm, tilt effect), visual illusions (Ehrenstein illusion, neon colour, abutting grating illusion), and long-range interaction (phi-motion, factor of common fate, fading and filling-in). While some of these studies succeeded in linking perception to neuronal behaviour, others did not. The task of probing the human brain by using phenomena in search of mechanisms continues to be a challenge for the future.

[Supported by DFG grant SP 67/9-3/]

ORAL PRESENTATIONS

THEORY AND MODELS

◆ **A model of velocity aftereffects: Two temporal filters and four free parameters**

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The perceived speed of moving patterns changes over time. Adapting to a moving pattern leads to an exponential decrease in its perceived speed. However, under certain conditions, perceived speed increases after adaptation. The time course of these perceptual effects varies widely. We measured the perceived speed of 1 cycle deg^{-1} sinusoidal patterns over a range of adaptation and test speeds (2–20 deg s^{-1}) and at a variety of adaptation durations (0–64 s). The results indicate that adapting to slow speeds results in an increase in the perceived speed of faster images and a reduction in the perceived speed of images of the same or slower speeds. Adapting to high speeds led to an exponential reduction in the perceived speed of all subsequently presented images. Thus, any model of perceived speed must capture both increases and decreases in perceived speed contingent upon prevailing conditions. We have developed a model that comprises two temporally tuned filters whose sensitivities reduce exponentially as a function of time. Perceived speed is taken as the ratio of these filters' outputs. The model has four free parameters that determine the time constants of exponential decay and the asymptotic response attenuation for the temporal filters. The model assumes that the decay of each filter's sensitivity over time is proportional to the relative sensitivity of that filter to the adaptation frequency. The model captures both increases and decreases in perceived speed following adaptation, and describes our psychophysical data well, resolving around 96% of the variance. Moreover, the parameter estimates for the time constants of the underlying filters (~ 8 s) are very close to physiological estimates of the time course of adaptation of direction-selective neurons in the mammalian visual system. We conclude that a physiologically plausible ratio model captures much of what is known of speed adaptation.

◆ **A neurocomputational model for describing and understanding the temporal dynamics of perisaccadic visual perception**

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Several experiments have shown that the plan of making an eye movement affects visual processing. Under certain conditions, briefly flashed stimuli are mislocalised towards the saccade target (Ross et al, 1997 *Nature* **386** 598–601). This effect starts before the eyes move and is strongest around saccade onset. The spatial pattern of mislocalisation is asymmetric in space and depends on stimulus position (Kaiser and Lappe, 2004 *Neuron* **41** 293–300). In V4, perisaccadic receptive field (RF) shifts have been reported (Tolias et al, 2004 *Neuron* **29** 757–767), and several, primarily oculomotor related areas, show perisaccadic remapping (Kusunoki and Goldberg, 2003 *Journal of Neurophysiology* **89** 1519–1527). However, neither the underlying RF processes, nor the phenomenon of the 'compression' of visual space are well understood. We have developed a neurocomputational model of perisaccadic perception in which an oculomotor feedback signal is directed towards the saccade target and changes the gain of the cells in extrastriate visual areas. As a result, the cortical activity profile induced by a flashed dot is distorted towards the saccade target. The model can reproduce the temporal course and the 1-D spatial pattern of mislocalisation as measured by Morrone et al (1997 *Journal of Neuroscience* **17** 7941–7953) and the 2-D mislocalisation data of Kaiser and Lappe (2004). It further inherently predicts RF dynamics. For the selected parameters, we observe a perisaccadic shrinkage and shift of RFs towards the saccade target as reported for V4. Our oculomotor-feedback hypothesis differs from remapping, since the RF shifts are directed towards the saccade target. Thus, we suggest a further universal mechanism that is likely to occur in intermediate areas within the visual hierarchy. The oculomotor-feedback hypothesis is the first integrative account for both electrophysiological measurements of receptive field shifts and for psychophysical observations of spatial compression.

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- ◆ **Brightness integration: Evidence for polarity-specific interactions between edge inducers**
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We present a computational framework for analysing data on the spatial integration of surface brightness. Our framework builds on the hypothesis, originating in Retinex theory, that brightness is computed by integrating induction signals generated at edges (log luminance ratios) in a scene. The model of Rudd and Arrington (2001 *Vision Research* **41** 3649–3662) generalises Retinex theory by characterising how neighbouring edges can interact to partially block the flow of induction signals from one another. We show that both the Rudd–Arrington model and Retinex theory are special cases of a broader class of models in which opposite-polarity edges are parsed into separate half-wave rectified channels before spatial integration. Each model incorporates different polarity-specific constraints on the interactions between neighbouring edges. We fit these models to psychophysical data on spatial brightness integration (Hong and Shevell, 2004 *Visual Neuroscience* **21** 353–357; *Vision Research* **44** 35–43), comparing performance using a statistical technique for quantifying goodness-of-fit relative to the number of model parameters. We find that a model which strongly impedes the flow of induction signals across neighbouring edges of the same polarity, but does not restrict, or weakly restricts, flow across edges of opposite polarity, is most likely to be correct. Our results are at odds with published variants of the filling-in theory of brightness perception, which predict either unrestricted flow across edges of the same polarity or no flow at all. The framework can also be used to quantitatively assess models of colour perception, where putative polarity-specific interactions can be defined in terms of cone-specific contrasts, as implied by Retinex theory, or cone-opponent contrasts.

[Supported by grant 051.02.080 of the Cognition program of the Netherlands Organization for Scientific Research (NWO).]

- ◆ **Can perception violate laws of physics?**

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We can see impossibilities; even paradoxes, such as the Penrose triangle. But can perception violate laws, such as Curie's Principle, that symmetries cannot produce systematic asymmetries? Some repeating, and so globally symmetrical figures (the Café Wall), are distorted by accumulating local asymmetries. But others (the Pogendorff) seem to create global distortions in one top–down step. I discuss how this might occur, with implications for brain representations.

[Supported by the Gatsby Trust.]

- ◆ **Dynamics of motion representation in short-latency ocular following: A two-pathways Bayesian model**

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The integration of information is essential to measure the exact 2-D motion of a surface from both local ambiguous 1-D motion produced by elongated edges and local non-ambiguous 2-D motion from features such as corners, end-points, or texture elements. The dynamics of this motion integration shows a complex time course which can be read from tracking eye movements: local 1-D motion signals are extracted first and then pooled to initiate the ocular responses; 2-D motion signals are then taken into account to refine the tracking direction until it matches the surface motion direction. The nature of these 1-D and 2-D motion computations is still unclear. Previously, we have shown that the late, 2-D-driven, response components to either plaids or barber-poles have very similar latencies over a large range of contrast, suggesting a shared mechanism. However, they showed different contrast response functions with these different motion stimuli, suggesting different motion processing. We designed a two-pathways Bayesian model of motion integration and showed that this family of contrast response functions can be predicted from the probability distributions of 1-D and 2-D motion signals for each type of stimulus. Indeed, this formulation may explain contrast response functions that could not be explained by a simple Bayesian model (Weiss et al, 2002 *Nature Neuroscience* **5** 598–604) and gives a quantitative argument to study how local information with different relative ambiguity values may be pooled to provide an integrated response of the system. Finally, we formulate how different spatial information may be pooled, and draw an analogy between this method and methods using the partial-derivative equations. This simple model correctly explains some

nonlinear interactions between neighbouring neurons selective to motion direction which are observed in short-latency ocular following and neurophysiological data.

[L Perrinet was sponsored by the «ACI Temps et Cerveau» (CNRS).]

◆ **Knowing where we are going: Solving the visual navigation problem by following the VI–MT–MST cortical pathway**

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Current biologically based models of visual self-motion estimation are unable to use 2-D images as input. They all assume that the retinal image motion at the eyes of the observer has somehow been magically converted into a velocity vector representation (the flow field). These models ignore the problems associated with extracting motion from images, eg variations in contrast, spatial frequency differences, and the aperture problem. This situation has been rectified, and I have developed a self-motion estimation system which is able to use input stimuli identical to those used in electrophysiological and human psychophysical experiments. The system uses 2-D motion sensors based on neurons in the VI and middle temporal (MT) region of the primate brain (Perrone and Thiele, 2002 *Vision Research* **42** 1035–1051; Perrone, 2004 *Vision Research* **44** 1733–1755). These sensors can overcome the aperture problem and display many of the properties of MT pattern neurons. The MT-like sensors have been incorporated into self-motion estimation ‘templates’ (see Perrone, 1992 *Journal of the Optical Society of America* **9** 177–194; Perrone and Stone, 1994 *Vision Research* **34** 2917–2938) that are tuned to the global patterns of image motion that occur when we move through the environment. These templates mimic the properties of some medial superior temporal (MST) neurons, the putative processors of self-motion information in primates. The new self-motion estimation system uses: (i) a set of templates tuned to a range of heading directions and combinations of body rotations (pitch, yaw, and roll), and (ii) a mechanism for modifying the templates driven by (known) eye movements. I show that this dual neural-based system can extract self-motion information (heading direction, body rotation, and relative depth) from digital image sequences, as well as account for a wide range of psychophysical data on human heading estimation (eg Li and Warren, 2004 *Vision Research* **44** 1879–1889).

◆ **Optimal noise levels enhance sensitivity to weak signals in the human visual system**

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‘Stochastic resonance’ (SR) refers to the broad range of phenomena where the addition of weak noise levels enhances information transfer. Several models that specify which conditions lead to SR have been developed. Most of them imply a hard threshold mechanism or something comparable. SR effects have been demonstrated at several levels in biological information-processing systems, including the human tactile and auditory perceptual system. We investigated discrimination of barely detectable low-contrast stimuli in white luminance noise. Stimuli were 3 cycles deg^{-1} Gabor-patches of 45° and -45° orientation. Five contrast levels (leading to $d' \approx 0$ to $d' \approx 3$) were combined with nine noise levels (0 to $2 \times 10^{-6} \text{ deg}^2$ noise spectral density). When optimal noise levels were added, sensitivity was strongly enhanced. For the subthreshold contrasts, sensitivity rose to a single peak in function of noise level, after which it decreased again. This is the essence of the SR phenomenon. These results are consistent with a hard threshold mechanism in the human early visual system, although other explanations are possible. We tried to model our results with a very basic contrast perception model that focused on additive pre-threshold noise, the threshold itself, and additive post-threshold noise. For all subjects, the contrast threshold was estimated to be about 0.004, and post-threshold noise to be about 10 times stronger than pre-threshold noise. This model fitted the data well. Since a hard threshold prevents weak signals being detectable, it does not seem to lead to any functional advantage. However, some possible benefits of a threshold mechanism in contrast perception will be discussed.

◆ **The Topographica cortical map simulator**

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The goal of the Topographica project is to make large-scale computational modeling of cortical maps practical. The project consists of a set of software tools for computational modeling of the structure, development, and function of cortical maps, such as those in the visual cortex.

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These tools are designed to support: (i) rapid prototyping of multiple, large cortical maps, with specific afferent, lateral, and feedback connectivity patterns, and adaptation and competitive self-organisation, with the use of firing-rate and spiking neuron models; (ii) automatic generation of inputs for self-organisation and testing, allowing user control of the statistical environment, based on natural or computer-generated inputs; (iii) a graphical user interface for designing networks and experiments, with integrated visualisation and analysis tools for understanding the results, as well as for validating models through comparison with experimental results. The simulator is user programmable, generalises to different network arrangements and phenomena at different scales, is interoperable with general-purpose analysis and visualisation tools and low-level neuron simulators, and runs on widely available computing hardware. With Topographica, models can be built that focus on structural, functional, or integrative phenomena, either in the visual cortex or in other sensory cortices. The first full release of Topographica is scheduled for late 2005, and it will be freely available over the internet at topographica.org. We invite cortical map researchers in all fields to begin using Topographica, to help establish a community of researchers who can share code, models, and approaches.

[Supported in part by the US National Institute of Mental Health under Human Brain Project grant R01-MH66991.]

SPATIAL VISION

◆ **Is motion imagery accompanied by a spatiotemporal evolution of attention?**

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Subjects with the gaze in central fixation extrapolated in imagery the motion of a spot rotating on a circular trajectory after its disappearance. A saccade had to be made to a flash presented with various displacements relative to the position of the currently imagined spot. Saccadic latency was delayed by as much as 50 ms when the flash appeared displaced, either backward or forward, from the imagined spot. In an 'observation' condition, in which the spot did not disappear, latencies were similarly delayed, but only for backward displacements. In 25% of the trials, a beep was presented instead of the flash, with various SOAs. Subjects made a saccade to the currently imagined spot position. Mental rotation speed, estimated by the saccadic direction: latency ratio in the beep trials, was on average 9% slower than stimulus speed. Compensating for individual mental rotation speed confirmed the latency cost of making a saccade to a location different from the currently imagined location. [Powerpoint presentation]

◆ **Priming in visual search: Context effects, target repetition effects, and role-reversal effects**

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In the literature on visual perception there are many examples of how what has previously been perceived affects subsequent perception. Repetition of the same target stimulus in a visual-search task speeds task performance, and a stimulus that must be ignored in a particular setting is processed more slowly than otherwise if it must subsequently be acted upon in another context. We set out to obtain a thorough characterisation of such history effects in visual search requiring speeded judgments of target presence or absence among a set of distractors. Our results show that such priming effects have a major influence on visual-search performance. Large priming effects are seen when a target is repeated between trials, and our results also show that priming does not only occur for the target but that there is considerable priming due to repeated distractor sets, even between successive trials where no target was presented on either trial. The search also proceeds faster if the same distractor sets are repeated, even when the current target is different from the last target. This suggests that priming can operate on the context of the search, rather than just on the target in each case. Furthermore, we investigated the effects of role reversals of particular display items, from being a target on one trial to being a distractor on the next, and vice versa, showing that such role reversals also affect search performance, over and above the priming effects themselves. We discuss how temporary representations based on previous history may be crucial for visual-scene analysis, and how the results provide some clues about how the stability of the visual world is maintained. Finally, we discuss the importance of priming of perceptual groups, and of the repetition of context for visual perception.

[AK was supported by a grant from the Human Frontiers Science Program and JD was supported by the Wellcome Trust and the Medical Research Council.]

- ◆ **Cholinergic enhancement increases signal-to-noise ratio of BOLD signal in human visual cortex**
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Previous physiological studies have suggested that acetylcholine increases the signal-to-noise ratio (SNR) of sensory responses in early visual cortex. We administered the cholinesterase inhibitor donepezil (Aricept) to healthy human subjects and used fMRI to measure the BOLD responses in visual cortex to passive visual stimulation. The cortical representations of the stimulus were defined, separately for each subject, in visual areas V1, V2, and V3 by standard retinotopic mapping techniques. The resulting regions of interest were used to assess the effects of cholinergic enhancement in scanning sessions that were separate from the retinotopic mapping sessions. 3 h before scanning, 5 mg of either donepezil or placebo was administered in a double-blind procedure. Subjects passively viewed a contrast-reversing checkerboard annulus that was presented in a block-alternation design, with periods of 10 s of continuous stimulus presentation alternating with 10 s of a blank screen. A 0.05 Hz sinusoid (same frequency as the stimulus cycle) was fit to the fMRI time series for each voxel, and the coherence between this sinusoid and the time series was computed. This coherence value quantified signal-to-noise ratio in the measured fMRI time series, taking a value near 1 when the stimulus-evoked response at the block-alternation period was large compared to the noise (at all other frequency components) and a value of 0 if the stimulus-evoked response was small relative to the noise. Cholinergic enhancement with Aricept increased the signal-to-noise ratio in visual cortex in all four subjects. Experiments are under way to determine the relative contributions of neural and vascular processes to this increase in signal-to-noise ratio. [Supported by NIH, grants RO1 MH63901 and F32 EY14520.]

- ◆ **Orientation-selective adaptation to first-order and second-order stimuli in human visual cortex measured with fMRI**
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The neuronal mechanisms of second-order texture perception remain poorly understood. We have used fMRI adaptation to localise neurons tuned to the orientation of first-order and second-order grating patterns. We measured fMRI responses in three subjects to single presentations of first-order and second-order gratings after adapting to high-contrast first-order or second-order gratings. A separate session was run for each adapter orientation and stimulus type. Sessions consisted of pre-adaptation for 100 s, followed by 10 scans, each 42 trials long. Trials consisted of the adapter for 4 s, a blank screen for 1 s, the test stimulus for 1 s, and a blank screen for 1.2 s. The test stimulus was parallel or orthogonal to the adapter, or blank (adapter only trials). Stimuli were horizontal or vertical gratings presented within an annulus around fixation. First-order stimuli were generated by modulating the background luminance (LM). Second-order stimuli were generated by modulating the contrast (CM) or orientation (OM) of a first-order carrier. We used four stimulus combinations (adapter : test): LM : LM, CM : CM, OM : OM, and LM : OM. The fourth condition tested for cross-adaptation between first-order and second-order stimuli. Attention was diverted from the stimulus by a demanding task at fixation. Data were analysed for each of several visual areas, defined by retinotopic mapping. Both first-order and second-order stimuli elicited orientation-selective adaptation in most visual areas. In condition LM : LM, the adaptation was as large in extrastriate areas as in V1, implying that the adaptation originated in V1. For second-order stimuli (CM : CM and OM : OM), the amplitude of adaptation was larger, relative to the absolute response amplitudes, in several extrastriate areas including V3 and V4. There was little difference in the strength of adaptation between the second-order conditions. No consistent effect of adaptation was found in condition LM : OM, in agreement with psychophysical evidence of separate first-order and second-order mechanisms.

- ◆ **Rapid and direct access to high spatial-frequency information in visual categorisation tasks**
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A dominant hypothesis in cognitive sciences suggests a coarse-to-fine bias in scale processing, meaning an advantage of low spatial frequencies (LSF) for objects or natural scene categorisation (Bullier, 2001 *Brain Research Reviews* 36 96–107; Parker et al, 1992 *Perception* 21 147–160, 1997

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Perception **26** 1169–1180; Schyns and Oliva, 1994 *Psychological Science* **5** 195–200). Two alternative hypotheses could underlie these results. On the one hand, longer behavioural answers produced by human subjects when exposed to high spatial-frequency (HSF) information could be generated by longer physiological processes (implying access to parvocellular layers). However, it was shown that fast access to HSF information can occur after sensitisation phase on HSF images constituted of pseudo-hybrids (Oliva and Schyns, 1997 *Cognitive Psychology* **34** 72–107). Pseudo-hybrids consisted of meaningful information at one scale (either LSF or HSF) and structured noise at the other scale. Therefore, an alternative hypothesis suggests that longer behavioural response to HSF stimuli could be due to a simple computational problem related to the statistics of the inputs. Computational modelling provided some evidence that fine spatial resolution could be noisy for categorisation tasks and might contain confusing details, making visual categorisation processes difficult in distributed neural systems [French et al, 2002, in *Proceedings of the 24th Annual Conference of the Cognitive Science Society, Washington DC* (New York: LEA) pp 322–327]. In another paper, Mermillod et al (2005 *Brain and Cognition* **57** 151–157), were able to identify specific categories which allow better categorisation performance on the basis of HSF rather than LSF information. We report here behavioural data showing a reversing of the coarse-to-fine results (meaning faster processing of HSF than LSF information). This reversing was obtained by means of HSF scales identified by the artificial neural network as more efficient to resolve the categorisation task. These results suggest that the coarse-to-fine bias might be related not to physiological constraints but to computational properties of the visual environment. [PowerPoint presentation.]

◆ **Detailed metric properties of human visual areas V1 and V2 from 0.3 to 16 deg eccentricity**
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It is well known that the relationship between visual field eccentricity and cortical distance from the fovea can be described approximately by a logarithmic function. The function describing the increase in width of visual areas with eccentricity is not known, however. The complete mapping between visual space and cortex is a combination of these two functions. Before the human cortex was measured by fMRI, Schwartz (1980 *Biological Cybernetics* **37** 63–76) proposed a complex logarithmic mapping function as a model for human visual cortex. We examined the fit of this function to retinotopic mapping data for V1/V2 that were obtained with the use of advanced fMRI procedures. We used the atlas fitting functions from the VISTA-toolbox (Dougherty et al, 2003 *Journal of Vision* **3** 586–598) to semi-automatically define the borders between visual areas together with their iso-eccentricity and iso-polar lines within the reconstructed 3-D cortical manifold. Using retinotopic procedures with a log-scaled eccentricity stimulus and a fine fixation cross to optimise the stability of fixation, we could reliably map the representation of the eccentricity down to 0.3 deg radius, which is substantially closer to the foveal centre than in previous studies. We found an increase in V1 width up to 8 deg eccentricity (by a factor of 3.1, from 17.4 ± 3.4 mm at 0.37 deg to 54.5 ± 2.8 mm at 8 deg) with no significant increase thereafter. The combined measurements of eccentricity magnification functions and width magnification functions within the cortical manifold define the amount and isotropy of cortical area devoted to visual space at any eccentricity. This analysis provides a detailed framework to compare with theoretical treatments of the mapping of visual space to cortex. In detail, these results are inconsistent with the mapping function $\log(z + a)$ with an estimated $a < 0.8$ deg, proposed by Schwartz, and constrain more elaborated models, such as the conformal dipole mapping (Balasubramanian et al, 2002 *Neural Networks* **15** 1157–1163).

◆ **Interocular masking and summation indicate two stages of divisive contrast gain control**
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Our understanding of early spatial vision owes much to contrast masking and summation paradigms. In particular, the deep region of facilitation at low mask contrasts is thought to indicate a rapidly accelerating contrast transducer (eg a square-law or greater). In experiment 1, we tapped an early stage of this process by measuring monocular and binocular thresholds for patches of 1 cycle deg^{-1} sine-wave grating. Threshold ratios were around 1.7, implying a nearly linear transducer with an exponent around 1.3. With this form of transducer, two previous models (Legge, 1984 *Vision Research* **24** 385–394; Meese et al, 2004 *Perception* **33** Supplement, 41) failed to fit the monocular, binocular, and dichoptic masking functions measured in experiment 2. However, a new model with two-stages of divisive gain control fits the data very well. Stage 1 incorporates nearly linear monocular transducers (to account for the high level of binocular summation and slight dichoptic facilitation), and monocular and interocular suppression (to fit the profound

dichoptic masking). Stage 2 incorporates steeply accelerating transduction (to fit the deep regions of monocular and binocular facilitation), and binocular summation and suppression (to fit the monocular and binocular masking). With all model parameters fixed from the discrimination thresholds, we examined the slopes of the psychometric functions. The monocular and binocular slopes were steep (Weibull $\beta \approx 3-4$) at very low mask contrasts and shallow ($\beta \approx 1.2$) at all higher contrasts, as predicted by all three models. The dichoptic slopes were steep ($\beta \approx 3-4$) at very low contrasts, and very steep ($\beta > 5.5$) at high contrasts (confirming Meese et al, loco cit.). A crucial new result was that intermediate dichoptic mask contrasts produced shallow slopes ($\beta \approx 2$). Only the two-stage model predicted the observed pattern of slope variation, so providing good empirical support for a two-stage process of binocular contrast transduction.

[Supported by EPSRC GR/S74515/01.]

◆ **Spatial and temporal recognition processes in reading**

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Consider reading as serial object recognition, where each word is an object. Using RSVP, we measured the proportion of words correctly identified as a function of letter-to-letter spacing and word presentation rate. The results are separable in space and time, indicating that observers must isolate each letter in space and each word in time.

SURFACE AND SHAPE PERCEPTION

◆ **Amodal unification of surfaces with torsion requires visual approximation**

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We explored a new stereoscopic phenomenon, demonstrating that the perceived slant of untextured surfaces is constrained by occlusion geometry, beyond point-by-point matching. Displays were characterised by two vertically aligned rectangles, one frontoparallel and the other slanted about the vertical axis. Their relative slant was judged to be smaller when the two rectangles were perceived as a single object amodally unified behind a frontoparallel occluder, either luminance-specified (experiment 1) or illusory (experiment 2), than in the baseline condition in which two separate objects were perceived. Two hypotheses were considered: (i) visual approximation, when limiting cases of unification are met (eg when the smooth unification of non-coplanar surfaces and the minimisation of their deviation from coplanarity requires torsion) with image parts modified to allow for spatial unification; and (ii) occluder presence alone, when two regions have a common border, so that the near one inhibits the far one pulling the common border toward the depth level of the near region (Nakayama et al, 1989 *Perception* **18** 55–68). In experiment 3, we compared perceived slant of a rectangle, either joinable or not, with or without the occluder. Two sets of non-joinable displays were used in which spatial unification was disrupted even when the occluder was present, by means of junction's geometry or misalignment. Observers made a speeded judgment of whether the two rectangles flanking on either side of the occluder or gap had either 'positive' or 'negative' twist. Occluder presence alone reduced slant sensitivity (as well as classification speed), even when no interpolation could occur. When surfaces could be amodally unified, we found both a greater loss of slant sensitivity (with respect to baseline) and an inverse relation between the amount of loss in slant sensitivity and stereo-slant. Results indicate that visual approximation is effective when surface interpolation requires torsion, within a limited range of twist angle.

[Supported by MIUR-COFIN2003 and US NEI EY13518.]

◆ **Effects of temporal context on amodal completion, response times and magneto-encephalograph results**

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We investigated amodal completion of partly occluded figures with a same-different paradigm in which test pairs were preceded by sequences of two figures. The first of these could be congruent to a local or global completion of an occluded part in the second figure, or a mosaic interpretation of it. A superadditive facilitation of response times was obtained when the simple figure was congruent to an interpretation of the following occluded figure. This effect was obtained for local, global, as well as mosaic interpretations of the occluded figure, but only when the latter was presented briefly (50 ms). The results indicate that prior exposure primes possible interpretations in ongoing completion processes. In a follow-up experiment, we recorded and

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analysed the magneto-encephalogram for the occluded figures under these conditions. Compared to control conditions in which unrelated primes were shown, occlusion and mosaic primes reduced the peak latency and amplitude of neural responses evoked by the occlusion patterns. Compared to occlusion primes, mosaic ones reduced the latency and increased the amplitude of neural activity. This suggests that processes relating to a mosaic interpretation of the occlusion pattern can dominate at an early stage of visual processing. The results do not, however, constitute evidence for the presence of a 'mosaic stage' in amodal completion, but rather for parallel computation of alternative interpretations, including a mosaic interpretation. This last one can rapidly emerge in visual processing when context favours it. The results show a clear effect of temporal context on the completion of partly occluded figures.

◆ **Measuring the Kanizsa illusion: Revisiting brightness-nulling, depth-nulling, and contour-positioning studies**

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We previously reported a computer model to reproduce the perception of the Kanizsa figure and a wide range of variation figures, based on depth-cue-detection and surface-reconstruction algorithms (Kogo et al, 2002 *Lecture Notes in Computer Science* **2525** 311–321). In our model, the local depth cues are first detected and then globally integrated in a process of surface construction to determine the 3-D structures. The model predicts that this 3-D information plays a key role in the different perceptions of the variation figures. To support this view, we first revisited the psychophysical experiments [Halpern, 1987, in *The Perception of Illusory Contours* Eds E Petry, G E Meyer (New York: Springer) pp 171–175; Guttman and Kellman, 2004 *Vision Research* **44** 1799–1815] that have been reported to measure the brightness perception in the central area (brightness-nulling experiment), and the perceived positions of the subjective contours (contour-positioning experiment). As predicted, the Kanizsa figure showed the perceived brightness being different from the surrounding area, and the positions of the subjective contours were perceived more inwardly than in the figures with no illusion. The variation figures that do not evoke the illusion did not result in these properties. Importantly, the figures that consist of an equal number of white and black objects on a neutral grey background also showed the contour positions inwardly as well, while the brightness was not different from the surrounding area. Next, using a stereoscopic setup, subjects were asked to change the disparity of the central area until it was perceived to have the same depth as the surrounding objects (depth-nulling experiment) (Gregory and Harris, 1974 *Perception & Psychophysics* **15** 411–416). The brightness-nulling and contour-positioning experiments were repeated after the subject found the nulling position in depth. We compared the measurements of the perceived brightness and contour positions before and after the depth-nulling and evaluated the results against our model predictions.

◆ **Separate aftereffects for the shapes of contours and textures made from contours**

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We describe a novel aftereffect in which adaptation to a sinusoidal-shaped contour produces a shift in the apparent shape frequency of a subsequently presented test contour, in a direction away from that of the adaptation stimulus. The shape aftereffect is observed also for textures made up of parallel contours, or 'contour-textures'. However, a contour adaptor produces relatively little aftereffect on a test contour-texture, and vice-versa. While one might not expect a contour adaptor to have much of an effect on a test contour-texture, the opposite is not the case: the coverage of the contour-texture would normally be expected to make it a more powerful adaptor than a single contour. A possible explanation of the relative lack of an aftereffect on a test contour when using a contour-texture adaptor lies in the different luminance spatial-frequency spectra of the two stimuli: the shape of the contour might be encoded by luminance spatial-frequency filters that are not stimulated by the contour-texture because of its narrower luminance spatial-frequency bandwidth. We tested this possibility using contour-texture adaptors of a variety of luminance spatial frequencies and a test contour of fixed luminance spatial frequency. However, none of the contour-texture adaptation luminance spatial frequencies produced much of an aftereffect on the test contour. Our results constitute powerful evidence that there are separate mechanisms for encoding the shapes of contours and contour-textures, and that contour-shape encoding mechanisms are rendered largely inactive by the presence of surround parallel contours. The possible neurophysiological substrate of these findings is discussed.

[Supported by NSERC (Canada) grant OGP 0121713 given to FK.]

◆ **The tangent illusion**

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Here is a new geometrical illusion. Draw three disks of increasing size, all tangent to a pair of non-parallel straight lines. Ask observers (or yourself) to visually extrapolate the tangents to the two smaller disks and to evaluate whether the largest disk is also tangent or, if not, whether it is too large or too small. Surprisingly, perception of common tangency fails to occur. The largest disk appears too large, relative to the extrapolated tangents. A similar illusion is obtained if observers are asked to visually extrapolate the tangents to the two larger disks and evaluate the smallest disk. In this case, the smallest disk appears too small: observers perceive the three disks as having common tangents when the smallest disk is larger than the objectively tangent disk. Several hypotheses may account for the effect. According to the categorical hypothesis, the largest disk is overestimated and the smallest disk is underestimated, as an effect of induced categorisation. Asking observers to visualise the tangents to two disks would favour their grouping and the consequent differentiation of the third disk (in the direction of either an expansion or a shrinkage), with a paradoxical loss of collinearity. According to a distortion-based hypothesis, the illusion depends on the underestimation of the angle between the two tangents; ie on the tendency to perceive the two tangents as if they were closer to parallelism than they actually are. A more general hypothesis derives from the nonlinear shrinkage of interfigural distances, demonstrated in other visual phenomena. We ran a parametric study of the tangent illusion and varied the rate of growth of the three disks (ie the size of the angle between the two geometrical tangents) and the relative distance between their centres. Using the method of constant stimuli, we obtained data supporting the categorical hypothesis.

[Supported by MIUR-COFIN2003.]

◆ **Ultra-rapid visual form analysis using feedforward processing**

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The speed with which humans and monkeys can detect the presence of animals in complex natural scenes constitutes a major challenge for models of visual processing. Here, we use simulations using SpikeNet (<http://www.spikenet-technology.com>) to demonstrate that even complex visual forms can be detected and localised with a feedforward processing architecture that uses the order of firing in a single wave of spikes to code information about the stimulus. Neurons in later recognition layers learn to recognise particular visual forms within their receptive field by increasing the synaptic weights of inputs that fire early in response to a stimulus. This concentration of weights on early firing inputs is a natural consequence of spike-time-dependent plasticity (STDP) (see Guyonneau et al, 2005 *Neural Computation* **17** 859–879). The resulting connectivity patterns produce neurons that respond selectively to arbitrary visual forms while retaining a remarkable degree of invariance in image transformations. For example, selective responses are obtained with image size changes of roughly $\pm 20\%$, rotations of around $\pm 12^\circ$, and viewing angle variations of approximately $\pm 30^\circ$. Furthermore, there is also very good tolerance to variations in contrast and luminance and to the addition of noise or blurring. The performance of this neurally inspired architecture raises the possibility that our ability to detect animals and other complex forms in natural scenes could depend on the existence of very large numbers of neurons in higher-order visual areas that have learned to respond to a wide range of image fragments, each of which is diagnostic for the presence of an animal part. The outputs of such a system could be used to trigger rapid behavioural responses, but could also be used to initiate complex and time-consuming processes that include scene segmentation, something that is not achieved during the initial feedforward pass.

◆ **Visual and haptic perception of roughness**

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In this study, we are interested in the following two questions: (i) how does perceived roughness correlate with physical roughness, and (ii) how do visually and haptically perceived roughness compare? We used 96 samples of everyday materials, such as wood, paper, glass, sandpaper,

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ceramics, foams, textiles, etc. All samples were characterised by different physical roughness measures, all determined from accurately measured roughness profiles. These measures consisted of spectral densities measured at different spatial scales and industrial roughness standards (Ra, Rq, and Rz). Six subjects (four naive) were instructed to order the 96 samples according to perceived roughness resulting in a line of almost 10 m in which the samples varied from smooth to rough. In the visual condition, subjects were allowed to see the samples but not to touch them; the experimenter placed the samples in the line following the subject's instructions. The experiments took place in a classroom with all lights on and the windows blinded. In the haptic condition, the subjects were blindfolded and the experimenter helped them to place the samples in the line. The rank orders of both conditions were correlated with the various physical roughness measures. The highest value of the Spearman rank order correlation for each subject ranged from 0.52 to 0.83 for the visual condition and from 0.64 to 0.82 for the haptic condition. It depended on the physical roughness measure whether haptic performance was slightly better than, or equal to, visual performance. It turned out that different subjects ordered the samples using different criteria; for some subjects the correlation was better with roughness measures that were based on higher spatial frequencies, while others seemed to be paying more attention to the lower spatial frequencies.

[Supported by Netherlands Organisation for Scientific Research (NWO).]

◆ **Where features go to in human vision**

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Several studies have shown that features can be perceived at locations other than their retinotopic locations. This non-retinotopic perception of features has been interpreted as binding errors due to the limitations of parallel information processing. Using a Ternus–Pikler display, we show that non-retinotopic feature attributions are not perceptual errors, but precisely follow rules of grouping. In the first frame of a two-frame display, we presented three vertical Verniers of which only the central one was offset either to the left or right. The outer Verniers were aligned. In the second frame, after an ISI of 100 ms, we displayed three aligned Verniers shifted to the right. Thus, the centre element of the first frame was presented at the same position as the leftmost element in the second frame. When observers attended to this leftmost element, Vernier-offset discrimination was quite weak, even though the Vernier offset was presented at this retinotopic position in the first frame. Surprisingly, Vernier offset discrimination improved if the central element of the second frame was attended, even though this element and the retinotopically corresponding element of the first frame were not offset. In the case where the centre elements of the two frames were both offset, these offsets were perceptually integrated when the centre element of the second frame was attended, even though these elements were at two different spatial positions. This non-retinotopic feature integration is in accordance with a correspondence of elements between the two frames established by group motion as it occurs with this kind of Ternus–Pikler displays.

FRIDAY

SYMPOSIA

THE ROLE OF CONTEXT IN RECOGNITION

◆ **Detection of cryptic targets in avian vision: A field study**

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There are several strategies available to animals to avoid being detected by predators. The most complex is mimicry, where the animal resembles another specific object, such as a twig. Somewhat less demanding is crypsis, in which the animal seeks to resemble its general background. Crypsis makes the animal hard to detect when it is on an appropriate background, but will fail if the background is inappropriate. Finally, the animal may display high-contrast markings designed to disrupt its prototypical shape; this strategy, known as disruptive coloration, was recently investigated by us and found to reduce predation of artificial moths by birds in a natural woodland setting (Cuthill et al, 2005 *Nature* **434** 72–74). We investigated the role of crypsis in avian predation, using similar techniques to the earlier study. Photographs of different trees were obtained, and used to produce a series of morphed photographs spanning the range between the trees. Stimuli were made from these photographs on a calibrated laser printer, and cut into triangular ‘moths’. A dead mealworm served as bait, and the moths were attached to mature and young trees in natural English woodland. Survival analysis of the worms gave an estimate of the predation rate. Results are presented about the survival probabilities of ‘specific’ and ‘generalist’ moths. In general, this methodology allows ‘field psychophysics’ to be performed in a natural setting on a wild population of birds.
 [Supported by BBSRC Grant number S18903.]

◆ **Modeling scene context for object search in natural images**

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At the beginning of a search task, attention and eye movements are guided by both low-level image properties and top–down contextual information. However, it remains a puzzle how human observers represent and use contextual information at the beginning of the search process, as well as how salience and context interact to produce visual-search scanning patterns. I present behavioural and computational results investigating the role of contextual priors in guiding visual search. By monitoring eye movements as participants search novel and very familiar scenes for a target object, we asked the question when contextual priors benefit visual exploration (early stage, before initiating a saccade, during the search phase per se, or at the object recognition stage). Our experiments manipulated two types of contextual priors: categorical priors (the association between a scene category and an object category) and identity priors (the association between a specific scene exemplar and a specific object). Various data are discussed in terms of the implications of context-dependent scene processing and its putative role in various stages of visual search. [In collaboration with A Torralba, B Hidalgo-Sotelo, N Kenner, and M Greene.]

◆ **The contribution of top–down predictions to visual recognition**

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We see the world in scenes, where objects typically appear together in familiar contexts. In spite of the infinitely diverse appearance of these scenes, such context-based associations can give rise to expectations that benefit the recognition of objects within the scene. Building on previous work (Bar, 2003 *Journal of Cognitive Neuroscience* **15** 600–609; Bar and Aminoff, 2003 *Neuron* **38** 347–358), we proposed a mechanism for rapid top–down and context-driven facilitation of object recognition (Bar, 2004 *Nature Reviews Neuroscience* **5** 619–629). At the heart of this model is the observation that a coarse, low-spatial-frequency representation of an input image (ie a blurred image) is sufficient for rapid object recognition in most situations. Specifically, a low-spatial-frequency image of a scene can activate a set of associations (ie ‘context frame’) that provide predictions about what other objects are likely to appear in the same environment. For example, a ‘beach’ context frame will include the representation of a beach umbrella, a beach chair, a sand castle, and so on, as well as the typical spatial relations among them. In parallel, a low-spatial-frequency image of a single target object within the scene can considerably limit the number of alternative interpretations that need to be considered regarding the identity of this object. For example, a low-spatial-frequency image of a beach umbrella can be interpreted as a

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beach umbrella, a mushroom, a lamp, or an umbrella. The intersection of these two sources of information, the context and the object alternatives, would result in a unique identification of that object. The resulting representation can then gradually be refined with the arrival of details conveyed by the high spatial frequencies. The logic and behavioural and neuroimaging data that support various aspects of the proposed model are outlined.

[Supported by NINDS R01NS44319, NINDS R01NS050615, and the James S McDonnell Foundation #21002039.]

◆ **Beyond the face: Exploring rapid influences of context on face processing**

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In our natural world, a face is usually not encountered as an isolated object but as an integrated part of a whole body. For example, the emotional state of an individual is conveyed at the same time by the facial expression, the tone of voice, and the emotional body language. A correct interpretation of all these different signals together is important for survival. Likewise, rapid detection of a discrepancy between a facial expression and the accompanying emotional body language contributes greatly to adaptive action. Moreover, faces also appear within external contexts typically consisting of natural scenes. For example, the presence of a natural scene and also its emotional valence may influence how a facial expression is judged and may also determine how well faces are subsequently remembered. In order to arrive at an ecologically valid theory of face processing, the impact of these various context effects has to be taken into account. I present recent results from behavioural and brain-imaging experiments investigating how face processing is indeed influenced by context. The overall goal of these experiments is to picture the different types of context influences and to obtain insight into their time course. I discuss the importance of context effects on face processing for traditional theories of face recognition and for face-processing deficits.

CROSSMODAL INTERACTIONS IN VISUAL PERCEPTION

◆ **Coordinate transformations and visual–auditory integration**

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Visual information is originally eye-centred and auditory information is originally head-centred. How does the brain reconcile these disparate reference frames when combining visual and auditory information? It has recently been reported that some neurons in the primate inferior colliculus and auditory cortex carry information about eye position (Groh et al, 2001 *Neuron* **29** 509–518; Werner-Reiss et al, *Current Biology* 2003 **13** 554–562). The reference frame was complex, suggesting that auditory signals in these brain areas are neither head- nor eye-centred, but carry a mixture of sound and eye-position-related information. Do auditory signals undergo further transformation before they are combined with visual signals in multimodal structures such as the parietal cortex? To address this question, the reference frame of both visual and auditory signals in the lateral and medial banks of the intraparietal sulcus (areas LIP and MIP) was investigated. The activity of 275 neurons was recorded in two monkeys performing visual or auditory saccades. The reference frame patterns of visual and auditory signals were similar both to each other and to those of auditory signals in the IC and auditory cortex. Visual response patterns ranged from head- to eye-centred, as did auditory responses, with the majority of response patterns being no more consistent with one reference frame than with the other. Why does the brain mix head- and eye-centred coordinates, rather than creating a pure code in one format or the other? The answer to this question may lie in the eventual output: motor commands. The pattern of force needed to generate a saccade depends on both the head- and eye-centred positions of the target. Thus, the ultimate output of the system is a mixture of head- and eye-centred information which may be similar to the representation contained in the intraparietal sulcus and other brain areas.

[Supported by NIH NS 17778, NIH NS50942, NSF 0415634, Alfred P Sloan Foundation, McKnight Endowment Fund for Neuroscience, Whitehall Foundation, John Merck Scholars Program, ONR Young Investigator Program, EJLB Foundation.]

◆ **Integrating sensory modalities in the perception of motion**

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There is increasing recognition of the importance of multisensory integration in obtaining accurate and coherent representations of the environment. Some of the classic demonstrations, including the ventriloquist illusion and the McGurk effect, are based on the perceptual consequences of presenting conflicting information to different senses. However, these traditional lines of research have often focused on spatially static stimulation, in contrast with the highly dynamic nature of everyday scenes. We have used the principle of intersensory conflict to address the contribution of multisensory integration in the perception of motion. Our initial studies show that motion judgments in one sensory modality (audition) can be strongly influenced by the direction of motion in other modalities (vision). As in other multisensory phenomena, these influences are not always bidirectional and extend to other modality combinations. Furthermore, several lines of evidence strongly support the idea that the integration of motion information has a perceptual basis, and that it cannot be accounted for solely by the local interactions occurring at the level of static information (the ventriloquist illusion). In light of the data presented, we argue that these integration processes are based on motion representations and that they occur automatically, with little or no voluntary control by the observer.

[Supported by Ministerio de Educacion y Ciencia (TIN2004-04363-C3-02), and the McDonnell Centre for Cognitive Neuroscience, Oxford.]

◆ **Anomalous cross-modal interactions in synaesthesia**

N Sagiv (Department of Psychology, University College London, London WC1E 6BT, UK) Synaesthesia is a condition in which stimulation in one sensory modality evokes an additional perceptual experience in a second modality. The condition is more common than previously thought, affecting over 1% of otherwise normal population. Synaesthesia offers a unique point of view on conscious visual perception. I discuss a number of studies examining not only how such anomalous cross-modal interactions become possible, but also what they tell us about normal perception. Among the questions discussed are: Does synaesthesia rely on cross-modal mechanisms common to us all? How do we obtain objective measures of such unusual experiences? What is the time course of synaesthesia? What is the role of attention in synaesthesia? Additionally, I discuss some prevalence data, possible modes of inheritance, and the use of synaesthesia as a model for cognitive genomics.

◆ **Combination of visual and auditory information in fixation and during saccades**

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Information processed by our five different senses must be combined at some central level to produce a single unified percept of the world. Recent theory and evidence from many laboratories suggest that the combination does not occur in a rigid, hard-wired fashion, but follows flexible situation-dependent rules that allow information to be combined with maximal efficiency. For example, when vision and audition give conflicting information about spatial position, vision usually dominates (the well-known ‘ventriloquist effect’). However, when visual information is degraded (by blurring, for example), auditory information contributes to and may even dominate spatial localisation. Importantly, localisation with dual (visual and auditory) sensory input is always more precise than with a single sensory modality, as predicted by models assuming a statistically ideal combination of signals. This technique has recently been extended to the study of visuo-auditory combination at the time of saccades. Many studies have shown that briefly displayed visual (but not auditory) stimuli presented near saccadic onset are systematically mislocalised, seen compressed towards the saccadic target. However, when visual and auditory stimuli are presented together at the time of saccades, audition dominates, causing both to be perceived veridically. Again, the results are consistent with a simple model of statistically optimal cross-modal combination. Other interesting cross-modal interactions (such as the cross-modal flash-lag effect) are also discussed, many of which are not readily explained by simple models such as statistically optimal combination.

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ORAL PRESENTATIONS

EYE MOVEMENTS

◆ **An information theoretic analysis of eye movements to natural scenes**

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The choice of where we move our eyes is determined by a number of factors including high-level constraints (such as what task is performed by the subject), and low-level constraints (such as the fixations being more probable to 'salient regions'). We used information theoretic techniques, more traditionally used for the analysis of neuronal spike trains, to estimate the contribution of high-level and low-level factors to the distribution of fixation locations in natural images. Our method requires no arbitrary decisions about which low-level image statistics contribute to low-level salience. For eye movements recorded when viewing natural images, task-dependent factors accounted for 39% of the eye-movement-related information, whereas task-independent factors accounted for 61%. Over the course of several seconds of viewing, we found that the contribution of task-independent factors was time invariant, whereas the contribution of task-dependent factors increased.

◆ **Blazing an efficient walking path with one's eye**

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Opposing views currently exist regarding the role of eye movements in locomotion. One view is that eye movements mask information useful for locomotion, and as a consequence some type of compensation is required to undo their retinal-image effects. A second view is that eye movements aid in the discovery of one's aim point by scanning the environment to find some lawful aspect in the retinal flow. We suggest that eye movements play yet another beneficial role in locomotion. Using an immersive virtual environment, we show that eye movements aid walkers by seeking out efficient paths prior to moving in a particular direction. Twenty participants were instructed to walk as quickly as possible to a target, avoiding obstacles. Head position and orientation were recorded, and used to determine point of view and path taken. Eye recordings were made and used to construct eye-on-scene (gaze) movies. Gaze deviation (RMSE of gaze from path) and path inefficiency (distance traveled minus optimal distance) were computed from 600 trials, and tested with a 40 deg and a 10 deg field of view (FOV). Regression analysis showed that (log) gaze deviation was linearly related to (log) path inefficiency ($p < 0.0001$ for both FOVs). Navigation was more efficient when one's gaze was near the path taken. Gaze deviation accounted for half the variability in path inefficiency. Efficient walkers, defined as those with inefficiency scores below the median, looked ahead 3.1 m before they arrived at the point on the path. This distance increased to 3.7 m with a 10 deg FOV. For inefficient walkers, preview distance was 2.8 m for both FOVs. These findings suggest that efficient walkers adopt scanning strategies that enable them to get to their goal with a minimum expenditure of energy—by letting their eyes do the walking before their feet.

[Supported by US Army grant W911NF-04-1-0059.]

◆ **Eye movements on a display with gaze-contingent temporal resolution**

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We investigated the influence of high temporal frequencies in the visual periphery on the control of saccadic eye movements. To this end, we used a gaze-contingent system capable of foveating the temporal resolution of movies (1024 × 576 pixels, 30 Hz) in real-time. Previous approaches have been limited to varying only spatial resolution (see eg Perry and Geisler, 2002 *SPIE* **4662** 57–69). We used a multiresolution pyramid to create six temporally downsampled versions of an image sequence. Depending on eccentricity, the different levels of the pyramid were then interpolated in the upsampling reconstruction step to yield a varying temporal resolution across the visual field, currently defined by a sigmoidal falloff from the centre. Thus, moving objects in the periphery became blurred or even seemed to disappear completely, while full temporal resolution was kept at the centre of gaze. Because only at eccentricities exceeding about 20 deg the reduction in resolution becomes significant, this real-time selective filtering remains unnoticeable to the subject. We measured the effect of such gaze-contingent stimulation on eye movements. Eight subjects watched four temporally foveated video clips of natural scenes (20 s duration each)

while their eye movements were recorded. The data were compared with a large collection of gaze data on the same, but unfoveated, videos (fifty-four subjects). Results show that the number of saccades with an amplitude of more than 20 deg is reduced by about 50% ($p < 0.01$). A further significant effect is an increased preference for the centre of the display. Thus, we can conclude that temporal transients in the visual periphery are highly important for the guidance of saccadic eye movements. We plan to predict eye-movement paths by manipulating these transients, in an attempt at more efficient image communication (see <http://www.inb.uni-luebeck.de/ltap>).

[Supported by the German Ministry of Education and Research (BMBF) under grant number 01IBC01B.]

◆ **Eye movements to pictures of normal faces, and the same people made up to be disfigured**

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There have been many eye-movement studies of faces, but only a few on disfigured faces. This is partly because it is difficult to get examples of disfigured faces. We have resorted to using faces made up to be disfigured (Brown and Looney, in preparation), so have normal and disfigured versions of the same face. We investigated eye movements to pictures of faces made up to be disfigured on the right or left and also to the same people but non-disfigured—using the ASL eye tracker with gaze-tracker software. We also measured skin conductance and heart rate responses to these faces. Each face was zoned into a disfigured region and a matching mirror-image non-disfigured region. The normal non-disfigured pictures of the same people were given the same zones. Eye fixations were counted in the zones. The normal faces showed a significantly greater number of fixations in the right-hand zones compared to the left-hand ones (relative to the visual field of the observer). When the disfigurement was on the left, there was very little difference between the disfigured left zone and the non-disfigured right zone. When the disfigurement was on the right, there was a significantly greater number of fixations to the disfigured right zone. This suggests that normal faces are fixated more on the right than on the left, which means that most of the face is in the left visual field for more time than it is in the right, which would enable more right hemispheric processing. The effect of disfigurement is to attract eye movement; so, when on the left, the disfigurement reduces the normal right/left difference; and when on the right, it increases it. Results of the skin-conductance responses to the normal and disfigured faces will be reported.

◆ **How do eye movements change during visual learning?**

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Eye movements reliably signal conscious cognitive processes, such as task planning or recognition, but are they linked to the gradual learning of the underlying structure in unfamiliar visual scenes? We investigated changes in the characteristics of eye movements during the viewing of many multi-shape scenes containing hidden underlying structures defined by the co-occurrence of particular shapes. Twelve shapes were grouped into six 2-element base-pairs, with elements in base-pairs appearing together only in a fixed spatial arrangement. Fifty subjects were tested in a two-phase observational learning paradigm. During the practice phase, subjects viewed 144 displays composed of a random arrangement of three base-pairs while their eye movements were monitored. The subjects' only task was to explore the scenes. In the following test phase, subjects viewed one base-pair and one arbitrary pair in each trial of a temporal 2AFC task, and were asked to choose the more familiar pair based on the practice phase. Subjects were grouped into good ($> 67\%$ correct) and bad learners ($< 56\%$) on the basis of their 2AFC performance, and their eye movements during the practice phase were compared. There was no significant difference between good and bad learners in basic eye-movement metrics (number of fixations, total fixation time per scene). The proportion of saccades between two elements of the same base-pair compared to saccades between different base-pairs did not change differentially with practice ($p > 0.9$) in the two groups. However, by the end of the practice phase, good learners looked significantly fewer times ($p < 0.05$), but each time significantly longer ($p < 0.02$), at elements of base-pairs that they identified successfully during the 2AFC test. Thus, statistical learning of visual structures alters the pattern of eye movements, reflected in longer durations of fixation of significant spatial structures, even before the likelihood of repeatedly fixating those structures exceeds chance.

[Supported by NIH HD037082 and Packard Foundation (2001-17783).]

Friday

◆ **Picking up where you left off: The timecourse of target recovery after a gap in multiple object tracking**

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Observers in multiple object tracking (MOT) experiments can successfully track targets which disappear for up to 500 ms [Alvarez et al, 2005 *Journal of Experimental Psychology: Human Perception and Performance* 31(4)]. How quickly can targets be recovered after they reappear? We devised a reaction time (RT) variant on the standard MOT paradigm. Observers tracked four of eight moving gray disks for 1–3 s, at which point the disks disappeared for a fixed gap duration, then reappeared at updated positions as if they had continued to move during the gap. Following a variable stimulus onset asynchrony (SOA) from the time of reappearance, one disk (the probe) turned red, and observers had to make a speeded response indicating whether the probe was a target or non-target. In experiment 1 ($N=8$), we compared no-gap (0 ms gap) and gap (133 ms) conditions, with SOAs of 0, 80, 160, 320, and 1280 ms. Gap condition RTs were slower than no-gap RTs at 0 ms SOA, then dropped to the no-gap level by 80 ms. In experiment 2 ($N=8$), we used SOAs of 0, 40, 80, 120, 160, and 1280 ms. Here gap condition RTs reached no-gap levels by 40 ms. In experiment 3, we used SOAs of 0, 40, 80, 120, 160, 320, 960, and 1280 ms, and varied gap duration from 133 to 307 to 507 ms. The same timecourse was observed for all three gap durations, with RT reaching a minimum at 40 ms. These data suggest that observers are able to recover targets within 40 ms of reappearance. Such a rapid time course suggests that targets are recovered in parallel, rather than one by one.

[Supported by NIH MH65576.]

◆ **Saccadic suppression of retinotopically localised stimuli in V1: A parametric fMRI study**

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Vision is an active process involving a close interplay between sensory and oculomotor control systems in the brain. Psychophysical data have shown that the decrease in visual sensitivity experienced during the execution of saccades starts ~ 75 ms before the onset of the actual eye movement. The perception of briefly presented stimuli during the pre-saccadic interval is impaired, despite the fact that these stimuli are projected onto the stationary retina. We studied the cortical responses to flashed visual stimuli presented immediately before the onset of a saccade to a peripheral target. Exploiting the random nature of saccadic latencies and Bayesian theorem, we adaptively presented four Gabor patches during 8 ms in each of the four visual quadrants at different times during the pre-saccadic period. Trials were sorted according to the resulting delay between stimulus and eye movement (SOA). Subjects were asked to judge the relative orientation of the Gabor stimuli. Clusters encoding each of the four stimuli were retinotopically localised and used to define regions of interest later used in the fMRI analysis. In an event-related design, the SOA was introduced as a parametric modulator to the BOLD signal changes elicited by the Gabors in V1, which consistently decreased with decreasing SOA. Even though their retinal images were identical, Gabors presented very close to the saccadic onset were often not perceived and induced no significant signal changes in V1, as opposed to Gabors presented far away from the saccadic onset (SOA > 100 ms) or when no saccadic eye-movement preparation was in course. Our findings suggest that saccadic suppression is evoked at a subcortical level, before stimulus-driven activity reaches visual cortex and its 'suppressing' effects can be measured with fMRI in V1.

[Supported by Deutsche Forschungsgemeinschaft SFB 517 Neurokognition.]

◆ **The possible purpose of microsaccades**

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We have modelled the effects of microsaccades on the contrast detection and discrimination capacities of cones and cone-driven ganglion cells in the human fovea. Typical human micro-saccade patterns were applied to achromatic contrast patterns corresponding to stationary borders and lines passed through the foveal line-spread function and projected onto the human foveal cone mosaic. The resulting temporal contrast modulation over a cone receptive field was convolved with the response kinetics of primate cones as reported by Schnapf et al (1990 *Journal of Physiology* 427 681–713), and the output of the cone-driven ganglion cells was calculated by

the difference-of-Gaussians receptive field model of Donner and Hemilä (1996 *Visual Neuroscience* **13** 173–186). We find that microsaccades may dramatically enhance sensitivity to edges and lines, and, especially, help to distinguish two or several closely spaced lines from a single line. Being under neural control, the microsaccade patterns (forward–return) and velocities appear to be ‘tuned’ to the spatio-temporal properties of foveal cones and ganglion cells. To our knowledge, the effects of microsaccades and other small (fixational) eye movements on these primary signals of the visual system have not previously received attention, although they set boundary conditions for performance at any subsequent stage.

[Supported by the Academy of Finland, grant 206221.]

3-D VISION

◆ Bayesian modelling of binocular 3-D motion perception

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Introducing uncertainty to existing models of binocular 3-D motion perception results in different predictions for perceived trajectory angle and velocity of a target moving in $x-z$ space. The first model uses velocity constraints in the left and right eye to recover trajectory angle. Uncertainty in velocity encoding produces likelihood distributions for angular velocity in the left and right eye. A suitable prior condition for this model favours slow motion (Weiss et al, 2002 *Nature Neuroscience* **5** 598–604). Determining the maximum of the resulting distribution gives an estimate of trajectory angle and velocity in $x-z$ space. The second model is based on uncertainty in binocular disparity encoding. The prior condition of this model is defined in disparity space favouring zero disparity (Read, 2002 *Neural Computation* **14** 1371–1392). The effect is computed for the endpoint of a target and trajectory angle, and velocity estimates are derived. Predictions from both models were tested in an experiment where changing binocular disparity and interocular velocity difference served as cues for 3-D motion perception. Stimuli were presented to the left and right eye on a calibrated flat CRT monitor in a split-screen Wheatstone configuration with a refresh rate of 120 Hz. On each trial, subjects verged on a fixation-cross flanked by vertical nonius lines and horizontal grids at 114 cm before two target dots above and below fixation moved on parallel trajectories. Trajectory angle (0° to 360°) and distance travelled (25 to 33 mm) varied in randomly intermixed trials. In separate blocks, four subjects indicated trajectory angle and distance travelled by adjusting markers on screen. The results confirm that trajectory angle (Harris and Drga, 2005 *Nature Neuroscience* **8** 229–233) and velocity in $x-z$ space are systematically biased. Both observations support the notion of a stereo-motion system that first encodes disparity.

◆ Fourier cues to 3-D shape

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If you pick up a typical vision text, you’ll learn there are many cues to 3-D shape, such as shading, linear perspective, and texture gradients. Much work has been done to study each cue in isolation and also how the various cues can be combined optimally. However, relatively little work has been devoted to finding commonalities between cues. Here, we present theoretical work that demonstrates how shape from shading, texture, highlights, perspective, and possibly even stereopsis could share some common processing strategies. The key insight is that the projection of a 3-D object into a 2-D image introduces dramatic distortions into the local image statistics. It does not matter much whether the patterns on a surface are due to shading, specular reflections, or texture: when projected into the image, the resulting distortions reliably cause anisotropies in the local Fourier spectrum. Globally, these anisotropies are organised into smooth, coherent patterns, which we call ‘orientation fields’. We have argued recently [Fleming et al, 2004 *Journal of Vision* **4**(9) 798–820] that orientation fields can be used to recover shape from specularities. Here we show how orientation fields could play a role in a wider range of cues. For example, although diffuse shading looks completely unlike mirror reflections, in both cases image intensity depends on 3-D surface orientation. Consequently, derivatives of surface orientation (curvature) are related to derivatives of image intensity (intensity gradients). This means that both shading and specularities lead to similar orientation fields. The mapping from orientation fields to 3-D shape is different for other cues, and we exploit this to create powerful illusions. We also show how some simple image-processing tricks could allow the visual system to ‘translate’ between cues. Finally, we outline the remaining problems that have to be solved to develop a ‘unified theory’ of 3-D shape recovery.

[Supported by a fellowship from the Max Planck Society.]

Friday

◆ **Perspective images and vantage points: Geometrical analyses versus the robustness hypothesis**
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Every linear perspective image involves a projection centre. When observed from that position, it provides a stimulus geometrically equivalent to the stimulus provided by the original scene. However, this is not true if the image is observed from a different vantage point. There are two hypotheses concerning the effect of the variation of the position of the vantage point on the perceived spatial structure of the 3-D scene conveyed by the image. Geometrical analyses suggest that displacements of the vantage point lateral to the image plane should induce shears of the perceived scene, whereas orthogonal displacements should induce compressions/dilatations. In contrast, the robustness hypothesis claims that, except in special cases, the perceived scene structure is not affected by such displacements, thanks to a constancy-like perceptual mechanism which compensates for variability of vantage point positions. Most previous research has indicated that vantage point positions do affect the perceived scene structure to some extent. However, such research has often used images lacking salient perspective cues, and was rarely based on detailed geometrical predictions of the effects of vantage point variation. I report three experiments, one using a specially constructed image, and two with drawings by de Vries, involving strong perspective cues. In the first experiment, I used lateral displacements of the vantage point, with subjects judging the 3-D direction of colonnades depicted in the image. In the other two experiments, I used orthogonal displacements. In the second experiment, subjects judged the depth extent of a depicted pedestal; and in the third, they judged the angle of depicted pillars with respect to a terrace. The results are generally in accord with the geometrical analyses, but show some systematic deviations from predictions, which are more likely due to visual angle effects and flatness cues in images, rather than to compensation mechanisms envisaged by the robustness hypothesis.

◆ **Cue recruitment and Pavlovian conditioning in visual perception**

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Up until fifty years ago, associative learning played a fundamental role in theories of perception [Berkeley, 1709 *Essay Towards a New Theory of Vision*; Condillac, 1754 *Treatise on Sensations*; Kant, 1781 *Critique of Pure Reason*; Helmholtz, 1878 *The Facts of Perception*; James, 1890 *Principles of Psychology*; Hebb, 1949 *Organization of Behavior* (New York: John Wiley); Ames, 1953, in *Vision and Action* Ed. S Ratner (New Brunswick, NJ: Rutgers University Press); Brunswik, 1956 *Perception and the Representative Design of Psychological Experiments* (Berkeley, CA: University of California Press)]. Since then, however, perceptual learning has frequently been defined as an improvement in the ability to discriminate that comes with practice [Gibson and Gibson, 1955 *Psychological Review* **62** 32–41; Drever, 1960 *Annual Review of Psychology* **11** 131–160; Fahle, 2002 *Introduction, Perceptual Learning* (Cambridge, MA: MIT Press)]. Does associative learning for arbitrary signals occur in perception? We developed the ‘cue recruitment’ experiment, an adaptation of Pavlov’s classical conditioning paradigm [Pavlov, 1927 *Conditioned Reflexes* (Oxford: Oxford University Press)], to systematically study associative learning in perception. Trainees viewed movies of a rotating wire-frame cube. This stimulus is perceptually bistable. On training trials, perceived direction of rotation was disambiguated by the addition of depth cues (stereo and occlusion). Critically, arbitrary visual signals (position or translation) were also added, contingent on the direction of rotation. On test trials, stimuli contained the new signals, but not the stereo and occlusion cues. Test trials were monocular to minimise the potency of motion-specific stereo adaptation aftereffects on test trials. Over 45 min, the new signals acquired the ability to disambiguate rotation direction on their own. As with classical conditioning, this learning took place without conscious effort, grew incrementally, lasted, and interfered with subsequent learning of the opposite correlation. The results were consistent across trainees. These findings are qualitatively different from previous results: the effect was positive (unlike most adaptation aftereffects) and the associations were arbitrary [not between stimuli that are naturally related (Sinha and Poggio, 1996 *Nature* **384** 460–463)].

[Supported by NIH grant R01-EY 013988 and the University Research Foundation of the University of Pennsylvania.]

◆ **Disparity and texture gradients are combined in a weighted sum and a subtraction**

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Different combinations of depth cues are relevant for different perceptual judgments. For judgments of slant, disparity and texture gradients should be combined in a weighted sum. For judgments of texture homogeneity (ie shape constancy), the gradients should be compared, which can be accomplished by subtracting one from the other. An analogous transformation occurs in colour vision where L- and M-cone signals are added in luminance channels and subtracted in colour-opponent channels. Does the same occur with disparity and texture signals? Specifically, are disparity and texture combined in a weighted summation for slant estimation and subtracted for judging texture homogeneity? And is access to the disparity and texture signals themselves lost in the combination? To answer these questions, we presented planes whose slants were defined by independently varied disparity and texture gradients. There were two types of stimuli: Voronoi-textured planes and square-lattice planes. The former minimised the detectability of texture homogeneity; the latter maximised its detectability. There were three types of trials. (i) 3-interval 'oddyity', in which three stimuli were presented, one (or two) at a base slant with no conflict between disparity and texture and two (or one) at a comparison slant with conflicting modulation of texture and disparity. Observers indicated the interval containing the 'odd' stimulus, using any criteria. (ii) 2-interval 'slant', in which two stimuli were presented, one with conflict and one without. Observers indicated the interval containing greater perceived slant. (iii) 2-interval 'homogeneity', in which two stimuli were again presented, one with conflict and one without. Observers indicated the interval containing the less homogeneous texture. With both stimulus types, the slant and homogeneity thresholds predicted the oddity thresholds. This finding is consistent with the hypothesis that disparity and texture cues are combined by weighted summation to estimate slant and by subtraction to estimate texture homogeneity.

◆ **Investigation of the relative contributions of 3-D and 2-D image cues in texture segmentation**

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Segmenting a texture of 45° bars from another of -45° bars is more difficult if a task-irrelevant texture of spatially alternating horizontal and vertical bars is superposed. The elements of the two textures share the same grid locations. In other words, the superposed texture of horizontal/vertical bars interferes with the task (Zhaoping and May, 2004 *Society for Neuroscience* abstract online No. 20.1). In this study, we ask if the degree of interference changes when the interference pattern is placed in a different depth plane. Subjects performed a two-alternative forced-choice (left or right) localisation of the texture border and their reaction times were measured. The stimulus patterns consisted of 30 × 22 texture elements, extending about 50 deg × 36 deg in visual angle, with the texture border located between 8 deg and 19 deg eccentricity laterally. Superposing an interference pattern leads to a prolonged reaction time. When the interference pattern was at a non-zero disparity while the task-stimulus pattern was at zero disparity, the interference effect was reduced. Since the disparity difference was created by shifting the interference pattern horizontally in the stimulus input for one eye but not for the other, we further investigated whether this 2-D stimulus shift without stereo cues is sufficient to reduce interference. When the identical stimulus pattern with this non-zero horizontal shift between task-relevant and interference pattern was presented to the two eyes, interference effects were indeed reduced. Interference by irrelevant orientations, and its reduction by non-zero shifts between the two textures, have been predicted by Li's theory (2002 *Trends in Cognitive Sciences* 6 9–16) of V1 as a salience map. Our current results suggest that V1, which does not solve the stereo fusion problem (Cumming and Parker, 2000 *Journal of Neuroscience* 20 4758–4767), may be largely responsible for the reduction of the interference.

◆ **Motion parallax influences the way we place objects on slanted surfaces**

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Various sources of visual information determine the perceived slant of a textured surface. We measured the relative contributions of such sources (motion parallax, binocular disparity, texture gradients, and accommodation) using a simple placing task. Most previous experiments on slant perception have been performed in virtual environments. Often, a chin-rest or biteboard was used. In such cases, motion parallax is irrelevant as a slant cue. We used an apparatus in which the surface slant could be rotated independently of the texture, creating a conflict between texture and other cues, to evaluate the possible role of motion parallax. Conditions with and

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without a biteboard were compared. The task of the subject was to place a flat cylinder on the slanted surface. The position and orientation of the cylinder were measured throughout the movement. The relative contributions of various cues were determined by eliminating the cues one by one, and measuring the weight of texture relative to the remaining cues. Binocular cues contributed most strongly to the perceived slant of nearby surfaces. Surprisingly, motion parallax proved to be as important as the texture cues. All subjects moved their heads considerably when placing the cylinder (at least 40 mm in the lateral direction). There was no evident correlation between the amount of head movement and the weight given to motion parallax. Thus, motion parallax contributes to our actions even in conditions in which we are under the impression that we are standing still.

- ◆ **The role of texture in shape from shading: Are humans biased towards seeing relief textures?**
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When a textured surface is modulated in depth and illuminated, the level of illumination varies across the surface, producing coarse-scale luminance modulations (LM) and amplitude modulation (AM) of the fine-scale texture. If the surface has an albedo texture (reflectance variation) then the LM and AM components are always in-phase, but if the surface has a relief texture the phase relation between LM and AM varies with the direction and nature of the illuminant. We showed observers sinusoidal luminance and amplitude modulations of a binary noise texture, in various phase relationships, in a paired-comparisons design. In the first experiment, the combinations under test were presented in different temporal intervals. Observers indicated which interval contained the more depth stimulus. LM and AM in-phase were seen as more depth than LM alone which was in turn more depth than LM and AM in anti-phase, but the differences were weak. In the second experiment the combinations under test were presented in a single interval on opposite obliques of a plaid pattern. Observers were asked to indicate the more depth oblique. Observers produced the same depth rankings as before, but now the effects were more robust and significant. Intermediate LM/AM phase relationships were also tested: phase differences less than 90 deg were seen as more depth than LM-only, while those greater than 90 deg were seen as less depth. We conjecture that the visual system construes phase offsets between LM and AM as indicating relief texture and thus perceives these combinations as depth even when their phase relationship is other than zero. However, when different LM/AM pairs are combined in a plaid, the signals on the obliques are unlikely to indicate corrugations of the same texture, and in this case the out-of-phase pairing is seen as flat.

[Supported by the Engineering and Physical Sciences Research Council (EPSRC).]

VISUAL AWARENESS

- ◆ **Colour in mind: Stability of internally generated colours in synesthesia**

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Synesthesia refers to a condition where a sensory stimulation may result in perception within another sense; for example, an auditory stimulus may result in perception of a specific colour. Similarly, within a modality, cross-feature interactions may take place such that, for example, a letter may result in perception of specific colour (form colour). fMRI investigations have shown evidence that colour form synesthesia is a result of cross-activation between form-selective and colour-selective brain areas (Hubbard et al, 2005 *Neuron* **45** 975–985). Using a colour-matching paradigm, we have investigated the reproducibility of mental colours in two participants with form colour synesthesia. In experiment 1, we have shown that form–colour matching, for those colours that could be reproduced on a CRT monitor, in both synesthetes was as accurate as simultaneous colour matching in normal observers ($N = 20$), and was significantly better than delayed colour matching in normal observers. In experiment 2, we compared the ability to reproduce colours of familiar objects from memory in normal observers and one synesthete with red–green form colour synesthesia. The data show that consistency of the synesthete participant to reproduce blue and yellow object colours was similar to normal controls, but for red–green targets, which could be internally represented, performance of the synesthete was significantly better than that of normal observers. In conclusion, we present psychophysical evidence for a precise connection, mapping specific forms with a precise colour rather than a diffuse cross-feature connection. In addition, the findings cannot be accounted for by a generally enhanced memory for object colours in synesthesia.

◆ **Correlation of neural activity in early visual cortex and subjects' responses—fMRI and EEG measurements of change detection**

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A central question in the scientific study of perceptual awareness is the extent to which neuronal activity in distinct cortical areas correlates with conscious experience. In particular, does neuronal activity in primary visual cortex (V1) relate to subjects' visual perception? We addressed this question by exploiting the phenomenon of 'change blindness'. We presented a flickering stimulus, consisting of several ring segments centred on a red fixation mark. Each ring segment was filled with a grating tilted either $+45^\circ$ or -45° from the vertical midline. Subjects had to report on the location of occasional 90° flips in the orientation of single rings by means of button presses. However, the synchronous flicker of the stimulus effectively masks these local orientation changes and they are frequently missed. Our fMRI data show that there is a transient, spatially localised BOLD signal increase in V1 (and other retinotopically organised early cortical areas) following reported—but not missed—orientation changes. Our findings suggest that, already in the earliest stages of the visual cortical hierarchy, neuronal activity correlates with subjects' conscious perception and behaviour. In addition, we present our ongoing EEG study using a similar stimulus and task. We describe stimulus- and response-locked ERP components induced by perceived and non-perceived changes and their neuronal sources. We discuss how the higher temporal resolution of our EEG measurements can complement our fMRI data.

◆ **fMRI evidence for temporal precedence of right inferior frontal activity changes associated with spontaneous switches in bistable perception**

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When looking at ambiguous visual stimuli, the observer experiences transitions between two competing percepts while physical stimulation remains unchanged. A central process subserving the continuous reinterpretation of the visual input has been suggested to be involved in the initiation of spontaneous perceptual transitions. While recent evidence from functional magnetic resonance imaging (fMRI), showing frontal and parietal activations during perceptual switches, seems to support this view, it is unclear whether these activations indeed reflect a top-down process of perceptual reorganisation or rather a bottom-up process signalling the salience of perceived switches. We sought to characterise the functional roles of different regions showing switch-related activations by investigating the temporal relationships between responses to spontaneous and those to externally generated perceptual switches. Twelve subjects participated in an fMRI experiment at 3T during which they viewed a bistable apparent-motion stimulus and indicated spontaneous direction reversals by key presses. In a control condition, the subjects' sequence of perceptual switches during bistability was replayed, for which a disambiguated version of the stimulus was used. Event-related responses to both spontaneous and stimulus-driven perceptual switches were observed in hMT+/V5 bilaterally, and in several frontal and parietal regions, including right inferior parietal and bilateral inferior frontal cortices. Greater activations during spontaneous, compared to stimulus-driven, switches occurred in right inferior frontal gyrus and left frontal opercular cortex. Detailed analyses of the event-related signal time-courses showed that response onsets to spontaneous, compared to stimulus-driven, switches in the right inferior frontal gyrus occurred on average 784 ± 200 ms earlier ($p < 0.002$), whereas such a difference was absent in other frontal and parietal regions and hMT+/V5 (condition-by-region interaction, $p < 0.003$). The temporal precedence of activations in the right inferior frontal gyrus indicates this region's involvement in a higher-order process initiating spontaneous switches in perception during constant physical stimulation.

[Supported by Volkswagen-Stiftung and Deutsche Forschungsgemeinschaft.]

Friday

◆ **Cortical adaptation of unconscious perceptual representations**

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We investigated how the cortical representation of a stimulus is altered by conscious experience. To this end, we used object substitution masking to manipulate conscious awareness, in conjunction with an fMRI-adaptation paradigm to evaluate how the internal representation of the stimulus is altered. In each trial of the experiment, the adapting stimulus was a notched diamond with the top, bottom, left, or right corner removed. This stimulus was presented randomly to one of four spatial locations, introducing the spatial ambiguity considered necessary for object substitution masking. The adapting stimulus was then immediately masked by four dots surrounding the stimulus. Following the masked stimulus, a second notched diamond, either the same or different in orientation from the adapting stimulus, was presented to test for adaptation. The subject's task was to report the orientation of the notch for the adapting stimulus (ie the masked presentation), which was either consciously perceived by the observer or not, depending on whether masking was successful. Trials were later binned according to the correctness of the response for analysis of the functional imaging data. In separate functional imaging runs, we independently identified the four regions corresponding to the four stimulus locations in primary visual cortex (V1), and lateral occipital cortex (LO). In V1, the cortical responses for correct and incorrect trials did not differ significantly. The response in LO, however, was dependent on the subjects' conscious experience: trials on which subjects correctly reported the orientation of the notch evidenced attenuation of the hemodynamic response for repeated presentations, whereas incorrect trials did not. These results indicate that the cortical representation of a stimulus in LO is shaped by an observer's conscious experience, whereas the representation in V1 is not.

◆ **Emotional meaning affects awareness of faces**

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An important question in perception is how stimuli are selected for access to awareness. There is increasing evidence that selection is based on an interaction between low-level stimulus features (eg sudden onset) and high-level factors, such as the meaning and relevance of stimuli to the observer. In four experiments we investigated the impact of emotional meaning on detection and awareness of faces using the attentional-blink paradigm. The attentional blink refers to the phenomenon that detection of a visual target presented in a rapid stream of visual stimuli is impaired if it appears within about 400–700 ms after a first target, which observers have to identify. The results showed that faces presented in an attentional-blink task were detected more frequently when they displayed an expression of fear compared to the same faces displaying neutral or a happy expressions. Furthermore, the likelihood of detecting a face was directly related to the intensity of the expression of fear in the face; the more intense the expression, the better detection. Finally, we showed that manipulation of the emotional meaning, by means of fear conditioning, enhanced subsequent detection. Detection of neutral faces increased following association with an aversive loud noise, while detection of non-conditioned faces did not change. Our results extend previous reports of preferential detection of emotionally meaningful words or schematic objects, to more naturalistic stimuli, namely human faces. In addition, the results of the conditioning experiment indicate that fear conditioning is one way by which neutral stimuli can acquire the emotional significance that allows preferential access to awareness. The modulation of awareness through fear conditioning is in line with reports that the amygdala, a brain structure thought crucial for fear conditioning, is also involved in enhanced perception of emotionally significant stimuli.

◆ **Surround suppression explains crowding in normal observers and amblyopes**

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When viewed peripherally, targets 'crowded' by nearby distractors are hard to identify. This phenomenon has been explained by limitations of various high-level processes (eg attention resolution; feature-pooling between the target and its surround). Instead, we argue that the surround suppression observed physiologically in primary visual cortex can explain the crowding phenomenon. First, we use normal observers to show that surround suppression is remarkably similar to crowding: both phenomena are (i) strong only in the periphery; (ii) saturate quickly as a function of the surround contrast; (iii) are narrowly tuned to orientation and spatial frequency of the surround; and (iv) extend over a large region determined primarily by the target's eccentricity

rather than its scale. These results are based on contrast detection thresholds measured for a Gabor target surrounded by a sine-grating annulus. Next, we used amblyopic subjects to show that abnormal crowding and surround suppression observed in such subjects are strongly correlated. Unlike normal observers, some amblyopes experience crowding even when the target is positioned in the fovea. We measured contrast thresholds for letter identification and Gabor detection tasks for the same amblyopic observers. Our results demonstrate that the observers that showed foveal crowding showed a similar amount of (abnormal) foveal surround suppression. Conversely, observers without abnormal surround suppression had no crowding in the fovea. Our results strongly suggest that difficulty in target identification in the presence of nearby stimuli can be explained by a distortion (or loss) of small but crucial features of the target due to surround suppression.

[Supported by NEI EY06644 and NEI National Research Service Award.]

NATURAL SCENES AND VISUAL SEARCH

◆ Opponent channel responses to changes in the illuminant of natural scenes for primates and birds

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Evidence suggests that the red–green opponent system is optimised for the task of detecting fruit against a dappled background of leaves. One reason the red–green opponent (RG) system aids the detection of fruit is its relative insensitivity to shadows and other variations in the illuminant. This is because the peak sensitivities of the L and M cones are close together; where the light becomes redder or bluer, the response of the RG system tends to vary only a little in comparison with the blue–yellow opponent (BY) channel. Using time-lapse recording with an LMS calibrated camera and a spectrometer, we examined the opponent responses to a scene containing foliage and fruit from dawn until dusk. Opponent responses were computed for primates (human) and birds (starling) using the Macleod–Boynton RG and BY equations. The contrast between the fruit and the surrounding region was assessed with d' . As expected, responses of RG opponent channels were more stable than those of BY channels under varying illuminants, and d' scores were higher. Furthermore, primate RG responses were more reliable than bird responses; this was due to the fact that bird cones are not only more widely spaced but also because the action spectra of the L and M cones have a narrower bandwidth.

[This Research was supported by BBSRC (ref S11501) and EPSRC/Dstl (ref RG/S56405/01).]

◆ On the relationship between reaction times and discriminability in visual search

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Within the classical account provided by the feature-integration theory (Treisman and Gelade, 1980 *Cognitive Psychology* 12 97–136) the slope of the plots of the reaction times (RTs) as functions of set size indicates the underlying processing architecture, with positive and flat slopes corresponding to serial or parallel mechanisms, respectively. An alternative view, based on the signal detection theory (SDT), explains differences in search time vs set size in terms of discriminability (d') of the target relative to the distractors (Verghese, 2001 *Neuron* 31 523–535). We tested this hypothesis in a visual-search task for a Gabor patch tilted off-vertical among vertical distractors of varying number (0 to 15). The relationship between search times and discriminability was investigated by a technique in which fast binary response requiring classification of the direction of the target tilt (clockwise vs counterclockwise) was followed by precise classification of the perceived angle of the target. If RTs were a function of the stimulus discriminability (ie the stronger the internal evidence the faster the response) rather than of the serial/parallel nature of the search process, then plotting the perceived tilt vs set size would answer this question with high precision. Indeed, RTs increased steadily as a function of set size both when plotted, collapsing all the angles tested within each set size, and when we equated the physical d' (plotting only RTs for angles around or above threshold). However, equating the perceived rather than the physical tilt at different set sizes produced completely different functions that were virtually flat from set size 2 up to set size 16. This result provides support for the SDT interpretation of search times indicating that, once d' is balanced across conditions, the only change in search time indicates a switch between discrimination of a unique stimulus and the status of search with two or more stimuli.

Friday

◆ **A novel threshold: One for meaningful change**

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Discrimination thresholds for parameters such as orientation and spatial frequency are well established for the human visual system. However, under some task conditions, these thresholds are not the determining factor in performance. We wondered whether a higher-order threshold might exist, used by the visual system across tasks to indicate meaningful change in multi-element displays. Identical elements were combined to form either a Ternus display or a classic visual search array. Stimuli were either Gabor patches or minimum-luminance discs. In the latter case, size was manipulated; whilst in Gabor conditions carrier orientation, spatial frequency or contrast were varied. The Ternus displays always had a 0 ms inter-stimulus interval, and the element characteristics were varied systematically from frame to frame: small changes resulted in a percept of element motion, large changes in one of group motion, as previously reported (Scott-Samuel and Hess, 2001 *Perception* **30** 1179–1188). For search displays, the target was defined by differences in element characteristics with reference to the distractors; the transition point between efficient and inefficient search was noted, as determined by the gradients of the search slopes. For both Ternus and search displays, the magnitudes of orientation, spatial frequency, contrast, and size change at the transition point between the two percepts (either element and group motion, or inefficient and efficient search) were far larger than normal discrimination thresholds for these parameters (8 deg orientation difference; 20% spatial frequency change; 50% contrast change; 10% surface area change), implicating high-level processing. In the Ternus condition, subjects reported that change was visible long before it was sufficiently large to elicit a group-motion response. We propose that similar processing may underpin the analysis of both types of display, and that the measured thresholds reflect a higher-level distinction between meaningful and non-meaningful change.

[Supported in part by the Wellcome Trust.]

◆ **A fast heuristic algorithm for human visual search**

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Visual search for a known target is fast when the target has a unique feature, and slow when the target is defined by the absence of or conjunction of features (Treisman and Gelade, 1980 *Cognitive Psychology* **1** 97–136). Here, a fast heuristic search algorithm is described that mimics these aspects of visual search. The proposed visual search model consists of two components: parallel feature clustering and serial search. In feature clustering, the image is decomposed into local features, which are clustered hierarchically according to feature similarity and proximity. Each cluster has a ‘signature’ that lists all the features in the cluster. In the serial search stage, a specified target is given a signature of the list of features it possesses. Search proceeds by comparing cluster and target signatures. If the target could be contained in the cluster, its subclusters are examined; if not, the cluster is ignored and the next cluster examined. This visual-search procedure produces ‘parallel’ search when the target has a unique feature, and ‘serial’ search otherwise. It also predicts that serial search for an object having two features is twice as fast as serial search for an object missing a feature. The model also accounts for effects of spatial layout such as ‘feature contrast’ (Nothdurft, 1991 *Vision Research* **31** 1073–1078). Finally, the model uses the heuristic that each object maps to a cluster at some level. If this is violated, this algorithm will fail; and indeed humans also find this kind of search very difficult.

◆ **The red rectangle: A celestial example of the pyramid illusion?**

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The pyramid illusion (also called the Vasarely illusion) is a striking perceptual effect related to the Mach band, Chevreul, and Craik–O’Brien–Cornsweet effects. It has been incorporated into many op art paintings such as *Arcturus II* by Victor Vasarely. The effect can be produced by stacking concentric squares (or other geometrical figures such as rectangles or hexagons) of linearly increasing or decreasing size and lightness, one on top of another. We have constructed controllable Flash applets of this effect as part of the NSF supported “Project LITE: Light Inquiry Through Experiments”. They can be found in the vision section of the LITE web site at <http://lite.bu.edu>. Recently, the Hubble Space Telescope (HST) produced spectacular images of an astronomical object called the ‘Red Rectangle’. This is thought to be a binary star system undergoing recurrent mass loss episodes. The image-processed HST photographs display the same

characteristic diagonal lightness enhancements as those that are seen in the pyramid illusion. While some of the observed effect is probably photometric (due to limb brightening by the emissive nebula), psychophysical enhancement also seems to be involved in the visual impression conveyed by the HST images, much as Mach band effects have been reported in medical x-ray images. In this presentation, we examine to what extent the visual impressions of the Red Rectangle and other extended astronomical objects (including the Sun, Moon, and Saturn) are purely physical (photometric) in origin, and to what degree they are enhanced by psychophysical processes. To help assess the relative physical and psychophysical contributions to the perceived lightness effects, we have made use of a centre-surround (difference of Gaussians) filter we developed for MatLab. We conclude that lateral inhibition can contribute to the lightness features seen in astronomical objects like the Red Rectangle, though it may not be the only factor involved. [Project LITE is supported by US National Science Foundation Grant #DUE-0125992.]

◆ **Perception of natural images with exponential luminance frequency distributions**

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The luminance frequency distribution of many rural scenes can be approximated by an exponential function (Pinto, 2004, MPhil thesis, UMIST, Manchester, UK) but, in psychophysical experiments where luminance frequency distributions were manipulated, observers seem to prefer an exactly exponential dependence over the original approximately exponential dependence (Pinto et al, 2005 *Investigative Ophthalmology & Visual Science* **46** E-Abstract 4574). The purpose of this work was to investigate what properties of the scenes determine such preference. Images of rural scenes were obtained with a hyperspectral imaging system (Foster et al, 2004 *Visual Neuroscience* **21** 331–336) and, for each image, its luminance frequency distribution was computed and a set of images with exactly exponential distributions but with different coefficients was derived. The images resulting from these manipulations were displayed on a calibrated colour monitor. In each experimental trial, the observer had to express a preference between the original image and a version with an exactly exponential luminance frequency distribution. The pattern of responses was analysed and correlated with the luminance properties of the scenes. It was found that the degree of preference for an exact exponential function was stronger for distributions with intermediate widths and weaker for short- and long-tailed native luminance frequency distributions. These data suggest that the visual system may be optimised for exponential luminance distributions with specific decay parameters.

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BIOLOGICAL MOTION

◆ **Discrimination of biological motion in noise**

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Viewing a stimulus embedded in noise impoverishes the analysis of the stimulus. For a biological-motion stimulus in noise, Neri et al (1998 *Nature* **395** 894–896) reported two different behaviours for the detection and discrimination of the stimulus's walking direction. When subjects had to detect the stimulus, a linear relationship between the number of stimulus dots and the number of noise dots was observed. This behaviour could be assigned to the use of local motion signals. In contrast, when subjects had to discriminate the walking direction, a nonlinear relationship was reported. The reason for this remained speculative. We presented a biological-motion stimulus in noise, and varied in two tasks the amount of local motion signals in the stimulus. We asked human observers to discriminate the walking direction of the stimulus. We simulated the experiments with a form-based template-matching model. Previous results showed that behaviour of humans in discrimination tasks without noise can be explained by this model (Lange et al, 2004 *Perception* **33** Supplement, 100). The results of the model simulations replicated the results reported by Neri et al, independently of local motion signals. The behaviour of humans revealed the same results and confirmed the model predictions, as the results did not rely on local motion signals, either. Model simulations and psychophysical data showed that the results of the discrimination task reported by Neri et al are independent of local motion signals. We conclude that a template-matching process may be an adequate explanation for the results of this study and the results reported by Neri et al. We suggest two distinct processes for visual analysis of a stimulus in noise: one mechanism for detection and segregation of the stimulus from the background, which may benefit from local motion signals, and subsequently, an analysis of the walking direction of the stimulus, which can be explained by a template-matching process.

[Supported by Bundesministerium für Bildung und Forschung.]

◆ **Activation in superior temporal sulcus parallels a parameter inducing the percept of animacy**

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An essential, evolutionarily stable feature of brain function is the detection of animate entities, and one of the main cues to identify them is their movement. We developed a model of a simple interaction between two objects, in which we could control the percept of animacy by varying one parameter. The two disk-like objects moved along separate random trajectories but were also influenced by each other's positions, such that one object followed the other, in a parametrically controlled fashion. An increase of the correlation between the object's movements varied the amount of interactivity and animacy observers attributed to them. Control animations were only different from the experimental in terms of the interactivity level, but not in terms of object speed and separation. Twelve observers lying in a magnetic-resonance-imaging scanner had to rate the amount of interactivity and the overall speed of the objects in separate, subsequent tasks. Behavioural results showed a significant difference in interactivity ratings between experimental and control stimuli, but no difference in speed ratings, as expected. There was no response-time difference between the tasks. The fMRI data revealed that activation in the posterior superior temporal sulcus and gyrus (pSTS/pSTG) increased in relation to the degree of correlated motion between the two objects. This activation increase was not different when subjects performed an explicit or implicit task while observing these interacting objects. These data suggest that the pSTS and pSTG play a role in the automatic identification of animate entities, by responding directly to an objective movement characteristic inducing the percept of animacy, such as the amount of interactivity between two moving objects. These findings are consistent with literature showing that, in monkey and human, pSTS and pSTG respond to stimuli displaying biological motion.

[Supported by the Wellcome Trust.]

◆ **Biological motion activates the STS in a retinotopic manner**

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The human visual system is equipped with highly sensitive mechanisms for recognising biological motion. A putative functional role of biological-motion perception is to register biological movements anywhere within the visual field. However, in previous imaging studies of biological motion only the neuronal network for centrally presented stimuli was investigated. In the present study, we investigated activations in the neuronal network for biological-motion recognition with peripheral stimulation. In an event-related fMRI experiment, subjects discriminated the orientation of point-light walkers at -20 deg, 0 deg, and $+20$ deg eccentricity. They were instructed to fixate a central fixation dot at 0 deg during the experiment. Eye movements were controlled by an eye-tracker system. We found that subjects discriminated the walker's orientation well, both centrally and peripherally. Central and peripheral walkers activated similar brain areas. The right posterior superior temporal sulcus (pSTS) was activated. Compared against baseline, the location of right pSTS activity depended on the retinal location of the walker. In detail, the peak activation shifted systematically with the walker's retinal location. We suggest that not only human low-level visual areas, but also the high-level area STS are organised in a retinotopic manner.

◆ **Throwing like a man: Recognising gender from emotional actions**

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One aspect of the kinematic-specification-of-dynamics hypothesis is that, since active movements provide greater amplitude of joint kinematics, it is easier to decode active movements into the underlying dynamic and person properties. To explore this hypothesis, we investigated the recognition of gender from throwing movements done in angry, happy, neutral, and sad styles. Throwing movements were recorded from twenty-nine actors (fourteen male) who were asked to perform throws in these different affective styles. A subsequent analysis of kinematics revealed that the ordering of average wrist-velocities of the movements were angry, happy, neutral, and sad, in descending order. Thus, it was predicted that recognition of gender would be best for angry movements. Point-light displays of six points on the arm were constructed and shown to naive observers who were asked to recognise the gender and provide a confidence rating for each display. Results showed that, consistent with the prediction, both proportion correct and confidence ratings were highest for angry throws. Closer examination of the proportion correct, however, revealed a substantial trend in the participants' responses to judge angry movements as male and sad movements as female. One possible explanation that is consistent with a kinematic analysis of the throwing data is that there is a trend to identify fast movements as male. However, other explanations exist and we are currently examining the possible interplay between perceptual and social biases in the recognition of gender from point-light displays.

[Supported by EPSRC.]

◆ **Effects of spatial attention on perception of a point-light walker superimposed by 3-D scrambled walker mask**

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Our perception of a point-light walker is effectively interrupted by a 'scrambled walker mask'. This mask consists of position-scrambled dots that mimic the motion corresponding to the walker's joints (Cutting et al, 1988 *Perception & Psychophysics* **44** 339–347). In this study, we added binocular disparity to the mask and walker to investigate whether the segregation in depth between the two facilitated the perception of the walker. Three spatial relations between the walker and mask were adopted: the walker moved in front of the mask, the walker moved at the back of the mask, and both moved in the same depth plane. The performance in the last condition was set as the baseline. As a result, the performance improved dramatically when the walker was in front of the mask, whereas it remained at the same low level as the baseline when the walker was at

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the back of the mask. In the next experiment, when a prior guide to indicate the depth location of the walker by sound was given to the observers, the performance improved even when the walker was at the back of the mask. These tendencies were specific to the perception of biological motion because they were not confirmed in the control experiment in which translational motion was used. The binocular disparity thus facilitated observers' performance regardless of the two spatial relations or the prior guide. The scrambled walker mask does not hold the global configuration of the walker, but still contains the local motion of each joint of the walker. Therefore, these results suggest that the local motion in front of the mask captures observers' attention in a default manner, and it makes it difficult to segregate the walker and the mask by binocular disparity. This implies that the local motion is the strong attractive factor in perceiving the biological motion.

◆ **Mid-level motion features for the recognition of biological movements**

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Recognition of biological motion probably needs the integration of form and motion information. For recognition and categorisation of complex static shapes, recognition performance can be significantly increased by optimisation of the extracted mid-level form features. Several algorithms for the learning of optimised mid-level features from image data have been proposed. It seems likely that the visual recognition of complex movements is also based on optimised features. Exploiting a new physiologically inspired algorithm and classical unsupervised learning methods, we have tried to determine mid-level motion features that are maximally useful for the recognition of body movements from image sequences. We optimised mid-level neural detectors in a hierarchical model for the recognition of human actions (Giese and Poggio, 2003 *Nature Reviews Neuroscience* **4** 179–192) by unsupervised learning. Learning is based on a memory trace learning rule: Each detector is associated with a memory variable that increases when the detector is activated during correct classifications, and that decreases otherwise. Detectors whose memory variable falls below a critical threshold 'die', and are eliminated from the model. In addition, we tested a classical principal-components approach. The model is trained with movies showing different human actions, from which optic flow fields are computed. The tested learning algorithms extract mid-level motion features that lead to a substantial improvement of the recognition performance. For the special case of walking, many of the extracted motion features are characterised by horizontal opponent motion. This result is consistent with psychophysical data showing that opponent horizontal motion is a dominant mid-level feature that accounts for high recognition rates, even for strongly impoverished stimuli (Casile and Giese, 2005 *Journal of Vision* **5** 348–360). As for the categorisation of static shapes, recognition performance for human actions is improved by choosing optimised mid-level features. The learned features might predict receptive field properties of complex motion-selective neurons (eg in area KO/V3B).

[Supported by the DFG, HFSP and the Volkswagen Foundation. CBCL is supported by NIH, Office of Naval Research, DARPA and National Science Foundation.]

◆ **How fast brain object categorisation allows top – down processes of segmentation**

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Biological motion recognition refers to our ability to recognise a scene (motion or movement) based on the evolution of a limited number of tokens. Much work has been done in this direction showing how it is possible to recognise actions based on these points. Following the work of Giese and Poggio (2003 *Nature Reviews Neuroscience* **4** 179–192) and using some recent results of Thorpe and Fabre-Thorpe (2001 *Science* **291** 260–263) we have proposed an alternative approach based on the fact that neural information is, in the fast brain, coded by the relative order in which these neurons fire. The result of these simulations is that information from early visual processes appears to be sufficient to classify biological motion. In the next step, we explored whether this fast brain labelling mechanism can be used as a feedback input to help segmenting motion, considering the simple fact that the classification process is not only able to give a label but also to evaluate, for each token, whether its contribution to the labelling has been positive (inlier) or negative (outlier). One way to implement this mechanism is to simply inhibit the contribution of each token and evaluate whether this transient deletion improves

or impairs the quality of the labelling level, which is output by the SVM-like classifier. As a local feedback, this loop acts as an oscillation mechanism which stabilises at a local optimum. This inlier/outlier segmentation may help segmenting the object with respect to the background. The biological plausibility of the present model is based on the proposed Hebbian implementation of a statistical learning algorithm related to SVM and based on the Thorpe and Delorme neuronal models. It is shown that the top-down feedback is easily implemented as an interaction between the classification map (as observed in IT) and earlier cortical maps, taking into account the way feedbacks act in the brain.

CLINICAL VISION

◆ Glare sensitivity in myopic and emmetropic subjects as assessed by facial EMG

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In a previous study we have shown that myopic subjects generally exhibit longer glare recovery time than the emmetropes (Kurtev and Given, 2004 *Perception* 33 Supplement, 128). To extend the comparison, objective measurements were made of glare sensitivity. EMG was recorded from facial muscles (mostly orbicularis oculi) while presenting a glare-inducing stimulus in a simple identification task following the procedure outlined by Murray et al (1998, Transport Research Laboratory Project Report N13740). Although the procedure as described was used for objectively measuring discomfort glare, using low level of glare and analysing the initial response makes it suitable for studying glare sensitivity as well. Two different glare conditions were used in order to be able to assess the contribution of the startle response and the effect of glare level and pattern of presentation. The experiments were conducted at a low photopic/high mesopic level of luminance. For the recordings and stimulus presentation, use was made of the Biopac system with EMG and SuperLab modules. The results showed that myopes have different EMG response to glare as compared to emmetropes. The difference seems to affect more the overall pattern and frequency spectrum than the latency and magnitude of the response. The differences, however, were not as pronounced as with glare recovery time obtained under similar stimulation parameters. The data further suggest that the differences in visual performance in myopic and emmetropic subjects depend not only on physical but on physiological factors as well.

◆ A test of bipolarity hypothesis underlying colour harmony principle: From the evidence on harmony production and estimation correspondence and individual difference

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Recent studies on information processing of perception and affection (or Kansei) suggest that the stages of processing for negative (unpleasant or ugly) and positive (pleasant or beautiful) affections should differ (Hakoda et al, 2001, IEICE Technical Report HCS2000-50, pp 31–37; Kawabata and Zeki, 2004 *Journal of Neurophysiology* 91 1699–1705). On the other hand, studies on colour harmony are not necessarily concerned with stages of processing in Kansei, but just assume the bipolarity of affection: a continuum from harmony to disharmony with a neutral or zero category. The present study was designed to test this simple bipolarity hypothesis by making clear the relationship between harmony and disharmony of colour combination, and to infer the stages of harmonious/disharmonious information processings, noticing the degree of individual difference in producing and estimating harmony on colour combinations. In experiment 1, four colour combinations arranged in square-shape to be used as test patterns for harmony estimation (experiment 2) were produced by forty-two graduate and undergraduate students, following three degrees of harmony: high (harmonious), medium (neutral), and low (disharmonious), by using colour cards based on the Japanese Color Research Institute colour system (called PCCS). In experiment 2, harmony estimations (harmony, neutral, or disharmony) for the test patterns were made by thirty-four graduate and undergraduate students. How much the production and estimation corresponded was measured for each test pattern. It was found that these correspondences significantly differed depending on the degree of harmony: disharmonious colour combinations were much more consistently produced and estimated than neutral and harmonious colour combinations. This implies that there are smaller individual differences for disharmonious colour combinations than for harmonious ones, suggesting that the principles of colour harmony and disharmony should be derived from different stages of information processing of affection.

Tuesday

◆ **Visuo-spatial recognition in Williams syndrome: Dissociative performance in non-motor tasks?**

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Williams syndrome (WS) is a rare neurodevelopmental disorder (1:20 000), caused by a submicroscopic deletion in the band q11.22-23 of chromosome 7. The WS patients have a unique cognitive phenotype (Bellugi et al, 2001 *Clinical Neuroscience Research* **I** 217–229), classified as mildly to moderately retarded (mean IQ is 55, with a range rarely reaching above 50) associated with generalised difficulties in general problem solving, arithmetic, and typically unable to achieve fully independent living. They also present an unusual socio-emotional and personality attributes, characterised by an excessive sociability. Despite their low IQs, individuals with WS display characteristic patterns of cognitive performance with peaks and valleys of abilities. Specially striking is a well-documented dissociation between relatively spared linguistic abilities and severely impaired visuo-spatial cognition, which is disproportionately impaired (particularly at the level of global organisation). However, there are incongruities within spatial cognition, where WS subjects display preserved areas, with face-processing abilities being a remarkably strong area of performance (Farran et al, 2001 *Journal of Child Psychology and Psychiatry* **42** 719–728). Using two spatial perception recognition tasks (Benton's line orientation test and Benton's test of facial recognition), nonverbal, and both requiring processing pictures (different stimuli—lines and faces), but without involving visuo-constructive abilities, we studied the performance of Williams syndrome subjects. In order to do this, we evaluated a Williams syndrome group ($N = 8$) in these specific non-motor perceptual tasks to study the referred high performance of individuals with WS on face-processing tasks, despite their severe impairment on the other visually based cognitive tasks.

◆ **Substantial loss of chromatic contrast sensitivity in subjects with age-related macular degeneration**

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In subjects with normal vision, chromatic contrast sensitivity continues to increase as spatial frequency decreases. When contrast is expressed in terms of combined cone contrast, red–green chromatic sensitivity at a low spatial frequency of, for example, $0.4 \text{ cycle deg}^{-1}$ is higher than luminance contrast sensitivity by a factor between 6 and 10, depending on age (and increasing for still lower frequencies). In the yellow–blue direction, the factor is between 1 and 3. This means that for low spatial frequencies one needs far less modulation of the cones in order to reach a certain chromatic threshold than to detect an equally small achromatic difference. Small differences in colour therefore represent an effective cue for detection and discrimination of objects in normal vision. However, in the case of visually impaired subjects with age-related macular degeneration (AMD) the situation is different. We have addressed this issue as part of a larger study of visual function and AMD. For a selected group of twelve elderly subjects with AMD (mean age 75 years) and no other diseases affecting vision, we have compared achromatic and isoluminant chromatic contrast sensitivities as a function of spatial frequency of sinusoidal gratings. Variability was large between subjects, but, in the AMD group, sensitivity to achromatic contrast was generally less severely affected at low than at high spatial frequencies. Relative to an age-matched control group, the group-average achromatic sensitivity at $0.4 \text{ cycle deg}^{-1}$ was one-third of the normal value. Sensitivity to red–green and yellow–blue contrasts of the same spatial frequency was on average only about one-tenth of the normal age-matched sensitivity. This implies a more dramatic loss of chromatic than of achromatic vision at low spatial frequencies in AMD.

[Supported by the Norwegian Association of the Blind and Partially Sighted. Thonning Owsen's Foundation.]

◆ **Impairments of colour contrast sensitivity thresholds in cases of damage of chiasma opticum**

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The purpose of our study was to estimate how the narrowing of outer visual field sectors affects colour contrast sensitivity. Correlation was made between colour contrast sensitivity thresholds

and narrowing of the visual field of each eye of 24 patients with pituitary adenomas and 186 healthy controls. The mean age of the subjects was 35.1 years and all had normal visual acuity. The visual field was tested by Goldman's perimeter; the computerised colour contrast test was used. The subjects were shown a computer-generated stimulus, consisting of a line surrounded by grey background. The line colour saturation was then varied by increasing or decreasing its red, green, or blue phosphor luminance starting from the initial grey of the background. Simultaneously, the orientation of the line was randomly varied between horizontal and vertical. The subjects were then asked to judge the orientation of the line. The threshold was established when the observer was no longer able to accurately detect the orientation of the line, and it was defined in terms of distance between colour of the line and the background in the L^* , a^* , b^* system of coordinates (CIE 1976). The mean contrast sensitivity of the right eye was 2.1 (95% CI 1.7–2.5) and of the left eye 2.5 (95% CI 1.6–3.4). The mean contrast sensitivity of the right eye of the controls was 1.7 (95% CI 1.6–1.7). The difference between the means of colour thresholds of the patients and controls was significant (for the right eye $t = 4.3$, $p < 0.001$; for the left eye $t = 4.5$, $p < 0.001$). We found no strong correlation between the narrowing of the visual field and colour contrast sensitivity in patients with damage of chiasma opticum (for the right eye $r = 0.44$, $p = 0.03$; for the left eye $r = 0.46$, $p < 0.025$).

[We need financial support.]

◆ **Topographical characteristics of contrast sensitivity of subjects with physiological myopia**
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In previous study, evidence was provided that subjects with physiological myopia display lower contrast sensitivity to positive and negative contrast when stimulation is performed in the central fovea. The purpose of the present study was to investigate the same characteristics of the vision, but of the larger part of the central retina for a zone of 10 deg along the horizontal meridian. The study included four subjects: two emmetropes, one myopic subject with spherical equivalent of myopia 2.5 D, and one with spherical equivalent of myopia 5.5 D. The monocular contrast thresholds for positive and negative contrast were measured at photopic (100 cd m^{-2}) and mesopic (2 cd m^{-2}) conditions at 1, 2, 3, 4, and 5 deg left and right of the central fovea. Thresholds were determined through a change of the letter contrast by applying the staircase procedure and a visual stimulus generator (Cambridge Research Systems). The results show that myopic subjects have a smaller area with relatively high contrast sensitivity than emmetropes and the tendency of space reduction is equal to the spherical equivalent of myopia.

◆ **The effects of ageing and Parkinson's disease on visuospatial attention: Sex and modality differences**

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Cognitive and perceptual abilities tend to decline with age as a result of cerebral changes, but there is increasing evidence that the decline is not uniform with respect to sex, brain function, or region. Here, we report results from a new task battery designed to delineate the effects of ageing and disease on visuospatial attention. The battery includes: simple and choice reaction-time tasks (SRT and CRT) requiring motor responses to simple visual stimuli distinguished by colour, form, or motion; and cued and non-cued visuospatial attention tasks requiring detection of colour changes only (CCD) or tracking of multiple objects distinguished by motion and location only (MOT). In a pilot study, we tested three groups: young healthy controls [YC; age 23.80 (± 1.82) years; $N = 15$]; aged healthy controls [AC; age 77.85 (± 5.54) years; $N = 13$]; and Parkinson's disease outpatients [PD; age 76.69 (± 5.57) years; $N = 13$]. Numbers of males and females were near-equal in each group. Our findings are as follows: (i) reaction times (RTs) decline with age for all tasks, but the decline is greater for motion-related tasks than for colour-related or form-related tasks. (ii) Accuracy also tends to decline with age, and declines most severely for the most difficult colour changes, the highest-attentional-load tasks, and the tasks requiring endogenous shifts of attention. (iii) Young males tend to outperform young females, but male performance tends to decline more severely with age and disease than female performance. (iv) On almost all tasks the PD group performs no worse than the AC group; the exceptions are the SRT and CCD tasks, and for these PD performance is significantly worse only for the males. We conclude that low-level as well as high-level visual cortical functions are differentially affected by age and disease in males and females.

Tuesday

◆ **Test variability in glaucomatous visual fields tested with high-resolution perimetry**

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High-resolution perimetry (HRP) is a computer-based diagnostic technique that allows a detailed assessment of the detection of suprathreshold stimuli in the central visual field of ± 20 deg vertical and ± 27.0 deg horizontal eccentricity. The purpose of this study was to evaluate the test variability in glaucomatous visual fields measured by HRP. Five patients (five eyes) with primary open-angle glaucoma who were well controlled on medical therapy were studied. The stage of the glaucoma varied from incipient to advanced. Visual field was assessed six times within a six-week period. We described and analysed the concordance between the variability indices, the number of detected stimuli, fixation rate, false positive responses, and reaction time by the non-parametric statistical Friedman test. Intraindividual variability was $>10\%$ in two patients for the number of detected stimuli, in three patients for the fixation rate, and in all patients for the false positive responses. However, group comparisons revealed no significant changes of repeated HRP examinations regarding the number of detected stimuli ($\chi^2 = 3.506$, $p = 0.657$), the fixation rate ($\chi^2 = 1.296$, $p = 0.948$), and the false positive responses ($\chi^2 = 5.497$, $p = 0.375$). The mean reaction time decreased systematically, on average 38 s over the six measurements ($\chi^2 = 14.885$, $p = 0.03$). We conclude that HRP is a useful tool for measuring the glaucomatous visual field. Because of the test-to-test variability within individuals, repetitive examinations are necessary for a stable baseline. The decreased reaction time refers to possible learning effects in HRP. To compare the relationship between the variability indices of healthy subjects and glaucoma patients, normal values will be collected.

◆ **Motion processing in dyslexia and Asperger syndrome: an fMRI study**

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Deficits in motion processing but not form processing have been reported in dyslexia. Deficits in both motion and form processing have been reported in autism, but the data are less equivocal for Asperger syndrome. To investigate the neural bases of these visual deficits we conducted an event-related fMRI study of form and motion processing on a group of adults with dyslexia, a group with Asperger syndrome, and a control group. The purpose of this study was to identify the loci of deficits in spatial integration and motion integration with the use of form-coherence and motion-coherence detection tasks. The stimuli consisted of Glass patterns comprising dot triplets separated by a rotational transformation in space to generate a static form-coherence pattern, or dots rotated over time to generate a coherent motion display. Fixed levels of stimulus coherence were used from 0.0 (all dot transformations in a random direction) to 1.0 (all dot transformations in the coherent direction). The Glass pattern was embedded in a field of random dots and a participant's task was to identify its location to either the left or right of the central fixation point. The order of events was permuted in a pseudo-random fashion. A number of areas have previously been identified as responding to motion coherence and to form coherence (Braddick et al, 2000 *Current Biology* 10 731–734), and these were used as the basis for a region-of-interest analysis. The BOLD response to form coherence did not differ significantly between experimental groups. The BOLD response to motion coherence was nonlinear in V5 for the dyslexia group, compared to the linear relationship for the Asperger syndrome and control groups.

◆ **Deficits of visual information processing in schizophrenic patients and their healthy relatives**

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Schizophrenic patients show strong deficits not only in cognitive and mental functions but also in visual information processing. Strong visual deficits occur with visual backward masking tasks. We presented a Vernier target that was followed by a grating mask. We determined the SOA between the Vernier and the grating onset for schizophrenic patients, their healthy first-order relatives, and a healthy control group. Schizophrenic patients were diagnosed by DSM IV. Different neuropsychological tests were assessed to determine verbal and non-verbal intelligence, working memory, learning capacity, and sustained attention (PS3, CVLT, WCST, CPT). Schizophrenic

patients need SOAs about three times longer than healthy controls to reach a predefined criterion level. Neuropsychological testing shows clear deficits compared to the healthy controls. Surprisingly, also the healthy relatives show significantly longer SOAs than the controls (but better performance compared to the schizophrenic patients). However, the neuropsychological scores of the relatives are comparable to the controls. It seems that deteriorated performance in visual backward masking reveals an innate vulnerability to suffer from schizophrenia rather than being an expression of the illness itself. Hence, in the relatives there must be altered circuits in the brain accounting for deteriorated processing. Therefore, studies on healthy relatives of schizophrenic patients allow one to study prolonged processing without the effects of the illness itself or a corresponding drug treatment.

[Supported by the Volkswagen Foundation and by the NATO Science Program.]

◆ **Colour determination changes due to damage of chiasma opticum**

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The purpose of the work was to characterise the dichromatopsia in persons with bitemporal visual field defects, and to determine colour discrimination defect and its relation to the right or left temporal narrowing of visual fields in chiasma-opticum-damaged persons. Computerised Farnsworth–Munsell 100 Hue test and Goldman perimeter were used. Both eyes were tested separately. Colour determination error scores were analysed in twenty-four persons with damage of chiasma opticum and temporal visual field defects as well as in one hundred and eighty-six controls. All of the statistics were calculated by using total and selective error scores in colour determination and narrowing in degrees of the visual field. Colour determination error score in chiasma-opticum-damaged persons was for the right eye 142 (95% CI 106–179) and for the left eye 143 (95% CI 107–180). The mean of temporal narrowing of the visual field was for the right eye 27.1 deg (95% CI 11–43.1) and for the left eye 30.4 deg (95% CI 13.5–47.4). The visual field of healthy persons was normal for the right and left eye and colour determination error score was for the right eye 84 (95% CI 80–88) and for the left eye 86 (95% CI 81–91). The colour determination scoring averages differed significantly between the groups of healthy persons and patients with damaged chiasma opticum (for the right eye $t = 6.8$, $p < 0.001$; for the left eye $t = 6.2$, $p < 0.001$). The correlation coefficient between temporal narrowing of visual fields in chiasma-damaged persons and colour-discrimination score was for the right eye $r = 0.55$, $p = 0.006$, and for the left eye $r = 0.57$, $p = 0.004$.

◆ **Pattern pulse versus frequency doubling illusion: Sensitivities and specificities in optic neuritis patients**

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We compared the diagnostic capabilities of pattern pulse (PP) and frequency doubling (FD) illusion-based multifocal visual evoked potentials (VEPs) in normal subjects, and multiple sclerosis (MS), and optic neuritis (ON) patients. Twenty-seven normal subjects and fifty MS patients, twenty-six of whom had experienced optic neuritis (ON+), participated in our study. The patient groups were matched for length of disease and number of clinical attacks. All subjects had refraction corrected to 6/9 or better. The recordings were obtained dichoptically stimulating 8 regions per eye. Contrast threshold testing was performed by a FD technology perimeter, consisting of low-spatial-frequency ($0.25 \text{ cycle deg}^{-1}$) sinusoidal gratings that underwent rapid (25 Hz) counterphase flicker. The FD stimulus was presented at 95% contrast to each location. PP VEPs were recorded to the pattern pulses (the small chequerboards being presented transiently but infrequently against a neutral grey background) of one video frame at 1.3 presentations s^{-1} . Compared to the responses of normal subjects, those of MS patients had significantly smaller response amplitudes, lower signal-to-noise ratios, more complex response waveforms, and longer response delays. To estimate sensitivities and specificities for the different stimulus types, we used the receiver-operator-characteristic plots (ROCs). Bootstrap estimates of the accuracies of the ROCs for the PP VEPs template delays indicated 92% sensitivity at a false positive rate of 0% in ON+ patients. The results were similar for patients with no history of ON. The accuracy of the classification model based upon the FD VEPs was poor in ON+ patients: the model performed at a specificity of 62% for a sensitivity of 63%. This finding suggests that PP VEPs have better diagnostic capabilities than FD VEPs.

Tuesday

◆ **Weak contextual suppression can make people with schizophrenia more accurate at contrast discrimination**

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Context is central to several theories of the diverse cognitive deficits associated with schizophrenia. For example, Phillips and Silverstein (2004 *Behavioral and Brain Sciences* **26** 65–82) argue that people with schizophrenia fail to disambiguate information using context because of hypoactivity in NMDA glutamate receptor channels. Here, we consider how poor contextual processing affects vision in schizophrenia. A common form of contextual interaction in visual cortex is centre-surround inhibition which serves as a form of local contrast-gain control and explains illusions such as a contrast-contrast [where texture appears of lower contrast in the presence of a high-contrast surround, than in isolation (Chubb et al, 1989 *Proceedings of the National Academy of Sciences of the USA* **86** 9631–9635)]. We asked if reduced contextual suppression might make schizophrenics less prone to contrast-contrast. We used a temporal 2AFC contrast discrimination task, presenting a reference texture-patch (fixed 40% contrast) that either was or was not surrounded by a high contrast (95%) surround, followed by an isolated patch of variable contrast. We collected psychometric functions in both surround and no-surround conditions for fifteen chronic schizophrenics, thirteen non-schizophrenic clinical controls (with a range of diagnoses including bipolar disorder), and twenty non-clinical controls. We report that schizophrenic observers are consistently less prone to the illusion than controls; 12/15 were more accurate in the surround condition than the most accurate control subject. This finding represents a rare instance of schizophrenic observers being less error-prone than controls at a behavioural task, and therefore cannot be attributed to a general cognitive deficit. That our results arise from a 'low-level' visual task suggests that weak cortical suppression from context may be a general feature of schizophrenia.

[Supported by BBSRC.]

◆ **Form and motion processing in dyslexia and Asperger syndrome**

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There is a large body of research on visual perception deficits in both people with dyslexia and Asperger's disorder. However, to date no study has ever compared sensitivity to global form and motion between these two populations. In this experiment, we measured form-coherence and motion-coherence detection thresholds for a group of adults with dyslexia, a group of adults with Asperger syndrome, and a matched control group. A coherent visual patch was depicted by dots separated by a rotational transformation in space (form coherence) or space-time (motion coherence). Stimuli were presented for 0.25 s to prevent serial-search strategies. Coherence was progressively reduced from 1.0 until an error was made, in the manner of a 2-up, 1-down staircase, with thresholds calculated as the mean of six reversals, ignoring two initial reversals. We report that adults with dyslexia do not show a deficit in visual motion, contradicting previous findings (Hansen et al, 2001 *NeuroReport* **12** 1527–1530). Results also show that adults with Asperger syndrome perform at the same level as dyslexics and controls in motion processing, replicating our previous studies with children. However, it is found for the first time that people with Asperger syndrome show lower form-coherence thresholds, which may go some way to explain their superior performance in certain visuospatial tasks. The results of the study are discussed with respect to the involvement of the M/dorsal and P/ventral pathways in developmental disorders.

COGNITION

◆ **Influence of monetary incentive on performance in a selective-attention flanker-interference task**

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In the human performance literature there has been a great deal of interest in the effect of anxiety and arousal on visual attention (eg see Janelle, 2002 *Journal of Sports Sciences* **20** 237–251). Often such experiments have focused on complex tasks such as driving simulation, sport-specific skills, and dual-task situations, sometimes with seemingly conflicting results. In this experiment, we test the effect of anxiety or arousal, as manipulated by a monetary incentive, in a simple selective-attention flanker-interference task. Participants responded to a central target (X or Z) while ignoring an irrelevant flanking distractor item that could be compatible or incompatible with the target response. Perceptual load on the central target task, as well as distance of the distractor item from the target, were manipulated. Reaction times (RTs) in compatible

target–distractor conditions were subtracted from incompatible target–distractor conditions to produce interference RT scores. There was no main effect of incentive condition on the interference RTs, although interference effects for error rates were generally lower in the high-incentive condition. Most interestingly, results suggest an interaction between incentive condition and perceptual load for the interference RT measure; the expected effect of perceptual load on distractor interference was seen in the low-incentive condition but not in the high-incentive condition. Results are discussed in terms of the effect of anxiety/arousal on spatial attention by mechanisms of perceptual capacity and cognitive control (eg Lavie, 2004 *Journal of Experimental Psychology: General* **133** 339–354).

◆ **Visual inference of categories of two dimensions with use of sequential sampling**

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Categorical inference tasks could be performed by using many procedures. In this study, we used a sequential sampling procedure in which participants observe, or sample, some instances of the category one by one until their samplings are sufficient to determine the category. Using this procedure, we investigated properties of the visual inference of 2-D categories. The two dimensions meant that categories were determined by two quantitative attributes (eg luminance, height, or width), not by qualitative ones. We focused on the performances in three tasks: 2-D object task, 2-D face task, and 2-D pair task. In all tasks, the stimulus consisted of a pair of objects: an elliptic disk and a triangle. In 2-D object task, the ellipse and triangle constituted a projected image of one object (a cone). In 2-D face task, they constituted a configurative pair of a face (a mouth and nose). In 2-D pair task, they constituted a separated pair. In experiments, both the luminance (or width) of the elliptic disk (L) and height of the triangle (H) were category cues. We prepared two sets of category stimuli drawn from two Gaussian distributions:

$$N(L_1, H_1; \sigma_L^2, \sigma_H^2) \quad \text{and} \quad N(L_2, H_2; \sigma_L^2, \sigma_H^2),$$

where $L_1 < L_2$ and $H_1 > H_2$. The former distribution corresponded to the target category. For example, in the 2-D object task, the target category consisted of cones with larger height and darker (or narrower) base. A pair of instances continued to be presented simultaneously until participants terminated their sampling. We found that the number of samplings had a tendency of being smaller both in the 2-D object and 2-D face tasks than in the 2-D pair task when using the two dimensions of width and height, which indicated that objects and configurative figures contribute to more efficient samplings of their constituents in category inference.

◆ **Coherent-motion-onset event-related potentials in dyslexia**

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One of the theories of dyslexia suggests that dyslexics suffer from deficits in the magnocellular system. To assess this theory, we examined eighteen dyslexics (adolescents and young adults) and twenty-two controls with visual event-related and evoked potentials. The experiment was an oddball task, in which infrequent target stimuli were presented randomly among frequent standard stimuli. The frequent stimuli were alternating sequences of random-dot motion and coherent rotation. 20% of the rotation sequences were randomly replaced by target sequences in which the dots were in coherent expanding motion. The subjects had to press a button when seeing a target. Recordings were made at two different levels of coherence: 100% and 60%. With common average reference, the most prominent feature in the responses to coherent rotation onset was a long-lasting (~150–~900 ms) occipito-parietal positivity. The amplitude of this positivity was much larger at 100% than at 60% coherence. A similar positivity was also present in the global-field-power waveform. In addition, there was a negative–positive–negative series of waves between 180 and 300 ms at the occipito-parieto-temporal region. There were only minor differences between dyslexics and controls in these responses. However, there was a significant group difference in the responses to target stimuli. The parietal positivity at about 600 ms (corresponding to the visual P300 response) was much larger in controls than in dyslexics at both levels of coherence. Equal averaged responses to coherent-motion onset suggest that the average neural signals in dyslexics and controls are equal. The significant amplitude difference in responses related to cognitive decisionmaking suggests that the input to the decision process has more noise in dyslexics than in controls. Thus, the magnocellular deficit in dyslexia may be due to increased amount of neural noise in the motion-detection system.

Tuesday

◆ **The role of spatial contiguity in perception of causality**

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Adults see causality in schematic events: if square A moves towards B, which moves immediately upon contact, they report that A launches B—physical causality; but if B moves before contact, so that both move simultaneously for some time, observers report that B tries to escape from A—social/psychological causality. In two experiments, we examined how the spatial and temporal configurations of events affect these causality illusions. In study 1 we varied: (i) size of the gap between A's final and B's initial location, (ii) which object moved first, and (iii) whether objects moved contiguously or simultaneously. Twenty-three observers rated degree of physical and psychological causality for 5 replications of the $7 \times 2 \times 2$ within-subjects factorial design. A-first contiguous motion received high physical and low psychological ratings. The reverse appeared for the other three events. Gap size affected only A-first contiguous motion: physical ratings decreased with it, but psychological ratings increased. Overall, causal impressions depended on event type and spatial contiguity. Event-type effects, however, could be spatial contiguity effects in disguise: identical gaps between trajectories produce different gaps at the point when the second object starts to move for different temporal configurations. For instance, in A-first contiguous motion the objects come closer than in simultaneous motion where B moves away before A reaches it. Thus lower physical ratings for the latter may be due to larger gaps at the point of closest approach. Accordingly, in study 2 (unfinished), event configurations were equated on the gap present as the second object started to move. Results show clearly that ratings for all event types depend on gap size, but that event type has independent effects. Taken together, these findings help clarify the role of spatial contiguity in perceptual causality: it contributes to the distinction between physical and psychological causality, but is not its only determinant. [Supported by ESRC project grant RES-000-23-0198.]

◆ **Visual perception of physiognomic properties and meanings in relation to stress or comfort states**

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Shapes and colours can convey meanings that are more or less easily grasped by average observers, such as feelings, emotions, intentions. In this regard, there has been talk of 'expressive qualities' and 'valences' [Koffka, 1935 *Principles of Gestalt Psychology* (Harcourt & Brace); Metzger, 1954 *Psychologie Steinkopf*]. Even the terms 'physiognomic properties', 'tertiary qualities', and 'affordances' [Gibson, 1979 *The Ecological Approach to Visual Perception* (Boston, MA: Houghton Mifflin)] have been used. Arnheim (1949 *Psychological Review* 56 156–171) illustrated some examples of structural isomorphism between objects and self-perceptions. However, emotional and motivational factors were generally underestimated. Our investigation has focused on these. We applied an already-tested experimental technique consisting of recalling personally stressful experiences or, their opposite, relaxing and comforting events, through drawings. This noninvasive procedure enables the reactivation of temporary tolerable states of stress or, conversely, of comfort: assessed by applying self-appraisal scales before and after each treatment [Biasi and Bonaiuto, 1997, in *Colour and Psychology* Ed. L Sivik (Scandinavian Colour Institute) pp 54–65]. To evaluate the perception of expressive qualities, the test 'linear shapes and coloured bands' [Bonaiuto, 1978 *Forme Lineari e Bande Colorate* (Università di Roma 'La Sapienza')] was used. Young adults, both genders equally represented, were individually examined. Ten 'linear shapes' were examined before the stress or comfort treatment, and another ten at the apex of each treatment. Each shape was shown with a multiple choice of meanings, only one being the appropriate on a statistical basis, the other meanings being inappropriate or irrelevant. Double-blind conditions and systematic rotations were guaranteed. The capacity to grasp the shared meanings decreases after stress, while comfort improves this perceptual performance. The effects are particularly conspicuous when positive' type emotional qualities (goodness, kindness, comicalness) must be detected, and may be explained as a combination of psychological defences. Considering the role of meaning perception in interpersonal relations, in comprehension of art and in aesthetic experience, it seems important to underline the close interaction, previously neglected, between cognitive and affective processes, such as those activated in stress and comfort situations.

◆ **A pilot study of the temporal condition for the perception of life in communication with computers**

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Robots have been developed not only for industries but also for homes, and their psychological aspects as well as technological ones have become more important. Interaction with computers is not a special activity in our modern daily life; we use them all the time, whether we are aware of this or not. Thus, psychological enrichment concerning the man/machine interaction is not a matter of the limited domain of robotics. We are interested in the perception of life in the interaction with machines. We may treat the machine as a nonliving material, but if we feel something resembling human communication, its usability will be changed. Our main purpose is to clarify the condition in which people feel interaction with the machine as communication with something alive. When the machine reacts to a certain human approach, do we feel something more than automatic and mechanical response? We note the perception of causality, a phenomenon when we see some causal relationships or meanings in a sequence of mechanical or physical occurrences. Perception of communication with the machine is also an event like perceptual causality, so that the temporal condition is crucial. Therefore, as the first step in a series of studies, we investigated temporal conditions for the perception of life in communication with computers. Simple interactive animations were prepared and presented to naive subjects. They were not aware of the purpose of study, and were instructed just to describe their impression of the operation of animations where a rectangle changed its colour in response to a click by the subject. Colour, speed and latency of change, and the number of changes were variables. As a result, the subjects spontaneously reported the perception of life under certain conditions; the rectangle seemed to be alive, pulsate, or give a warning in certain cases. Latency and length of time before the change may be important factors.

LEARNING AND MEMORY

◆ **Neural correlates of category learning**

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Category learning by prototype abstraction is an excellent model of plasticity; however, its neural correlates are currently unknown. We used event-related fMRI to measure patterns of cortical activity during retrieval of familiar prototypes and new exemplars of portraits, landscapes, and abstract paintings by Modigliani, Renoir, Van Gogh, Pissarro, Miro, and Kandinsky. During the encoding session, subjects memorised 15 prototypes from each category that were presented 4 times each. Four days later, the retrieval session was performed in the MR scanner. The old prototypes were presented with new exemplars, and subjects pressed a button to indicate whether they had seen the pictures before. The new exemplars were either visually similar to the old prototypes, ambiguous, or non-similar. The old prototypes were correctly detected in 87% of the portraits, 62% of the landscapes, and 57% of the abstract paintings (mean latency: 1284 ms). The response to the similar items was less accurate (false alarms: 12%) and slower (1317 ms), as compared with the response to ambiguous (5%; 1208 ms) and non-similar (3%; 1062 ms) items. Visual perception of the paintings evoked activation in category-selective regions in the visual cortex; portraits activated the lateral fusiform gyrus, amygdala, and the superior temporal sulcus; landscapes evoked activation in posterior and medial fusiform gyri, and in the parahippocampal gyrus; abstract paintings elicited activation in the inferior occipital gyrus. Additionally, we observed differential activation in inferior frontal gyrus, intraparietal sulcus, and the anterior cingulate cortex, where old and similar items evoked stronger activation than ambiguous and non-similar items. Our results suggest that category learning is mediated by activation in a cortical network that includes regions in visual cortex where stimulus-specific representations are stored, attention-related areas where familiar prototypes are detected, and memory-related areas where new items are classified as a match or a mismatch.

◆ **Perceptual learning in monocular superimposed masking**

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We examined the effect of practice in monocularly superimposed masking and the transfer of learning. Observers were trained to improve their ability to detect Gaussian windowed sine-wave

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gratings (target) in the presence of sine-wave gratings (masker). Targets and maskers were presented monocularly and always had the same spatial frequency ($2 \text{ cycles deg}^{-1}$), orientation (45° or 135°), and phase (0° or 180°). These conditions of stimuli (the eye to which the stimuli were presented, orientation, and phase) were fixed during training. Target contrast thresholds were measured for 11 masker contrasts in each session. After training for 3–5 sessions, thresholds decreased except for conditions in which no maskers were presented. The practice effect at least partially transferred to untrained eye, untrained orientation of stimuli, and untrained phase of stimuli. We simulated changes in thresholds using our processing model [Maehara and Goryo, 2005 *Optical Review* **12**(2) 76–82] and fitted the model to the data. The model is a revised version of Foley's model (Foley and Chen, 1999 *Vision Research* **39** 3855–3872). The revised model has two characteristics. First, it receives two monocular inputs. Second, excitations and inhibitory signals are subjected to nonlinear transducer functions before and after summation of monocular signals. On the basis of simulation and parameter values estimated by fitting, it is shown that the effect of practice can be described as changes in the nonlinear transducer functions for divisive inhibitory signals.

◆ **Learning and strategy changes in a binocular time-to-contact judgment task**

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Time-to-contact (TTC) is the time remaining before an object collides with the observer. It has been demonstrated that, in laboratory settings, expert observers can make accurate judgments of TTC. However, it is not clear what the role of feedback and learning is in such studies. Unlike size, distance, or speed, TTC is not an intuitive visual variable. Also, TTC is correlated with other sources of information under natural circumstances. We report an experiment in which we explore the use of different sources of information and the influence of feedback on TTC judgments. Observers watched two sequentially presented trajectories of an approaching faceted ball. The task was to judge in which of the two trajectories the ball was the closest in time (had the shortest TTC) when it disappeared. By judicious choice of parameters (in particular, variation of projectile diameter), we were able to ensure that on 25% of trials, judgments based on looming rate would lead to the opposite response to judgments based on TTC. Examination of these particular trials allowed us to assess which particular source of information is being used without recourse to the introduction of an unnatural conflict between them. The role of feedback was explored by the use of alternate blocks with and without feedback. Pilot data suggest that observers rely on looming rate initially, but when given feedback learn to use TTC.

[JK is supported by the School of Psychology, Cardiff University.]

◆ **Does selective attention filter out distractor information in visual working memory storage?**

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Visual working memory (VWM) capacity has been estimated to be limited to up to 3–4 visual items (Luck and Vogel, 1997 *Nature* **390** 279–281). Memory load can be reduced by selecting only targets while ignoring distractors. Selective attention is considered to filter out distractors to limit the amount of information processing at higher-order perceptual and cognitive stages. Recently, it has been shown that selective attention depends on perceptual load to filter out distractors in an early or a late selection modality (Lavie, 2005 *Journal of Experimental Psychology: Human Perception and Performance* **21** 451–468; 1995 *Trends in Cognitive Sciences* **9** 75–82). Is this true for VWM storage? If distractors are not filtered out from VWM storage we would expect them to interfere with target memory retrieval and change detection. To test this hypothesis we used a very rapid change detection (VRCD) paradigm where subjects were presented with a sample array (100 ms) of coloured targets and distractors. Subjects had to select and store the targets in visual working memory while ignoring the distractors. After a short delay (1000 ms), a probe array was presented very quickly (100 ms) and one of the targets could have changed colour. Subjects had to detect as correctly and as fast as possible whether a cued target had changed or not. In half the trials, the distractors changed colour at probe array. We analysed response times and correct responses comparing conditions across same or different distractors at probe displays, but also across different memory loads and distractor loads. By modifying these parameters, we were able to test (i) the relation of response times and memory load in a VRCD task, (ii) the relation between target and distractor information in visual working memory, and (iii) the role of non-relevant perceptual load in the effective filtering of selective attention for VWM storage.

- ◆ **Working-memory characteristics during invariant visual-recognition processing in monkeys**
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To clarify the role of working memory during invariant visual-recognition processing in monkeys, we studied their working memory characteristics in a delayed (0–8 s) discrimination task before and after any modification of stimuli. After complete training in discrimination, three rhesus monkeys were tested in discriminating stimuli with different visual attributes (geometrical figures of various shape, size, orientation, various spatial relationships between components of objects) during development of a delayed instrumental reflex (associated with mechanisms of working memory). Next, monkeys were tested on recognising the same stimuli after their transformations such as variation in size, shape, and spatial relationships. An analysis of monkeys' working-memory characteristics (correct decisions, refusals of task decision, motor reaction time) revealed significant differences caused by visual attributes. These results demonstrate that correct decisions and duration of information storage after transformations of stimuli markedly decrease (by a factor of 2–3) in monkeys in delayed discrimination of images with different spatial-relationship features. These changes of monkeys' characteristics were accompanied by a significant increase of refusals of task decision and motor reaction time. The invariance of this delayed discrimination is achieved by additional training. After discrimination of black-and-white geometrical figures of different shape or orientation, under some variation in shape of objects the invariance was legible. This transformation practically did not influence correct decisions and duration of information storage, though refusals of task decision and motor reaction time were increased. The results obtained indicate that working memory takes part in invariant visual-recognition processing by forming separate channels to retain the information concerning the demarcating features of objects and their spatial relationships. The existence of these channels in working memory allows visual recognition to be performed invariantly along with estimation of the variants of an image.

- ◆ **Perceptual learning: No improvement under roving?**
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Training on simple discrimination tasks can improve perception. The mechanisms of this so-called perceptual learning are not yet well understood. In recent years, an increasingly complex pattern of results was found. It is, for example, possible to improve performance in Gabor contrast discrimination and line bisection with two stimulus alternatives but not if more alternatives have to be learned with randomly interleaved presentations (roving). A bisection stimulus comprises, for example, three parallel lines. In each trial, the central line is closer to one of the two outer lines and the task of the observers is to indicate the closer line. Here, strong learning occurs. However, we found no improvement of performance when the distance between the outer lines could vary randomly from trial to trial, being either 20 or 30 min of arc. Why does learning not occur under these roving conditions? For example, are the bisection stimuli too similar? Here, we show also that no learning occurs when we present interleaved bisection stimuli of two different orientations. Hence, roving seems to be a rather unspecific effect. It seems that learning two related tasks is a feat the human brain can hardly accomplish with about 3840 trials. Is learning with interleaved bisection stimuli impossible in general? We presented vertical bisection stimuli with outer line distances of either 20 or 30 min of arc randomly interleaved in ten sessions (18 000 trials per observer). After a period of rather constant performance (about 5000 trials), improvement of performance occurs. Hence, the human brain can manage to learn under roving conditions. [Supported by the Volkswagen Foundation and NATO Science Program.]

- ◆ **Neural responses of the memorising and recalling process in spatial mechanism measured by MEG**
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We have two types of spatial representation of environment. The first is an egocentric one that represents real-time change of sight from our own point of view. The second is an exocentric one that represents bird's-eye view of the environment. It has been found by PET and fMRI studies that the egocentric representation of space is located at the parietal lobe, the exocentric representation of space at hippocampus, and spatial working memory at frontal lobe. However, the temporal relationship among neural activities in these substrates during spatial-information processing is not clear because of the indirect and slow nature of PET and fMRI. Therefore, we used MEG as the non-invasive system to find dynamic characteristics of human spatial mechanisms. We investigated

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processes for memorising and recalling spatial memory. Observers were asked to memorise spatial configuration of a virtual-reality maze with egocentric or exocentric information. We measured spontaneous MEG response during the memorising process. Theta-wave activation was found at almost all parts of the brain including the frontal lobe. After observers memorised spatial configuration of the maze, sequences of egocentric views were presented as test stimuli. The sequence was sampled from the memorised maze in the 'true' condition. The last view did not correspond to the memorised maze in the 'false' condition. Observers responded whether the test stimulus was 'true' or 'false'. Evoked responses were averaged by using the onset of the last view as a trigger. The estimated locations of current sources of neural activity for recalling spatial memory were on the occipital lobe at 160 ms, on the parietal lobe at 280 ms, and on the frontal lobe at 640 ms. This propagation of activity suggests sequential involvement of visual, spatial, and memory mechanisms for spatial-information processing.

◆ **Retrieval of abstract drawings modulates activity in retinotopic visual areas**

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Growing evidence suggests that brain regions that process incoming sensory information can also be involved in the subsequent retrieval of that information from memory. Recent neuroimaging studies have shown content-specific retrieval activity, corroborating this hypothesis. Mental-imagery experiments have also found that activation patterns are material-dependent. In particular, activation of primary visual cortex (V1) has been reported for visual-imagery tasks requiring examination of fine spatial features. Here, we used functional magnetic resonance imaging (fMRI) to study the episodic encoding and subsequent retrieval of a set of line drawings and a set of words. The line drawings were composed of simple shapes with a complex abstract configuration and episodic encoding was achieved by asking subjects to perform angle comparisons. Group statistical analysis revealed stimulus-related and task-related activity in occipito-temporal and parietal areas, which were used to functionally define regions of interest (ROIs). Contrast between activations induced by old versus new items during retrieval was found to be significant in areas within these ROIs, including retinotopic visual cortex extending as early as V1. No such modulation could be observed during retrieval of words. These results support the hypothesis of reinstatement upon retrieval of the perceptual activity engaged during episodic encoding. Most notably, they seem to suggest involvement of retinotopic visual areas during retrieval of line drawings, possibly because these cannot easily be categorised as objects and therefore require examination of fine spatial features. This observation is consistent with findings from visual-imagery experiments. Further studies with fine mapping of retinotopic and non-retinotopic areas should clarify the content specificity of the observed modulations.

[Supported by FCT-POCTI/NSE/46438/2002.]

◆ **The time series of statistical efficiency in visual pattern learning**

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We investigated the time series of storage of information in supervised visual learning of prototype patterns. We prepared two prototype mosaics before each learning session. In each trial in a session, we added Gaussian luminance noises to the mosaics, and required participants to discriminate those noisy patterns. Since original prototypes were never presented to the participants, they had to learn or estimate the prototypes from the noisy patterns in the trials. The only cue to the learning was the feedback to the responses. While the prototypes were black-and-white, presented patterns were gray-scaled because of the added noise. The performances of human learners were compared to those of the theoretical learner based on the maximum-likelihood method. The theoretical learner was assumed to store (or use) all the information given in previous trials. Thus, the comparison showed how efficiently human learners stored the presented information in the learning course. We derived indices of storage efficiency in each trial from cumulative percent correct for both human and theoretical learners, and investigated how these indices changed as learning developed. We set three conditions of mosaic size (2×2 , 3×3 , and 4×4), and two conditions of similarity between prototypes. The results showed that human learners stored information highly efficiently in the early stage of learning (eg until about the 10th trial in 3×3 mosaic conditions), and then the efficiency declined and remained at a moderate level. Storage efficiency was higher as a whole in the conditions in which the mosaic size was smaller and two prototypes were similar, though the transitional pattern of the efficiency was almost the same in all the conditions.

◆ **The decay of trajectory traces in memory when tracking multiple trajectories**

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When detecting a deviation in a bilinear 'target' trajectory in the presence of linear 'distractor' trajectories, observers cannot process more than a single trajectory accurately (Tripathy and Barrett, 2004 *Journal of Vision* 4 1020–1043). Even when the 'distractor' trajectories disappear halfway through the trial, deviation thresholds rise rapidly as the number of distractor trajectories increases (Narasimhan et al, 2004 *Journal of Vision* 4 361a). If memory plays a role in the above set-size effects, then one expects that the same stimulus presented within a single frame (ie using static 'traces') would result in less decay of the trajectory information in memory and consequently lower thresholds. On the other hand, a limit imposed by attentional capacity would predict thresholds that are further elevated if single-frame stimuli were used. The stimulus was presented in a single frame in our first experiment; deviation thresholds were relatively unaffected by the number of distractor 'traces' (varied between 0 and 9). This suggests that the set-size effects in our previous study resulted from memory limitations. In our second experiment, there were three trajectories on each trial, each moving at 4 deg s^{-1} . The three trajectories were presented for 51 frames (816.67 ms). The target trajectory deviated and changed colour on frame 27, and a temporal delay (16.67–400 ms) was introduced between frames 26 and 27 (ie at the point of deviation). If the memory of trajectory traces decays with time, then thresholds should increase monotonically as the duration of the delay increases. Our results were consistent with this prediction, thresholds for delays longer than 250 ms being more than 3 times the thresholds when the delay was 16.67 ms. The two experiments along with the experiments in our previous study suggest that the retrieval of trajectory information is severely compromised when recall is delayed.

◆ **Information about the sequence of presentation does not reduce the visual working memory capacity**

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We investigated subjects' performance during 'memory recall' (Luck and Vogel, 1997 *Nature* 390 279–281) and 'sequence recall' [Henson, 2001 *The Psychologist* 14(2) 70–73] tasks to examine whether they are competing for the visual-working-memory resources. We used five different categories of the objects (alphabets, colours, orientations, tools, and irregular objects), which also enabled us to measure any contribution of object complexity on the subjects' performance. In contrast to the previous studies (Alvarez and Cavanagh, 2001 *Psychological Science* 15 106–111), we used the sequential presentation method that ensures individual object encoding and eliminates any contribution of pattern encoding which can exaggerate visual-working-memory capacity (Nasr et al, 2005 *Journal of Experimental Psychology: Human Perception and Performance* submitted). To rule out contributions of verbal working memory, we used an articulatory suppression procedure during the experiments (Baddeley and Hitch, 1974 *Psychology of Learning and Motivation* 3 47–90). In experiment 1, we measured subject's performance during a 'memory recall' task. The result of this experiment revealed that the performance is very different for various categories of visual objects ($p < 0.001$). In contrast to previous studies of working memory, this difference was largely correlated with objects meaningfulness instead of with their complexity. The results of experiment 2 showed that subject performance for 'sequence recall' is highly correlated with the results of experiment 1. The results of experiment 2 revealed that the amount of error in sequence recall was significantly different for various categories of the objects with no correlation with their complexity ($p = 0.001$). In experiment 3, we examined whether involving subjects in both tasks simultaneously would affect their performance in comparison with the results of experiments 1 and 2. The results revealed no significant impairment compared to those of experiment 1 ($p > 0.39$) and experiment 2 ($p > 0.67$). We suggest that information about the sequence of presented objects does not occupy any resources of working memory in excess of those necessary for retaining objects themselves.

◆ **Long-range perceptual learning with line stimuli?**

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Long-range lateral interactions between iso-oriented visual stimuli are present for gaps bigger than one-third of a degree. Polat and Sagi (1994 *Proceedings of National Academy of Sciences of the USA* 91 1206–1209) showed that, in this spatial regime, practice of contrast detection with

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Gabor patches did not improve target detection, or even made it worse by increasing the threshold elevation with practice (defined as logarithm of test over control thresholds). Indeed, in the first case they found that threshold elevations were stable through sessions and equal to zero, and in the second case they increased with practice (negative effect on lateral interactions). They reported these results for vertically oriented stimuli. Here, we tested the hypotheses of vertical and horizontal orientation differences in learning effects in the long-range regime, by measuring this effect with line stimuli (width: 0.025 deg; lengths: target 0.33 deg, inducer: 0.66 deg; visual gap: 1.5 deg). Ten subjects without previous experience in psychophysical experiments with line stimuli ran successively 1 control session, 4 test sessions, and 1 last control session per day. The experiment lasted two days and each session comprised 200 trials in a 2A-temporal-FC paradigm. Two interleaved staircases were used for stimulus presentation. Five subjects participated for the horizontal orientation, the remaining for the vertical orientation. Control thresholds did not vary systematically through practice. The global long-range regime interactions showed a stable facilitative effect through practice and no differences between orientations. Analysis of individual data demonstrates strong variability between subjects, some presenting suppression (threshold elevation above zero), and others facilitation (threshold elevation below zero), some clearly varying with practice, others not. These results show important variability between subjects for vertical and horizontal orientations on long-range perceptual learning.

◆ **Dissociation of object-based and space-based inhibition of return by working memory**

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Inhibition of return (IOR) refers to the delayed response to a location or an object that has recently been cued. Researchers in previous studies used spatially separate objects (which happen to involve 2-D space representations) to demonstrate object-based IOR, and used object-like stimuli (which happen to involve object representations) to demonstrate space-based IOR. In order to avoid the confounding from 2-D space representations, we used overlapping objects to probe object-based IOR. And we used similar but less object-like stimuli to probe space-based IOR. In order to dissociate object-based and space-based IOR, we adopted a dual-task paradigm, in which the primary task was to discriminate the luminance change associated with an object or a location, and the secondary task was to make a judgment about the central pattern that either did or did not involve spatial working memory. We found, on the one hand, that the space-based IOR was disrupted by the secondary task which was assumed to involve spatial working memory, whereas the object-based IOR remained intact. On the other hand, the object-based IOR was disrupted by the secondary task which was assumed to involve non-spatial working memory, whereas now the space-based IOR remained intact. These results suggest that space-based IOR is modulated by spatial working memory and that object-based IOR is modulated by non-spatial working memory.

[Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE.]

◆ **Perceptual learning of faces and textures is tuned to trained identities**

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Perceptual learning, although typically specific to properties of the trained stimulus, will transfer across stimuli under some conditions. Transfer of learning is sometimes obtained with complex visual stimuli, suggesting that, in such cases, learning alters processing at higher stages of the visual pathway. Although our previous work has shown category-specific enhancements of identification performance for faces and textures, whether such enhancements are indifferent to changes in stimulus identity has not been investigated. We addressed this question by using ten-alternative forced-choice texture and face identification tasks that were performed by separate groups of observers on two consecutive days. The faces were cropped to display only internal features, and equated for spatial-frequency content. Textures were band-limited noise patterns. Two sets of each stimulus category with equivalent spatial attributes were created, differing only in stimulus identities across sets. All stimuli were displayed at one of seven contrasts, in one of three external noise levels for a total of 21 stimulus conditions. For each stimulus category, one group of observers performed the task with the same stimulus set on both days. The other group was exposed to one set on the first day and the other on the second day. Method of constant stimuli was used to estimate 50% correct identification thresholds; learning was defined as a reduction in contrast thresholds from the first day to the next. With both textures and faces, performance

improvements were substantially greater for the group that was exposed to identical stimuli on both days; thus, perceptual learning did not transfer across changes to stimulus identity. It appears that, in both cases, the learning mechanism effectively localises informative regions of the stimulus that most efficiently enable individuation from other members of the same stimulus category. Surprisingly, fluency from prior experience with faces did not facilitate transfer of learning.

[Supported by NSERC PGS-D (ZH), NSERC Discovery grants (42133 and 105494), and the Canada Research Chair Program.]

◆ **Relational information in visual short-term memory as an explanation of the ‘visual sensing’ effect**

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In a change-detection paradigm, Vidal et al (2005 *Journal of Vision* 5 244–256) investigated how the relations between visual items determined the accessibility of each individual item in visual short-term memory (VSTM). They presented a sample screen composed of coloured squares and, after a blank, a test screen where one of the items was cued as target. The subject had to decide if the target had changed colour. Two kinds of changes could be made: a minimal change (only the target could change colour on the test screen) and a maximal change (all the non-targets changed colour). A decrement in change-detection performance was observed for the maximal-change condition, showing that relational information plays a role in recall from VSTM. Could this contextual effect be considered as a subject strategy or visual-noise effect? We conducted two experiments using the same paradigm as described earlier. In experiment 1, we asked the subjects to indicate the level of confidence of their answers on a three-level scale. In experiment 2, supplementary squares (visual noise) appeared on the test screen for half the trials. A second question we asked was: what is the exact role of the relational information? In experiment 3, when the subject detected a change, he had to recall the initial colour of the target. The results of experiments 1 and 2 confirm that the contextual-change effect is neither a strategic nor a noise effect. In experiment 3, we observed that subjects detect changes even if they don’t report the initial colour of the target. The experiments lead us to suggest that contextual changes produce false change perception and that relational information is strongly implicated in the change-detection mechanism. Moreover it could be the basis of the ‘visual-sensing-without seeing’ effect reported by Rensink (2004 *Psychological Science* 15 27–32).

◆ **Prism adaptation by gain control**

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To grasp objects, we have to translate retinal images into ‘world-centred’ representations of these objects, taking into account both retinal position and gaze direction. When wearing prisms deflecting the ray paths horizontally, subjects continue to fixate the target but their arm movements initially deviate sideways, adapting within a few movements. Hence, arm trajectories change though retinal projection stays constant. Upon removal of the prisms, movements first deviate in the opposite direction, indicating a negative aftereffect. A dozen subjects performed ballistic arm movements towards a visual target before, while, and after wearing prisms. After adaptation to the prisms, the aftereffect was examined, with either head or trunk rotated relative to the adaptation period. The target was always fixed foveally. The aftereffect increases, almost linearly, with trunk rotation in the direction of the aftereffect, whereas it decreases with trunk rotation in the opposite direction. Moreover, the size of the aftereffect decreases for head rotation in the direction of the aftereffect whereas it increases for head rotation in the opposite direction. The effect of trunk rotation is especially pronounced; the aftereffect is almost three times larger for a 90° rotation in one direction compared with the opposite rotation. Grasping a target and then repeating the identical arm movement after a trunk or eye rotation would cause a strong deviation from the target. Neck muscle proprioceptors usually prevent us from this fate, adjusting the arm trajectory to the changed relation between trunk and head and thus ensuring successful grasping. Our results indicate that prism adaptation relies on a change in gain rather than on a linear shift. After adaptation, signals from neck muscle receptors signalling the rotation between head and trunk obviously exert too weak an influence to compensate for the effects of the underlying trunk rotation.

[Supported by the German Research Council.]

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MULTISENSORY INTEGRATION 1◆ **Effects of accompanying sound on visually perceived motion**

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The purpose of this study was to demonstrate the effects of sound on the appearance of a moving object. Total impression of rebound and perceived path of occluded motion varied with accompanying sound. The subject was presented with an upper white rectangle area, which was 591 pixels in height and 1024 pixels in width, and a lower gray rectangle, which was 177 pixels in height and 1024 pixels in width on the computer display. A black disc, 32 pixels in diameter, moved at the constant speed of ~ 200 pixels s^{-1} down from the upper left area to the lower centre area of the display. Then the disc changed its direction of movement to upper-rightward after contact with the gray area; that is, the motion of disc followed a V-shaped locus. Simultaneously with the contact, some varieties of sound were presented. The higher in pitch and/or the shorter in duration the sound was, the harder the gray area appeared and the higher the perceived speed of rebound was. When a large time lag was introduced between the contact and the sound, regardless of the temporal position of the sound, the observers perceived no relation between them. In this condition, a white rectangular screen, 228 pixels in height and 348 pixels in width, was presented in the centre of the display to hide the point where the moving disc changed direction. Under this condition, the position of amodally perceived turning point was dependent on the temporal position of the accompanying sound.

◆ **Changing vision by changing breath**

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Previous studies have suggested that breathing can influence emotional states and, more in general, cognitive mental states such as perceiving [Benussi, 1925 *La Suggestione e l'Ipnosi come Mezzi di Analisi Psicologica Reale* (Bologna: Zanichelli); Boiten et al, 1994 *International Journal of Psychophysiology* 17 103–128]. Two experiments were run to investigate the possible effect of breathing on visual perception. In experiment 1, observers completed a line bisection task. Four different stimuli, each subtending 14.65 deg, were used: two horizontally oriented Brentano–Müller-Lyer figures with leftward-pointing or rightward-pointing outer wings, respectively, and two matched control figures with middle wings pointing in the same direction as the outer wings. One group of observers performed the bisection task after having breathed out slowly and smoothly for 4 min, whereas the other group performed the task after having breathed spontaneously. An optoelectronic motion analyser was used to record breathing movements of the chest wall and abdomen. Heart rate, galvanic skin response, and external temperature were also recorded. In experiment 2, observers performed a target-detection task under the same breathing conditions as in experiment 1. The target was a red point (diameter = 0.30 deg) presented in an expanding optic flow at four possible eccentricities with respect to the origin of the flow (ranging from foveal presentation to extrafoveal presentation). Optoelectronic data revealed that most of the observers actually breathed as they were required. No effect of breathing on both accuracy and precision in performing the line-bisection task was found: The Brentano–Müller-Lyer illusion resisted breathing variations. In contrast, response times in the target-detection task were influenced by breathing. Observers were faster in detecting the visual target after having breathed spontaneously than after having breathed out slowly and smoothly. This finding suggests that breathing can modulate the sensitivity of the visual system.

◆ **Auditory – visual fusion space in darkness depends on lateral gaze shift**

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Most multisensory studies concern cross-modal effect and only recently they have focused on auditory – visual (AV) fusion in space (Godfroy et al, 2003 *Perception* 32 1233–1245). Multisensory space perception implies the overlap of sensory modalities with various spatial frames of reference [Paillard, 1991 *Brain and Space* (Oxford: Oxford University Press) pp 163–182]. So, the relative involvement of each frame in the resulting percept needs to be clarified. The effect of dissociating the auditory and the visual egocentric reference frames on AV fusion was investigated first (Roumes et al, 2004 33 *Perception* Supplement, 142). Results supported the conclusion that the reference frame for AV fusion is neither visual nor auditory, but results from a cross-modal interaction. The luminous conditions of this initial study may have provided visual contextual cues. A large set of experiments revealed an effect of these allocentric cues on visual localisation (Dassonville et al, 2004 *Vision Research* 44 603–611). To prevent any bias due to visual context,

in the current experiment, we investigated the effect of a shift between the auditory and the visual reference frames on AV fusion in full darkness. Subjects sat in an obscured room, at the centre of a hemi-cylindrical screen. A 7×5 matrix of loudspeakers was located behind the screen. A broadband noise burst and a 1 deg spot of light made the bimodal stimulation. They were simultaneously presented for 500 ms, with a random spatial disparity. Participants had to judge their degree of unity (ie common location in space). To test the effect of a spatial dissociation between the visual and the auditory reference frames, the subject's head was kept fixed and the gaze, under eye-tracker control, was oriented either straight ahead or 20° laterally shifted. Results showed that fusion limits varied according to the position of the gaze. In darkness, the auditory–visual fusion space still results from a cross-modal interaction.

◆ **Cross-modal interference in rapid serial visual – tactile, tactile – visual presentations**

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The cross-modal interference from the tactile task to the visual task (and from the visual task to the tactile task) was examined. Dual-task paradigm in the rapid serial-presentation method was employed. The visual stimuli were alphabetic letters presented on the display. The tactile stimuli were presented on a forefinger of the dominant hand with eight pins (the piezoelectric element) that were arranged to form a rectangle (2×4). These visual and tactile stimuli were presented synchronously. The presentation duration was 30 ms and ISI was 70 ms. The distractor for the visual task was one of eight letters, and for the tactile task was one of eight pins. The first task was to decide whether the presented target was one of two pre-designated patterns: the visual task, to decide whether the target was P or R, and in the tactile task, whether the four pins of the upper side or the four pins of the lower side went up. The second task was to detect a pre-designated stimulus: in the visual task, to detect X, and in the tactile task, to detect the pattern composed of four pins of the centres. In the visual–tactile condition, the performance of the second task (the tactile task) was delayed after the first task (the visual task) for 300–400 ms. The attentional deficit found in the visual–tactile experiment is consistent with our previous study (Hashimoto et al, 2003 *Perception* 32 Supplement, 98), but the tactile–visual experiment showed no significant effect. This result seems to be caused by the high error rate of the first task (tactile task). Further studies are necessary to examine the cross-modal attentional interference from touch to vision.

◆ **Role of perceptive expectations and ground texture in motion sickness**

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We investigated the role of perceptive expectations and ground texture in the inducement of motion sickness in virtual reality. Visual flow structure depends strictly on observer action in reality but in virtual reality it depends only in part on observer action. Hence, it is possible to introduce a conflict between perceptive expectations and observer's perception. Furthermore, visual ground information plays a prominent role for terrestrial species, including humans. Thus, the different regions of the visual scene may influence the development of motion sickness to a different degree. In the experiment, a virtual scene was back-projected on a large screen ($2.8 \text{ deg} \times 2.1 \text{ m}$); it depicted three trees as seen by an observer moving on a circular path centred on one of the trees. The thirty-two participants were instructed to fixate their gaze on a particular tree and had to estimate repeatedly their motion sickness. The perceptive expectations of the participants were modified by asking them to look at the tree that was not aimed at by the virtual camera. Visual ground information was modified by the presence or absence of ground texture. When ground texture was deleted, only the relative movement of the trees remained (due to the movement of the camera). Motion sickness increased gradually during the experiment as the participants were subjected to the moving scene. Postural sway of participants was greater when their perceptive expectations were modified. Motion sickness was greater with a textured ground. Therefore, visual information which increases realism of the visual scene may play a role in the appearance of motion sickness.

◆ **The effect of 'non-informative' vision on tactile sensitivity**

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Recent studies have indicated that tactile acuity is enhanced if subjects view the stimulated region of skin shortly before application of a tactile stimulus (Kennett et al, 2001 *Current Biology* 11 1188–1191). This visual input was 'non-informative', in that it provided no information about

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the identity of the tactile stimulus. Here, we investigate how tactile sensitivity is affected by a similar non-informative view that is concurrent with tactile stimulation. To create visual input that contained no information about the tactile stimulus, we provided a mock view of the tested hand using a mirror-reflection of the opposite unstimulated hand. This mock view reduced tactile sensitivity, increasing detection and discrimination thresholds. Tactile sensitivity was also reduced when subjects were given a mock view of empty space (reflected in a mirror) where the hand and stimulus were actually located. Thus, perception of the tactile stimulus was disrupted by visual misinformation that there was no stimulus in that location. However, this form of visual misinformation does not suppress all consequences of tactile stimulation—further experiments revealed that a view of the hand enhanced the adaptive shift in tactile sensitivity induced by prolonged suprathreshold stimulation. These findings might represent two distinct effects of vision on touch: visual input interacts with the somatosensory processes that lead to conscious perception of tactile stimuli, and independently modulates processes leading to adaptation. Alternatively, visual input pertaining to the location of a hand might provide direct input to bimodal (visuo-tactile) systems, or feedback to somatosensory systems, that combines with tactile responses. If the visual input carries no information about the tactile stimulus, it would serve to add only noise to the tactile processing, thereby interfering with detection and discrimination. Nonetheless, the additional visual input might elevate response so as to increase the amount of adaptation in that system.

[Supported by the Australian Research Council]

◆ **The temporal limits of binding sound and colour**

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Perceptual features need to be combined to make sense of the world. Recently, there has been much focus on the visual domain, eg how different visual attributes such as colour and motion are bound temporally (Arnold et al, 2001 *Current Biology* **11** 596–600; Moutoussis and Zeki, 1997 *Proceedings of the Royal Society of London, Series B* **264** 393–399). However, organisms also integrate information from other senses. In this study, we investigated the temporal aspects of binding sound and colour. Participants were presented with a 0.75 deg disc, 3 deg above fixation. The disc changed from red to green (interleaved with a blank ISI) and vice versa with different alternation rates ranging from 1 to 5.5 Hz (step size of approximately 0.5 Hz). A 5 ms high (2 kHz) or low (1 kHz) sound was presented through headphones at the onset of each coloured disc. When the high sound accompanied the red disc, the low sound coincided with the green, and vice versa. Which sound coincided with which colour was randomly varied across trials. Participants were asked to attend to the colour and sound of the stimulus while fixating. After each trial (duration: 3 s), subjects indicated which beep (high or low) accompanied the red disc by using a keyboard press. The results show that the performance gradually decreases with increasing alternation rate. Above an alternation rate of 2.5–3 Hz participants are no longer able to match sound and colour. This limit is of the same order of magnitude as for binding visual features that are presented spatially separate (Holcombe and Cavanagh, 2001 *Nature Neuroscience* **4** 127–128) and shows the involvement of attentional systems (Verstraten et al, 2000 *Vision Research* **40** 3651–3664).

◆ **Can auditory cues influence the visually induced self-motion illusion?**

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It is well known that a moving visual stimulus covering a large part of the visual field can induce compelling illusions of self-motion ('vection'). Lackner (1977 *Aviation Space and Environmental Medicine* **48** 129–131) showed that sound sources rotating around a blindfolded person can also induce vection. In the current study, we investigated visuo-auditory interactions for circular vection by testing whether adding an acoustic landmark that moves together with the visual stimulus enhances vection. Twenty observers viewed a photorealistic scene of a market place that was projected onto a curved projection screen (FOV 54 deg × 40 deg). In each trial, the visual scene rotated at 30° s⁻¹ around the Earth's vertical axis. Three conditions were randomised in a within-subjects design: no-sound, mono-sound, and spatialised-sound (moving together with the visual scene) played through headphones using a generic head-related transfer function (HRTF). We used sounds of flowing water, which matched the visual depiction of a fountain that was visible in the market scene. Participants indicated vection onset by deflecting the joystick in the direction of perceived self-motion. The convincingness of the illusion was rated on an 11-point scale

(0–100%). Only the spatialised-sound that moved according to the visual stimulus increased vection significantly: convincingness ratings increased from 60.2% for mono-sound to 69.6% for spatialised-sound ($t_{19} = -2.84$, $p = 0.01$), and the latency from vection onset until saturated vection decreased from 12.5 s for mono-sound to 11.1 s for spatialised-sound ($t_{19} = 2.69$, $p = 0.015$). In addition, presence ratings assessed by the IPQ presence questionnaire were slightly but significantly increased. Average vection onset times, however, were not affected by the auditory stimuli. We conclude that spatialised-sound that moves concordantly with a matching visual stimulus can enhance vection. The effect size was, however, rather small (15%). In a control experiment, we will investigate whether this might be explained by a ceiling effect, since visually induced vection was already quite strong. These results have important implications for our understanding of multi-modal cue integration during self-motion.

[Supported by the EU-funded POEMS Project (Perceptually Oriented Ego-Motion Simulation, IST-2001-39223).]

- ◆ **Nonlinear integration of visual and auditory motion information for human control of posture**
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It is well known that we control our posture with both vestibular and visual information. However, the effect of auditory information on the postural control is not explicit but weak (Soames and Raper, 1992 *European Journal of Applied Physiology and Occupational Physiology* **65** 241–245; Tanaka et al, 2001 *Ergonomics* **44** 1403–1412). We focused on the interaction of visual and auditory motions, which would modulate postural sway. We presented visual motion (sinusoidal grating, $71.6 \text{ deg} \times 53.7 \text{ deg}$, $0.56 \text{ cycle deg}^{-1}$) and auditory motion (white noise with binaural intensity modulation, stereo loudspeakers, 70 dB) horizontally back and forth. In experiment 1, the horizontally cyclic motion was at 0.167 Hz for both vision and audition, and we set four conditions. Visual and auditory motions were (i) in the same direction (A–V congruent condition), (ii) in the opposite directions (A–V conflict condition), otherwise (iii) auditory source remained constant at the centre, or (iv) silent while visual motion was presented. Observers fixated the centre marker and the posture was measured by a force plate for 36 s stimulus presentation. Postural sway was induced in the direction of visual motion, and more in the A–V congruent condition than in the other conditions. However, sway in the A–V conflict condition was almost the same as in the constant sound and the silent conditions (i) > (ii) = (iii) = (iv). In experiment 2, we varied the cyclic frequency of auditory motion (0.128, 0.167, 0.217 Hz, and constant sound) while that of visual motion was fixed (0.167 Hz) to investigate the effect of phase incongruence. We again found enhancement of body sway in the congruent condition (0.167 Hz), but there was no difference between the other conditions. Conflict or incongruence of visual and auditory motions did not inhibit the postural sway in comparison with the constant-sound condition. These results suggest that the congruent auditory motion enhances visually induced postural sway, but the conflict or incongruent sound does not affect it.

[Supported by Grants-in-Aid for Scientific Research, Encouragement of Young Scientists (B) by MEXT Japan, and Nissan Science Foundation.]

- ◆ **Cross-modal repetition deficit**
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When two stimuli with the same phoneme are presented closely during a rapid serial presentation, we cannot recognise one of the two stimuli. This phenomenon is called repetition deficit, which occurred in both visual and auditory modalities (repetition blindness, RB: Bavelier and Potter, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 134–147; repetition deafness, RD: Nakajima and Kikuchi, 2003 *Japanese Journal of Psychonomic Science* **22** 41–42). It is suggested that RB and RD are a consequence of an encoding failure or of some confounds in memory. However, the cause of them remains unknown. In this study, we investigated whether the cross-modal repetition deficit occurs, using combinations of visual and spoken digits (when presented at a rate of 120 ms per digit). In experiment 1, participants were presented lists of five to seven visual and spoken digits. The lists often contained two digits that were the same. Results showed that visual–auditory order caused a repetition deficit but auditory–visual order did not. Experiment 2 showed the same results under low memory load, with lists of three to five digits. These results support an encoding failure hypothesis as the cause of repetition deficit. We suggest that differential speed for encoding produced these results. Phonemic encoding in auditory modality is faster than that in visual modality. Visual digits are converted into phonemes

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after form information is analysed, whereas spoken digits are direct phonemes. Because under visual–auditory order condition a subsequent auditory stimulus catches up with a preceding visual stimulus in encoding stage, one of the two stimuli cannot be recognised. However, under auditory–visual order condition the two stimuli can be recognised because an auditory stimulus is encoded so fast that a visual stimulus does not overlap in encoding stage.

◆ **Visual discrimination of intermodal launching events**

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Several experiments have demonstrated that causality judgments increase when an additional auditory event marks the collision in a launching event. These results suggest that intermodal unity is the main source of the perception of causality (Guski and Troje, 2003 *Perception & Psychophysics* 65 789–800). In the present study, I investigated the influence of a sound in visual discrimination of launching events. In the preliminary experiment, the Michotte's launching effect paradigm was used [Michotte, 1946/1963 *The Perception of Causality* (London: Methuen)]. The launching effect varied because of the contact delay (0, 40, 80 ms). Subjects judged the animation with 0 ms of contact delay the best simulation of launching. In the second experiment, a sound (440 Hz) of different duration (30, 150 ms), was added at the time of contact between the two moving objects. Different pairs of events (only visual or intermodal) were shown. Subjects were required to pay attention to the visual animation only, and give a same/different answer. The results show that subjects are less accurate in the intermodal condition: intermodal integration occurs despite intentional efforts to filter out auditory stimulation.

◆ **Cross-modal mere exposure effects between visual and tactile modalities**

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There has been little study of mere exposure effects between different modalities. We investigated the cross-modal mere exposure effects between visual and tactile modalities using 3-D novel objects. We prepared sixteen novel objects, eight target and eight distractor stimuli. There was no significant difference in preferences for the target and the distractor stimuli. Sixty participants were allocated to four conditions ($N = 15$) including two experimental conditions (VT or TV) and two control conditions (V or T). In the VT condition, the participants were visually exposed to the target objects (exposure task), then 2 or 3 days later were asked to rate the preferences (rating task) for the target objects mixed with the distractor objects after touching them. In the TV condition, the participants touched the target objects, and later rated the preferences for the targets and the distractors after seeing them. The participants in the V and the T conditions were asked to rate the preferences for all stimuli in either visual or tactile modality without the exposure task. We found that in the VT condition the participants significantly preferred the target to the distractor objects. In contrast, in the TV condition, there were no significant differences in the preference ratings between the target and the distractor objects, and those ratings were generally higher than the ratings in the V condition. In both control conditions, there were no significant differences in the preference ratings between the targets and the distractors. These results suggested that the cross-modal mere exposure effect occurred depending on which modality was used in the exposure and the rating task, indicating the asymmetric influence of sensory modalities on affective judgments.

◆ **Differential neural activity during perception of coherent audiovisual motion**

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We investigated the cortical activations associated with coherent visual motion perception in the presence of a stationary or moving sound source. Twelve subjects judged 5 s episodes of visual random-dot motion containing either no (0%), meager (3%), or abundant (16%) coherent direction information. Simultaneously, a moving or stationary auditory noise was presented. In a 4AFC response paradigm, subjects judged whether visual coherent motion was present, and, if so, whether the auditory sound source was moving in-phase, was moving out-of-phase, or was not moving. T2*-weighted images were acquired with a 1.5 T Siemens Sonata. To eliminate interference with the noises created by the gradient system, a sparse imaging design was employed, in which we temporally separated audio-visual stimulation from the gradient switching. An SPM2 fixed-effects analysis revealed significant BOLD clusters in extrastriate and associational visual cortex that increased with visual coherence level. Auditory motion activated an extended region

in the STG confirming an earlier study (Baumgart et al, 1999 *Nature* **400** 724–726). Combined audio-visual motion led to significant activation in the supramarginal gyrus and STG and the effect size is larger with congruent movement direction. Our findings indicate that the lateral parietal and superior temporal cortex underlies our ability to integrate audio-visual motion cues. [Supported by the Deutsche Forschungsgemeinschaft, Bayerische Forschungsförderung]

◆ **A cue-combination model for the perception of body orientation**

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Visual and non-visual cues affect perception of body orientation with respect to gravity. In the rod-and-frame effect, a rolled visual frame alters an upright observer's percept of Earth vertical. We asked whether this effect is the consequence of combining visual and non-visual cues to body orientation in a statistically optimal fashion. To do so, we measured the perception of body orientation in three conditions: non-visual, visual, and combined. In the non-visual condition, rolled observers viewed an ambiguous letter (a horizontal 'p' or 'd') in an otherwise completely dark environment. They indicated whether they saw a 'p' or a 'd', ie whether the shaft of the letter was oriented clockwise or counterclockwise relative to Earth horizontal. Using a 2AFC procedure, we estimated the mean and variance of the non-visual estimates for various body rolls. Eye torsion was measured and taken into account for each roll position. In the visual condition, supine observers viewed a stereo version of the rod-and-frame stimulus—a letter-and-cube stimulus—and indicated what letter they saw; judgments were relative to body midline. Because observers were supine, non-visual gravitational cues were irrelevant to the judgments. From observer responses, we estimated the mean and variance of the visual estimates for various frame rolls. Non-visual and visual responses were used to predict statistically optimal cue-combination responses for the combined condition. We then compared the predictions to behaviour. In the combined condition, rolled observers viewed the letter-and-cube stimulus and indicated what letter they saw relative to Earth horizontal. Some observers showed behaviour consistent with combining cues in a statistically sensible manner. Others responded in a way that resembled their responses in the visual or non-visual conditions, suggesting that these observers were making judgments based on one or the other modality.

[Supported by AFOSR F49620-01-1-0417.]

◆ **Optokinetic or simulator sickness: Objective measurement and the role of visual – vestibular conflict situations**

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Simulators are being used more and more: for research and development purposes, but also for education, training, and even for recreation. We work with driving simulators, and have conducted a series of studies on a problem that often occurs with these (and other) simulators: simulator sickness. This phenomenon closely resembles the classically experienced motion sickness. It can affect a user enough to make him/her abort a simulator run within minutes, or interfere with the task(s) to be performed. We present an experiment in which we studied the psychophysical reactions of subjects and recorded their neurovegetative activity. Our goals were to improve understanding of the underlying causes of simulator sickness, testing in particular the visual – vestibular conflict hypothesis. Ultimately, we intend to develop an objective measure for monitoring purposes, so that sickness can be detected before it becomes incapacitating. We used a fixed-base simulator, running an urban circuit with many sharp turns and traffic lights. Subjects were asked to indicate continuously their discomfort on a visual-analogue scale while exploring the town. We studied fifty-one normal volunteers (thirty-four became sick). Sickness correlated strongly with anxiety. The subjective discomfort readings correlated well with simultaneous neurovegetative data (especially skin resistance and temperature), and with a symptom-scoring test administered after the experiment. There was no clear indication of an age or gender effect. We also present some initial evidence that visual – vestibular conflict may not be a sufficient condition to provoke simulator sickness: other factors probably play an (equally?) important role (anxiety, nauseating odours, etc).

[Supported by the European Union (QLK6-CT-2002-00151: EUROKINESIS)]

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ART AND VISION◆ **Aversion to contemporary art**

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Migraine has been a source of inspiration for many artists, including Debbie Ayles. When Ayles's work is viewed, observers often complain that her paintings give them a headache. We find that, unsurprisingly, ratings of aversion to the paintings are negatively correlated with ratings of the artistic merit of the paintings. What is perhaps more surprising is that it is possible to explain more than 10% of the variance in ratings of aversion simply on the basis of a particular spatial periodicity of the paintings and their average colour saturation (CIE 1976 SUV). The findings apply not only to Ayles's art but also extend to a sample of non-representational art by a wide variety of contemporary artists. We propose a model of aversion that can be applied to contemporary art. [Supported by a Wellcome Sciart Award.]

◆ **What a beautiful stump! Ecological constraints on categorical perception of photographs of mutilated human bodies**

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We investigated the categorical perception of photographic images of mutilated and intact human bodies in the specific context of competitive sports. Twenty photographs of mutilated and intact female and male bodies, all either actively or passively involved in competitive sports of various kinds such as swimming, marathon running, or handball, were presented in random order on a computer screen to four groups of twenty young students (ten females and ten males) each. In a two-alternative forced-choice task, observers of each group had to assign each photograph to one of two possible perceptual categories: 'beautiful' versus 'ugly', 'natural' versus 'artificial', 'familiar' versus 'strange', or 'dynamic' versus 'static'. The results show that, in general, categorical judgments of 'beautiful' are positively correlated with 'familiar', 'natural', and 'dynamic'. They also reveal that positively connoted perceptual judgments such as 'beautiful' do not depend on whether a body represented in a given image is visibly mutilated or intact, but on whether the activity represented in the image is likely to be perceived as 'natural' or as 'dynamic'. The findings suggest that the nature of subjectively connoted perceptual judgments can be predicted on the basis of specific ecological constraints, which is discussed.

◆ **A look through the expert's eyes: Art expertise and aesthetic perception**

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According to the model of aesthetic experience proposed recently by Leder et al (2004 *British Journal of Psychology* **95** 489–508), the nature and intensity of a person's aesthetic experience strongly depend upon the person's art-related expertise and her/his affective state when entering the aesthetic episode. Expertise is believed to foster style-related processing, thus helping people 'read' and interpret an artwork (Gaver and Mandler, 1987 *Cognition and Emotion* **1** 259–282). In fact, the literature on aesthetic behaviour contains a lot of evidence suggesting differences in perception and preferences between art experts and novices (Hekkert and van Wieringen, 1996 *American Journal of Psychology* **109** 389–407). Yet, there is much less empirical evidence concerning the exact processes behind these differences as well as the question which aspects of expert knowledge are most relevant in this respect. In order to shed more light on these issues we chose different methodological approaches. For example, we experimentally manipulated knowledge by giving persons information on some artists' styles while controlling for their expertise and affective state. The results point to an interaction between affective state and experimentally acquired stylistic knowledge. In another study we examined the perceptual spaces for contemporary art both for art experts and novices. Moreover, the method of priming is employed to test the mnemonic and perceptual effects of style acquisition. The studies are discussed within the framework of the above-mentioned model of aesthetic experience.

◆ **The effect of Gestalt factors on aesthetic preference**

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The present study was designed to examine the role of combined Gestalt factors in the aesthetic preference for a cross-shaped configuration composed of five squares. Proximity in distance and

similarity in hue and lightness of figural components were systematically varied. A total of 48 combinations of proximity–similarity were used as test configurations. Seventeen graduate students participated in the experiment. They were asked to make aesthetic preferences for each test configuration using a 7-point scale. An ANOVA was applied to average scale values of aesthetic preference. Main effects of proximity and similarity were found to be significant: interactions between proximity and hue, and between hue and lightness were significant. As regards proximity, preferences were stronger with the shorter distance than with the longer distance between figural components. As regards similarity, preferences were much stronger for combinations of the same hue and different lightness and weaker for combinations of different hue and lightness, and intermediate for combinations of same hue and same lightness. In addition, the effect of proximity was found to enhance the similarity effect.

◆ **The relationship between visual anisotropy and aesthetic preference for disk arrangement**

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Morinaga [1954, “Experimental studies on aesthetic arrangement” *Proceedings of the Annual Meeting of Japanese Applied Psychology Association* (in Japanese)] investigated Gestalt factors determining aesthetic arrangement. In his study, participants were asked to arrange the most beautiful one, two, or three black disks in a white rectangular framework, demonstrating that the centre of gravity of aesthetic arrangement coincided with the centre of the framework. However, his study was not concerned with the size of the disks. Arnheim [1954/1974 *Art and Visual Perception* (Los Angeles, CA: University of California Press)] argued that the impression of a visual weight was determined by figural positions in the framework in line with Morinaga’s finding. Moreover, Arnheim argued that there would be an anisotropy of the visual field. Accordingly, although the size of objects may be equal, the perceived size of an object in the right side may be larger than that of the object in the left side. Thus, a balanced state as a whole would then be achieved when the right object is slightly smaller than the left one. Furthermore, the perceived size of an upper object is larger than that of a lower one. Mitsui and Noguchi [2002, “Searching for basic rules on aesthetic arrangement” *Proceedings of Annual Meeting of Japanese Psychonomic Society* (in Japanese)], using two disks, support Arnheim’s concept of visual balance when the size combination of disks is different. These results therefore imply that visual anisotropy is reflected in the aesthetic arrangement. The present study was designed to examine whether a similar anisotropy is observed when a rating method is used instead of the arrangement method. The higher scale values of aesthetic preference were found when the centre of the subscribed circle of two disks coincided with the centre of the framework, rather than when it deviated from the centre of the framework. Also, higher scale values of aesthetic preference were found when the smaller disk was placed in the upper area, and the larger one was placed in the lower area. The present study confirms that aesthetic arrangement and preference are governed by visual balance.

◆ **How we look at photographs: Lightness perception and aesthetic experience**

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Black-and-white photography is a form of art, a language in which luminance contrast relationships are its letters. Contrast discrimination, therefore, is a necessary ability for reading this language, perhaps even more influential in the aesthetic experience than the represented subject itself. Moreover, the neuroaesthetic aspect suggests tonal expression produced by the photographer and that preferred by the viewer to match. To investigate the roles and interferences of local and global elements in lightness perception and object recognition processes of photographs, we examined whether contrast discrimination is a response to spatial configuration properties, or also to conceptual contents and its relation to preference.

(i) We compared contrast discrimination performance for grey-scales to that for three categories of black-and-white photographs by Ansel Adams in which discrete tonal regions of the characteristic curves were altered systematically. We found substantial differences in response to contrast, depending on the tonal region at which contrast alteration occurred, without significant effect of the conceptual content. Moreover, low performance in the shadow region of grey scales, significantly improved in photographs, presumably because of their complex configurations. We also found differences in performance between photographs of daylight and night scenes. These findings are in line with Gilchrist’s ‘anchoring theory of lightness perception’.

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(ii) Next, we performed a contrast-preference-evaluation task in a 'dislike-like' scale on the previously examined photographs. Observers showed preference for the unaltered photographs, which decreased systematically with contrast alteration. Like discrimination performance, preference also varied with region—it was higher for contrast alteration at shadows than at highlights or mid-tones. These results are consistent with the common rules for creating and appreciating art as an extension of the function of the brain proposed by Zeki in 2000, and the laws of artistic experience based on neurobiological strategies suggested by Ramachandran and Hirstein in 1999.

- ◆ **Effects of brightness, contrast, and colour tone on the affective impressions of photographic images**
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To investigate affective impressions of brightness, contrast, and colour tone on photographic images, we performed three experiments. In experiment 1, black-and-white photographs were used to see the affective impressions of brightness and contrast. The brighter photographic images were more positive and more dynamic, and lighter feelings were rated. The varying contrast did not show any significant effect on the dynamic-static dimension, while it added more negative and heavier impression to the overall stimuli. When colour photographs were used in experiment 2, it gave similar results to experiment 1; however, the affective impressions were less obvious in bright conditions than in dark ones. In experiment 3, each photograph was filtered through colour tones of cyan, magenta, yellow, black, red, green, blue, and white. Black-and-white tone filtering produced similar effects to those of brightness-change condition, showing comparable results to previous experiments. The other six colour-filtering procedures did not give any obvious affective impressions, while the changes of impression on the static and heavy dimensions were slightly mediated by blue and yellow tones.

[Supported by Korea Research Foundation Grant (KRF-2002-074-AM1021).]

- ◆ **How alike are natural scenes and paintings? Characterising the spatial statistical properties of a set of digitised, grey-scale images of painted art**
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Natural scenes share a number of statistical properties including power spectra that are distributed as $1/f^2$ (f = spatial frequency), sparse spatial structure, and similar edge co-occurrence statistics. Painted artworks form an interesting class of images because they are human-created interpretations (and often representations) of the natural world. But, whereas natural scenes comprise a wide range of illuminations and viewing angles, paintings are limited by their smaller range of luminances and viewing distances, their roughly 2-D format, and their typically indoor setting. Nevertheless, paintings have captivated humans for millennia, and statistical similarities in their spatial structure could grant insights into the types of spatial patterns humans find compelling. We investigated the spatial statistics of a large database of digitised paintings from the H F Johnson Museum of Art in Ithaca, NY, and compared them to a set of randomly chosen natural-scene images. A set of randomly chosen, grey-scale images of paintings from the Johnson database—which included a diverse set of paintings of Western and non-Western provenance—was characterised in terms of pixel statistics, power spectra, local operator statistics, and other measures. We found that our set of paintings showed lower skewness and kurtosis than the set of natural scenes, both in its intensity distributions and in its response distributions following convolution with a difference-of-Gaussians operator. The set of painted art images was found to have a typical spatial-frequency power spectrum similar to that of natural scenes. We also used a novel over-complete coding technique to give an estimate of the information content for our set of artworks and our set of natural scenes. For all of our statistical measures, noise whose power is distributed as $1/f^2$ and whose pixel intensities were Gaussian-distributed served as a control.

[DJG was supported by NIH EY0153932; DJF and DMC were supported by NGA contract HM 1582-05-C-0007 to DJF.]

- ◆ **Estimating the best illuminant for art paintings by computing chromatic diversity**
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The visual impression of an artistic painting is strongly influenced by the spectral profile of the illuminant. The goal of this work was to estimate the best illuminant to appreciate artistic oil

paintings by computing chromatic diversity for several types of illuminants. Hyperspectral imaging over the visible range was used to digitise a set of oil paintings from the collection of the Museu Nogueira da Silva, Braga, Portugal. The hyperspectral imaging system had a low-noise Peltier-cooled digital camera with a spatial resolution of 1344×1024 pixels (Hamamatsu, C4742-5-12ER), and a fast-tuneable liquid-crystal filter (VariSpec, model VS-VIS2-10HC-35-SQ, Cambridge Research & Instrumentation, Inc., MA, USA) mounted in front of the lens. The spectral reflectance of each pixel of the paintings was estimated from a grey reference surface present in the scene. Illuminant spatial non-uniformities were compensated for by measurements of a uniform surface imaged in the same location and conditions as the paintings. The radiance from each painting under CIE Standard Illuminants D65 and A, normal halogen and Solux-type light sources, and fluorescent lamps with CCT 2940 K, 4230 K, and 6500 K, was estimated and the corresponding luminance and chromaticity distributions computed. In each case, the number of discernible colours was estimated by computing the painting representation in CIELAB space and by counting the number of non-empty unit cubes in that space. It was found that for all paintings the illuminant producing the largest number of discernible colours was the CIE Standard Illuminant D65 followed by Solux; fluorescent lamp with CCT 6500 K was the best of the remaining set. These results suggest that the ideal light for illumination of this type of artistic paintings is close to average daylight.

◆ **Dürer's choice: Representing surface attitude in engravings**

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Artists effectively convey three dimensionality in engraved images through collinear and cross-hatched etch lines. Suggested relationships between etch lines, texture flows, and shading flows (Ben-Shahar and Zucker, 2004 *Vision Research* **44** 257–277; Zucker, 2004 *The Depictive Space of Perception: A Conference on Visual Thought, Bolzano, June*) motivated an investigation into how high and low spatial-frequency components in etchings affect surface attitude perception. Effects were measured with so-called gauge figures or surface probes (Koenderink et al, 1992 *Perception & Psychophysics* **52** 487–496) applied to stimulus images comprising etchings of spheres, of identical size and low-pass shading flows but drawn with different etch-line configurations. Results indicate that line configuration, and thus high-spatial-frequency content, significantly biases the outcome. Surface probing proves to be a genuinely useful investigative tool, by providing hints of how etch lines affect surface perception. For example, local orientation of etch lines biases surface perception. Biasing of perceived shading flow by high spatial frequencies was then tested with etched figures with conflicting etch-line and shading-flow information. As pointed out elsewhere (Koenderink and van Doorn, 1995 *Image and Vision Computing* **13** 321–331), local judgment of surface attitude depends on global shape. Similarly, more complex pictorial influences of etch lines are observed for more intricate etchings. Cross-hatching of etch lines is shown to neutralise biases in perceived surface attitude. I suggest that Albrecht Dürer, a genius in the art of etching, was especially gifted in selecting and using lines that enriched the sense of looking into his art works. Dürer's artistic intuitions deepen our insight into the relationship between actively perceived pictorial object surface and computable image attributes, such as texture and shading flows. In fact, he may have been drawing loci of active perception.

[Supported by the Japan Society for the Promotion of Science (JSPS).]

◆ **Leonardo da Vinci's "Mona Lisa" in light of his studies of the brain**

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According to Giorgio Vasari, Leonardo kept the "Mona Lisa" from having a melancholic look by entertaining her with musicians and entertainers. The question then is how, in terms of Leonardo's science, did these entertainments keep her amused, or in Leonardian terms, how did they stir her mind? Such a question was all important for Leonardo who considered the rendering of "moti mentali" the object of portraiture. Luckily for us, Leonardo drew maps of the function of the brain so we can trace the paths of mental stimuli. The purpose here is not to judge the facts of his anatomy, but rather to use his extant anatomical drawings to understand how he would have imagined enjoyment working in the brain. I will read his diagrams like the London subway map, made to indicate function rather than geography. I will then listen to and analyse a popular Renaissance song of the type that might have been played for the Mona Lisa: Josquin Despres's (c.1450/7–1521) frottola, "El grillo" ("The cricket"). I will demonstrate that the pattern of the listener's awareness can be traced on Leonardo's map of the mind. When all is said and done, we will find that Leonardo's map of the brain works well enough to give us a general sense of the process of enjoyment expressed in Mona Lisa's countenance.

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◆ **Motion perception in art and design research**

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What happens when visual perception theory and practice become a tool for art and design? How can the science of vision be interpreted in such a way as to provide new techniques for drawing and animation? We present the outcome of research from an art and design perspective that uses science as both inspiration and problem solver. From exhibitions in the UK, Europe, and Korea, we show biological motion used to create an illusory army of figures marching around a quarry wall; path-guided apparent motion to provide a means of providing low-bandwidth mobile phone media; and how depth and motion can be used to create a new way of drawing. In addition, we introduce a new research programme where we are investigating how new physical forms can be created with the use of visual motion perception.

◆ **Hermann – Hering grids: The impact of sound on vision**

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The reverberations of sound on light have not been restricted to theories of the nature of the stimulus. In the confined context of the acoustic figures described initially by Robert Hooke in 1665 and in more detail by Ernst Chladni in 1787 (often referred to as Chladni figures), a novel visual phenomenon was observed. Chladni investigated the vibrations of flat plates, and the patterns produced by certain sounds. He scattered fine sand evenly over a horizontal glass or metal plate, clamped at one end, and set it in vibration with a violin bow; symmetrical patterns were formed where the sand gathered. The nodal lines represented the parts of the plate that vibrated least and sand collected in these areas that were relatively still. In his drawings of the acoustic figures, Chladni represented the nodal lines as black on a white ground. Several decades later, when Charles Wheatstone experimented on the acoustic figures, he drew the nodal lines in white on a black ground, and many different patterns were presented in a 5×6 matrix of squares. John Tyndall so represented them in his book *On Sound* published in 1867; they were displayed in smaller dimensions and in a 5×8 matrix. Two years later, Ludimar Hermann, when reading the German edition of the book, noted the dark dots between the black squares on which the Chladni figures were shown; the illusion is now called the Hermann grid. In 1907, Ewald Hering drew attention to its converse (a black grid on a white background) producing the Hering grid. However, the light dots observed by Hering had been described in 1844 by Rev. W Selwyn, and they were similarly interpreted in terms of simultaneous contrast.

◆ **Drawing as an experience of seeing**

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My paper deals with drawing as a particular and privileged process of visual perception, and the visual perception of a drawing. The experience of seeing, when drawing, is profound and intense. Looking at an object, then drawing it, implies a disciplined and organised observation, and establishes a clear difference between a vagrant look over things and the active look over what is being drawn—what one wants to see. In this way, drawing is a way of acquiring knowledge and of investigating the visual world. What is drawn undresses itself before our eyes from the mist that melts everything into the whole and acquires a presence and a defined visual percept. We draw because our eyes see. We draw because our brain tends to identify profiles, outlines, and is able to accept a representation in the place of what one wants to present. To identify, with the means of recognising, refers directly to identity. Originally, however, it means: the twosome making just one. The fact that drawings contain not only the real register of the gesture of drawing but contain also, concealed, all the movements made to obtain that result, provokes in the perception of the observer a recognition of the lines drawn and of the movements needed to accomplish them. As Skoyles shows, there is a motor perception identified through the eyes that gather memories of identification of the gesture that was made, according to our own ability of performing that gesture. So, what the eyes see when looking at a drawing challenges our brain to physically experience gestures and actions that in reality we may not be able to accomplish, but nevertheless are able to identify, in the full sense of recognising in our own body what actions were needed to result in the lines we see.

ATTENTION 1◆ **Decreased detectability of targets in non-stimulated regions of the visual field**

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Recent fMRI studies demonstrated negative BOLD response beyond the stimulated regions within retinotopic visual areas (Shmuel et al, 2002 *Neuron* **36** 1195–1210). It has been suggested that this negative BOLD response is a reflection of automatic withdrawal of attention when a large stimulus is presented in the visual field (Smith et al, 2004 *NeuroReport* **11** 271–277). We investigated psychophysically whether stimulating large parts of the visual field significantly impairs the detection of a small target stimulus in the non-stimulated parts of the visual field. In half of the trials subjects had to detect a Gabor patch (target) of full contrast, presented either centrally (2–4 deg) or peripherally (8–10 deg) relative to a rotating checkerboard ring (stimulus) with an eccentricity of 4.5–7.5 deg. In the other half of the trials, the subjects had to detect the target in the central or peripheral region in the absence of the stimulus. Fixation had to be maintained on a spot in the centre of the screen. The target was presented at random orientation, time, and location within the central or peripheral region. Subjects indicated the detection of the target by pressing a button. We observed that the reaction times in both the central and the peripheral region are higher when a stimulus is presented than when no stimulus is presented (centre: $p < 0.001$, two-tailed paired t -test; periphery: $p < 0.001$, two-tailed paired t -test). Our results suggest that stimulating a large part of the visual field might cause automatic withdrawal of attention from the non-stimulated parts of the visual field.

◆ **Spatiotemporal characterisation of presaccadic allocation of attention**

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Stimuli presented during the preparation of a saccade are more accurately perceived when their location coincides with the saccadic target. This phenomenon has strengthened the notion that a tight link exists between oculomotor programming and the deployment of covert spatial attention. A previous study (Castet et al, 2004 *Perception* **33** Supplement, 16) has characterised the temporal course of human performance in an orientation-discrimination task during the period preceding a saccade. Discrimination thresholds were measured with the discrimination target (a tilted Gabor patch) presented at different delays after the onset of the saccadic cue (a central arrow) and masked after 50 ms. Threshold values were found to significantly decrease with time within about 150–200 ms, both when the discrimination target was at the same location as the saccadic target or at a distinct one. Here, we present new experimental findings allowing us to characterise in more detail the spatiotemporal evolution of presaccadic discrimination performance and to gather insight about its nature. First, we present evidence that the temporal benefit is dramatic when the location of the tilted Gabor patch is cued (focused attention), whereas it is absent or much reduced when the location is randomly chosen, on any given trial, among eight possible locations (distributed attention). Second, we find that by reducing the luminance contrast of the mask, which is somehow equivalent to increasing the time of presentation of the oriented patch, discrimination acuity increases overall, and that the temporal benefit tends to disappear. These findings suggest that the perceptual improvement results from a progressive increase of the amount of focal attention deployed at the discrimination-target location. Other possible explanations, based more generally on an effect of temporal cueing or fixation disengagement, seem to be ruled out.

[Supported by European Network PRA—Perception for Recognition and Action.]

◆ **Temporal dynamics of the interaction between working memory and attention: A neuronal model of a Wisconsin-DMS-Task**

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To study the basic processes involved in visual information processing, we developed a Wisconsin-like ‘what-where-delayed-matching-to-sample’ task to be accomplished by human subjects and a neurodynamical model. In this task, a pair of visual stimuli, separated by a fixed delay, is presented to the subjects who have to indicate whether these stimuli match one of two possible

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feature dimensions: same object or same position on the screen. The valid rule changes without notice (Wisconsin-like paradigm) at random intervals. Analysis of response times (RTs) revealed that subjects not only store the relevant stimulus dimension, but also memorise the irrelevant stimulus dimension; hence, answers were fastest in cases where both stimulus dimensions matched. In trials with a match in the relevant stimulus dimension, RTs were slower and still increased for trials with a match in the irrelevant stimulus dimension. For simulation of the task, we used a biophysically detailed neuronal model which consisted of various pools of neurons: two rule pools, responsible for the maintenance of the active rule, and two times two memory pools reflecting the stimulus dimensions 'object' and 'space'. The simulations allowed the replication of the RT distributions as generated by the subjects. Further on, the model makes it possible to calculate the resulting fMRI signal and thus allows a comparison with experimentally determined fMRI signals in similar tasks. These results prove that the developed model is a realistic neuronal implementation for these kinds of tasks. The experimental setup used is shown and results obtained by human subjects are presented. The neurodynamical model is explained and simulation results in terms of spiking rates of the participating neuronal pools as well as response times achieved by the model are outlined.

[Supported by the German Science Foundation (DFG), Project No. FOR 480/1-1.]

◆ **Implicit learning of divided visual-spatial attention allocation in easy and difficult tasks**

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Implicitly acquired knowledge of task-relevant locations in the visual field improves visual search task performance over time following the deployment of selective attention to those locations. Task difficulty also guides the deployment of attentional resources, with easy tasks leading to general learning and difficult tasks leading to specific learning (eg Ahissar and Hochstein, 2000 *Vision Research* **40** 1349–1364). To date, only unitary associations between target and location have been assessed. We examined whether anticipatory knowledge of probable target locations improves visual search task performance and whether the modulating force of task difficulty on visual-spatial deployment of attention manifests itself following learning of dual target-location associations within the same visual scene. Control (both targets in all visual field regions) and experimental (each target confined to specific visual field regions) groups showed implicit learning—decreasing response time and increasing accuracy. With an easy task, both groups showed no change in performance during the test (both targets in all visual field regions). With a difficult task, the performance of the control group improved during the test, whereas that of the experimental group deteriorated. The results are discussed in light of learning under conditions of divided attention.

[Supported by NSERC (MvG) and FQRSC Équipe.]

◆ **Attention sharpens selectivity**

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There is a debate whether attention sharpens tuning function of processing units to play its role in enhancement of visual processing. Using an adaptation paradigm, we tried to investigate changes in orientation tuning in attended and non-attended conditions. In the first experiment, we showed that the magnitude of tilt aftereffect (TAE) for a 90° target stimulus is maximal when adapting and target stimuli have 20° difference in their relative orientations; ie most effective adapting stimulus was a 70° orientation. The magnitude of the TAE decreases when this difference becomes either smaller or larger by a skewed Gaussian-like function with its peak at 70°. Kohn and Movshon's adaptation model for MT (2004 *Nature Neuroscience* **7** 764–772) was used for determining the relative distance between target stimulus and the most effective adapting stimulus by kurtosis of tuning function of processing units. We investigated whether engagement/disengagement of attention during the adaptation could change this relative distance. In the second experiment, a staircase paradigm was used to determine the most effective adapting stimulus for a 90° target stimulus. Subjects were fixating on the adapting stimulus while their covert attention was either directed to (attended condition) or diverted from (non-attended condition) the adapting stimulus. Relative distances between the most effective adapting stimulus and target stimulus in these two conditions have significantly different distributions ($p = 0.004$, Kolmogorov–Smirnov test). In the attended condition, this difference was $8^\circ \pm 0.07^\circ$

smaller than the non-attended condition. These data could be interpreted by changes in tuning function in Kohn's model and are suggestive of sharpening of tuning function of orientation processing units of attention.

◆ **Mechanisms of covert attention revealed by contrast adaptation**

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Psychophysical and neurophysiological studies have shown that covert attention enhances contrast sensitivity by increasing the gain of the neurons processing a stimulus. Conversely, adaptation reduces contrast sensitivity by reducing neuronal gain. In this study we characterised the mechanism(s) by which attention affects sensory processing by quantitatively contrasting the effects of transient (exogenous) attention and contrast adaptation on contrast sensitivity. In each block a 70 s adaptation phase was followed by 20 test trials. There are two adaptation conditions. Adapt-100: two vertical Gabors (4 cycles deg^{-1} , $\sigma = 2$ deg) at 100% contrast were presented for 70 s on opposite sides along the horizontal meridian. The stimuli were counterphase flickered at 7.5 Hz. Adapt-0: observers fixated for 70 s a blank field of the mean luminance (0% contrast). Top-up: the adaptation stimulation (either adapt-100 or adapt-0) was repeated for 2.5 s before each test stimulus. Test-stimuli: in each trial, two Gabor patches were presented at the same locations of the adaptors (same size and spatial frequency). The target Gabor was randomly tilted $\pm 2.5^\circ$; the other stimulus was vertical. Observers discriminated the orientation of the tilted target; stimuli were presented with contrast randomly selected from a set of 7 levels, in the range 1%–80%. Accuracy was assessed at each contrast. In each test trial there were two possible attentional conditions. Peripheral cue: a horizontal bar appeared above the target. Neutral cue: the bar appeared at fixation; a 1 s delay followed the top-up before the cue appeared (50 ms, 50 ms ISI). Stimuli were displayed for 100 ms. We plotted contrast response functions. Adaptation effect: performance in neutral trials was better in the adapt-0 than in the adapt-100 condition. Attention effect: performance in peripheral trials was better than in neutral trials. Performance in peripheral trials was comparable for the adapt-0 and adapt-100 conditions. These results suggest that transient attention acts on the same or similar mechanisms of contrast adaptation. [Supported by the Beatrice and Samuel A Seaver Foundation.]

◆ **Limits on continuous monitoring of the features of multiple objects**

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In previous studies, people's ability to continuously monitor the locations of moving objects (Pylyshyn and Storm, 1988 *Spatial Vision* 3 179–197) or to detect changes in the features of objects (Luck and Vogel, 1997 *Nature* 390 279–281) has been examined. In these studies, performance limits of around four objects have been reported. When participants have to monitor the features and spatial locations of objects together, performance is much worse (Saiki, 2003 *Journal of Vision* 3 6–21), and the limit may be as low as one object. Whether this is a limit on monitoring non-spatial features, or on monitoring locations and features together, is unresolved. We examined continuous monitoring of non-spatial features without the demand of spatial monitoring. Five luminance gratings constantly changed orientation in a smooth and random manner. At the start of each trial, between one and five of the gratings were marked as targets for monitoring. After a quasi-random interval all gratings disappeared and the location of one grating was cued. Participants reported the last orientation of this grating. We chose a performance criterion where a judgment was recorded as correct if the error was less than 30° . The proportion of correct responses was high when one grating was marked as a monitoring target. The proportion correct dropped with each additional target added to the monitoring task, and furthermore dropped significantly between monitoring one and monitoring two targets. With a stricter 10° error criterion, performance was no better than predictions based on a monitoring capacity of one object. These preliminary results indicate that precision is lost with every object added to the attentional load. Tripathy and Barrett (2004 *Journal of Vision* 4 1020–1043) found a similar pattern for spatial tracking. We tentatively suggest that the similarity could indicate a common underlying mechanism.

◆ **Crowding and salience-based attention**

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In a recent article, Pelli et al (2004 *Journal of Vision* 4 1136–1169) have suggested that feature binding is mediated by hard-wired integration fields instead of spotlight of spatial attention

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[as assumed by Treisman and Gelade (1980 *Cognitive Psychology* **12** 97–136)]. Consequently, the visual features can be correctly conjoined only when there are no other competing features within a circle with radius of about $0.5E$ (E = eccentricity of the target object). This claim can be falsified by an observation that we can easily see, for example, the orientation of a single blue bar within a dense array of differently oriented red bars. In the present study, possible determinants of the extent of crowding (or feature integration) zones were analysed with feature (colour) singletons as targets. The number of distractors was found to have a dramatic effect on crowding. With few distractors, a usual crowding effect was observed. However, with increasing number of distractors, crowding effect was remarkably reduced. Similar results were observed when the target and distractors were of the same colour, and only a circle of different colour indicated the target location. The results can be explained by bottom-up attention that facilitates the processing of information from salient locations in the visual field. The relative salience of distractors is reduced when other similar distractors surround them. The higher-level integration fields can 'see' the representation already modified by salience-based exogenous attention.

◆ **Spatial attentional orienting and synchrony priming**

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When a 3×3 matrix of 90° corner junctions, detection of a Kanizsa-type square is facilitated when the target display is preceded by a 40-Hz flickering 'premask' matrix of 3×3 crosses, with four of the crosses oscillating in synchrony at the subsequent target location (Elliott and Müller, 1998 *Psychological Science* **9** 277–283). To examine whether this 'synchrony-priming' effect is influenced by visuo-spatial attention, we introduced a spatial-cueing manipulation (eg Posner, 1980 *Quarterly Journal of Experimental Psychology* **32** 3–25) into Elliott and Müller's synchrony-priming paradigm. Observers were presented with a spatial precue (a symbolic visual, direct visual, or direct auditory cue) to indicate the display quadrant in which the target Kanizsa square was likely to appear, and this could be the quadrant of the synchronous premask crosses or another quadrant. Symbolic (central) cues, with long cue-target SOAs, had no effect on the synchrony-priming effect, suggesting the priming occurs at a stage not influenced by spatial attention. However, direct (visual and auditory) cues, with short cue-target SOAs, modulated the synchrony-priming effect such that the effect was larger for noncued (invalid) compared to cued (valid) locations. This pattern of results suggests that, when the system is in a reflexive mode of spatial orienting, either the synchronous premask itself, or the expedited formation of the target, acts as a nonconscious 'salience' signal that competes with the cue for the allocation of spatial attention.

◆ **Capturing focused attention**

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The question whether onsets capture attention automatically was examined by asking whether (a) the intentionality, and (b) load criteria are fulfilled. When attention is in a diffuse state, an onset captures attention. Yet, when attention has already been cued to an object or a location, the same onset would fail to capture attention (Theeuwes, 1991 *Perception & Psychophysics* **49** 83–90; Yantis and Jonides, 1990 *Journal of Experimental Psychology: Human Perception and Performance* **16** 121–134). These results have been used as evidence that onsets fail the intentionality criterion of automaticity. In the previous studies, the onsets appear very frequently over trials. In the experiments reported here, it is shown that, if onsets appear infrequently (< 20% of trials), capture would occur even when attention has been prioritised elsewhere. Thus, the intentionality criterion is fulfilled. It is further shown that, even when perceptual load is high, attention capture would occur, thus fulfilling the load criterion. Over time, the capture effect dissipates. The results are explained within the orienting response framework. An onset captures attention when its advent is novel and thus bears information. But when it appears frequently, its appearance becomes an expected occurrence and, over time, it is incorporated into the neuronal model. When this obtains, onsets fail to capture attention.

[Supported by a NUS Grant R-107-000-042-112.]

◆ **Does attention affect the identification of multiple directions in transparent motion?**

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Human observers are able to separate several motion directions in transparent motion stimuli, but we don't know how many directions can be encoded simultaneously in the human visual system.

Previously, we have shown that selective attention helps observers to identify a specific direction of motion in random-dot kinematograms (RDKs) with dots moving in up to 6 different directions, whereas an unattended direction can be identified in no more than 3 directions. Our pattern of results suggested that the limiting factor for identifying a given direction in a transparent RDK is the angular separation between directions, and that providing a cue prior to stimulus presentation can reduce the minimum angular difference. That study thus provided clues about the early encoding of transparent motion, but did not answer the question of how many motion directions can be detected simultaneously. To address this question, we designed two new experiments based on the same stimuli. In the first experiment, observers were simply asked how many directions they detected in RDKs containing 2–8 directions. Whereas reports were reliable for 2 or 3 directions, they dropped to chance for 4 or more directions. A cue indicating only one specific direction of motion prior to stimulus presentation, unsurprisingly did not affect these results. In the second experiment, observers were shown a set of direction vectors after a RDK containing 2, 3, or 4 directions and were asked whether the stimulus was composed of these directions or not. In half of the trials one direction was incorrect, and in half of the trials a precue indicated the set of directions to be attended to. Observers could solve this task for 2 directions, but were at chance for 4 directions, and did not benefit from precues, suggesting that our ability to resolve several motion directions in transparent RDKs simultaneously is severely limited.

[Supported by BBSRC (I11/S1711)]

◆ **Attentional modulation of lateral interactions depends on eccentricity**

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Visual attention has been found to facilitate texture segmentation in periphery by increasing spatial resolution (Yeshurun and Carrasco, 1998 *Nature* **396** 72–75). Campana and Casco (2005 *Perception* **34** Supplement, this issue) show that attention not only increases spatial resolution but also reduces the effect of inhibitory short-range spatial interactions only in periphery. Casco et al (2005 *Vision Research* **45** 2384–2396) found that attention produces a specific facilitation of texture segmentation when texture elements are oriented as the texture boundary (iso-oriented), probably resulting in enhancement of spatial interaction between texture elements. Is this modulation of facilitation by attention dependent on eccentricity? By using a RSVP paradigm, we manipulated, at 0 and 5 deg of eccentricity, the amount of attention allocated to orientation discrimination of a 3-Gabor-group, either horizontal or vertical, in which individual Gabors were either iso-oriented or ortho-oriented and differed by 45° in orientation from background Gabors. Our results show that when attentional resources are largely available, orientation discrimination of the iso-oriented group is facilitated both in fovea and in periphery. In contrast, the reduction of attention has different effects depending on eccentricity: a larger decrease in performance for iso-oriented than ortho-oriented groups in fovea, and a decrease in performance with ortho-oriented groups only, in periphery. Furthermore, whereas in periphery iso-oriented groups are far better discriminated than ortho-oriented ones, in fovea this difference is strongly reduced. These results indicate that in fovea attention is more engaged in grouping iso-oriented elements, whilst in the periphery only grouping of ortho-oriented elements needs attention. Overall, these results suggest that attention affects the strength of lateral interactions differently in fovea and periphery: reducing attention in the fovea reduces the strength of facilitatory lateral interactions between both iso-oriented and ortho-oriented Gabors, whereas in the periphery only the strength of facilitatory interactions between ortho-oriented Gabors is reduced.

[Supported by Ministero dell'Istruzione dell'Università e della Ricerca, grant PRIN 2003.]

◆ **Attentional modulation of visual search depends on the relation between eccentricity and spatial interactions**

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We investigated whether the improvement by attention in visual search is due to the exclusion of distractors, change of decisional criteria, or signal enhancement. Observers searched for the presence of a target line with small (10°) or large (20°) orientation differences from 2, 4, or 8 background elements that were either close or sparse, and either presented at large (~5 deg) or small (~1.5 deg) eccentricity. Results show that element separation affects target sensitivity in opposite directions: d' is higher at small spacing for less eccentric elements, and is higher at large spacing for more eccentric elements. Cueing relevant elements in displays with small spacing and a fixed number of eight elements improves visual search only in the periphery, where the difference in sensitivity due to orientation differences and the reduction in performance at small spacing both disappear. These results make it possible to distinguish a general increase of sensitivity for the target

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in the periphery (signal enhancement) from a more specific modulation of spatial interaction by attention, with the consequent reduction of crowding (distractor exclusion).

◆ **What does attention select in visual search, and why?**

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Space-based accounts of visual attention assume that attention enhances processing of a limited spatial region, independently of the number of objects it contains. Object-based accounts propose that attention selects a limited number of objects, independently of their spatial location. With a series of visual-search tasks, we investigated potential boundary conditions on the operation mode of attention, and related it to the function attention may serve in each task. Search target was always a horizontally oriented ellipse among differently oriented distractor ellipses. Across four experiments, we orthogonally manipulated target–distractor similarity (TD) by the shapes of ellipses, and distractor–distractor similarity (DD) by homogeneous or heterogeneous distractor orientations. We assessed the nature of processing limitation in each experiment with the following design: different numbers of objects were presented tachistoscopically in four concentric areas. A central cue manipulated the spatial extent of the attentional focus. Low-level visual effects were controlled by M-scaling. Overall performance was best in the low-TD-high-DD search (classic pop-out). Here, object number did not limit sensitivity but spatial focus size did. High-TD-low-DD equally reduced overall performance. In both cases, object number affected sensitivity, but only in the high-TD-high-DD condition did spatial focus size also affect sensitivity. High-TD-low-DD search produced the worst overall performance, and sensitivity was an effect of object number but not of spatial focus size. In sum, spatial processing limitations correlated with DD, and object-based limitations with overall task performance. We conclude that attention selects information in limited spatial regions if target detection is supported by grouping homogeneous items. Attention selects objects if target identification is not automatic (because of perceptual similarity, or lack of sufficient distractor grouping). The function of attention in visual search may thus be twofold: it can enhance image segmentation or target identification, each when necessary. The operation mode depends on which process needs attentional modulation.

◆ **Asymmetry of stimulus-driven attentional capture by non-contingent onsets and colour distractors**

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Attentional capture refers to the phenomena that attentional orienting is directed by a task-irrelevant stimulus. It has been argued that only the stimulus that shares the same feature with the target captures attention [the contingent attentional capture hypothesis (eg Folk et al, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 1030–1044)]. This hypothesis excludes the possibility of attentional capture by a stimulus that is not contingent on the properties of the target (ie purely stimulus-driven attentional capture). Nevertheless, stimulus salience increases with display size, and this increases the possibility of stimulus-driven capture. Furthermore, stimulus-driven activation is highest around the time the stimulus appears. It is thus possible that, by increasing display size, stimulus-driven capture can be found at short but not at long cue-to-target stimulus onset asynchrony (SOA). To test this conjecture, we used the same paradigm as Folk et al (1992), but increased display size and manipulated SOA. The target was defined by either a colour or a sudden onset, and a cue preceded the target that either had the same colour, or also had a sudden onset. The target feature or location was never contingent on the cue, and participants were also instructed to ignore the cue as much as possible. Our results show (i) that a non-contingent onset nevertheless captures attention, (ii) that this capture effect occurs early and decreases with SOA, and (iii) that only non-contingent onsets capture attention, and colour cues do not. In conclusion, purely stimulus-driven attentional capture by non-contingent onsets does occur, despite that this violates the contingent attentional capture hypothesis. The fact that onsets capture attention, and colour does not, suggests that onsets are unique in capturing attention after all.

[Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE.]

◆ **Effect of attentional load, habituation, and fatigue on motion-onset VEPs**

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Motion-onset visual evoked potentials (M-VEPs) resulting from an extended series of stimulus presentations can be influenced (apart from the physical parameters of stimuli) particularly by

three factors: attention, adaptation/habituation (active processes), and fatigue. Many authors described modulation of visual motion processing and subsequently also changes in the M-VEPs by attention (Torriente, 1999 *Vision Research* **39** 4122–4139) or adaptation (eg Hoffmann et al, 1999 *Vision Research* **39** 437–444). However, the effect of habituation and fatigue on M-VEPs has not yet been systematically studied. M-VEPs to radial motion outside the central 5 deg of the visual field were recorded in 9 blocks of 120 stimuli (200 ms of motion, 1 s of stationary phase). The duration of one block was 144 s and inter-block rest intervals were 20–30 s. Session duration was about 30 min. M-VEP amplitudes and latencies were evaluated in ten healthy subjects (age span 20–50 years). In each block, subjects completed tasks of three difficulty levels, using random digits generated in the central part of the stimulus field during each stationary phase. The most significant effect observed was amplitude decrease and latency prolongation of the M-VEP dominant peak as a result of inter-block habituation and fatigue. This was particularly strong for the M-VEPs with the easiest task during the stationary phases. With an increase of task difficulty, the effect was less pronounced. The intra-block M-VEP changes exhibited a non-systematic behaviour, influenced probably by fluctuating attention, which seemed to be out of the subjects' control. The study shows that motion-onset detection is not corrupted, but it can even benefit from attentional load since the latter decelerates the habituation/fatigue process.

[Supported by the Ministry of Education of the Czech Republic (grants VZ 0021620816 and VZ 0021620820)]

- ◆ **Influence of a moving object on visual information capacity expressed by span of attention**
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The purpose of this study was to confirm the influence of a moving object on the so-called 'span of attention'. It is well known that human attention is attracted by any moving objects in the visual field. We carried out experiments by presenting a pattern composed of random dots in the display for a short time. Subjects were asked to state how many dots they perceived. Thus the span of attention was measured. We employed two kinds of patterns: one was composed of stationary random dots from 2 to 20 (static pattern), and the other consisted of stationary random dots with 1 moving dot (dynamic pattern). The moving dot in the dynamic pattern was arranged at the top, bottom, right, or left area of the display in order to investigate the influence of the location of the moving object presented. Each pattern was displayed for 165 ms in order to avoid eye movements. The results expressed by the relationship between the number of dots presented and the percentage of correct answers indicated that the span of attention for the dynamic patterns was smaller than that for the static patterns. This shows that human attention was, in fact, attracted by a moving object. Further, we found that the span of attention came down greatly when 9 dots were presented, whereas in the case of dynamic patterns it came down greatly when 8 dots were presented. In addition, the span of attention for the dynamic patterns was smaller when the moving dot was presented at the top of the display than when it was presented elsewhere.

- ◆ **Action modulates object-based selection**
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Cueing attention to one part of an object can facilitate discrimination in another part (experiment 1; Duncan, 1984 *Journal of Experimental Psychology: General* **113** 501–517; Egly et al, 1994 *Journal of Experimental Psychology: Human Perception and Performance* **123** 161–177). We show that this object-based mediation of attention is disrupted when a pointing movement is prepared to the cued part; when a pointing response is prepared to a part of an object, discrimination does not differ between (i) stimuli at locations in the same object but distant from the part where the pointing movement is programmed, and (ii) stimuli at locations equidistant from the movement but outside the object (experiment 2). This remains true even when the pointing movement cannot be performed without first coding the whole object (experiment 3). Our results indicate that pointing either (i) emphasises spatial selection at the expense of object-based selection, or (ii) changes the nature of the representation(s) mediating perceptual selection. In addition, the results indicate that there can be a distinct effect on attention of movement to a specific location, separate from the top–down cueing of attention to another position (experiment 3). Our data (Linnell et al, 2005 *Vision Research* **45** 2268–2286) highlight the interactivity between perception and action.

[Supported by a Co-op grant from the Medical Research Council of the UK to GWH and AMW.]

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◆ **Illusory motion attenuates attentional blink**

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Attempts to report the identity of two temporally closely spaced 'targets' leads to a phenomenon known as the 'attentional blink' (AB) (Raymond et al, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 849–860). The AB has been replicated many times, though a number of experimental situations have emerged where the phenomenon does not occur. Recently, one such report by Olivers and Nieuwenhuis (2005 *Psychological Science* **16** 265–269) revealed that, with only the addition of a non-task-demanding musical background, the AB is largely attenuated. In the present experiment, we sought to determine if (i) the background must be auditory, at the same time creating a cross-modal stimulus condition, and (ii) if there might be a spatial attentional component. In three conditions, we required different groups of participants to perform an AB task at the centre of the display. In two of the three conditions, we created an apparent-motion background with a field of dots moving in one group away from the central AB task, and in the other group toward the central task. In the control group, the same number of dots remained stationary. In contrast to the control group revealing a normal AB, both 'motion' background groups revealed an attenuated AB, with the greatest attenuation occurring in the 'moving outward' condition. We argue that the effect shown by Olivers and Nieuwenhuis (a) is not limited to an auditory background (and thus may be shown within modalities as well as between modalities), and (b) is sensitive to a spatial attentional manipulation such as is created by the illusion of apparent motion. We speculate that ours and the original effect shown by Olivers and Nieuwenhuis may be due to the background task attenuating an unnecessary over-allocation of attention to the first target. [Supported by the Wellcome Trust.]

LIGHTNESS, BRIGHTNESS, AND CONTRAST 1

◆ **Contrast variations in bisection stimulus with flanking stripes**

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In psychophysical experiments, subjects reported the two intervals of the three-dot stimulus to appear different in length in the presence of flanking stripes. The inside flanking stripes caused underestimation of the interval length, while the outside ones, conversely, induced overestimation. The illusion strength was affected by the stripe, dot, and background luminance changes. The illusion diminished when the stripe luminance approached the background luminance value, and the stripes were difficult to discern. When the stripe luminance increased or decreased, in comparison to the background luminance, the illusion strength grew symmetrically, but it saturated at certain luminance and remained approximately constant at higher contrasts. Different background luminances yielded curves similar in shape. The maximum values of the curves increased with dot-luminance decrease. The obtained results follow with predictions of the assimilation theory (Pressey, 1967 *Perceptual and Motor Skills* **25** 569–572) and the weighted averaging model (Anderson, 1974 *Tex Rep CHIP-43*, La Jolla, CA: University of California, San Diego, Center of Human Information Processing, June, pp 215–298): the focal stimulus excitation assimilates (or is averaged with) the excitation magnitude of the contextual figures flanking the focal stimulus.

◆ **Predicting the effect of spatial articulation on lightness**

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Agostini and Bruno (1996 *Perception & Psychophysics* **58** 250–258) found that, under Gelb lighting (an illumination border is made to coincide with the outer border of the display and the rest of the visual field is left in near darkness), the magnitude of the simultaneous lightness contrast effect increases significantly relative to measures taken under homogeneous illumination, and that a similar increase is observed on using CRT simulation. Few years ago, Agostini and Galmonte (1999 *Perception & Psychophysics* **61** 1345–1355) studied the effect of spatial articulation on simultaneous lightness contrast, on the Benary display, and on related displays by using both methods: Gelb lighting and monitor presentation. Both methods revealed a decrease of the simultaneous lightness contrast effect as the spatial articulation increases. In the present work, the same stimuli have been simulated on a CRT monitor and a model of human visual perception (ACE) has been applied to them in order to verify its ability in predicting lightness induction. Observers had to perform lightness matches by choosing from a simulated Munsell scale; these data have been compared with ACE processing result. Agostini and Galmonte's results have been replicated. Furthermore, ACE shows an interesting precision in predicting quantitatively the induction effects. ACE is a

powerful model for predicting human visual perception. Developing a computational tool, like the one considered in this work, has the advantage that a particularly complex configuration can be first analysed by ACE and then tested by psychophysics methods.

◆ **A local contrast metric**

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Local luminance metrics are useful for the quantitative prediction of signal detectability on nonuniform backgrounds. When the background for signal detection is uniform, it makes sense to compute the contrast of a point in the image relative to the overall background luminance, but when there are slow variations in the background, the local background luminance appears to determine the effective contrast (Bowen and Wilson, 1994 *Vision Research* **34** 645–657). In one detection model (Ahumada and Beard, 1998 *SID Digest* **29** 641–644), an ‘optical-blur’ low-pass filter generates a blurred luminance image $B(x, y)$, then a ‘luminance-spread’ low-pass filter is applied to generate a local luminance image $L(x, y)$. The ‘visible’ contrast at each point is then computed as $B(x, y)/L(x, y) - 1$. For near-threshold targets on a uniform background, almost the same ‘visible’ contrast values are obtained by first computing luminance contrast from the uniform background and then filtering the image with a contrast-sensitivity function (CSF) computed as the difference between the two low-pass filters. Thus, if we estimate a two-component model CSF from uniform background detection thresholds, such as those from the ModelFest (<http://vision.arc.nasa.gov/modelfest>), we obtain a measurement of the local luminance spread function for predicting detection on nonuniform backgrounds. Best-fitting difference-of-Gaussian CSFs were found for the 16 ModelFest observer thresholds for images 1 to 10 (constant-width cosine-phase Gabor images). The equal-volume model (zero DC response model) with one luminance spread for all observers gives a good fit to the thresholds (standard deviation of the errors is 3 dB). The estimated standard deviation of the luminance-spread function is 0.4 deg. If spread of activity in the horizontal cell layer is the primary physiological substrate for the local luminance calculation, this analysis provides a psychophysical estimate of the width of this spread in the fovea. [Funding for this work was provided by NASA and the FAA.]

◆ **Role of luminance range and relative area in computation of lightness**

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Surrounding observers’ heads with large opaque domes allowed us to study the computation of lightness in minimal images composed of two gray shades that fill the entire visual field. We specifically tested predictions made by anchoring theory about the role of luminance range and relative area. In the first study, we tested a predicted tendency, called scale normalisation, to normalise the perceived lightness range on the 30 : 1 white : black range. Lightness matches were obtained in three domes, each divided into two shades of gray, with luminance ratios of 1.1 : 1, 3.5 : 1, and 10 : 1. Plotting perceived range against actual range produced a shallower slope than +1, as predicted by the anchoring model, but the lightness range generally showed compression rather than the predicted expansion. In the second study we tested a prediction called the area rule, that while the lighter region will always appear white, the darker region will become lighter as it gets larger, but only when it has a greater area than the lighter region. Each of nine domes was viewed by a separate group of twenty subjects. Each dome contained the same two shades of gray but the domes differed in the relative size of light and dark radial sectors. The results were consistent with the area-rule prediction. These results support the claim that lightness computation in simple images follows the same rules as lightness computation in illumination frameworks embedded in complex images.

[National Science Foundation: BCS-0236701; Public Health Service: GM 60826-02.]

◆ **Adding diagonals to the scintillating grid**

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Recently, Geier et al (2004 *Perception* **33** Supplement, 53) reported that the Hermann grid illusion disappears with simple sinoid distortion of the grid, an observation that cannot be easily reconciled with an explanation based on concentric receptive fields of retinal ganglion cells as proposed by Baumgartner’s model. Rather, it favours (additional) cortical mechanisms, as suggested before, Lingelbach et al (1985 *Perception* **14** Supplement, 7), who showed that the Hermann grid illusion disappears if diagonals are added to the orthogonal grid (for a review see Spillmann, 1994 *Perception*

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23 691–708). We investigated whether adding diagonals to the scintillating grid would likewise weaken or extinguish its strong illusion. A grid (15 deg × 15 deg) showing an optimal scintillating effect—matrix of 9 × 9 black squares, separated by orthogonal medium-grey lines (10 min of arc width) with white dots (15 min of arc diameter) at their intersection—served as reference pattern (A). Diagonals inserted in A were either of the same width as the orthogonal grid bars (B) or thinner: 0.5 (C) or 0.2 (D) times their width. In addition, patterns B–D were modified in that the diagonals were sinusoidally curved leaving the intersections right-angled (E–G). Six observers judged the strength of the scintillating illusion in the modified patterns relative to reference A (100%). The scintillating effect was virtually absent in patterns B (8%) and E (3%) and still markedly reduced with thinner, straight (C, D) or curved (F, G) diagonals, illusory magnitudes ranging from 18% to 32%. Our results show that the above-mentioned influence of diagonals on the Hermann grid also strongly affects the scintillating grid, hence suggesting the involvement of orientation-sensitive cortical mechanisms.

[Supported by ZVA (Zentralverband der Augenoptiker Deutschlands).]

◆ **Laws of figurality and lighting, backlighting, and watercolour illusions**

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Our purpose is twofold. (i) We report new phenomena, called ‘lighting’ and ‘backlighting’, derived from geometrical conditions similar to those inducing the watercolour illusion, ie juxtaposition of two parallel lines varying in brightness and chromatic content. The novel effects were obtained by changing the number of lines (2–6) and the luminance profile (ramp and symmetrical or asymmetrical sawtooth). They demonstrate ‘lighting’ as an emergent percept, the way ‘light’ appears to fall upon an object and how arrangements of ‘lights’ along the boundaries model volume and strengthen the illusion of depth. (ii) We extract from these boundary profiles the ‘laws of figurality’. The Gestalt laws of organisation of Wertheimer (1923 *Psychologische Forschung* 4 301–350) explain how individual elements group into parts that in turn group into larger wholes separated from other wholes (‘objects’), while the laws of figure–ground segregation of Rubin [1915 *Synsoplevede Figurer* (Copenhagen: Gyldendalske Boghandel)]; 1921 *Visuell wahrgenommene Figuren* (Copenhagen: Gyldendalske Boghandel) determine what appears as figure or ground (the boundaries belong only to the figure). The laws of figurality add to these laws by defining the phenomenal appearance of what is perceived as a figure within the 3-D space and under a perceived illumination. They determine the ‘figurality’: the colour and the volume of the object with lit and shaded regions, and the direction and the colour of the light emerging from the object. The main question they answer is how luminance-gradient profiles across boundary contours define both the 3-D appearance of a figure and the properties of the light reflected from the volumetric shape. In other words, the laws of figurality define the specific figural properties of a 3-D illuminated object. Several laws of figurality were demonstrated and, through psychophysical experiments, were shown to be independent from both grouping and figure–ground segregation laws.

[Supported by Fondazione Banco di Sardegna, ERSU and Fondo d’Ateneo ex 60%. Special thanks to Maria Tanca for assistance in testing the subjects.]

◆ **Context effects in assimilation and contrast**

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We have systematically studied the change of lightness appearance in an ambiguous visual pattern. Fuchs (1923 *Zeitschrift für Psychologie* 92 249–325) found that differently coloured parts assimilate, whereas Agostini et al (1993 *Perception* 22 263–272) described the opposite effect: contrast between the subparts. To explore these quite different results in which the perceived organisation could trigger either assimilation effects or contrast effects, we have constructed an ambiguous pattern in which lightness differences between parts could lead to assimilation or contrast. More specifically, we have constructed a visual pattern that could be perceived as a pattern of adjacent straight grey stripes, or as a pattern of adjacent but phase-shifted grey vases. The ambiguous parts, that were darker or lighter than the grey, could belong perceptually to either the stripes or the vases. We asked the participants to judge the relative lightnesses of the grey parts in the stripes and vases. By means of a strong contextual and attentional cue, focusing on either the stripes or the vases, we have induced the perception of one of these structures. It turned out that for any pattern with fixed luminance relations between the different parts, participants could be divided in three classes: one for which contrast dominates, one for which assimilation dominates, and one mixed class. This division turned out to be consistent for each participant.

◆ **Which has the bigger effect: Higher luminance vs luminance adjacency**

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Lightness illusions usually consist of two sets of targets that share the same luminance and/or reflectance but appear different due to local and global photo-geometric features. Here, we present a lightness illusion in which a target (T, luminance 243 cd m^{-2} , reflectance 19.8%) appears lighter than another coplanar surface that has both higher luminance and reflectance (mg, 463 cd m^{-2} , reflectance 30%). The illusion is serendipitous, as it was observed during an experiment with a modified configuration of the staircase Gelb illusion (Cataliotti and Gilchrist, 1995 *Perception & Psychophysics* **57** 125–135), an illusion that in its standard configuration withstands explanations by both contrast and albedo theories, but appears to be well accounted for by the anchoring theory (Gilchrist et al, 1999 *Psychological Review* **106** 795–834). The original purpose of the experiment was to study local luminance interactions among surfaces that are adjacent either at a proximal level of stimulation or also perceptually. The set of stimuli consisted of five adjacent squares ($5 \text{ cm} \times 5 \text{ cm}$) arranged in a row as follows: black (b1, 42.6 cd m^{-2}), light gray (lg, 863 cd m^{-2}), middle gray (mg, 463 cd m^{-2}), dark gray (dg, 165 cd m^{-2}), and black (b2, 42.6 cd m^{-2}). Adjacent to three sides of b2 was T, shaped as a square semi-annulus that measured 2 cm in width from the borders of b2, and 7 cm per side. T and the five squares shared the same special illumination. In order to have a clear view of the interactions at play, we asked our naive observers to match all surfaces, including T, with grey chips from a 35 step Munsell chart. The mean match for T was 8.9, while the mean match for mg was 8. We are currently conducting parametric studies to understand the dynamics of the illusion, and to check whether the illusion is related to classic studies by Wallach.

◆ **Do cortical neurons spatially integrate luminance or edge signals to encode surface properties?**

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Studies of human brightness perception emphasise the importance of long-range spatial integration. One prominent theory posits that the brain spatially integrates polarity-sensitive edge signals to encode surface properties (Retinex theory). Another theory predicts that surface properties are encoded by computing local luminance signals relative to a global estimate of luminance (mean-luminance theory). We developed models that capture these different principles using only a few parameters (3 and 5 for the mean-luminance and Retinex models, respectively). Each model is fit to individual response profiles obtained from 67 surface-responsive macaque V1 neurons (Kinoshita and Komatsu, 2001 *Journal of Neurophysiology* **86** 2559–2570). The Retinex model explains more than 70% of the response variance (an arbitrary value) in 75% of neurons, while the mean-luminance model achieves similar fits in only 49% of cases. We selected for further analysis 52 neurons for which at least one model achieves an acceptable fit. Performance was assessed by a technique for quantifying goodness-of-fit relative to number of parameters, giving the relative probability of each model being correct. We calculated that the mean-luminance model, having fewer parameters than the Retinex model, has a high probability ($p > 0.9$) of being correct in 40% of selected neurons, while the Retinex model is highly likely to be correct in only 12% of selected neurons (the remaining 48% giving no clear-cut result). Thus, the mean-luminance model outperforms the Retinex model by a factor of about three. Our analysis leads to the testable prediction that a small fraction of surface-responsive V1 neurons spatially integrate edge information and a much larger proportion of neurons spatially integrate luminance signals.

[Supported by Grant 051.02.080 from the Cognition Program of the Netherlands Organization for Scientific Research (NWO).]

◆ **A reverse correlation study of the spatiotemporal properties of brightness perception in real and illusory stimuli**

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It has been proposed that the brightness of a uniform surface is determined by the local border contrast responses which are propagated in space by an active, temporally extended filling-in mechanism. Brightness illusions, such as the Craik–Cornsweet–O’Brien illusion where a luminance border gives rise to an illusory brightness percept, have been taken as evidence for this view.

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Here, a reverse correlation technique was used to assess the spatiotemporal characteristics of brightness perception for both 'real' (luminance defined) and 'illusory' surfaces. A contrast polarity discrimination task was used for (i) a 2.6 deg wide bar of uniform luminance and (ii) a 1-D COC bar in which the edges induce the perception of a 2.6 deg wide illusory bar. The target stimulus was flashed quickly, (4 frames, 67 ms) in the middle of a dynamic 1-D white noise sequence of 36 frames. A fixation mark was used to indicate both the location and the duration of the target stimulus. The resulting spatiotemporal classification images show that the brightness perception in both physical and illusory stimuli is associated with two spatiotemporally distinct responses: (i) a spatially local, temporally short border response, and (ii) a weaker response that was similar in both conditions and corresponds spatially to the brightness percept. This response is spatially and temporally more extended than the border response and resembles the output of a spatiotemporal low-pass filter. The maxima of both responses occur rather simultaneously; we could not find significant delays related to the propagation of the brightness signal. There were no marked differences in the classification images in the real and the illusory conditions, suggesting that both low-contrast physical and illusory surfaces are processed by mechanisms having similar spatiotemporal properties.

[Supported by the Academy of Finland.]

◆ **The effect of white-noise mask level on sine-wave contrast detection thresholds**

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The critical-band masking model predicts that the typical U-shaped contrast threshold curve for sinusoidal gratings progressively flattens out and shifts upwards when the gratings are masked by white noise of increasing power spectral density (N0), at least for spatial frequencies below 10 cycles deg⁻¹. To test this prediction, we used Bayesian staircases in a 2IFC paradigm to measure contrast thresholds of horizontal sinusoidal gratings (0.25–8 cycles deg⁻¹) within a fixed Gaussian window, masked with one-dimensional, static, broadband white noise which had one of five power spectral density levels ($0.002 \times 4^k \times 10^{-3}$ cycles deg⁻¹, with $k = 0, \dots, 4$). Raw data showed a progressive flattening of threshold curves with increasing noise level. Theoretical threshold curves from the critical-band masking model were fitted simultaneously to the data at all noise levels, by means of visual filters with log-normal spectral shapes. Assuming channels whose bandwidth in octaves decreases as an affine function of their log centre frequency, the fit was adequate when detection was mediated either by the channel tuned to the frequency of the stimulus or by the channel that maximised the signal-to-noise ratio.

◆ **The Hermann – Hering grid illusion: Human parafoveal perceptible field centre size estimations and establishment of a new methodology for investigative application**

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It is generally accepted that lateral inhibition processes within the receptive fields of retinal ganglion cells influence the Hermann grid illusion (HGI). First, the HGI was used to estimate the perceptible field centre sizes (PFCSs) in the parafoveal area of the human eye with a newly developed methodology based on a nulling technique. Second, the vertical bar luminance and bar width of an isolated intersection of a Hermann grid were adjusted to maximise the illusion strength. A computer-monitor based psychophysical test with randomly interleaved staircases measured the minimum intensity of a patch of light required to null the HGI at different bar widths (range 0.22–1 deg) at three different retinal eccentricities (1.5, 3, and 6 deg) in three normal subjects. An isolated intersection of a Hermann grid was presented with a luminance range of the vertical bar between 0.42 and 138 cd m⁻² whilst the luminance of the horizontal bar was fixed at 138 cd m⁻². A subset of this parameter space was investigated in a further eight normal subjects. The results indicate that PFCS for an optimum HGI strength increases from approximately 20 min of arc at 1.5 deg eccentricity to approximately 35 min of arc at 6 deg eccentricity. As previously reported, there appears to be a broad distribution of PFCSs at each specific retinal eccentricity. We observed differences between subjects in the vertical bar luminance that maximised the strength of the HGI, although all were lower than 7.95 cd m⁻². It is concluded that reliable measurements of the strength of a localised HGI can be made with a nulling technique. These demonstrate an increase in PFCS with increasing retinal eccentricity in the parafoveal human eye and that a range of PFCSs is likely at each eccentricity.

◆ **Distortion tolerance of the Hermann grid**

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Earlier we showed (Geier et al, 2004 *Perception* 33 Supplement, 53) that the Hermann grid illusion disappears by applying certain distortions to the lines. In the absence of an explanation for this new phenomenon, we used psychophysical measurements. The dependent variable was the 'distortion tolerance': at a given distortion type, starting from straight lines and increasing the distortion step by step, we wished to establish a measure when the illusion disappeared for a given subject. The independent variables were the distortion type and the line width. The applied distortion types were sinusoid lines (sinus curves while the intersections rotated, but remaining right angled), wavy lines (sine curves with one period in the middle), humped lines ('humps' in the middle), knotted lines (thicker middles of the lines), and one-sided knotted lines (thicker middles on one side only). Stimuli were shown in random order on a computer monitor: $d = 15$ inches, 1024×768 pixels, viewing distance 60 cm, gazing with free eye movements. Distorted Hermann grids included 7×5 white lines on a black background, with 3 different line widths (11, 17, and 23 pixels), with constant line spacing (102 pixels). There were twenty-two subjects. A two-way ANOVA showed that the main effect of distortion type is highly significant ($p < 0.01$); the main effect of line width is not significant; and interaction is not significant. Pairwise comparison showed that differences between the one-sided knotted line and every other line type were significant; differences between all other pairs were not significant. Our conclusion is that the main cause of the Hermann grid illusion is the straightness of the black–white edges; the line width plays no significant role. Documentation in support of these results can be found at <http://www.geier.hu/ECVP2005>.

◆ **Influence of the coherence of a glaring source on the contrast sensitivity function**

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The contrast sensitivity function (CSF) describes the range of luminous contrasts that can be processed by the visual system. A glaring source in the visual field affects the CSF. The current study was carried out in order to compare contrast sensitivity degradation with a non-coherent glaring light (xenon light) and with a laser glare. CSF was determined with 2-D difference-of-Gaussians profile stimuli. Such stimuli have a 1.0 octave spatial-frequency tuning, with spatial extent fitted to the spatial-frequency content. They are therefore optimal for CSF assessment. Six stimuli were used, ranging from 0.6 to 19.2 cycles deg^{-1} . The two glaring sources were a HeNe laser source and a xenon source chromatically filtered for the same wavelength. Each produced a discoid spot (2.0 deg in diameter, 8.0 deg in eccentricity). The glare luminous flux was 0.0004 lumen (ie retinal illuminance was 209000 td). The test stimulus and the glaring light were strictly superimposed by means of an optical bench and focused for infinity. There were twelve subjects, all volunteers. Data showed no qualitative specific effect from the laser source: the contrast thresholds increased mainly at the low and medium spatial frequencies. But a magnitude in contrast sensitivity degradation occurred with the laser glaring source. Changes in spatial distribution of luminance, due to transmission of laser light through optic structures, and highlighted through local luminance measurements, can account for such a quantitative difference between coherent and non-coherent glare. [Supported by DGA/DSP/SHP, contract no.00CO019 from PEA no.990804.]

◆ **The additive and multiplicative component contribution into Adelson's snake lightness illusion**

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It was recently shown that Adelson's snake lightness illusion could be observed even when the targets had the same contrast as their immediate surround ('iso-contrast snake pattern') (Logvinenko and Ross, 2005 *Spatial Vision* 18 25–72). We studied how the lightness illusion produced by the iso-contrast snake pattern depends on its multiplicative and additive components of the atmosphere transfer function [Adelson, 2000, in *The New Cognitive Neurosciences*, 2nd edition, Ed. M Gazzaniga (Cambridge, MA: MIT Press) pp 339–351]. The multiplicative component alone induced a shadow-like percept which was accompanied by the lightness illusion that gradually increased with its magnitude. The additive component alone produced a 'haze-like' percept accompanied by the lightness illusion that gradually increased with the magnitude of the additive component as well. We measured systematically the illusion strength as a function

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of the magnitude of both components for four observers, using the same techniques as Logvinenko and Ross (2005, loco cit.). The effectiveness of both components was found to be approximately equal (two Munsell units at the maximum of the illusion).

◆ **The orientation dependence of the Hermann grid illusion**

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The Hermann grid illusion (HGI) is the apparent darkening of the intersections of white stripes lying on a dark background. It is currently assumed that the HGI is produced by the operation of antagonistic centre-surround receptive fields (CSRFs) at the early stages of the visual pathway, with the major contribution stemming from the lateral-inhibition circuits of the retina. According to this view, centres of CSRFs located at the intersections of the grid would receive more inhibition from the white stripes than those located along a stripe and flanked by two squares. However, for most people, an oblique presentation of the grid has two effects: (i) a reduction of the HGI, and (ii) the presence or strengthening of spurious lines running diagonally through the squares of the grid ('Prandtl lines'). We present a quantitative characterisation of the HGI elicited by a grid in horizontal-vertical and oblique orientations. The reduction of the HGI elicited by the oblique grid seems inconsistent with the modest anisotropy of retinal and geniculate cell responses, and with their mainly radial orientation bias. Therefore the HGI, so far considered as the prototypical low-level CSRF-originated brightness illusion, might be the result of higher-level mechanisms of the visual system associated with horizontal-vertical biased orientation processing. [Supported by Centro de Investigacion y de Estudios Avanzados del IPN, Mexico.]

◆ **Filling-in of the blind spot: Edge effects in the visual cortex**

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The blind spot is a fairly large (5 deg × 7 deg, centred 16 deg temporally) area of the retina that contains no photoreceptors. In binocular vision, the absence of information is compensated by the other eye, which receives input from the corresponding region of the visual field; but, even in monocular vision, the blind spot is not subjectively noticeable, as the colour and texture of surrounding regions are perceptually filled in. It is debated whether this filling-in reflects higher-order cognitive processes or is generated by neural mechanisms at cortical areas where the retinal topography is preserved. We have obtained evidence for the latter hypothesis in a series of experiments on the minimum information required for filling-in. The blind spots of six trained observers were carefully mapped on a computer screen, and individually fitted frames of colour or texture, having the same shape as the blind spot but varying in width, were generated in Adobe Photoshop. Frame and background luminances were 35.0 and 4.0 cd m⁻², respectively. With narrow frames, owing to the influence of eye movements and Troxler fading, filling-in might be short-lived and partial, ie colour or texture invaded part of the blind spot but left minor areas unfilled or 'foggy'. Observers rated the area subtended by the filling-in on a ten-step scale. With red, green, and blue frames, frame widths broader than 0.26 deg produced complete filling-in (> 90%) on all trials, and complete filling-in was occasionally observed with frames as narrow as 0.06 deg. With texture, complete filling-in (> 90%) of dot patterns and horizontal as well as vertical gratings (1.5 and 2.3 cycles deg⁻¹) was observed with frame widths of 0.43 deg and broader, and occasionally with frames of 0.22 deg. We suggest that filling-in is generated by local mechanisms of the cortex, analogous perhaps to the mechanisms generating the Craik-O'Brien-Cornsweet illusion.

[Supported by DFG-grants SP 67/8-2 and SP 67/9-1.]

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◆ **Length matching distortions in the presence of distracting stripes**

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In the horizontal three-dot stimulus, two vertical flanking stripes were displayed inside one of the stimulus intervals and the third outside the other. Subjects reported that the spatial intervals between dots appeared different in length when their physical extents were equal. To establish the perceived length equality, the subjects changed the test interval length by adjusting its end-dot position. The length matching error grew up proportionally with stimulus size and approached

6%–12% of the stimulus reference interval length. The error increased with increase of the gaps between the dots and the distracting stripes. It reached maximum at the gaps equal to 10%–15% of the reference interval length and monotonously diminished with the following gap increase. The experimental curves appeared to be symmetrical in accordance with the zero gap and showed opposite signs of the illusion strength depending on whether the inside or outside stripes were combined with the reference interval. The experimental findings show the presence of a certain positional averaging, which agrees with predictions of the perceptual assimilation theory (Pressey and Bross, 1973 *Perception* 2 211–217): a shift of the perceived position of the end-points of the stimulus intervals toward the position of appropriate flanking objects, and may be described quantitatively by means of the spatial filtering procedures (Bulatov and Bertulis, 2004 *Informatica* 15 443–454).

◆ **Poggendorff bridges Müller-Lyer and rod-and-frame**

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Since its creation, the Poggendorff illusion has been extensively studied and several theories have been proposed to explain it. Many studies successfully accounted for stretching and modifying the illusion, and the Poggendorff now comes in more than twenty flavours. Lateral inhibition, amodal completion, perspective scaling, perceptual compromises, and configural effects have all been proposed as models to account for the collinearity bias. Here, we approach this illusion using the more general notion of visual frame of reference, and we ask whether the collinearity judgments are based on visual computations of length, orientation, or both. We used a square (as inducing figure) and two oblique lines (as test figures). We measured subjective collinearity. We manipulated the size and orientation of the configuration, the angle between the square and the lines, and the position of the test lines relative to veridical collinearity. We found a main effect of the angle between the test lines and the inducing figure, independent of size, which disappeared when the test lines were vertical or horizontal relative to gravity. The orientation of the lines along the vertical or horizontal axes affected the Poggendorff illusion, indicating a main role of gravitational computations. Our data show that, when the square is upright, the Poggendorff figure behaves like a Müller-Lyer revealing a main effect of angle/length; when the test lines are vertical, the Poggendorff behaves like the a rod-and-frame revealing a main role of gravitational axis. Here, we show that the Poggendorff illusion exposes the signature of a more general visual processing principle called by the Gestalt psychologists 'frame of reference'.

◆ **Size perception in an expanding room: Is stereo and motion parallax information lost without trace?**

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In an immersive virtual-reality environment, subjects fail to notice when a scene expands or contracts around them, despite correct and consistent information from stereopsis and motion parallax, resulting in gross failures of size constancy (Glennerster et al, 2003 *Journal of Vision* 3 490a). We determined whether subjects could be trained using feedback to respond to the stereo and motion parallax signals. Subjects compared the size of two objects, each visible when the room was a different size. As the subject walked across the room it expanded (or contracted). We determined the matched size of the comparison object using a staircase procedure. Twenty psychometric functions were interleaved in each run of 800 trials: 5 changes in room size ($\times 0.25, 0.5, 1, 2, 4$) and 2 distances of the reference and comparison objects. During feedback trials, incorrect responses were signalled by a tone. Size matches were determined before, during, and after the run in which feedback was given. We found that size matches were less dependent on the change in size of the room after feedback. However, matches did not always become more veridical. For conditions in which the comparison was closer than the reference object, subjects made matches that were about 30% smaller than when the comparison and reference were at the same viewing distance. Conversely, matches were about 30% larger when the comparison was more distant than the reference. This was true even in the normal, non-expanding room where, paradoxically, feedback made responses less veridical than before. This pattern of results suggests that in the expanding room subjects do not have independent access to information from stereopsis and motion parallax, even when feedback should help them to use it.

[Supported by the Wellcome Trust and the Royal Society.]

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◆ **Spatial asymmetries: Enhancing the outer unit**

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A well-known but unclear effect in peripheral vision is that letters displayed at a certain eccentricity are recognised better when presented on the peripheral outward side of a string than on the foveal inward side. In early research, this central–peripheral asymmetry had been attributed to serial processing from outward to inward characters. In current models, however, parallel processing is assumed. To study recognition performances of outward versus inward stimuli, Landolt rings were presented in isolation as well as with a flanking bar on the horizontal and on the vertical meridian. The data show that already the recognition of gaps in isolated rings is better when the gaps are presented on the outward side of the ring. Moreover, the side of a flanking bar did not affect the central–peripheral asymmetry, showing that flanking characters are not a prerequisite for the effect. Instead, it is suggested that the outward unit of a stimulus is amplified. This enhancement might be functional for directing visual attention necessary for identification processes. A comparison with isolated and flanked letter recognition performances revealed certain differences in the spatial asymmetries suggesting that the probably attention-driven mechanisms underlying the asymmetry are based on information about the kinds of stimuli.

◆ **Contour processing and the local cross-scale spatial-phase alignment of natural-scene images**

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It is well agreed upon that the phase spectrum of any given Fourier-transformed natural-scene image plays a central role regarding where in the image contours occur, thereby defining the spatial relationship between those features in the formation of the overall structure within a given image. While a handful of anecdotal studies have demonstrated the relevance of the Fourier phase spectrum with respect to human visual processing, none have demonstrated the relative amount of local cross-scale spatial-phase alignment needed to successfully extract meaningful contours from an image. Here, we examined this using a match-to-sample task with a large set of natural images (varying in the degree to which they contained carpentered structures), grouped with respect to their level of sparseness. The phase spectra were band-pass filtered such that the phase angles falling under the filter's pass-band were preserved, and everything else was randomised. The filter width was systematically varied (in 0.3 octave steps) about one of three central frequencies (3, 6, and 12 cycles deg^{-1}) across images (ie test images did not repeat). All images were assigned the same isotropic $1/f$ amplitude spectrum and RMS contrast (50%). On any given trial, following a 250 ms presentation of a partially phase-randomised image, participants were simultaneously shown (for 2 s) four content-matched images and asked which one corresponded to the previously viewed partially phase-randomised image. Results indicated that the bandwidth of local cross-scale spatial-phase alignment needed to successfully match image contours depended on the amount of content (ie relative sparseness) present in the original image, with less sparse images requiring much more phase alignment before image contours could be matched. In addition, there appeared to be a bias favouring content around 6 cycles deg^{-1} , as the amount of local phase alignment needed was often less in that range compared to the other two central spatial frequencies.

[Supported by Canadian Institutes of Health Research (CIHR) grant MT 108-18 to RFH.]

◆ **Analysis of the combination of frequency and orientation cues in texture-orientation perception**

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Visual perception of shape from texture has led to numerous studies aiming to unravel which cues are effectively used by observers. Recently, Li and Zaidi (2004 *Journal of Vision* 4 860–878) have suggested that it is necessary to distinguish between frequency and orientation cues. Following this distinction, we evaluated the contribution of frequency gradients and linear perspective for the perception of shape from texture. We present here several experiments with purposely designed stimuli. Each stimulus represents a plane covered by a homogenous texture composed of Gabor patches. The plane is oriented in depth with a particular slant and tilt and is viewed under perspective projection. Importantly, the frequency of each Gabor patch is determined by the local spatial-frequency gradient defined by the projection. Similarly, the orientation is determined by the local vanishing point induced by linear perspective. This makes it possible to independently manipulate the frequency and the orientation gradients in order to obtain a texture with a specific combination of cues. We synthesise textures presenting only a frequency gradient

or an orientation gradient, or both gradients. For each texture, a slant and a tilt discrimination tasks are performed. We found that frequency-defined textures are better discriminated for large slant angles, and orientation-defined textures are better discriminated when the texture orientation is close to horizontal and vertical. In addition, a perturbation analysis revealed that frequency gradients dominate over linear perspective. These results validate the use of our stimuli for the study of the perception of shape from texture and the decomposition of the texture cue into elementary components.

◆ **Spatial scale and second-order peripheral vision**

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There is ongoing debate concerning the relationship between the second-order visual system and the spatial scale of its first-order input. We sought to investigate this issue by examining the role of spatial scale in determining second-order sensitivity in peripheral vision. Stimuli were spatial-contrast modulations (f_{mod}) of a relatively high-spatial-frequency first-order luminance-modulated carrier grating (f_{carr}). Detection thresholds for the second-order modulation were measured for a parameter space defined by combinations of f_{mod} and f_{carr} in both central and peripheral vision. We were particularly interested in whether the concept of spatial scaling holds for second-order vision. In other words, can second-order vision be equated across eccentricity simply by a change in stimulus scale (size)? Results demonstrate that this is indeed the case, but only for fixed ratios of $f_{\text{mod}}/f_{\text{carr}}$. In other words, stimuli need to be scaled in every respect (both modulation and carrier) in order to be equated across eccentricity. This argues for a strict relationship between second-order vision and the scale of its first-order input. Nonetheless, different $f_{\text{mod}}/f_{\text{carr}}$ ratios each possessed similar spatial scales with respect to eccentricity, indicating a parallel arrangement of dedicated second-order mechanisms having a common eccentricity dependence. Finally, in agreement with previous studies, the spatial scale of the second-order system was found to be quantitatively similar to that for simple first-order stimuli.

◆ **Visual backward masking: Effects of mask homogeneity**

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The majority of studies on visual masking have focused on temporal aspects. However, recently several studies have demonstrated that also the spatial layout of the mask has a profound effect on the masking strength. Especially changes that reduce the homogeneity of a mask greatly enhance its effectiveness. In our study, we investigated the effects of the spatial homogeneity of a grating mask on offset discrimination of a preceding Vernier target. To break homogeneity, the length of some lines of the standard grating was doubled. For example, we used a grating with two longer lines at the two positions next to the Vernier target. By this increase in line length, the visibility of the target was strongly reduced in comparison with a condition in which a standard grating (all lines of equal length) served as a mask. Surprisingly, masking was much weaker if every second line was longer in an alternating fashion (one longer line, one line with normal length, one longer line, etc). Performance for this alternating-line-length mask was comparable to when all grating elements had the same length. However, masking strongly increased when we placed these long lines in a less regular fashion along the grating (ie non-alternating). Therefore, the number of long lines per se cannot explain masking. Our findings indicate that the overall homogeneity of the mask determines its masking effectiveness. Simulations with a Wilson–Cowan type model, consisting of an inhibitory and an excitatory layer, show that simple local interactions between neighbouring elements can explain the effects of mask homogeneity.

◆ **The role of directionality in Giovanelli's illusion**

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When each dot, of a sequence of horizontally aligned dots, lies within a circle, and the circles are not horizontally aligned, the dots are illusorily perceived misaligned (Giovanelli, 1966 *Rivista di Psicologia* **60** 327–336). Previous studies have suggested that the illusion of Giovanelli is based on the influence of the frame of reference. In the present research, we tested the role of the directionality factor on the illusory misalignment. A sequence of misaligned circles was used to induce the illusion. The directionality (the inclination of the sequence of circles) was 0.5° . The adjustment method was adopted: participants varied the position of each dot, from the left to the right of the sequence, until an aligned sequence of dots was obtained. The results indicate

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that the directionality of the sequence of inductive stimuli increases the horizontal misalignment. We conclude that the frame of reference and also the influence of directionality is crucial in providing a comprehensive account of the illusion. The model of orientation maps (Kenet et al, 2003 *Nature* **425** 954–956) is discussed.

◆ **Grouping in the Ternus display: Identity over space and time**

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In the classical Ternus display, the 'group' or 'element' motion percepts reflect biases towards within-frame or across-frame grouping (Kramer and Yantis, 1997 *Perception & Psychophysics* **59** 87–99; He and Ooi, 1999 *Perception* **28** 877–892). With variable ISIs, spatially continuous internal element structure biases within-frame grouping (Alais and Lorenceau, 2002 *Vision Research* **42** 1005–1016). Using a novel configuration of the Ternus display with no ISI, we investigated spatiotemporal grouping by manipulating internal structure of the stimulus elements across space and time. Each of five stimulus frames consisted of three elements (Gabor, SD 0.25 deg, 2 cycles deg⁻¹ carriers): two central elements to either side of a fixation dot, plus one outer element alternating left to right. They were subjected to the following: (i) each stimulus frame was temporally subdivided, with carrier orientation oscillating back and forth about vertical on alternate subdivisions through angles varying from 0° to 90° across trials; (ii) each stimulus frame was subdivided into three frames alternating in orientation through 90° (central elements) or through an additional 0° to 45° range (outer elements); (iii) stimuli as for (i), but outer elements oscillated with a delay ranging from 0 to 100 ms. Observers reported their percept: element or group motion. We found (i) an increased number of subdivisions in each stimulus frame gave more group motion: temporal contiguity influenced within-frame grouping; (ii) larger orientation differences between central and outer elements gave more element motion (thresholds around 30°): spatial contiguity influenced across-frame grouping; (iii) longer delays gave more element motion (thresholds around 40 ms): temporal contiguity influenced across-frame grouping. Thus both spatial and temporal factors can interact to influence the percept of the Ternus display. These interactions have implications for perceptual grouping in Ternus displays, suggesting more complex dynamics than pure spatial interactions, and also challenge short-range/long-range accounts. [Supported by BBSRC.]

◆ **Measuring Vernier acuity with the use of a contrast-masking protocol**

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Contrast masking of a sinusoid target by a grating is dependent on the phase of the stimulus relative to the mask, with the classical view being that a greater phase offset will produce more masking, although performance is dependent on subjects' detection strategy (eg Foley and Chen, 1999 *Vision Research* **39** 3855–3872). We found that, with appropriately chosen stimulus parameters, a target presented between 45° and 90° out of phase with a grating of the same spatial frequency can produce lower thresholds than when the target is presented at 0°. This effect appears to be due to the presence of Vernier cues in the stimulus, displaying 'sub-pixel' Vernier offsets. Modified contrast-masking protocols were used to display sub-pixel offsets with a variety of stimulus configurations. The target was moved out of phase by different offsets relative to the mask. Contrast thresholds were obtained with a QUEST adaptive staircase procedure, by using the psychophysics toolbox for MATLAB (Brainard, 1997 *Spatial Vision* **10** 433–436). Perceived Vernier offset was calculated as follows:

$$\text{Offset} = |x - \pi/2| \text{ radians ,}$$

where $x = \arctan[(0.5 + k \cos \phi)/k \sin \phi]$, k is contrast threshold, and ϕ is phase offset. We obtained an optimal stimulus configuration when the mask was a Gabor patch and the target a small Gaussian-edged square grating, spatial frequency 1.7 cycles deg⁻¹, presented 90° out of phase (see also Little et al, 2005, paper presented at ARVO 2005, abstract 5647/B850). We show that thresholds obtained in this task cannot be explained in terms of contrast-masking mechanisms, that results correlate well with traditional measures of Vernier acuity, and that the target is resistant to blur compared to contrast masking with 0° offset. This novel protocol can be used to present Vernier stimuli at short test distances, overcoming the resolution limit that CRT monitors impose on traditional Vernier tasks.

◆ **Effect of positions of lines on the perception of the Ebbinghaus angular illusion**

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The Ebbinghaus angular illusion (tilt illusion) is a basic illusion which relates to line directions or angles between lines. We conducted a psychophysical experiment and found that perception of such illusions is also affected by positions of lines which consist of a basic line and a line moving on the basic line. In addition, a simulation model of VI in the brain, based on the physiological findings, has been constructed to find a neural architecture which invokes the phenomena. The neurons of this model have inhibitory connections with other neurons whose receptive fields are often different from presynaptic neurons. By using these inhibitory connections, outputs of our model can explain the results of the psychophysical experiments. This model will be useful for constructing a visual architecture with high quality in the near future.

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3-D VISION

- ◆ **Effect of depth perception cues produced by edge pattern for depth-fused 3-D display**
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Suyama et al (2004 *Vision Research* **44** 785–793) suggested a new 3-D display called 'depth-fused 3-D'. An apparent 3-D image in the display can be perceived from only two 2-D images displayed at different depths when an observer views them from the direction in which they overlap. Two 2-D images are created from an original 2-D image projected from 3-D space. The only difference between them is their luminance distributions, which are calculated according to the depth of each object in 3-D space. The authors reported that the depth cue was affected by the subjective edge perceived as binocular disparity. The perceived subjective edge was produced by the luminance ratio and different image positions when the front and rear images overlapped. The purpose of this study was to verify this perceived subjective edge model and examine the depth perception cues when the luminance distribution of image edges is changed. Stimuli were two images. The former was presented as a blurred image in the front or rear display and the latter as a sharp image. Blur values were created by convoluting a point-spread function that was approximated by a Gaussian distribution. In the experiments, a subject adjusted the depth distance of the depth-fused 3-D image for measurement so that the two images were perceived to be at the same depth. We found that when blur values were increased, the depth was changed. In the depth presented by depth-fused 3-D, we could perceive a change in depth, even when we did not change the luminance ratio in the front and rear images. Therefore, when front and rear images at different depths overlapped, there was a subjective edge. We conclude that the image was perceived to have a depth because the edge was perceived by binocular disparity.

- ◆ **Orientation sensitivity to solid and stereoscopic bars in area V1 of the monkey visual cortex**
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It is well known that cortical visual cells are able to detect the orientation of contrast edges. However, it remains to be shown whether these cells are sensitive to orientation of stereoscopic edges. We studied the activity of 225 cells recorded from area V1 in two awake monkeys (*Macaca mulatta*) trained to perform a visual-fixation task. Cell sensitivity to orientation for solid bars was assessed by means of a bright bar flashing over the receptive field with 8 different orientations. Cell sensitivity to orientation for stereoscopic bars was assessed with a stereoscopic bar generated by means of dynamic random-dot stereograms sweeping back and forth in 8 different orientations. Sensitivity to orientation was determined with a sensitivity index which is a normalisation of the ANOVA test:

$$F = \frac{S_{\text{between}}}{S_{\text{between}} + S_{\text{within}}},$$

where S_{between} is the variability inter-condition and S_{within} is the variability intra-condition. The significance level for considering a cell selective was $p < 0.05$. The mean sensitivity index for solid bars ranged between 0.28 and 0.99 (mean = 0.79) and between 0.24 and 0.98 for stereoscopic bars (mean = 0.56). In our sample 72% of cells showed orientation sensitivity for solid bars and 38% of the cells showed orientation sensitivity for stereoscopic bars. The correlation coefficient for orientation sensitivity between solid and stereoscopic bars was 0.84. Our preliminary data suggest that encoding orientation of visual stimuli in visual cortical cells of area V1 may share the same neural mechanisms for solid and stereoscopic figures.

[Supported by grant BFU2004-01839]

- ◆ **Effects of monocular depth cues on perceived distance, perceived velocity, and time-to-collision**
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In humans, perceived object speed in depth is not just derived from the time course of perceived object distance, but involves retinal velocity signals that must be scaled by depth information.

It is not known whether velocity scaling is based on perceived object distance. To address this question, we modified perceived object distance by adding monocular depth cues providing a stationary visual reference frame. We measured the effect of the visual reference frame on perceived distance and time-to-collision (TTC) estimate. TTC is most probably based on the ratio between perceived distance and perceived speed, rather than the ratio between retinal size and retinal expansion rate (tau strategy). The object appeared further away from the observers and TTC was shorter with, than without, the visual reference frame. That TTC was not invariant with respect to the visual reference frame provides further evidence against the pure retinal tau strategy. Moreover, the differential effect of the visual reference frame on perceived distance and TTC refers to the question how perceived object distance is used for velocity scaling. We demonstrate that our result is consistent with the hypothesis that perceived speed is computed by accurate velocity scaling based on perceived distance. Alternatively, perceived velocity may not exclusively depend on this instantaneous velocity-scaling mechanism, but may also depend on the time course of perceived distance. An optimal method to combine multiple measures for estimating object distance and speed in depth is provided by the Kalman filter theory. We analysed a filter using measurements of image size, image expansion rate, and distance derived within the additional visual frame of reference. This model also predicts, in agreement with our experimental data, a differential effect of the reference frame on estimated distance and TTC. This suggests that the velocity-scaling mechanism uses perceived object distance.

◆ **Is depth a psychophysical variable?**

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'Pictorial relief' is the surface of a 'pictorial' object in 'pictorial space'. Pictorial space is the 3-D impression that one obtains when looking 'into' a 2-D photograph. Photographs (any images) do in no way specify a physical scene. Rather, any photograph is compatible with an infinite number of possible scenes or 'metameric scenes'. If pictorial relief is a member of these scenes, the response may be called 'veridical', although the conventional usage is more restrictive. Thus, the observer has much freedom in arriving at his response. To address this ambiguity, we determined the pictorial reliefs for eight observers and for six stimuli. We used a method of cross sections to operationalise pictorial reliefs. We found that linear regression of the depths of reliefs for different observers often leads to very low (even zero) R^2 . It appears that the responses are idiosyncratic to a large degree. Perhaps surprisingly, we also observed that multiple regression of depth and image coordinates often leads to very high R^2 ; sometimes they increased up to about 1! Apparently, 'depth' is to a large extent irrelevant as a psychophysical variable, in the sense that it does not account for the relation of the response to the image structure. This clearly runs counter to the bulk of the literature on pictorial 'depth perception'. The invariant core of inter-individual perception is of an 'affine nature'.

◆ **Systematic deviations in a 3-D exocentric pointing task**

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Research on visual space has mostly been done in horizontal planes. In our previous research, observers had to direct a pointer towards a small ball by remote control. Here, we extended this 2-D exocentric pointing task into three dimensions. The pointer could rotate both in the horizontal plane and in the vertical plane. We varied the horizontal visual angle between the pointer and the ball, the ratio of the distances from these objects to the observer, and the vertical visual angle between the two objects. In all three experiments, the observers had to point from left to right and from above eye-height to below eye-height (and vice versa). First of all, we found rather large deviations in the horizontal plane. Second, for the conditions where the pointer was closer to the observer than the ball, we found increasing deviations with an increase of the horizontal visual angle. Third, we found that the observers were pointing further away than the ball actually was when the pointer was closer to the observer than the ball. However, when the ball was closer to the observer than the pointer, they were pointing in between the position of the ball and the observer. The last parameter, the vertical visual angle, had no effect on the horizontal deviations. These results imply that the distances towards the two objects are overestimated by the observers. In addition, enlarging the distance between the two objects increases the size of the deviations.

[Supported by the Research Council for Earth and Life Sciences (ALW) with financial aid from the Netherlands Organization for Scientific Research (NWO).]

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◆ **Spherical harmonic representation of illumination in complex, 3-D scenes**

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The spectrum of light reaching the eye from a surface depends not only on the reflectance properties of the surface but also on its orientation with respect to light sources in the scene. In a series of recent studies, we and others have shown that the visual system partially compensates for changes in surface orientation and therefore must represent some part of the spatial and spectral variation in scene illumination ('the light sphere'). Lighting in natural scenes (Sun, clouds, sky, inter-reflecting objects) can be extremely complex but not every detail of the light sphere is needed to perform every visual task. In particular, the high-pass variation in the light sphere has little effect on the light reflected by matte surfaces [Basri and Jacobs, 2003 *IEEE PAMI* 25(2) 383-390]. We propose that a biological visual system engaged in estimating surface properties might plausibly represent the light sphere using a spherical harmonics expansion (a spherical analogue of a Fourier series) and that the visual system may use different frequency bands for different visual tasks. We report two experiments concerning the relative importance of low-pass and high-pass information in the light sphere. The results of experiment 1 indicate that the human visual system is able to represent all of the low-pass band (denoted MS[9]) that controls the light reflected by matte surfaces at different orientations. In experiment 2 we compare colour perception in scenes with complex lighting to the same scene illuminated by an MS[9] low-pass approximation of the same lighting. Although we removed much of the high-pass light variation that creates cast shadows and specular highlight, the luminance of matte surfaces was almost identical in the paired scenes. We find differences in perceived surface colour, indicating that the visual system is also using high-pass components of the light-sphere above the MS[9] cutoff. [Supported by Grant EY08266 from the National Institute of Health; Grant RG0109/1999-B from the Human Frontiers Science Program.]

◆ **Stereomotion without changes of disparity or interocular velocity difference**

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Two binocular cues to motion in depth have been identified psychophysically: change of disparity (CD) and interocular velocity difference (IOVD). We evince a third stereomotion cue arising from changes in the extent of binocularly unpaired regions. In experiment 1, a solid black rectangle was presented to one eye, the other eye viewing two rectangles (each half the width of the larger one), separated by a central vertical gap (unpaired background stereopsis: Gillam et al, 1999 *Vision Research* 39 493–502). As these rectangles were moved further apart, subjects perceived a pair of frontoparallel planes moving in opposite directions in depth, despite a lack of any conventional motion in depth cues at the gap between the planes. Subjects adjusted a probe containing CD and IOVD cues to match the amplitude and phase of the motion in depth seen at the gap. Matches were as large for unpaired background stereopsis stimuli as for CD/IOVD stimuli, while no motion in depth was seen for synoptic or monocular targets. This effect was not due to the spreading of CD or IOVD information from the outer edges to the central gap in the unpaired stereograms, since little or no motion in depth (changing slant) was seen in the outer edges of stimuli lacking a gap. In experiment 2, subjects viewed a similar binocular figure whose outer edge remained stationary in both images (no CD or IOVD) while the gap smoothly increased and decreased in size in one monocular image. Subjects reported two planes, fixed at their outer edges, swinging in opposite directions in depth. Again, probe matches showed an equivalence of perceived motion in depth between CD/IOVD targets and their unpaired equivalents, in contrast to a lack of a stable motion in depth percept in synoptic or monocular stimuli.

[Supported by ARC DP0211698 to BG.]

◆ **Motion parallax and specularities on smooth random surfaces**

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When an observer moves through a 3-D scene, the resulting optic flow depends on the direction of heading and on scene depth. Any depth differences across the image give rise to motion parallax. Typical studies of motion parallax as a visual cue to depth consider depth discontinuities and surface slant. These studies assume that surface points are well marked, either by isolated dots or by a matte texture. These markings are needed so that the image velocities can be measured and these velocities correspond to projected velocities of surface points, relative to the

observer. This assumption of fiducial surface markings fails in the case of shiny surfaces, however. For shiny surfaces, objects are reflected in a mirror-like manner and the resulting image motion depends not just on observer motion and depth, but also on the surface curvature. Previous studies of specular motion have concentrated on simple surface geometries such as 3-D ellipsoids. Here, we use 3-D computer graphics to investigate specular motion for more complex surface geometries, namely random terrain surfaces generated by summing 2-D sinusoids. We show that, for such surfaces, motion parallax from specularities can have a similar behaviour to that of parallax from matte surfaces, namely the image motion tends to diverge from the direction of heading as in classical optic flow.

◆ **Investigation of accuracy of 3-D representation of a 3-D object shape in the human visual system**

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The aim of the work was to investigate experimentally a mean-square error of 3-D representation of a 3-D object shape in the human visual system under monocular observation and various aspects. To exclude influence of the texture of the test object surface and the influence of characteristics of the illuminance on the results of measurements, we used test objects uniformly painted white (similar to sculptures) under fixed localisation of standard light sources. In our experiments, we used 3-D images of various complexity, from geometrical primitives to human faces and figures that were generated by means of 3-D graphic editors. 3-D images of the test objects preliminarily distorted in shape and their undistorted references were presented to a group of human observers. The task of the observers was to define the threshold values of distortions under monocular observation and various aspects. On the basis of experimental results, we estimated the mean-square error of 3-D representation of a 3-D object shape in the human visual system. We show that this error depends on the quantity of aspects used in experiments. It decreases when the quantity of aspects increases. We found how the mean-square error depends on the characteristics of the human eye.

◆ **3-D volumetric object perception from the pantomime effect and shading cues**

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Human beings can perceive volumetric objects induced by many kinds of cues, and the binocular disparity and monocular shading cues are two of the most natural ones. In binocular cues, a visual effect named the pantomime effect was reported (Zhang et al, 1998 *Japanese Journal of Applied Physics* **37** L329–L332), in which an illusory 3-D volumetric object is perceived in binocular viewing owing to some stereoscopically displayed inducing objects. On the other hand, shading cues have been studied for a long time. The phenomenon of ‘shape from shading’ is thought to be an ‘early’ visual process computed in the occipital areas and is largely a bottom–up mechanism (Kleffner and Ramachandran, 1992 *Perception & Psychophysics* **52** 18–36; Mamassian et al, 2003 *NeuroReport* **14** 971–975). Our earlier fMRI study found that several brain areas in the left prefrontal cortex were activated when the volumetric object was perceived by the pantomime effect, while some right prefrontal cortical areas were activated by monocular shading cues (Zhang et al, 2004 *Perception* **33** Supplement, 40). Here, we measured the temporal response for the perception of different volumetric objects, and found that the perception induced by the pantomime effect was much shorter than that by monocular shading cues, and also shorter than 2-D perception, which is induced by stimuli similar to that for the pantomime effect but without binocular disparity. Therefore we propose that the perception of volumetric object from shading is not a simple early process, and the right prefrontal cortex processes information from the lower-level visual cortex and projects a top–down signal back to construct a volumetric object perception. On the other hand, the perception from the pantomime effect is accelerated by binocular information though it also recruits some higher-level cortex.

◆ **Summation of pictorial depth cues with motion and disparity gradients**

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Our unified experience of the world derives from a detailed analysis and subsequent recombination of its component parts. A good investigative tool for this process is the summation paradigm in which sensitivities (SENS) to each of a pair of independent signals (A and B) are measured. The two signals are then weighted in a compound stimulus to equate their detectability. A comparison of

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sensitivities to a signal alone (eg $SENS'_A$) and that measured in the compound (eg $SENS'_A$) gives the summation ratio ($SR = SENS'_A / SENS_A$). If the signals are detected independently, then $SR = 1$, though probability summation can increase this to about 1.2. If quadratic summation occurs, then $SR = \sqrt{2}$, consistent with linear summation of the two signals and independent limiting noise on each of the signal channels. Crucially, the observer must disregard the noise associated with the irrelevant signal in the single-signal conditions. If this is not possible (eg the signals are accessed only through the summation process), then signals and noise are summed, and $SR = 2$. Here we use this paradigm to investigate the summation of pictorial (size and contrast) and non-pictorial (disparity) depth cue gradients. Stimuli were two-dimensional arrays (13×13 elements) of grating patches arranged evenly over an invisible square grid, each subject to a small level of random positional jitter, and viewed through a circular aperture (diameter = 17.95 deg). Stimulus duration was 200 ms and black screens ensured there was no extraneous visual stimulation. Summation between pictorial depth cues was quadratic, suggesting the signals could be addressed independently, but summation between pictorial and disparity gradients was less than this, suggesting possible subsystems for pictorial and non-pictorial depth cues. This hypothesis will be tested by measuring summation between each of the present three gradients and a motion gradient. [Supported by the Wellcome Trust.]

◆ **The effect of active exploration of 3-D object views on the process of view generalisation in object recognition**

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Harman et al (1999 *Current Biology* 9 1315–1318) showed that active exploration of novel objects allowed faster visual recognition of these objects than did passive viewing. We examined whether active exploration of particular objects can facilitate subsequent view-matching of different objects within the same category. In a generalisation phase, participants performed a temporal 2AFC discrimination task between two views of novel paper-clip objects. When the two views were of the same object, these were related by rotation ($< 75^\circ$) about the vertical or horizontal axis. Subsequently, in an observation phase, participants were presented with another 5 paper-clip objects. One group of participants (the active group) explored actively each of the objects for 20 s using a track ball in a limited range (-45° to 45°) around the horizontal axis. The other group (the passive group) observed a replay of active exploration of each of those objects by the active group. Following this observation phase, the generalisation phase was repeated twice for both groups of participants. We found that only the active group showed a significant improvement of view generalisation. However, this improvement was limited to those views that were 45° apart about the horizontal axis. Furthermore, the improvement disappeared when we replicated the experiment using a smaller range of active exploration (-30° to 30°). The improved performance following active exploration cannot be due to an improvement in encoding particular object views, since the objects explored actively were different from those viewed in the generalisation phases. We, instead, suggest that active exploration can lead to learning of a rule for view transformation of objects within a particular category. This effect, however, appears to depend on the axis and range of active exploration.

◆ **Influence of visual context on surface deformation perception based on binocular disparity**

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Is the processing of disparity gradient in perception of surface deformation global or local (Devisme et al, 2004 *Perception* 33 Supplement, 93)? Disparity gradient estimation can depend on visual content. To study the influence of binocular disparity cues, sparse random-dot stereograms (RDSs) (small randomly and sparsely placed dots) are commonly used. In slant estimation tasks, perception was similar for sparse RDSs, which convey some depth information, and for a texture which is devoid of depth cues, like starry-night texture (Zabulis and Backus, 2004 *Journal of the Optical Society of America A* 21 2049–2060). In surface deformation detection tasks, stimuli have to be cyclopean images and adapted to a continuous variation of binocular disparity. Two experiments were performed with the same observer's task, but using different stimuli and a dichoptic display mode. The task consisted in detecting deformation of a frontoparallel plane. The first experiment used a stereoscopic stimulus which consisted of white open circles on a black

background with a semi-random distribution and interlaced-frame stereo display. The second experiment used a sparse RDS composed of white points on black background and frame-by-frame stereo display. Open circles and sparse RDSs permitted continuous deformation perception. However, contrary to RDS, the texture of the circles did not convey uniform visual information all over the stimulus. The texture of the circles could indicate that the display was frontoparallel, and then could conflict with disparity information. We were interested whether informational content of image on the whole visual field and display mode would affect deformation detection thresholds. The results suggested that in surface-deformation detection over a large visual field, the significant feature of stimulus was its ability to represent a continuous variation of binocular disparity, whatever the display mode was.

◆ **Preference judgments with stereoscopic stimuli**

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Stereoscopic images (or, possibly, any vivid simulation of depth) can be very striking, particularly on first viewing. Groups of stereo enthusiasts exist (eg 'The Stereoscopic Union') who make and share unusual stereoscopic images. Books of stereograms, especially the 'Magic-Eye' stereograms, have been best-sellers. What is it about these images that is so fascinating? Wade (1987 *Perception* 16 785–818) has suggested that the often unrealistically large disparities used in typical stereoscopic photographs provides an exciting stimulus for a naive observer. Zeki [1999 *Inner Vision* (Oxford: Oxford University Press)], on the other hand, might argue that pure stereoscopic images induce activity in those particular areas of the brain associated with stereoscopic processing, and that this in itself is aesthetically pleasurable. We investigated these issues further by presenting a short sequence of stereoscopic images to 359 members of the general public in the 'Virtual Science Theatre' of the Glasgow Science Centre. Three pairs of data projectors, driven by an SGI workstation, presented stereoscopic images onto a 9.25 m × 1.70 m panoramic screen. Image separation was obtained by using polarising spectacles. Five simple 3-D shapes (cube, sphere, cone, cylinder, pyramid) were presented at five different disparities (large near, small near, zero, small far, large far) in a mixed experimental design. Stimulus size covaried with disparity, so near objects were large and far objects small. Participants were asked to rank the shapes in order of preference. Whilst there was a significant preference, irrespective of shape, for the large near disparities over zero and far disparities, the main effect in the data concerned the shape rather than the disparity/size. This result suggests that the 'wow' response to very large, close stereoscopic stimuli is relatively subordinate to other factors which can be promoted either by attentional cueing or which evoke specific pleasurable associations in memory.

◆ **Extraction of rich and reliable scene representations making use of perceptual grouping and motion**

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An artificial visual system is presented that aims at the extraction of rich and reliable scene information from calibrated stereo sequences. Through the interaction of processes realising spatiotemporal predictions, a high degree of reliability can be achieved. These predictions are based on perceptual grouping mechanisms and 3-D motion. We present a quantitative assessment of the different processes involved and their contribution to the performance of the system. The lower layer of our architecture extracts a sparse map of local and multimodal edge descriptors called primitives. Visual information is coded in terms of multiple visual modalities such as colour, contrast transition, or optic flow. Those primitives are then used in a multimodal stereo matching scheme, associating a confidence to all possible stereo pairs. From those stereo hypotheses one can then reconstruct the associated 3-D scene features. The representation at this level lacks completeness and reliability, since it is based on local mechanisms. However, several schemes using feedback from higher visual processes, like motion estimation and perceptual grouping, are used to improve the overall performance of the system. Perceptual grouping of the extracted local primitives can be applied to draw additional constraints over stereo hypotheses. These constraints allow one to improve the matching quality as well the accuracy of the reconstruction process. We also show how prior knowledge of the camera motion can be used to achieve a richer and more robust representation of the scene. We present a quantification of the impact of the different modalities and of additional constraints drawn from perceptual grouping and 3-D motion on the quality of the scene reconstructed. We could show that the use of all visual modalities as well as the two mechanisms result in an improvement of the scene representations. Their combined use leads to robust and reliable representations.

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- ◆ **Investigation of the efficiency of the human visual system in the case of 3-D images observation**
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The aim of our investigation was to define the algorithm of identification of 3-D test objects by a human observer. The experimental conditions were as follows: the alphabet of the test objects was limited and known, aspects were varied arbitrary and could be not coincident with those at the stage of training. We applied our method of experimental investigation of algorithms of identification of 3-D images of test objects. In the experiments, a wide range of test objects was used: from images of simple 3-D objects to realistic images of 3-D human portraits. We investigated how the efficiency of the human visual system depends on the quantity and aspect angles of the test 3-D objects that were used in training and on a priori information which the observer has at his disposal during identification. On this basis, we found that accuracy and completeness of 3-D representation of 3-D object shape in the human visual system depends on the quantity of various aspects used in training. As a result of these investigations, we developed an algorithm for the identification of 3-D objects and a computer model of the human visual system operating in threshold conditions of observation of the test objects presented at arbitrary aspects.

- ◆ **Neural correlates of 3-D object learning**
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Our 3-D environment challenges the visual system by providing only partial information about the 3-D structure of objects. Learning to recognise and generalise from 2-D views is crucial for 3-D-object perception and discrimination. We used functional magnetic resonance imaging (fMRI) to investigate the cerebral substrates of such learning and recognition in twenty healthy right-handed volunteers. Prior to scanning, subjects were blindfolded to explore haptically 3 objects made of 5 elements arranged in distinctive 3-D structures: 2 objects were mutually mirror-symmetrical, whereas 1 had an internal rotational symmetry. Subjects were then scanned during a supervised learning phase in which they had to discriminate the 3 objects seen under 8 different views, followed by a generalisation test in which they saw learned views and new views from these objects, together with new visually similar objects. fMRI data were analysed as a function of the subjects' performance during both the learning and generalisation phases. Ten subjects were assigned to the 'good' performers group, achieving better 3-D object knowledge than the remaining ten subjects who were assigned to the 'bad' performers group. During the learning phase, the right hippocampus and inferior frontal regions showed increased activity in the good compared to the bad learners (second-level ANOVA), possibly underlying enhanced memory encoding in these subjects. During the generalisation phase, old views produced increased activation in the hippocampus and in left temporal regions when compared to new views, suggesting a special role of these brain regions in memory encoding and/or the reinstatement of memory traces for 3-D objects. Increased view-specific activity (old minus new views) in the good as compared with the bad learners was found in frontal regions, right STS, and the visual cortex, suggesting that enhanced monitoring and visual processing in this group might lead to better recognition performance.

- ◆ **Temporal property of stereoscopic depth discrimination around the fixation plane**
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In stereoscopic viewing, a small depth difference can be resolved when a reference pattern is near to a fixation plane: discrimination sensitivity falls rapidly when the reference plane deviates from the fixation plane. The aim of this study was to investigate a temporal property of stereoscopic depth discrimination when the reference pattern was on or away from the fixation plane. Experiments were conducted in a dark room. Frontoparallel random-dot patterns, with a size of 7.5 deg × 7.5 deg, were generated by a personal computer and displayed on a CRT monitor. Observers viewed them binocularly via mirrors. The viewing distance was 40.0 cm and the fixation distance was 60.0 cm throughout the experiment. In one condition, the pattern was on the fixation plane; in the other two conditions, it was at a position with 5.0 min of arc binocular disparity, crossed or uncrossed, from the fixation plane. In all conditions a square region, 2.5 deg × 2.5 deg area, at the centre of the reference pattern, had 5.0 min of arc crossed disparity

relative to the reference pattern in half the trials. The whole patterns were displayed for 27, 67, 133, 253, 507, 1000, and/or 2000 ms. In each trial, the observers viewed the pattern and responded whether the central square area was in front of the surrounding area. Results showed that ratios of correct response gradually rose with the stimulus duration in all conditions. The function rose quickly when the reference pattern was on the fixation plane. There was not a distinct difference between the conditions in which the reference was with crossed disparity with uncrossed disparity. These results are discussed with respect to properties in processing of binocular disparity information.

[Supported by a Grant-in-Aid for Young Scientists (B), Ministry of Education, Culture, Sports, Science and Technology, Japan.]

◆ **Functional brain imaging of the reverse-perspective illusion**

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Reverse perspective is an illusion of apparent movement in a static picture that is caused by the inversion of depth cues. False motion is seen when the viewer moves in relation to the picture, and is a consequence of a conflict between bottom-up information (the changing retinal image) and top-down information (the visual changes anticipated on the basis of self-motion). We studied the brain response to the illusion using an fMRI technique. As stimuli, a shadow-box (SB) object with normal depth cues and a reverse-perspective (RP) object with inverted cues were prepared. The stimuli were rotated 30° around the vertical axis back and forth during fMRI measurement. A block design method was used in which subjects watched the stimuli moving and stopping (contrast) repeatedly every 24 s. Ten university students participated in the experiment as subjects. Both in RP and SB results, strong activations in the visual area in occipital and parietal lobes, and weak activations in temporal and frontal lobes, were observed. Especially in RP, the activated area was more diffuse. On subtracting SB from RP results, the following four activations were identified. (i) *The boundary between area 19 and area 37, which corresponds to MT.* Although the displayed motion parallax was almost identical in RP and SB, the activation was stronger in RP. (ii) *Area 7.* Spatial information of the stimuli reaches here via the dorsal visual pathway. In the case of RP, the perceived false motion might have caused the strong activation in this area. (iii) *Area 37.* The monocular depth perception from the painted cues might occur in this area. (iv) *Area 8.* This region is related to eye movement. In the reverse-perspective illusion, the rivalry between motion parallax and depth from painted cues may be the cause of these activations.

◆ **Cue combination: No unnecessary loss of information**

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Natural visual scenes contain an abundance of depth cues (eg linear perspective, binocular disparity, texture foreshortening). It is widely assumed that the visual system processes such cues separately. It is typically assumed that some averaging takes place to harmonise the information coming from these cues. This averaging operation is assumed to take the reliability of the cues into account by weighting the cues accordingly. Support for these assumptions is obtained by comparing observers' measured reliabilities to model predictions. Typically, single-cue reliabilities are determined with single-cue stimuli and then used to predict the reliabilities and weights for two-cue stimuli. The actual weights in two-cue stimuli are determined by systematically perturbing (ie adding noise to) one of the cues and determining how much the other needs to be changed to get the same percept as without the perturbation. With this method, observers are forced to ignore cue conflicts even when they are visible. Experimenters using this method have claimed that people lose access to the independent sources of conflicting information. But is this really the case? We let subjects match the apparent slant and surface texture of a test surface to those of a simultaneously visible reference surface. We varied the surfaces in ways that we expected would favour different cues (monocular or binocular), or different comparisons between the surfaces (slant or surface texture). We examined the correlation between the variances in the settings of the two cues. In five different conditions, observers showed five different patterns of errors. We argue that this is not evidence that the cues were combined differently, because all the error patterns were consistent with our expectations. We conclude that (single-cue) information is only 'lost' during cue combination if there is no benefit in retaining the information.

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EYE MOVEMENTS◆ **Eye movements, anisotropy, and similarity**

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Eye-movement recording was used to study the effect of the difficulty of having to make a perceptual organisation contrary to the similarity principle, on the number of fixations and their duration. Another goal was to check how spatial anisotropy affects these two parameters of eye movements. We recorded eye movements of thirty-four students during a perceptual task under two experimental conditions: (i) perceptual organisation according to the gestaltic principle of similarity, and (ii) an organisation contrary to this principle. Under both conditions, the similarity was arranged in the vertical direction in half of the stimuli and in the horizontal direction in the other half. From our results we conclude that a greater response time, a greater fixations number, and a greater fixations duration reflect the difficulty of perceiving a configuration contrary to the similarity principle. The response time was less when the similarity was in the vertical direction than when it was in the horizontal direction. Furthermore, with similarity in the vertical direction, the fixation number was less and their duration was greater. These results show the important role of peripheral pre-processing in explaining fixation durations.

◆ **The effects of optokinetic nystagmus on the perceived position**

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Psychophysical investigations have shown that spatial locations of objects flashed briefly around the time of an impending saccade are distorted, shifting in the direction of the saccade and compressed towards the visual target (Ross et al, 2001 *Trends in Neurosciences* 2 113–121). Similarly, targets presented during pursuit eye movement are mislocalised in the direction of pursuit (Brenner et al, 2001 *Vision Research* 41 2253–2259). Here, we investigate the effects of optokinetic nystagmus (OKN) on visual localisation. Subjects passively viewed a large (100 deg × 70 deg) screen on which a sinusoidal grating drifted at 10 deg s⁻¹. This stimulus elicited strong OKN, comprising slow tracking phases interspersed with fast saccade-like corrective movements. Salient targets (1 deg × 70 deg bars) were flashed briefly at various positions on the screen (superimposed on the drifting grating), and at various intervals relative to saccade onset. The bars were seen shifted in the direction of the slow-phase tracking movement, but the shift was less when flashed near the time of the fast-phase 'saccade'. This result contrasts with that obtained when subjects make voluntary saccades while viewing the OKN stimulus, that caused both a shift in the direction of the saccade and compression, as previously observed with homogeneous fields. The results imply that mislocalisations also occur during reflex eye movements.

◆ **Trans-saccadic integration along the form pathway**

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While the input to the visual system is a series of short fixations interleaved with rapid and jerky shifts of the eye, the conscious percept is smooth and continuous. One possible explanation for this visual stability is that our brain's map of external space is re-mapped around the time of eye movements (Duhamel et al, 1992 *Science* 255 90–92), but there is no evidence for integration of visual patterns across saccades (Irwin, 1991 *Cognitive Psychology* 23 420–456). I tested whether visual form aftereffects showed evidence of re-mapping across saccades. The location of the adapter and test was either matched (spatiotopic integration) or mismatched across the saccade. I found that the magnitude of the face aftereffect was modulated by whether or not the adapter and test were spatiotopically matched. Contrast adaptation, however, did not occur across saccades under any condition. The tilt and shape aftereffects showed an intermediate result, with some spatiotopic-specific adaptation effects. Together, these results suggest that the visual system incorporates predictive and consistent information from the past without requiring pattern integration.

◆ **Eye movements influence how we intercept moving objects**

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Owing to neuromuscular delays and the inertial properties of the arm, people must aim ahead of moving objects if they want to intercept them. We have proposed that misperceiving objects in the direction of ocular pursuit helps people aim ahead of moving objects without them having

to judge the speed of the object. To test this proposal, we asked subjects to hit moving targets as quickly as they could. In separate blocks of trials, they either pursued the target with their eyes or else they fixated a point near the position at which they would hit the target. All targets moved at the same speed, but they started at slightly different positions. The results confirmed that eye movements influence how people intercept moving targets, but subjects started their movements in a direction that was less far ahead of the target (closer to the direction they were looking) during pursuit, rather than further ahead of the target. This difference was not accompanied by a difference in the subsequent movement time. The difference had disappeared by the time subjects hit the target. To examine whether visual information during the movement helped eliminate the initial difference we repeated the experiment, but this time subjects could not see their hand during the movement and received no feedback about whether they hit the target. The tendency to initially aim further ahead of the target when instructed to fixate still disappeared during the movement. It even became a tendency to hit further at the front of the target during ocular pursuit, as we had originally predicted (by a distance corresponding to 50 ms of target motion). Thus, our study confirms that eye movements play an important role in interception.

◆ **Impossible gap paradigm: Experimental evidence for autonomous saccade timing**

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Wing and Kristofferson (1973 *Perception & Psychophysics* **14** 5–12) proposed a model of rhythm production originally based on data from rhythmic finger-tapping experiments. Collins et al (1998 *Experimental Brain Research* **120** 325–334) demonstrated that some of the assumptions of the model are incompatible with data from conscious saccadic rhythm production. SWIFT (Engbert et al, 2002 *Vision Research* **42** 621–636) is a model of saccade generation in reading, based on the assumption of autonomous saccade timing. In reading, we typically find inter-saccade intervals much too short to be timed consciously (220 ms on average versus 400–500 ms on average in saccadic metronome-continuation tasks). In order to be able to observe autonomous saccade timing, we conducted a tracking experiment without explicit timing demands. A saccade target kept appearing at either one of two locations situated 3 deg apart. As soon as a tracking saccade crossed a certain boundary on its way to the target, the target was deleted and ‘reappeared’ at the location where the gaze had just moved from. Consequently, the attempt to keep track of the target resulted in oscillating fixation behaviour, and the time course cannot be attributed to any external metronome. Inter-saccade intervals from eight out of ten subjects showed good agreement with the predictions of the Wing–Kristofferson model, indicating that continuous saccade timing is possible and hence constitutes a plausible assumption in a computational model of eye movements. We found average inter-saccade intervals within the same range as those typical of reading. Results are discussed in light of the SWIFT model and its formal framework.

[Supported by Grant KL 955/3-4 from Deutsche Forschungsgemeinschaft.]

◆ **Microsaccade rate during (un)ambiguous apparent motion**

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Recently, microsaccades have been found to produce perceptual correlates (Martinez-Conde et al, 2000 *Nature Neuroscience* **3** 251–258) and to be influenced by attentional allocation (eg Engbert and Kliegl, 2003 *Vision Research* **43** 1035–1045; Laubrock et al, 2005 *Vision Research* **45** 721–730; Rolfs et al, 2005 *Experimental Brain Research* in press). Attentional influences were found in microsaccade orientation, and inhibition of microsaccade rate was observed in response to (visual or acoustic) display changes. Here we investigate whether microsaccade rate inhibition is an inevitable consequence of display change, or, rather, indicates an attentional orienting response. To this end, we used an apparent-motion display (Williams et al, 2003 *Nature Neuroscience* **6** 616–623) in a motion judgment task requiring ocular fixation. An apparent-motion display incorporates a series of display changes. Independent variables were (a) ambiguous or unambiguous motion direction (with constant velocity), and (b) horizontal or vertical motion. Furthermore, on a fraction of trials, irrelevant peripheral stimuli were presented before the onset of the motion display to induce now well-known effects on microsaccades. Results indicate that the distribution of microsaccade orientations is influenced by whether motion direction is horizontal or vertical. With respect to microsaccade rate, inhibition is mainly related to orienting, not display change. A stereotyped inhibition response is observed after both peripheral flashes and motion onset. However, during continuous motion, rate recovers, showing a higher peak for unambiguous motion. With longer motion intervals and continuous report of perceived motion direction, changes in microsaccade rate systematically precede manual response changes.

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◆ **Do consumers and designers perceive images of design products differently?**

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Earlier studies have shown that expertise affects gaze behaviour. In chess playing, Charness et al (2001 *Memory & Cognition* **29** 1146–1152) found that fixation and saccade metrics differed between expert and intermediate players: experts made fewer fixations and longer saccades. We are interested to see if expertise can also be identified from gaze behaviour while people are viewing design products. As a part of a wider study of perception of design, we studied the gaze behaviour of industrial designers and consumers while they were motivated by different tasks. An eye-tracking study with thirty-two participants was carried out to analyse perception of design products in two tasks: free observation and product evaluation. In free observation, photographs and drawn sketches of four products were shown to the participants. The products were two mobile phones, an axe, and a gardening hoe. Gaze data for this task were obtained from twenty-six participants (thirteen designers, thirteen consumers). In the product evaluation task, five different mobile phones were shown in different combinations for grading. Gaze data from twenty-four participants (ten designers, fourteen consumers) were obtained for this task. In the product evaluation task, there were statistically significant differences in fixation counts between the groups. Designers made fewer fixations on four phones, which is in line with earlier studies. There were no differences in fixation durations or saccade lengths. In the free-observation task, we found similar but smaller differences in fixation counts, durations, and saccade lengths between designers and consumers, and independent-samples *t*-tests of gaze data showed that these differences are not significant. Overall, it seems that motivation is a key factor of the differences in gaze behaviour of experts and novices. Without a motivation the difference is small, but with a clear task expertise affects the gaze.

◆ **Gaze behaviour of experienced and novice spotters during air-to-ground search**

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During the last ten years there have been 1635 crashes in Canada, commonly in remote regions characterised by challenging topography and dense vegetation. Downed aircraft must be located quickly, often by visual search from the air, so that any survivors can be rescued and treated for injuries. This study was designed to develop methods for evaluating the gaze behaviours of spotters during air-to-ground search, assess adherence to a prescribed scan path, estimate visual coverage of the search area, and determine the predictors of task success. Eye movements were measured in five experienced and five novice spotters while searching for ground targets. Spotters were also examined for static visual acuity and performance on a laboratory-based search task. Gaze relative to the head was transformed to gaze relative to the ground by using information from the scene. Patterns in the gaze were then analysed. Inter-fixation amplitude was significantly related to task success, which was independent of fixation rate, fixation duration, and inter-fixation duration. Importantly, experience did not predict task success. The derived measure of aerial coverage was related to the basic gaze measures but was unrelated to task success. Coverage values were generally low, possibly owing to an excessively large prescribed area. The occurrence of a dominant vertical scan frequency was unrelated to basic gaze measures, but was reflective of adherence to the scan path the spotters had been trained to follow. Spotters were instructed to direct their gaze in a regular, vertical scan path, and reports from spotters after the task confirmed that they believed they had adhered to such a pattern. However, gaze was relatively undisciplined, even for experienced spotters who had practiced these scan paths. Future improvements in task success will depend upon increased gaze discipline, perhaps from specific training, and the refinement of scan tactics and search parameters.

◆ **Stimulus-dependent variations in processing time revealed by the choice saccade task**

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Human responses to briefly flashed natural scenes have been analysed in ultra-rapid categorisation studies to determine the time needed to process different kinds of visual objects (VanRullen and Thorpe, 2001 *Journal of Cognitive Neuroscience* **13** 454–461). Recently, we showed that in a forced-choice task, in which two scenes are flashed simultaneously for 30 ms in both hemifields, participants can reliably make saccades to the side containing an animal in just 130 ms (Kirchner et al, 2003 *Perception* **32** Supplement, 170). In several different applications, including backward masking and image rotation, we replicated this high level of performance in the choice saccade

task with accuracy levels of up to 95% correct responses, with the most rapid saccades occurring below 150 ms. By repeatedly presenting a subset of target and distractor images, we show here that it is possible to reveal image-dependent variations: some targets are processed faster and more accurately than others. Intriguingly, in a manual go/no-go categorisation task, none of these images were associated with abnormally short reaction times, although some images were clearly more difficult than others (Fabre-Thorpe et al, 2001 *Journal of Cognitive Neuroscience* 13 1–10). Given our observation of extremely fast responses, it is of great interest to understand why these variations in processing time exist. An analysis of first-order and second-order image statistics showed that none could reliably be used by the subjects to perform the task. Although our targets and distractors differed on virtually all dimensions tested, removing the outliers from the two image sets failed to produce any change in overall accuracy and mean reaction time. We conclude that the choice saccade task is sufficiently sensitive to reveal even subtle differences in processing time between complex natural scenes, and could thus easily be adapted to study a wide range of visual problems.

◆ **Eye scanning activity influenced by temperament traits**

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Human eye movements are usually studied from the cognitive point of view. But the eye movements during scanning activity are not only a manifestation of cognitive processes, they are also influenced by temperament traits. In this study, the scanning activity of an unstructured material was compared with Cloninger temperament scales. Healthy subjects ($N = 25$) were administered through a computer a set of Rorschach tables and instructed to state the first interpretation during fixed time interval ($t = 15$ s). Their eye movements were recorded and after the experiment the subjects were administered Cloninger's TCI-R test. Total saccade trajectory length was measured and compared with TCI-R results. The results show that saccade trajectory length is positively related to the 'novelty seeking scale' and slightly negatively related to the 'persistence' scale. In other words, subjects with higher 'novelty seeking' manifest their temperament at the eye-movement level and tend to move their eyes over longer distances, probably in order to scan a larger area of the stimulus.

◆ **Visual tracking of dynamic stimuli with and without eye movements**

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Observers were instructed to track with or without eye movements a subset of three objects in a field of eight moving objects for a sustained period of several minutes. The eight objects moved randomly and uninterruptedly at a constant velocity, although the three relevant objects were maintained grouped, during the entire task, in a virtual triangle of constant area but varying in shape. One of the five irrelevant objects was displayed at the inner region of the virtual triangle at any given time. At random intervals, a target stimulus of brief duration appeared within any of the eight objects and observers were required to identify it. Results indicated that tracking with eye movements was best when the target appeared within a relevant object or within an irrelevant object displayed outside the area of the virtual triangle. However, when the target appeared within the interior irrelevant object, performance without eye movements was as good as performance with eye movements. These results suggest that eye movements may interfere with the perception of spatial relations among dynamic stimuli.

◆ **Possible influences of fixational eye movements on the neural encoding of natural stimuli**

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It is a long-standing proposal that an important function of the early stages of the visual system is to discard part of the redundancy of natural scenes to establish compact visual representations. In particular, it has been observed that the response characteristics of neurons in the retina and LGN may attenuate the broad correlations that characterise natural scenes by processing input spatial frequencies in a way that counterbalances the power-law spectrum of natural images. Here, we extend this hypothesis by proposing that the movement performed by the observer during the acquisition of visual information also contributes to this goal. During natural viewing, the projection of the stimulus on the retina is in constant motion, as small movements of the eye, head, and body prevent the maintenance of a steady direction of gaze. To investigate the possible influence of a constantly moving retinal image on the neural coding of visual information, we have analysed the statistics of retinal input when images of natural scenes were scanned in a way

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that replicated the physiological instability of visual fixation. We show that during visual fixation the second-order statistics of input signals consist of two components: a first element that depends on the spatial correlation of the stimulus, and a second component produced by fixational instability, which, in the presence of natural images, is spatially uncorrelated. By interacting with the dynamics of cell responses, this second component strongly influences neural activity in a model of the LGN. In the presence of fixational instability, the responses of simulated cells become decorrelated even if their contrast sensitivity functions are not tuned to counterbalance the power-law spectrum of natural images. The results of this study suggest that fixational instability contributes to the establishment of efficient representations of natural stimuli. [Supported by NIH grant EY15732-01 and NSF grant BIC-0432104.]

◆ **Eye movements do not explain visual illusory motion during neck-muscle vibration**

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Vibration of neck muscles induces illusory motion of an LED presented in a dark field, followed by an aftereffect of the illusory LED motion when vibration ceases (Lackner et al, 1979 *Aviation, Space and Environmental Medicine* **50** 346–354). Vibration excites muscle receptors that normally signal head movement, suggesting that possibly the illusory visual motion is the result of the central integration of the (false) head-movement signal and other relevant inputs specifying visual direction. However, vibration also induces nystagmic eye movements whose slow phases Popov et al (1999 *Experimental Brain Research* **128** 343–352) found in their participants to be in the direction opposite to the reported direction of illusory motion. They proposed that unregistered retinal slip, accumulated across the slow phases, is responsible for the illusory motion. Our goal was to test the latter proposal, using moment-to-moment measurements of both eye movements and perceived LED motion during neck muscle vibration and during the aftereffect. Periods of 15 s bilateral vibration of the sternocleidomastoid muscles were alternated with 15 s of no vibration. The participants' task was to fixate an LED presented in darkness, and to point at it at all times using a hand-held tracker. Five out of eight subjects perceived LED motion in the predicted direction (upwards) during vibration. The cumulative slow-phase eye position displaced the eyes downward in 63% of trials in which the upward illusory motion was perceived. There were marked individual differences, with some subjects having mostly upward rather than downward eye displacement. Illusory LED motion was often reversed during the 15 s with no vibration although the eyes, in 56% of those cases, continued to move in the same direction as during vibration. These results rule out retinal slip as the primary contributor to vibration-induced illusory visual motion and aftereffect, favouring the central integration explanation. [Supported by University of Sydney SESQUI grant to TSC, and NHMRC grant to IC.]

MOTION 1

◆ **Global motion affects local judgments of angular displacement**

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The object of this study was to examine whether estimates of the local rotation of a spinning object would be affected by the global movement of the object around a centre of gravity. The critical manipulation was whether the direction of rotation (clockwise—CW or counterclockwise—CCW) was the same or different at the global/local level. The target object was a nested-radial object (NERO)—3 concentric rings of 10 dots with phase shifts between the rings leading to structural variation—that spun locally around its own centre: 1 dot on the outer ring was white, the other 29 were black. Local rotation speed was four times greater than the global speed. Observers tracked the global movement of the NERO as it traversed a random section of a circular path centred on the middle of the screen. There were two tasks: first, remember the position at which the entire shape disappeared; second, remember the local angular position of the white dot around the local ring. Immediately after the NERO disappeared, observers could shift a central probe object using the mouse and click to indicate the estimated global point of disappearance. The probe object was visible at all times at the centre of the screen and was the same size as the target. It consisted of 3 complete circles rather than dots. Once the estimated global position of the target had been indicated, a single white dot appeared randomly on the outer ring of the probe. To estimate local rotation, the position of this dot could be adjusted by using two keys to shift CW or CCW. As in previous studies, local/global congruency had little effect on the remembered global position, with all responses shifted forward in the direction of motion. For local rotation, however, congruent displays gave rise to significantly larger shifts than incongruent displays. [Supported by the Max Planck Institute for Biological Cybernetics, Tuebingen, Germany.]

◆ **Motion-induced localisation bias in a motor control task**

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A moving carrier behind a stationary envelope can cause a perceptual misplacement of this envelope in the direction of the motion (De Valois and De Valois, 1991 *Vision Research* **31** 1619–1626). Yamagishi et al (2001 *Proceedings of the Royal Society* **268** 973–977) showed that this effect can also be found in visuomotor localisation tasks. We created a motor task in which a vertically moving, curved path on a monitor had to be kept aligned with the centre of a Gabor (stationary Gaussian and moving carrier either horizontally or vertically). The seventeen participants controlled the horizontal position of the path with a joystick. According to previous findings, we expected that the motion of the carrier would elicit a misalignment between path and carrier, with a relative displacement in the direction of the motion of the carrier. We found such a bias. Speed, orientation, and eccentricity of the Gabor were manipulated. The bias was enhanced with increasing speed and the orientation determines the direction of the perceptual misplacement. In addition, large eccentricities created an asymmetry in the bias: the bias was greater for inward than outward motion. Implications of these findings for the general understanding of this bias are discussed.

[Supported by the European Commission (HPRN-CT-2002-00226).]

◆ **Effects of a flash's internal motion on mislocalisation during smooth pursuit**

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Previous studies have shown that subjects mislocalise flashes in the direction of motion during smooth pursuit. Rotman et al (2005 *Vision Research* **45** 355–364) suggested that the absence of retinal motion with a flash caused mislocalisation. We wanted to test whether motion of the internal structure of a flash would affect localisation. To this end, subjects had to hit different kinds of flashes that appeared for 70 ms during smooth pursuit: a Gaussian patch without internal structure, a stationary Gabor patch (sine-wave \times Gaussian), a Gabor patch drifting in the direction of the pursuit target, which eliminates retinal motion of the internal structure, and a Gabor patch drifting opposite to the pursuit target, which doubled retinal motion of the internal structure. Foveal and peripheral eccentricities were presented. The results showed an effect of the type of patch when it appeared in the fovea, but not in the periphery. Greater mislocalisation was found with patches involving no retinal motion of the internal structure (a Gaussian patch without internal structure and a Gabor patch drifting in the direction of the pursuit) than with patches involving retinal motion of the internal structure (stationary Gabor patch and Gabor patch drifting opposite to pursuit). The size of the mislocalisation depended only on the presence or absence of motion of the internal structure of a flash and did not scale with its speed. As a drifting Gabor patch may induce an illusory position shift in the direction of motion, a control condition with stationary eyes was run. However, no bias was found in this control condition. In sum, our results support the assumption that the reason for the mislocalisation of foveal targets is the lack of retinal motion, and that global object motion, as well the motion of the internal structure, contribute to the error.

◆ **Responses of first-order motion energy detectors to second-order images: Modeling artifacts and artifactual models**

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Psychophysical studies (eg Smith and Ledgeway, 1997 *Vision Research* **37** 45–62) suggest that contrast-modulated static noise patterns may be inadvertently contaminated by luminance artifacts (first-order motion) when carrier noise elements are relatively large owing to persistent clustering of elements with the same luminance polarity. However, previous studies that have modeled the responses of conventional motion-energy detectors to contrast-modulated static noise patterns have found no evidence of systematic first-order motion artifacts when the mean opponent-motion energy was used to quantify performance. In the present study, we sought to resolve this discrepancy. We subjected first-order (luminance modulations of either static or dynamic noise) and second-order (contrast modulations of either static or dynamic noise) patterns to conventional motion energy analysis. Using space–time representations of the stimuli we measured the net directional response to each motion pattern, using either the mean or the

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peak opponent-motion energies. As luminance artifacts that can arise in contrast-modulated static noise are predominantly local in nature, model responses were studied for a range (1 to 4 octaves) of spatial and temporal filter bandwidths. When the frequency bandwidth of the filters comprising the motion detectors was relatively broad (more localised in space–time) the peak (but not the mean) opponent-motion energy correctly predicts that detectable, local luminance artifacts are sometimes present in contrast-modulated noise patterns, but only when static noise carriers with relatively large elements are used. Furthermore, the model predicts that when dynamic noise carriers are employed (eg contrast-modulated dynamic noise and polarity-modulated dynamic noise), patterns remain artifact free. As such, the modeling and psychophysical results are readily reconciled. Our findings also demonstrate that the precise manner in which computational models of motion detection are implemented is crucial in determining their response to potential artifacts in second-order motion patterns.

◆ **Effects of tilt and day/night simulation on perceived self-motion**

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It is well known that contrast and luminance affect the perceived speed of an object (Pulfrich, 1922 *Naturwissenschaften* **10** 533–564; Thompson, 1982 *Vision Research* **22** 377–380; Snowden et al, 1998 *Nature* **392** 450) and self-motion thresholds (Berthoz et al, 1975 *Experimental Brain Research* **23** 471–489). Contrast affects motion perception where higher contrast patterns are perceived as moving faster (Thompson, 1982 loco cit.) and are associated with a sensation of faster self-motion in driving simulators (Snowden et al, 1998 loco cit.). Thus, both sparse visual information and high-contrast effects might contribute to consistently greater estimates of distance travelled during nighttime simulations, yet there is little evidence indicating how far they have moved. In response to complaints by Canadian Forces pilots using simulators, we tested judgments of self-motion perception under both day and night conditions and found significant differences in judgments of the magnitude of motion with and without simulated physical motion (simulated by tilt). The magnitude of perceived self-motion for nine non-pilots was expressed as a ratio of response to stimulus distance (9 distances for each condition). These ratios were higher in the dark than in the light (1.11 ± 0.08 versus 0.85 ± 0.05) suggesting an overestimation of self-motion magnitude in the dark even in the presence of a physical motion cue (0.92 versus 0.78). Flight simulator designers/operators should consider these phenomena when using simulators for training measures, particularly in cases where fine scale simulation is important ($\pm 10\%$ of the actual distance).

◆ **Orientation cues to motion direction can be incompatible with image smear**

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A model of motion processing proposes that image movement produces motion streaks which indicate the axis of motion. The visual system confuses oriented lines with the streaks; both can determine perceived motion trajectory. Alternatively, Barlow and Olshausen (2004 *Journal of Vision* **4** 415–426) argue that the visual system detects orientation biases in the power spectrum of moving images; we show a more general mechanism is required. Orientation cues are created with micro-balanced, textured lines or dot-pairs which could not result from image smear and produce no spectral cue. Glass patterns were produced with these lines (and also lines defined by luminance increments). Rapid sequences of uncorrelated Glass patterns were displayed and observers were either asked to indicate the direction of apparent coherent motion (experiment 1) or to detect which of two intervals contained patterns producing a coherent motion percept (experiment 2). These contours provided a clear indication of the direction of motion and were as effective as luminance-defined stimuli in signaling coherent motion. The results show that contours can determine the perceived motion direction but contradict the view that only cues that could be produced by physical image smear are effective. The form-motion system receives inputs from texture-sensitive detectors as well. Subsequently (experiment 3) using dynamic, random, 22.5° orientation-bandwidth noise that was contrast-modulated by a drifting sinusoidal function, we have shown that first-order orientation cues also interact with second-order motion cues in motion-direction determination, the modulator drift-direction reported by observers being biased towards the orientation of the noise. The maximum influence occurred for angular differences of approximately 45° between the noise centre orientation and the sinusoidal modulator.

Overall, the evidence supports the use of spatial orientation cues in determining motion direction but is inconsistent with the view that only orientation cues that could be produced by motion smear are used in this manner.

[Supported by the Australian Research Council #DP0346084 and an Australian NHMRC Training Fellowship.]

◆ **Quantitative measurements of the peripheral-drift illusion**

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Fraser and Wilcox (1979 *Nature* **281** 565–566) found that stationary stimuli composed of sectors that gradually change from dark to light produce illusory motion in peripheral vision. They suggested that the direction of perceived motion is determined genetically. In the following studies, the direction of illusory motion was also thought to appear in the direction from dark to light (Faubert and Herbert, 1999 *Perception* **28** 617–621; Naor-Raz and Sekuler, 2000 *Perception* **29** 325–335). Recently, Kitaoka and Ashida (2003 *Journal of Vision* **15** 261–262) induced illusory motion through an effective stimulus configuration consisting of four degrees of stepwise luminance, ie spatial alternation of the combination of black and dark-gray and the combination of white and light-gray. However, their only method was phenomenological observation. Here, we tried to confirm the effectiveness of the stimulus configuration of Kitaoka and Ashida by investigating the duration of illusory motion in a quantitative analysis. We used two types of stimuli. We simplified grating stimuli used by Fraser and Wilcox in four-step luminance stimuli (FW-stimuli) and compared them with the stimuli Kitaoka and Ashida proposed (KA-stimuli). We presented these stimuli on a computer display with a mid-gray background. Subjects pushed one of four response keys corresponding to their percept. The data were analysed according to the direction and the duration of illusory motion. The results show that KA-stimuli induced movement longer than FW-stimuli and that the correlation between the luminance profile and the perceived motion direction was clearly stronger in KA-stimuli. We conclude that KA-stimuli produce a larger magnitude and more steady direction of motion illusion than FW-stimuli when they are presented with a mid-gray background.

[Supported by the 21st Century COE Program to Kyushu University from Ministry of Education, Culture, Sports, Science and Technology, Japan.]

◆ **Equivalent-noise analysis of optic-flow patterns across the visual field**

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An equivalent-noise paradigm was used to investigate contrast sensitivity to radial optic-flow patterns across the visual field in visually normal observers and patients with visual-field loss. Linear digital movies of the visual field at driving speeds of 50 km h⁻¹ were presented monocularly at 0 deg, 8 deg, and 16 deg. The movies (radius 4 deg) were presented in forward or reverse sequence in different levels of space–time filtered 1/f dynamic noise. Fixation was monitored with an eye-tracker. The rms noise contrast was fixed between 0 and 0.2; the rms contrast of the movie was under the control of a staircase. Observers identified whether the motion was forwards or backwards with feedback. By measuring contrast discrimination at various levels of added noise, we estimated how internal noise and efficiency changed across the visual field and following visual-field loss. Contrast sensitivity to optic-flow patterns fell with retinal eccentricity, and the equivalent noise analysis showed that the fall-off was due to both increased levels of internal noise and reduced efficiency for all observers. Patients with peripheral visual-field loss are further impaired relative to normal observers owing to higher levels of internal noise, but show similar levels of efficiency.

[Supported by the Wellcome Trust.]

◆ **Cortical activity during illusory motion sensations: The spinning disks illusion**

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It has been previously established that the human motion-sensitive area V5/MT is responsive when observers view a visual stimulus which conveys illusory motion (eg Zeki et al, 1993 *Proceedings of the Royal Society of London, Series B* **252** 215–222). The contribution of cortical information processing mechanisms to such experiences is not clear owing to, for example, confounding effects induced by eye movements or dynamic changes in the optical system. We have re-examined

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the responses in the brain to such stimuli using fMRI and a novel visual illusion: the Spinning Disks Illusion. In its static form, during eye movements or blinks concentric rings of disks filled with grey-level gradients appear to spin around the centre. Furthermore, dynamic modulation of the background luminance eliminates the dependence on retinal displacements and creates a reliable illusion during steady fixation which can thus be used in a highly controlled manner in psychophysical and physiological experiments. Participants viewed the illusion and a control optic flow stimulus designed to identify the V5/MT complex through specific BOLD responses. In both cases, participants fixated a central point which randomly changed colour at a rate of 1 Hz. Participants performed a colour counting task which aided fixation as well as controlling for different levels of attention and arousal that might be induced by the on/off nature of the block design. Robust activation was observed in the V5/MT complex in response to the optic flow stimulus. Responses to the illusion were found in the same locus, similar in spatial extent but always reduced in magnitude. In the absence of eye movements and attentional changes, these results demonstrate the activity of motion detectors in the absence of physical displacement, and support the notion that cortical motion processing mechanisms have a role to play in generating percepts of illusory motion.

◆ **Velocity judgments of moving visual stimuli are influenced by non-motion factors**

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The correct perception of motion is of great importance for humans and animals. Uses of motion perception include segmentation, judging time for an object to arrive, distance and depth, biological motion, estimating material properties, and tracking something during pursuit. We performed psychophysical experiments with six human subjects focused on factors that affect our subjective perception of speed. We studied some non-motion cues that enhance or reduce speed perception: size, luminance, background motion, motion aftereffect, and different delays between the stimuli. The subjects, sat in front of a screen of 26 deg × 16.5 deg, had to compare two different motion stimuli successively presented, and had to indicate which stimulus moved faster. Each stimulus consisted of a cloud of dots moving within a circular stationary aperture with a radius of 4 deg in normal cases. The responses obtained from subjects were fitted by psychometric functions (MatLab), and we estimated a threshold for correct responses in a given paradigm as inflection points of the fitted function. Control experiments were run where the only difference was speed in a range from -6 to 6 deg s⁻¹ (tested velocities were from 6 to 12 deg s⁻¹). In these curves, the difference in velocity of both stimuli perceived as the same velocity (inflection points, IP) tended to be 0 with a mean of -0.22 deg s⁻¹ and STD of 0.25 deg s⁻¹. In test experiments, we saw clear shifts of IP in cases such as size (radius change), motion adaptation (adaptation stimulus for 2 s in opposite direction), or background motion (moving background in opposite direction), with IP up to 1.34 deg s⁻¹ and STD of 0.32 deg s⁻¹. Otherwise there was no significant shift when we ran experiments of luminance (12.3 or 33.3 cd m⁻²) or different delays (from 1 to 1.5 s). Considering these results, we can say that some non-motion factors affect speed perception but not all of them to the same extent.

[Supported by the European EST 'PERACT'(MEST-CT-2004-504321.)]

OBJECT RECOGNITION

◆ **Figure – ground articulation in moving displays: The role of meaningfulness**

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Experiments on figure – ground articulation often utilise static patterns of black-and-white stripes, with stripes of a given colour possessing a property that favours their figural role. We improved this methodology by using a moving display. In experiment 1, we studied the geometric factor of parallelism (Ebenbreite), using patterns in which parallel-contour regions and nonparallel-contour regions were spatially alternated. In a recognition task, both accuracy (d') and speed were higher for parallel-contour regions, independently of the direction of movement and colour of the target region. In experiment 2, we modified the patterns of experiment 1 by making one nonparallel-contour region meaningful (a human profile). As predicted, recognition of the meaningful region improved. However, the face profile had only a local effect. Increased performance of the meaningful region did not propagate to other stripes of the same colour, as would have been expected if meaningfulness were to produce a global reversal. Interestingly, the rate of false alarms for face profiles ("yes" in negative trials) was high. This suggests that observers

remembered the meaning but not the exact shape of the target region. In general, regions included in movies without a face profile were recognised faster than regions included in movies with a face profile, independently of being bounded by parallel contours or not. Our results are consistent with a local model of figure–ground articulation.

◆ **Part-priming of object naming**

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Part-based theories of object recognition (eg recognition-by-components theory by Biederman, 1987 *Psychological Review* **94** 115–147) postulate that parts are extracted from the image and represented explicitly in a structural description. To provide direct empirical support for the relevance of parts in object recognition, a short-term priming experiment was performed. We used 112 outline stimuli derived from line drawings of common objects (De Winter and Wagemans, 2004 *Behavior Research Methods, Instruments, Computers* **36** 604–624). Naming times of the outline stimuli, presented for up to 2 s, were measured with a voice-onset key. The outline stimuli were preceded by a fixation cross (300 ms), a blank (300 ms), a prime (34 ms), and a blank (300 ms). Four different priming conditions were used in a within-subjects design ($N = 24$), with counterbalanced stimulus assignment and mixed blocks of trials. Object naming was correct in 88% of the trials and required about 800 ms on average. Correct naming times were significantly faster when salient parts (as derived from an independent segmentation study by De Winter and Wagemans, 2005 *Cognition* forthcoming) from the same outline were used as primes, compared to salient parts from a different outline (40 ms slower), other fragments from the same outline (25 ms slower), or a neutral baseline (30 ms slower). This priming effect, which may be largely automatic, indicates that object representations include salient parts but not other contour fragments with similar low-level properties. We relate our findings to possible neural mechanisms of object recognition including re-entrant processing, based on bottom–up and top–down activation of part and object representations.

◆ **Perceptual grouping by proximity, similar orientation, and good continuation in outlines and surfaces derived from objects**

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Since the early days of Gestalt psychology, we have known that perceptual grouping is influenced by proximity, similarity, and good continuation. In this study, we looked at the dynamic properties of these grouping principles by asking subjects to detect structure in displays that were presented for a variable duration and at different densities. Our stimuli consisted of Gabor elements (spatial frequency of 2 cycles deg^{-1} , space constant was one-fourth of the wavelength) whose orientation was manipulated to create a percept of an object. They could be aligned with the local tangent of the contour of the object ('curvilinear'), or all have the same orientation ('isolinear'). The elements were placed either on the outline of the object or on its surface. Object stimuli were derived from a set of line drawings of everyday objects (De Winter and Wagemans, 2004 *Behavior Research Methods, Instruments, and Computers* **36** 604–624), and were placed centrally on a background of randomly oriented elements. Objects subtended approximately 6–12 deg. We used a sequential 3AFC paradigm where the presentation time ranged from 50 to 1000 ms (with pre- and post-mask ISI of 700 ms). Target images contained any of five orientation combinations of contour and surface elements (curvilinear–random, curvilinear–isolinear, isolinear–isolinear, isolinear–random, curvilinear–random, respectively) at three different densities (corresponding to an average element separation of 1.86, 2.23, and 2.79 multiples of the Gabor wavelength). Distractor images contained elements of random orientation, and the task of the subject was to indicate in which he or she saw some structure. Our results showed that isolinear elements were detected at lower presentation times than curvilinear elements. Furthermore, the curvilinear elements were sensitive to a change in element separation, while the isolinear elements were not.

[Supported by the European Commission (HPRN-CT-2002-00226).]

◆ **Influence of complexity on human object recognition and its shape representation**

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Different theories have included complexity as an important factor in object recognition, stressing the advantages of simplicity, which are mostly documented for patterns. We measured human performance in recognising irregular, Fourier-descriptor-based shapes differing in complexity, and compared the results with the sensitivity of macaque infero-temporal (IT) neurons [see also

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Kayaert et al, 2003 *Journal of Vision* 3(9) abstract 514]. The response modulation of IT neurons to shape changes has been shown to systematically correlate with perceptual sensitivity. However, the earlier studies focused on the influence of the magnitude and nature of shape differences on both perceptual and neural sensitivity, rather than on the influence of global properties of the shape (ie the number of concavities and convexities, manipulated through the number of Fourier descriptors). The effect of complexity was measured for the sensitivity to two kinds of shape differences: straight versus curved contours and changes in the configuration of the concavities and convexities (eg their positions, manipulated through the phases of the Fourier descriptors). We observed that the recognition of two sequentially presented identical shapes by our human subjects was more accurate and faster for simple shapes. It was also easier to notice transitions between curved and straight contours in simple shapes. The detection of changes in the configuration of convexities and concavities of simple shapes was faster but not significantly better. The sensitivity of IT neurons corresponded with the human sensitivity for shape changes; there was an increased sensitivity to the simple shapes, but only for the transitions between curved and straight contours. Thus, the influence of complexity on the detection of shape changes is change-specific and linked to the sensitivity of individual IT neurons.

◆ **Character recognition and Riccò's law**

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The contrast threshold for the detection of patches of light depends upon stimulus size as described by Riccò's classical law of areal summation; the critical diameter within which Riccò's law holds increases with retinal eccentricity. Here, we present an analogue of Riccò's law for the recognition of characters at low contrast, and describe its variation with retinal eccentricity. Weber contrast thresholds for the recognition of singly presented digits were determined as a function of character size (0.2–5 deg), at 13 retinal eccentricities on the horizontal meridian up to 36 deg. Log–log contrast–size functions were analysed with respect to maximum slope and a slope of -2 . Stimulus size has a more pronounced effect on character recognition than it has on stimulus detection, such that the maximum slope of the (log–log) areal-summation function is much steeper than Riccò's (-2) slope. It ranges from -3 in the fovea to -7.5 at 30 deg eccentricity. At larger stimulus sizes, there is a range at which Weber contrast threshold C_w is proportional to the stimulus area S^2 (ie the slope is -2); we denote this as the Riccò size range. The latter increases with retinal eccentricity at the same rate as the receptive-field size. Furthermore, the effect size, $e = C_w \times S^2$, is a constant multiple of Spillmann's perceptive field size. The law will be formally related to that of Fischer and May (1970 *Experimental Brain Research* 11 448–464) for the cat. In conclusion, areal summation at the ganglion cell level does not predict areal dependence for character recognition. However, the dependence of the area-dependence function on retinal eccentricity is closely related to receptive and perceptive field size. It is well described by a compact set of equations.

[Supported by the Deutsche Forschungsgemeinschaft, STR 354/3-1.]

◆ **Orientation-invariant representations are activated first in object recognition**

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The time taken to recognise rotated objects increases systematically as an object is rotated further away from its usual (ie upright) orientation. This finding is generally interpreted to mean that the image of a rotated object must be normalised before it can be matched to a stored representation, implying that orientation costs are incurred early in the recognition process. In contrast, some recent studies suggest that early stages of object recognition (within the first ~ 100 ms) are mediated by orientation-invariant representations and that orientation costs arise at a later stage, as an item is consolidated for report (Harris and Dux, 2005 *Cognition* 95 73–93). Here, we used a priming paradigm to investigate how object recognition is affected by exposure duration and object orientation. In each trial, subjects saw a briefly presented photograph of an object (prime), followed by a 100 ms pattern mask, followed by an upright target object which they named as rapidly as possible. The prime appeared in one of 7 orientations (0° , 30° , 60° , 90° , 120° , 150° , 180°) and was either the same object as the target, or a different object. Prime duration (16 ms, 47 ms, 70 ms, 95 ms) was manipulated between subjects. Reliable priming (ie significantly faster naming of same-object targets, compared to different-object targets) was observed with a prime duration of 95 ms. Importantly, this priming effect did not vary as a function of prime orientation. In addition, there was no evidence whatsoever of any priming at the shorter prime durations. These results are inconsistent with normalisation accounts,

as they demonstrate that the initial activation of object representations is orientation-invariant. The viewpoint-dependent costs observed in many experiments must, therefore, arise at a later stage, after the memory representation of an object has been activated.

[Supported by the Australian Research Council.]

◆ **Reaction times for object detection in everyday-life scenes**

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To obtain information about differences in search times for different kinds of suprathreshold objects in everyday-life scenes we developed a computer-assisted object detection test consisting of photos in which a given object has to be found. Fifty-five healthy subjects (twenty-seven males, twenty-eight females) aged 15 to 74 years (mean age 34.9 years) were tested. Search times and rates of mistakes were measured by the computer program. Search times for two groups of seven objects per group were compared: objects with colour (colour objects) and objects presenting characters (character objects). The average search time was 1.82 s on average with a standard deviation of 0.62 s for colour objects. The average search time for character objects was 3.09 s with a standard deviation of 1.75 s. The average search times for colour objects and character objects differed significantly (Student's *t*-test, $p = 0.000$); colour objects were found to be significantly faster than character objects. Thus, different qualities of objects play a role in the detection and recognition of objects in everyday-life scenes.

[Supported by Magdeburger Forschungsverbund Partnerprojekt 1b, BMBF.]

◆ **Influence of orientation on rapid natural-scene discrimination: Psychophysics and physiology**

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We tested whether scene rotation has an influence on the dynamics of rapid scene processing in human observers, and used MEG to investigate the brain processes underlying these effects. All experiments used a 2AFC paradigm. Two photographs of natural scenes were presented to the left and right of the fixation, followed by a mask. All scenes contained one clearly identifiable object embedded in a background. The subject's task was to indicate the scene that contained an animal. The proportion of correct discriminations was measured as a function of scene-mask SOA, and psychometric functions were fitted to determine 75%-correct threshold SOAs. (a) One experiment was designed to investigate the effect of orientation on scene discrimination. Both photographs were presented at one of three orientations (0° , 90° , 180°) with multiple scene-mask SOAs. MEG recordings of the unmasked scenes were obtained. (b) A second experiment was used to evaluate the effects of an object and background orientation mismatch. Objects (Ob) and backgrounds (Bg) were rotated independently (Ob 0° /Bg 0° (all upright), Ob 0° /Bg 90° , Ob 90° /Bg 0° , Ob 90° /Bg 90°). Our findings were as follows. (i) For full scene rotation the discrimination threshold SOAs did not differ for upright and for inverted scenes. Rotations by 90° significantly raised the threshold SOA. The MEG activation differed between the two rotated conditions in parietal sensors between 280 and 380 ms. (ii) Compared to all upright presentation, any rotation by 90° had a significant detrimental effect on discrimination, irrespective of whether the object, background, or both were rotated. The thresholds for the three rotation conditions did not differ. Our psychophysical data indicate that rotation affects the rapid processing of natural scenes, although inversions may be processed very efficiently. The MEG data suggest that 90° and 180° rotated scenes are processed differently, possibly in a parietal rotation module in the brain. Object and background appear to be processed jointly even at very short processing intervals.

[Supported by DFG RI 1511/1-1 and Land Sachsen Anhalt FKZ0017IF0000.]

◆ **Why the temporal order of events determines feature integration**

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How features of an object are bound into a unique percept is one of the puzzling problems in the cognitive neurosciences. In order to investigate the temporal dynamics of feature binding, we used a feature fusion paradigm: a Vernier (V) was immediately followed by a Vernier with opposite offset direction (AntiV). Because of the very short presentation times of V and AntiV, feature fusion occurs, ie only one Vernier is perceived. We presented various sequences of Vs and AntiVs while keeping their total physical energy (duration \times luminance) constant. Surprisingly, the contribution of each Vernier to the fused percept depends not only on its energy but also on the temporal order of the elements. If, for example, a V is followed by an AntiV,

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the AntiV dominates the perceived offset (condition V–AntiV). Dominance changes when the V is subdivided into two equal parts, one of which is presented before and the other after the AntiV (condition $\frac{1}{2}V$ –AntiV– $\frac{1}{2}V$). In general, any level of performance can be achieved by arranging sequences of Vs and AntiVs appropriately—even when the total physical energy of V and AntiV is identical. We conclude that for a given physical energy of V and AntiV the temporal order of presentation determines the integration of features. We found that later elements within the sequence contribute more to the percept than earlier ones. Computer simulations suggest that neuronal decay is sufficient for explaining our experimental findings. Models of feature processing that are mainly energy-based while ignoring temporal aspects cannot account for our findings.

◆ **Sequence selectivity of form transformation in visual object recognition**

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Object motion, eg depth-rotation, provides visual information that might be useful for the reconstruction of an object's 3-D structure, hence increasing the recognition likelihood of any given moving object. Our aim is to demonstrate that object motion can, in itself, serve as an independent cue to object identity without particular recourse to form-retrieval processes. In this study, we used novel amoeboid objects that transformed nonrigidly over time. Two experiments are reported on the learnt recognition of such stimuli. During an initial study phase, participants learnt to identify these objects. At test, participants were either presented with an old/new recognition task (experiment 1) or with a two-alternative forced-choice task (experiment 2). Here, learnt stimuli were presented in either the studied sequence of shape transformations, or the reverse order. Although the shapes shown were the same in both instances, the overall findings indicate that participants performed significantly better in recognising the learnt objects when the same shapes were presented in the learnt sequence, than when they were presented in reverse sequence. If object motion facilitates recognition of the stimulus solely by contributing to the recovery of its form, the sequence of non-rigid transformation would not be relevant to its representation. Nonetheless, these findings suggest that human observers do not merely remember a visual object as a collection of different shapes. Instead, observers are also sensitive to how these shapes transform over time.

◆ **Contextual working memory for trans-saccadic object recognition using reinforcement learning and informative local descriptors**

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Previous research on behavioural modelling of saccade-driven image interpretation (Henderson, 1982 *Psychological Science* **8** 51–55) has emphasised the sampling of informative parts under visual attention to guide visual perception. We propose two major innovations to trans-saccadic object recognition: first, we model contextual tuning at the early visual processing stage. Saliency in pre-processing is determined from descriptors in terms of local gradient histogram patterns—SIFT features (Lowe, 2004 *International Journal of Computer Vision* **60** 91–110). SIFT features are scale-, rotation-, and to a high degree illumination-tolerant, in a substantial extension to previously used edge features (Rybak et al, 1998 *Vision Research* **38** 2387–2400) or appearance patterns (Paletta et al, 2004 *Perception* **33** Supplement, 126). Descriptors that are informative with respect to an information theoretic framework (Fritz et al, 2004, in *Proceedings of the International Conference on Pattern Recognition* volume 2, pp 15–18) are selected and weighted according to contextual saliency. Second, we develop a behavioural strategy for saccade-driven information access, operating on contextually selected features and attention shifts, being performed in terms of a partially observable Markovian decision process and represented by a short-term working memory generating discriminative perception–action sequences. It is developed under exploration and reinforcement feedback using Q-learning, a machine-learning methodology representing operant conditioning. Saccadic targets are selected for attention only in a local neighbourhood of a currently focused descriptor. The learned strategy proposes next actions that support expected maximisation of reward, eg minimisation of entropy in posterior object discrimination. We demonstrate the performance of using the sensory–motor context of trans-saccadic outdoor object recognition, efficiently identifying building facades from different viewpoints, distances, and varying illumination conditions.

◆ **Electrophysiological correlates of contour integration in humans**

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Integration of local features into global shapes has been studied in a contour-integration paradigm. We investigated the neural bases of contour integration with the help of event-related potentials (ERPs). We obtained ERPs while observers had to detect an egg-shaped, closed contour of Gabor patches on a background of randomly positioned and oriented Gabor patches. Task difficulty was varied by gradually rotating the Gabors from the predetermined path of the contour. This resulted in six levels of difficulty, and undetectable contours in about half the trials. We repeated the task at high and low contrast values for the Gabors. Difference waves were constructed by subtracting ERPs for undetectable from those of detectable contours. Contour integration (as reflected in the difference wave) was characterised by a more negative wave between 200 and 300 ms. This difference is generated by an enhanced negativity (at 260–280 ms) at occipito-temporal electrodes. Reducing the contrast of the images also led to an increase of the effect between 200 and 300 ms, and extended the difference to the negative component (at 350–380 ms) of the ERP. The time course of these results is consistent with earlier findings in the monkey cortex (eg Bauer and Heinze, 2002 *Experimental Brain Research* **147** 145–152; Zipster et al, 1996 *Journal of Neuroscience* **16** 7376–7389), suggesting the relevance of a later, ‘tonic’ response phase within the early visual cortex in the integration of orientation information across the visual field.

◆ **Global shape or semantic category preference in peripheral vision**

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The functions of peripheral vision (PV) for object perception remain largely unknown. Nevertheless, recent studies suggest (Levy et al, 2001 *Nature Neuroscience* **4** 533–539; Thorpe et al, 2001 *European Journal of Neuroscience* **14** 869–876) that PV can be used in object perception. In a previous work (Pins et al, 2004 *Perception* **33** Supplement, 74), we showed a preference for some object categories in PV. Nevertheless, this preference depends on the task. Semantic categorisation was easier for faces in PV, whilst discrimination and identification were easier for buildings. Information about global shape could be enough to perform the categorisation task, whilst some semantic information should be useful in both other tasks. Nevertheless, the two semantic categories used had different global shapes: faces are more or less round, whilst buildings are more angular. Thus, in the present study, the effect of stimulus global shape in PV was examined. Sixty subjects took part in the experiments. For each object category, both round and angular stimuli were used. They were displayed at 4 different eccentricities (from 6 to 60 deg), in 3 different tasks: categorisation (face/no-face), discrimination (same/different), and identification (edible/not edible). Categorisation was easier for round shape at large eccentricities whilst no differences between the 2 global shapes were observed in the discrimination and identification tasks. These new results suggest that the preference observed for faces in the categorisation task is determined by the global shape of these stimuli, as round shapes are easier to be categorised in PV. Otherwise, global shape does not seem to be responsible for the building preference, shown in our previous work, in PV for discrimination and identification tasks. This preference could be determined only by the semantic category itself. Thus, the preference for some object category in PV could depend on natural viewing (buildings are usually seen in PV).

◆ **Animals roll around the clock: The rotation invariance of ultra-rapid visual processing**

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The processing required to categorise faces and animals in rapid visual presentation tasks is not only rapid but also remarkably resistant to inversion (Rousselet et al, 2003 *Journal of Vision* **3** 440–456). It has been suggested that this sort of categorisation could be achieved by using the global distribution of orientations within the image (Torralba and Oliva, 2003 *Network* **14** 391–412), which, interestingly, is unchanged by inversion. But, if the subjects really did use a strategy based on global image statistics, image rotations other than inversion should impair performance. Here, we used a forced-choice saccade task (Kirchner et al, 2003 *Perception* **32** Supplement, 170) to analyse how performance varies with image orientation: sixteen subjects made a saccadic eye movement to indicate which of two scenes flashed for 30 ms in the left and right visual fields contained an animal. Both the target and the distractor images were presented randomly at 16 different orientations. The results showed that this form of processing

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is not only very fast, but remarkably orientation-invariant. There were no significant effects on mean reaction times (mean responses were between 236.5 and 244.3 ms for any orientation) and accuracy was also remarkably stable since only the 90° rotation produced a statistically significant, but relatively weak, 6% decrease in efficacy (78.7% correct detection) compared to performance at the best orientation (84.9%). The results imply that this form of rapid object detection could not depend on the global distribution of orientations within the image. One alternative is that subjects are using local combinations of features that are diagnostic for the presence of an animal and that the orientation invariance comes from them having learned to recognise these diagnostic features at a wide range of orientations.

[Supported by CNRS and SpikeNet Technology SARRL.]

◆ **A colour – size processing asymmetry in visual conjunction search**

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While we search for objects in our environment, we must often combine information from multiple visual modalities, such as colour or size. It is generally assumed that individual features are first processed independently prior to an integration stage. If this is correct, one might expect that, for fixed contrasts, the performance ratio between different features is the same for single-feature search as it is for conjunction search. We performed an experiment to assess this hypothesis. We first determined individual colour and size thresholds in which participants performed 70% correct in a single-feature search task. In the main experiment, subjects searched for single features and combinations of features while their eye movements were recorded. Subjects were cued (500 ms) to locate a target among twelve distractors in a circular arrangement (200 ms), followed by a mask (present until an eye movement was made). Across features, we found an asymmetry between the ratios of correct identifications in single-feature and conjunction search: overall, size performance dropped in conjunction search compared to single-feature search, while colour performance remained the same. Saccadic latencies for correct colour and correct size responses in conjunction search were not significantly different, ruling out the possibility of an explanation in terms of a speed–accuracy trade-off. The data suggest an interaction between processing of colour and size information in visual conjunction search. One possible explanation is the existence of visual channels that are conjunctively tuned to colour and size. Another one would be a selective attentional focus on colour in colour–size combination searches.

◆ **Parameters of ‘invisible’ masking affect incomplete image recognition**

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Earlier a new approach was proposed (Chihman et al, 2003 *Perception* **32** Supplement, 122), according to which figural incompleteness was considered to be the result of masking. It is as though the figure is partly occluded by a mask having parameters identical to those of the background. We assume that the visual system, on perceiving such incomplete images, not only picks out informative features in accordance with Biederman’s geons theory (Biederman, 1987 *Psychological Review* **94** 115–147), but determines characteristics of the ‘invisible’ mask for creation of the whole image as a Gestalt. We argue that recognition thresholds for incomplete images primarily reflect signal extraction from noise. To confirm this hypothesis we investigated in detail how parameters of ‘invisible’ masking affect recognition thresholds of fragmented images. The crucial aspect is the clarification of the threshold dependence only from the fragmentation properties, which can be random or well-ordered, differ in respect of the size, phase, and so on of fragments. The alphabet of 70 contour figures of everyday objects was presented in psychophysical experiments, and thresholds of their recognition were measured. Different geometrical structures with variable spatial-frequency characteristics and sizes were synthesised by means of the mask. We used both periodical structures and structures in the form of a noise. We obtained the number of recognised occluded figures as a function of the parameters of ‘invisible’ masking.

Our results strongly stress the role of spatial relations between image parts in the recognition of fragmented objects. The thresholds were found to decrease when spatial-frequency characteristics of the 'invisible' masking had pronounced orientation properties. The thresholds decreased when the masks were well-ordered as compared with masks with random structure. We found that the phase of the random mask is less important for the threshold of recognition at the first presentation, but becomes important in later presentations. We discuss the results in the light of match filtering theory.

◆ **Understanding text polarity effects**

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Scharff and Ahumada (2002 *Journal of Vision* 2 653–666) measured paragraph readability and letter identification for light text and dark text. For all tasks and conditions, responses to light text were slower and less accurate. Repetition of the letter-identification task on a single well-calibrated monitor has demonstrated that the result is not an artifact of apparatus. One potential explanation of the polarity effect is that it results from sensitivity and resolution differences between the ON and OFF pathways that differentiate in the retina. Another possibility is that the polarity effect is the result of increased experience with dark text on light backgrounds. To distinguish between these alternatives, we tried to separate the polarity of the contrast signal from the polarity of the letter by using a pedestal only slightly larger than the letters. The positive letters were placed on a negative pedestal so that the letter was at zero contrast with respect to the large background, but had positive contrast with respect to the local surround. Similarly, negative contrast letters were placed on a positive pedestal. If the physiological hypothesis is correct, the polarity of the pedestal, rather than the polarity of the letters, should control the performance. We presented randomised blocks of all combinations of three contrast levels and two polarities, both with and without a pedestal for the same 12 letters we used earlier. The task was to identify the presented letter as quickly as possible by typing it on a standard keyboard. The results without the pedestal replicated our earlier results. With pedestals, the polarity difference reversed with respect to text polarity. Negative pedestals (positive letters) led to faster and more accurate responses, thus supporting the physiological hypothesis. [Supported by the HMP Project of NASA's Airspace Systems Program.]

BINOCULAR VISION 1

◆ **The effects of the size and exposure duration of binocularly unmatched features on the phantom surface perception**

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When an opaque object occludes a distant surface, binocularly unmatched features exist. Previous investigators have reported some types of stereopsis based on binocularly unmatched features; one of them is phantom stereopsis (Gillam and Nakayama, 1999 *Vision Research* 39 109–112). When we fuse half images of the phantom stereogram, we can perceive the occluding phantom surface bounded by subjective contours in front of two vertical lines, but when we fuse the half images of the stereogram that was made by interchanging the half images of the phantom stereogram, we cannot. Two experiments were performed to investigate the effects of the size and exposure duration of binocularly unmatched features on the phantom-surface perception. The stimuli were the phantom and reversed-phantom stereograms. Observers were asked to report whether or not the phantom surface was perceived while keeping their eyes on the Nonius stimuli of the stereogram. The independent variable of experiment 1 was the line width (1.5, 3.0, 4.5, 6.0, 7.5 min of arc) corresponding to the size of binocularly unmatched features, and that of experiment 2 was the exposure duration of the stereograms (50, 100, 200, 400, 600, 1000 ms). The dependent variable of both experiments was discriminability which was represented by d' (signal detection theory). The results of the two experiments showed that (a) the discriminability was not affected by changing the line width, and (b) the discriminability was slightly decreased with the decrease of the exposure duration. Constructing the phantom surface could be rapid, and independent of the size of binocularly unmatched features.

◆ **Visibility modulation of rivalrous colour flashes with a preceding colour stimulus**

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When different colour flashes (eg red and green flashes) are presented to the corresponding region in the two eyes, observers usually report an unstable and rivalrous percept (binocular rivalry).

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Without changing the rivalrous colour flashes themselves, their visibility can be modulated by monocularly presenting a colour flash prior to the rivalrous flashes ('visibility modulation'). By systematically changing luminance contrasts of the preceding as well as the rivalrous stimuli, we investigated eye and colour specificities of visibility modulation. We used a preceding stimulus (red or green) of 1000 ms duration, 10 ms ISI, and red and green rivalrous flashes of 200 ms. A white surrounding field of 2 cd m^{-2} was always presented during the measurement. The results showed complex visibility modulation depending upon the combinations in colour and luminance between the preceding and rivalrous stimuli. When rivalrous flashes were equiluminant with the surrounding field, the preceding stimuli of lower luminances produced eye-specific enhancement (ie the visibility of the ipsilateral flashes was enhanced regardless of colour combinations between preceding and rivalrous stimuli), whereas the preceding stimuli at equiluminance produced colour specific suppression (eg the green preceding stimulus suppressed a green flash regardless of the eye to which it was presented). Colour-specific suppression was also observed when the preceding and rivalrous stimuli had higher luminances relative to the surrounding field. These results exhibit a clear contrast to 'flash suppression'—visual suppression of a monocular stimulus by the presentation of a different stimulus to the other eye (Wolfe, 1984 *Vision Research* **24** 471–478). Flash suppression has been demonstrated with similar stimulus sequences, but shown to be non-selective to stimulus parameters as long as two stimuli differ in their spatial structure. We are further exploring the nature of visibility modulation, but the present results suggest that these stimulus conditions would provide a good paradigm to investigate binocular colour interactions.

◆ **Spatiotemporal interpolation is processed by binocular mechanisms**

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When an object is occluded by a vertically oriented slit mask, observers see only various stripes of the object. When the object moves horizontally behind this mask, a succession of different slit views of the object is seen. However, subjects perceive the moving object as a whole, ie as if all parts were visible simultaneously (temporal interpolation), and, moreover, across the whole space rather than only within the slits, ie as if the mask was not there (spatial interpolation). To accomplish this task, the underlying brain mechanisms have to detect the motion direction and re-assemble the slit views in the appropriate order. Moreover, the slit views have to persist for a certain time within these mechanisms. We investigated the nature of the underlying motion and form mechanisms in two experiments. Stimulus displays presented multi-slit views of multiple objects, each of them being much smaller than the distance between the slits. Slits were 1 pixel wide, hence omitting local cues pointing to the overall motion direction. Using monocular and binocular presentations as well as critical dichoptic presentations, we show that (i) interpolation can be perceived when the only valid motion cue is presented dichoptically, and that (ii) interpolation performance is not better than chance when monocularly detectable motion is masked dichoptically. Hence, the motion detector underlying interpolation is binocular. Similarly, we presented forms that can only be identified when (i) the input of the two eyes is combined as well as (ii) monocularly identifiable but dichoptically masked forms. Results show that also the form detector is binocular. Our results show that spatiotemporal interpolation relies on standard binocular motion and form detectors. Hence they contradict the idea that the mechanism underlying spatiotemporal interpolation is identical to the monocular Reichardt motion detector described for V1.

◆ **Local mechanism for global adaptation in binocular rivalry**

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The visual system is highly developed for capturing salient features embedded in the visual field for survival. The percept in the visual field is constructed as a result of a fusion of the inputs from the two eyes. When the correlation between the binocular images is low, there is a competition between the two eyes, resulting in binocular rivalry. Thus, studying binocular rivalry in the presence of competing salient features is an effective platform for uncovering how the visual system captures salient features. In spite of many sophisticated studies, the exact nature of the neural mechanism underlying binocular rivalry remains to be clarified. Here, we report a striking example where the ocular dominance pattern in binocular rivalry appears to change in a global manner in which the visual system captures salient features (moving circles). Assuming that the dominance pattern in the double-circle condition could be approximated by a linear combination of the single-circle conditions, we made model predictions for the double-circle conditions from the single-circle data. We conclude that the apparent global dominance change can be explained by local interactions within the neural activities at an early stage of visual processing. We also

report a series of psychophysical experiments in which we studied the neural mechanism underlying the propagation of dominance wave. The apparently global dominance change in the presence of competing salient features has been analysed in detail, by the spatiotemporal sampling method (Taya and Mogi, 2005 *Neuroscience Letters* **381** 63–68). On the basis of the results, we constructed a generic model, where the coexistence of the local as well as the global spatiotemporal activity pattern supported by a small-world network architecture plays a crucial role in adapting to the dynamically changing external world.

◆ **Stereo kinetic pyramid**

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The existence of a smooth contour with constant curvature like the circle and the oval, is regarded as the necessary condition of the occurrence of the stereo kinetic phenomenon. Musatti pointed out that, when the Necker cube is rotated, the impression of substance is absent, though the figure is perceived as a solid. However, it has not been confirmed that the existence of the contour of constant curvature is a necessary condition for the stereo kinetic phenomenon, since a figure without constant curvature such as the rectangle also produces the usual stereo kinetic pattern. In this experiment, eight kinds of figures were presented. The forms were: the circle, the oval, the square, the rectangle, the equilateral triangle, the isosceles triangle, the shape of an island, and the shape of a star. Each figure was drawn on a white ground with a black line. In addition, there were two conditions for eccentricity, whether the centre of the figure corresponded to the centre of rotation or not. Each figure was rotated at 15 rev min^{-1} . The observation time was not restricted. Observers described their perception in sentences and figures. When the eccentric square pattern was rotated, the observers described it as a pyramid. When the island pattern was rotated, the observer described it as a vase. The solid is perceived even when there is no smooth contour of constant curvature. The observer also described an impression of a surface and subjective ridge lines. In the concentric circle pattern, the solid was not perceived. The existence of a smooth contour of constant curvature is not a necessary condition for the stereo kinetic phenomenon. For the perception of the stereo kinetic phenomenon, it is important that some distortions are present (for example, eccentricity) in the figure.

◆ **Anchors aweigh: The cyclopean illusion unleashed**

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The cyclopean illusion refers to the apparent movement of two stimuli positioned on a visual axis when accommodation is changed from one stimulus to the other. Recently, Erkelens (2000 *Vision Research* **40** 2411–2419) reported that the illusion does not occur when the two stimuli are presented against a random-dot background or when a spot on the background is substituted for one of the stimuli. Historically, Erkelens's finding is of interest, because he stands alone amongst a long list of researchers who have reported the robustness of this illusion, namely Wells, Helmholtz, Hering, Carpenter, and Enright. We have shown (2002 *Vision Research* **42** 1307–1324) that Erkelens's stimulus situation evoked eye movements that were too small to elicit the illusion for most observers, and we have hypothesised that the random-dot background used in his study contributed to the difficulty of producing the illusion. Our hypothesis was based on the observations that (a) the relative visual direction of the two stimuli with respect to the random-dot background remains fixed, and (b) the visual system tends to keep large backgrounds perceptually stationary. It predicts that the changes in the absolute visual directions of the stimuli are less likely to be noticed when a background 'anchors' the relative visual directions. Our experiment had four background conditions: random dots, vertical lines, horizontal lines, and dark. The idea was that the vertical-lines and the random-dots conditions would provide strong anchoring for the relative visual direction of the two stimuli, whereas the horizontal-lines and the dark-background conditions would not. In the anchoring conditions, the observers either did not experience the cyclopean illusion, as in Erkelens's study, or, if they did experience the illusion, it was much smaller than it was in the two non-anchoring conditions.

[Supported by NSERC.]

◆ **Fourier analysis of binocular reaction time distributions for luminance changes**

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I examined the temporal properties of binocular detection mechanisms for luminance signals in the frequency domain. Circular random stepwise achromatic pulses were presented on a colour monitor at a 1.5 deg field size. Their luminance was randomly selected between 3 and 27 cd m^{-2}

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in increments of 2 cd m^{-2} . A 15 cd m^{-2} achromatic reference stimuli was selected to provide supra-threshold luminance variations. For this arrangement, simple visual reaction times for manual responses were measured at the fovea under monocular and binocular observational conditions. Three human observers took part in the experiment. The transfer function of the binocular system was defined from the Fourier transform of probability density distributions. Standard filtering techniques were used to remove noise. Analysis of the power spectrum of the transfer function confirms the existence of attenuation at low frequencies, whereas gain was represented as band-pass filters at high temporal frequencies.

◆ **Stereo disparity benefits in minimally invasive surgery tasks and training**

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In minimal access surgery (MAS), surgeons control instruments in the patient's body using a television image relayed by a camera within the body. Although stereoscopic systems are available, they are not used routinely, despite evidence that binocular disparity usually improves depth perception in telepresence systems. The reluctance to use stereoscopic displays could be because experienced surgeons have learned to rely on the available monocular cues and because feedback from their actions compensates for lack of disparity. Here, we report two studies designed to evaluate the potential usefulness of disparity information in MAS. In experiment 1, performance on a 'pick-and-place' task that encapsulates key elements of surgical skill was measured with either monoscopic or stereoscopic viewing, and standard monocular depth cues were available, as in MAS. The availability of binocular disparity improved the speed of performance. In experiment 2, we tested the possibility that while surgeons might still be reluctant to use stereoscopic systems in surgery, they might find their use during training more acceptable. Provision of disparity during training could speed learning by making the early stages of practice easier, and by increasing the number of trials performed. However, this could produce dependence on binocular disparity and impaired performance under monocular viewing. Subjects practised two tasks (pick-and-place and pointing) over four 30 min sessions. The baseline group used a monoscopic display and the experimental group used a stereoscopic display for the first three sessions and a monoscopic display for the final (transfer) session. The experimental group performed better than the baseline group for the first three sessions, but only on the pick-and-place task, and on the transfer trial their performance dropped to baseline. Thus, nothing appears to be gained by training with a stereoscope if surgery is to be performed monoscopically.

◆ **Effects of depth on the Ouchi illusion**

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The Ouchi illusion is an apparent sliding motion perceived in a central disk portion and a surrounding portion with orthogonally oriented checkerboard patterns [Spillmann et al, 1993 *Investigative Ophthalmology & Visual Science* 34(4) 1031]. By adding actual depth to two portions of the Ouchi figure, we examined whether the illusion is sensitive to depth relationships. If this were the case, the checkerboard pattern of the central disk should show smaller or no amount of sliding motion when it is not coplanar with the pattern of the surroundings. Observers moved the stimuli and reported the amount of sliding motion of the checkerboard pattern in each portion, performing magnitude estimation in three conditions: the floating condition (the disk was closer to the observers than the surroundings), the hole condition (the disk was further than the surroundings), and the coplanar condition (the disk and the surroundings were on the same plane). Results showed that the amount of sliding motion in the floating and hole conditions was significantly smaller than that in the coplanar condition. The amount of sliding motion of the central disk was always significantly larger than that of the surroundings except in the floating condition. These results suggest that the actual depth order of the two portions in the floating condition has reduced the amount of sliding motion of the pattern in the disk. We conclude that the Ouchi illusion is sensitive to depth relationships, and the perceived depth order of the illusion between the central disk and the surroundings is consistent with their actual depth order in the hole condition.

◆ **Neural correlates of binocular rivalry in the human LGN and V1: An fMRI study**

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The neural mechanisms underlying binocular rivalry are still controversial. In early neuroimaging and single-cell studies, neural correlates of binocular rivalry were found in higher visual processing

areas, but more recent studies indicated that binocular rivalry is already resolved in V1. Here, we test whether neural correlates of perception during rivalry can be found as early as in the human LGN. Four subjects viewed rival dichoptic sine-wave gratings of two different contrasts and orientations through red/green filter glasses while echo planar images of the LGN and visual cortex were taken in a 3T head scanner (3 mm × 3 mm × 3 mm voxel size, TR = 1000 ms). The sensitivity of the LGN and V1 to stimulus contrast was used to compare responses evoked by gratings of 15% and 70% contrast between perceptual alternations during rivalry and physical stimulus alternations. Subjects indicated the perceived grating orientation by button presses. We reasoned that if rivalry were resolved in each structure, the BOLD signal evoked by the perception of high or low contrast gratings during rivalry would be similar to that during physical alternations of the same stimuli. We found that the hemodynamic response obtained during rivalry in the LGN and V1 increased when subjects perceived the high-contrast grating and decreased when subjects perceived the low-contrast grating. The pattern of responses was similar to that evoked during physical alternations. Our results confirm previous findings in V1 (Polonsky et al, 2000 *Nature Neuroscience* **11** 1153–1159). Importantly, they provide the first physiological evidence that neural correlates of binocular rivalry are present in humans as early as the LGN. In conclusion, binocular rivalry might be mediated by means of a selective suppression of LGN layers that process the input from one particular eye. The controlling modulatory input could be provided by feedback projections from the cortex where interocular competition is resolved.

◆ **Segmentation based on binocular disparity and convexity**

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Figure-ground segmentation enables contour curvature to be classified as either convex or concave, and it is known that convexity and concavity information affects human performance. At the same time, it is believed that in the process of segmentation itself there is a bias to maximise convexity [Kanizsa and Gerbino, 1976, in *Vision and Artifact* Ed. M Henle (New York: Springer) pp 25–32]. We report a series of experiments using random-dot stereograms (RDSs) in which observers discriminate which of two areas is nearer in depth. This leads to one half of the display to be seen as figure and the other as ground. Binocular disparity in the RDSs defines a correct response. In addition, by using an aperture, only one segment of the contour that separates the two areas is visible. The task is therefore a local judgment. By contrast, previous work in the literature used ambiguous stimuli with no single, correct interpretation, and complex shapes bounded by contours with a mix of local convexities and concavities. We hypothesised that if the system has a bias to assign figural status to the convex side of a local contour, performance will be better when binocular disparity is consistent with this bias, ie when the convex area is nearer in depth. Results confirm this hypothesis.

◆ **Oculomotor stability during stereo fixation with central and peripheral fusion locks**

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We studied the oculomotor stability during stereo fixation performed with or without zero-disparity fusion locks. Eighteen normal-sighted subjects had to fixate at centrally located stereo targets (circles of 1.2 and 3.2 deg in diameter; green–red separation filters) presented with crossed or uncrossed disparity (55 min of arc) in a dark environment. Bright line frames served as ‘fusion lock’; they were displayed on the screen surface centrally (forming an inner rectangular frame—1.3 deg vertical, 2 deg horizontal—superimposed on target area), or peripherally (inner frame of 10 deg vertical and 20.5 deg horizontal). Movements were recorded separately for each eye with unrestrained head posture (EyeLink system) prior to subjects’ fusion (signaled by keypress), and 60 s after the onset of fusion. Without fusion lock, all subjects showed different magnitudes of horizontal vergence drifts, fusion losses, and binocular instability as reflected by saccade patterns (frequencies, magnitudes, direction, etc). Mean times to fusion were 10.3 s without lock and were greatly reduced with peripheral fusion locks (5.5 s) along with improved binocular performance, whereas central locks impaired binocular performance and prolonged time to fusion (11.8 s), especially with uncrossed disparity (14.8 s). The adverse effects of central fusion locks are interpreted to reflect conflicting accommodative and vergence cues. With peripheral locks, dark background vergence cues are supposed to dominate accommodation, whereas central locks attract accommodation to screen surface, thus enhancing the conflicting situation. Our results support the role of remote peripheral zero-disparity images as triggers of

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a sustained vergence 'fusion-lock' mechanism during fixation. They also reveal effects of accommodation vergence that conflict with fixation vergence stability.
[Supported by a grant from C E Smith foundation, Jerusalem.]

◆ **Binocular summation at contrast threshold: A new look**

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Contrast sensitivity is better with two eyes than one. The standard view is that thresholds are about 1.4 ($\sqrt{2}$) times better with two eyes, and that this arises from monocular responses that, near threshold, are proportional to the square of contrast, followed by binocular summation of the two monocular signals. However, estimates of the threshold ratio in the literature vary from about 1.2 to 1.9, and many early studies had methodological weaknesses. We collected extensive new data, and applied a general model of binocular summation to interpret the threshold ratio. We used horizontal gratings (0.25–4 cycles deg⁻¹) flickering sinusoidally (1–16 Hz), presented to one or both eyes through frame-alternating ferroelectric goggles with negligible cross-talk, and used a 2AFC staircase method to estimate contrast thresholds and psychometric slopes. Four naive observers completed 20000 trials each, and their mean threshold ratios were 1.63, 1.69, 1.71, 1.81—grand mean 1.71—well above the classical $\sqrt{2}$. Mean ratios tended to be slightly lower (~ 1.60) at low spatial or high temporal frequencies. We modelled contrast detection very simply by assuming a single binocular mechanism whose response is proportional to $(L^m + R^m)^p$, followed by fixed additive noise, where L, R are contrasts in the left and right eyes, and m, p are constants. Contrast-gain-control effects were assumed to be negligible near threshold. On this model the threshold ratio is $2^{(1/m)}$, implying that $m = 1.3$ on average, while the Weibull psychometric slope (median 3.28) equals $1.247mp$, yielding $p = 2.0$. Together, the model and data suggest that, at low contrasts across a wide spatiotemporal frequency range, monocular pathways are nearly linear in their contrast response (m close to 1), while a strongly accelerating nonlinearity ($p = 2$, a 'soft threshold') occurs after binocular summation.
[Supported by EPSRC project grant GR/S74515/01.]

SCENE PERCEPTION

◆ **Effect of contrast and task on the interplay between low and high spatial frequencies in natural-scene perception**

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Fast scene perception studies suggested that spatial frequencies (SFs) of an image were analysed from low to high. However, Oliva and Schyns (1997 *Cognitive Psychology* **34** 72–107) showed that this coarse-to-fine processing was flexible: depending on visual demands, low or high SFs were preferred. We studied the influence of two factors on the relative contribution of low and high SFs in natural-scene categorisation: the stimulus contrast and the task that subjects realised. Stimuli were 24 images obtained from four basic scenes submitted to various filters: non-filtered, low-pass filtered, high-pass filtered, and hybrid images. A hybrid image (Schyns and Oliva, 1994 *Psychological Science* **5** 195–200) was composed of low SFs of a scene and high SFs of another scene. The first task consisted in identifying a sample presented for 30 ms by naming it verbally. The second task was a retain-to-compare paradigm: a sample was presented briefly followed by a target. The subject pressed a button if the sample matched the target. The sample was one of the 24 images and the target was one of the non-filtered images. The experiment was conducted for three contrast levels on twelve subjects. The results showed that the relative contribution of low and high SFs was similar for both tasks. For high-contrast stimuli, low-pass and high-pass filtered images were equally recognised and a decreasing contrast involved an increasing bias in favour of low SFs. Analysis of hybrid images showed that an increasing contrast implicated an increasing weight of high SFs compared with low SFs. High contrast induced a fine-to-coarse processing and low contrast reversed this strategy. Our work confirmed that the SF processing was flexible and showed that the image contrast was a factor modifying the relative weight of low and high SFs.

◆ **Relative contribution of low and high spatial frequencies: The effect of the level of scene categorisation**

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Psychophysical and computational research on natural-scene processing suggested that it would be more efficient to integrate information from the coarse blobs, conveyed by the low spatial frequencies (SFs) of the image, than from the more detailed edges, provided by the high SF.

However, Oliva and Schyns (1997 *Cognitive Psychology* **34** 72–107) provided evidence that relative contributions of low and high SFs for scene categorisation were not systematically determined. Their results led to the concept of a flexible processing that could change in order to adapt to perceptual conditions. The aim of the present work was to assess whether relative contributions of low and high SFs depend on the level of scene categorisation (ie basic-level versus subordinate-level). Thirty-four young adults participated in the experiment. Subjects were instructed to name verbally the category of the scene displayed. Four scenes were considered in the basic-level categorisation: indoor, landscape, city, and highway. Four different test images were generated for each scene: non-filtered, high-pass filtered, low-pass filtered, and hybrid images. Hybrid images were constituted by the low SFs of one scene and the high SFs of another scene. The filtering method was borrowed from Schyns and Oliva's study (1994 *Psychological Science* **5** 195–200). Images were displayed for 30 ms followed by a 40 ms mask. The 24 test images were displayed 6 times for each subject. The same experiment was conducted with 4 subordinate scenes (indoor scenes). Half of the subjects performed the categorisation task first at the basic-level. Results showed that the bias in favour of the low SFs was significantly stronger at subordinate level than at basic level. These results are interpreted in terms of object-centred and scene-centred approaches of natural-image perception.

◆ **Visual cues and distance estimation in sailing**

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Cognitive sport psychology is an emerging reality in experimental human science for understanding how athletes develop mental strategies to optimise performance. This aim can be achieved, for example, by using the paradigms of visual sciences in analysing sensorial cues available to the athlete when performing a specific action. In an ecological environment, a group of athletes of the 'optimist' category have been tested in the visual task of judging the distance between their position and the virtual line at the start of a regatta. It has been found that there is a good estimation of the distance in the proximity of both the jury boat and the buoy, while there is an underestimation of the distance at the centre of the regatta field, and an anomalous overestimation of the distance in the space between the central part of the alignment and the buoy.

◆ **The perceptual organisation with serially presented motion-picture shots**

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Suzuki and Osada (2004 *Perception* **33** Supplement, 80) suggested that a serial presentation of natural motion-picture shots often brings about their perceptual grouping. Observers perceive the continuity of actors' movement as a single event occurring through the shots. We investigated the cause of the continuity of actors' movement. We used natural (condition A) and geometrical (condition B) motion-picture shots in which the moving item (MI; an actor or a geometric circle) moved across the screen (natural scene or geometric rectangle) from right to left. The beginning and ending frames (0.06 s each) of the motion-picture shot were simultaneously removed so as to obtain 39 shots of different durations from 5.03 s to 0.03 s. We presented 39 motion-picture shots serially with each of them presented twice. Observers were asked to report their impressions whether movement of the MI would continue or not through the shots and whether the MI had a separate identity or not in the motion-picture sequence when they observed the sequence. Their impressions were qualitatively changed with the same temporal phase of both conditions. Observers could perceive the same events, such as repeated MI movement across the screen and several MIs turning around the observer, occurring in both conditions. Our results suggest that the cause of the continuity of actors' movement in serially presented motion-picture shots is not the context of natural scene of the movement of the MI but the spatio-temporal organisation of the motion-picture shots. When the motion-picture shots are serially presented, those shots would be perceptually organised as segregated several events or a continuous single event.

[Supported by a Rikkyo University Grant for the Promotion of Reserch.]

◆ **Reflections and visual space: Judgments of size and distance from reflections**

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The relative size of a target and its reflection is informative about the absolute distance of the target in units of the distance k between target and specular surface. For plane mirrors, the basic relationship is given by $d = 2k/r - 1$ where d is the distance of the viewpoint from the target

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object, and r is the ratio of the apparent sizes of target and virtual target. We presented observers with images of two target objects in front of a mirror and they made relative size and distance judgments (in separate experiments). Other visual cues to size and distance were eliminated from the stimuli. Results showed orderly psychophysical functions for both size and distance judgments, with steeper slope functions for distance judgments. Further experiments tested the effects of the horizontal offset of target and virtual images, presence of the observer in virtual image, and stereo presentation. Results indicate that even with the presence of binocular disparity, the additional depth cues provided by reflections significantly increased the accuracy of size and distance judgments.

[Supported by ESRC RES-000-22-0771.]

◆ **Categorisation of natural scene: Global context is extracted as fast as objects**

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The influence of the background of a scene on object identification is still controversial. On the one hand, the global context of a scene could be considered as an ultimate representation suggesting that object processing is done almost systematically before scene context. Alternatively, the gist of a scene could be extracted very rapidly and influence object categorisation. It is thus very important to assess the processing time of scene context. We used a go/no-go rapid visual categorisation task (previously used to study object categorisation) in which subjects had to respond by lifting a finger when they saw a ‘man-made scene’ (or ‘natural scene’) that was flashed for only 26 ms. Man-made and natural scenes were categorised with very high accuracy (96.4%–96.9%) and very short reaction times (RTs) (median RT: 383–393 ms, minimal RT: 288–313 ms). However, object salience impaired context categorisation. The categorisation of context was delayed by 20 ms when a salient object was present in the scene. When the object was incongruent with the context category (eg a man-made object in a natural scene), such interference induced a 15% accuracy decrease and an 80 ms RT increase. Compared with previous results of the group, these data show that coarse global context categorisation is remarkably fast: (i) it is faster than categorisation of subordinate categories like sea, mountain, indoor, or urban scenes (Rousselet et al, 2005 *Visual Cognition* **12** 852–877); (ii) it is as fast as object categorisation (Fabre-Thorpe et al, 2001 *Journal of Cognitive Neuroscience* **13** 171–180). Processing of a natural scene is thus massively parallel and the semantic global scene context might be achieved concurrently with object categorisation. These data suggest an early interaction between scene and object representations compatible with contextual influences on object categorisation.

◆ **Distortions in the visual perception of spatial relations: Implications for visual space**

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The visual experience is of a continuous and unique spatial manifold within which visible features and objects are embedded. Optical illusions of various types show that this manifold can be distorted by its contents, suggesting some form of relativistic space. The mapping from actual space to perceived space appears to be one-to-one and so the distortions experienced are not radical. However, we present data showing one-to-many distortions, indicating a non-unique visual space. For example, the size of the gap between the adjacent ends of two co-aligned lines is seen as less than the distance between two dots with the same physical separation. It is as if the lines are shrinking visual space along their axis. However, this effect only obtains when the two lines have the same orientation. The space is distorted by oriented objects, but only for objects of the same orientation and not for objects of other orientations in the same portion of visual space. This implies that it is necessary to talk of there being multiple visual spaces or manifolds, each one distorted independently of the others. This seems to threaten the experienced unity of visual space. Ultimately, we find it simpler to question the notion of visual space itself. To finish, we turn to a discussion of instances where visual space is not perceived, the best being an example of a regular tessellation from the floor of San Marco in Venice which is not seen as regular.

◆ **Non-reconstructive tasks in visual space perception: What is different about them?**

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Most psychophysical research on visual space perception employs ‘reconstructive’ tasks in which the observer typically adjusts the size or another selected spatial parameter of the comparison

target to match to that of a standard positioned remotely. The reason for this approach being used is to gather data directly comparable with the physical properties of space, ie data at a cardinal level of measurement. The tasks which do not require the observer to 'reconstruct' the spatial parameters in distal space are more likely to yield ecologically valid data (we usually do not modify the properties of physical space when perceiving it). Purely perceptual tasks, however, need to look for data which are only ordinal in order to be psychologically relevant. An example of a 'non-reconstructive' task would be an estimation of inter-object distances. We asked the observers to order the stakes located in the scene in front of them according to their distance from different locations in space. The visual scene was viewed successively from two viewing positions and in two scales. The data obtained by this procedure were subsequently compared with the data from a 'reconstructive' task (a map drawing of the given scene).

◆ **Estimation of light-field properties in a real scene**

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The appearance of an object is determined by its shape, surface structure, scattering properties, and the light field. Therefore one might expect perceptual interactions between light-field and object properties. We investigated the ability of human observers to match the directions of illumination of objects with various shapes, reflectances, and surface structures. Participants were asked to match the illumination direction of objects in a real 3-D experimental setup with the illumination direction in pictures of objects. The 3-D setup consisted of a vertically oriented arch over which a light source could be moved over 180°. The arch itself could be rotated over 360°, so that every direction of the light source could be achieved. Observers could control this direction from behind a screen (at a fixed distance). A test object was placed in the centre of the setup and the distance from the source to the object was constant. The matching consisted of comparing spherical stimuli to spherical test objects as well as test objects of a different shape. The stimuli differed from each other in optical properties, such as translucency, reflectance, and textured surface. We found that subjects are well able to match the light source direction of a real sphere with the illumination direction of a photographed sphere. In this case, the errors are of the same order of magnitude as the errors that we found in earlier experiments in which the illumination directions in photographs were matched with those of interactively rendered Lambertian smooth spheres. Matching the illumination directions of objects of differing shapes resulted in errors almost twice as large as of similar shapes, but in both cases participants were well able to estimate the direction of the light source. Estimates were more accurate for the azimuthal angle than for the polar angle. [Supported by the Netherlands Organisation for Scientific Research (NWO).]

◆ **Detection model predictions for aircraft targets on natural backgrounds**

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It is challenging to predict the visibility of small objects in the natural environment. In the aerial environment, detection of an aircraft is especially important but difficult since it appears tiny and within a variety of backgrounds. To seek an objective way to predict visibility of a target in the aerial environment, we compared the results of detection task with the predictions from two models considering the property of visual systems: a masking model by Ahumada and Beard (1998 *SID Digest of Technical Papers* 29 40.1) and a model proposed here based on sparse coding (Olshausen and Field, 1996 *Nature* 381 607–609). The masking model gives a prediction by applying filtering effects including blur, luminance, and contrast. In sparse coding, basis functions derived from natural images are comparable to spatial receptive fields in primary visual cortex and are characterised as localised, oriented, and bandpass. In the proposed model, we assume that the visibility of a target is worse if the target and background have similar coefficients (activation) of basis functions. The predictions from both models are generally similar, but are different in some conditions such as those including orientation factor. An airplane-shaped target was shown on gray natural images taken from the aviation environment and generated on a CRT monitor. The target was randomly presented in one of four quadrants. Subjects judged whether the target appeared and in which quadrant it appeared. Detection performance and reaction times were recorded. The results of detection and reaction times compared with the predictions of both models suggest that masking model predicts the detection better but the predictions from sparse coding may be better in some conditions.

[Supported by a grant to MC from the Department of Transportation, Federal Aviation Administration.]

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◆ **The psychophysical assessment of fused images**

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Image fusion involves the presentation of images from different sources (eg visible and infrared radiation) to human observers. Such techniques are now widespread in civil and military fields, necessitating accurate methods of assessment of fused image quality. Previously, such quality assessment has been carried out by computational metrics and with subjective ratings. We investigated an alternative psychophysical approach: task-based assessment of images. We designed an experiment using a signal-detection paradigm to detect the presence of a target in briefly presented images followed by an energy mask. In experiment one, eighteen participants were presented with composites of fused infrared and visible light images, with a soldier either present or not. There were two independent variables, each with three levels: image fusion method (averaging, contrast pyramid, dual-tree complex wavelet transform), and JPEG2000 compression (no compression, low, and high compression), in a repeated-measures design. Participants were presented with 6 blocks of 90 images—half target present, half absent—and asked to state whether or not they detected the target. Images were blocked by fusion type, with compression type randomised within blocks. In the second experiment, participants rated 36 pairs of images used in the first experiment on a 5-point Likert scale of subjective quality. Results for experiment one, analysed with repeated-measures ANOVAs, showed significantly greater d' and lower β for the complex wavelet, lower d' and higher β for the contrast pyramid, with the averaging method having smallest d' and greatest β . No significant main effect of compression was found. In contrast, the subjective ratings showed significant main effects of both fusion type and compression level. The results suggest that fusion method has a greater impact on signal detection than compression rate, whilst subjective ratings are affected by both fusion and compression and are therefore not a reliable predictor of performance.

VISUAL AWARENESS

◆ **Binocular rivalry dynamics are slowed when attention is diverted**

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To answer the question whether binocular rivalry alternations have an attentional component, rivaling orthogonal gratings were surrounded by an annulus of incoherent random-dot motion. Alternations in grating dominance were tracked while monitoring the surround for occasional weak motion pulses. Pulses of different strength were used to manipulate attentional demands in the distractor task. Observers indicated whether or not they had just seen a motion pulse each time a brief cue was presented. From a signal detection analysis, d' was calculated to measure task sensitivity. To verify that rivalry tracking was accurate while attention was distracted, observers tracked alternations, in pseudo-rivalry sequences, of monocular gratings (smoothly cross-faded) that mimicked actual rivalry alternations. Rivalry alternations were significantly slower when performing the attention task (relative to passive viewing). For difficult tasks (low coherence, low d'), reversal rate was slower than for easy tasks (high coherence, high d'). In pseudo-rivalry, correlations between stimulus alternations and subjects' tracking of alternations were high ($r \sim 0.9$), regardless of difficulty of the distractor task. Also, sensitivity (d') to the attentional task did not differ between real-rivalry and pseudo-rivalry conditions. Reversal rates were compared over four levels of grating contrast. While reversal rates decreased overall with decreasing contrast (as expected), performing the attentional task further decreased reversal rate. Interestingly, performing the attentional task retarded alternations as much as a halving of target contrast during passive viewing. Using a novel attention-distraction paradigm and signal detection, we thus demonstrated that a component of rivalry alternations is due to attention. Manipulating the difficulty of the distractor task showed that rivalry alternation rate correlates with available attentional resources. Performing a difficult attention-distracting task slows rivalry alternations by an amount equivalent to halving the contrast of the rival stimuli.

◆ **The phase of alpha wave correlates with the conscious perception of a masked target**

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When we perform a perceptual task, we often observe variability in performance even for physically constant stimuli. The variability on trial-by-trial basis can be attributed to various factors of the observer's internal state such as fluctuation of attention. Here, our aim was to find

what kind of internal states prior to stimulus onset correspond to the variability. More specifically, we were interested in whether the phase of occipital ongoing alpha wave (a slow oscillation at 8–12 Hz) influences visibility of a masked target. Observers performed an identification task of target letters, which were subsequently masked by a distractor, while their EEG was recorded. We examined whether the phase of ongoing alpha wave at the target onset correlated with performance. We used independent component analysis (ICA) to isolate the occipital components that exhibit ongoing oscillation in the alpha range (8–12 Hz). Using various interstimulus intervals, we found a point where the number of correct trials roughly equalled that of incorrect trials. Those trials were sorted according to task performance (correct or wrong response) and subjective confidence rating. The results show that performance correlated with the phase of the ongoing alpha wave. We found that the task performance in the trials in which the onset of the target coincided with the peak of the ongoing alpha wave was better than in other trials. Our results can be accounted for by the classical idea of discrete perception that one alpha cycle corresponds to one perceptual frame. When the target is presented near the peak, the target and the mask are likely to fall in separate cycles, resulting in a perceptual separation of the target and mask. For other phases, however, they seem to fall within a common cycle and are perceptually integrated. This hypothesis of perceptual frame can account for the variability in the backward-masking task.

◆ **Form discrimination and temporal sensitivity in blindsight**

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Residual visual capacity in subjects with lesions to primary visual cortex has been demonstrated in a number of studies, some of which identify a functional temporal channel from retina to cortex. Assuming sensitivity to regular temporal variation in stimulus activity we investigated the band-pass characteristics of mechanisms responsible for form discrimination in two subjects suffering visual field defects caused by damage to primary visual cortex. Discrimination performance was examined for the presence or absence of a discontinuity that bisected and offset two halves of a patch of horizontal gratings (with spatial Gaussian modulation). The bars were flickered in square waves or with transients removed by convoluting the square-wave signal with a temporal Gaussian. Calculating empirical ROC curves revealed, for the square wave presentations, that detection of the bisection was enhanced when stimuli were presented at flicker frequencies in the ranges 20–30 Hz and 47–62 Hz for one patient and at 91 Hz for the second. For temporally modulated presentations, detection accuracy was at chance or decreased to chance performance at around 30 Hz and then increased for both subjects to above chance performance within the range 40–60 Hz. The results of these experiments suggest blindsight may exploit temporal sensitivity with very particular band-pass characteristics that manifest themselves somewhere within the spectrum of the EEG gamma band.

◆ **First-order and second-order motion shifts perceived position with and without awareness of the motion**

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A number of striking illusions show that visual motion influences perceived position. While most of these demonstrations have used first-order, luminance-defined motion, presumably detected by passive motion-processing units, more recent demonstrations have shown that it may not be the physical or retinal motion that matters: the perception or awareness of motion may actually determine perceived position. In fact, all motion-induced position shifts may be a product of top-down processes such as inferred motion or attentive tracking-processes that require an awareness of motion. Here, we measured the perceived position of a stationary object containing either first-order (luminance-defined) or second-order (contrast-defined) motion, and found that both types of motion shifted the apparent location of the static object. To test whether these effects required an awareness of the motion, we used a crowding technique. Subjects adapted to either first-order or second-order moving patterns in a crowded scene filled with other moving patterns of the same type; because of the crowding, subjects could not identify the direction of motion in the adaptation pattern. Following adaptation, when a single static test stimulus (of the same type as the adaptation stimulus) was presented within the adapted location, subjects perceived the test stimulus to be shifted in position. Even when the test stimulus did not display a motion aftereffect, it still appeared shifted in position owing to the previous motion that subjects were not aware of. The results suggest that both first-order and second-order motion contribute to perceived position, and that the awareness of this motion is not necessary.

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◆ **Effects of transient attention on contrast sensitivity during binocular rivalry**

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We investigated the effect of transient attention on contrast sensitivity in an orientation discrimination task during binocular rivalry; we focused on the effects of attention on the signal during rivalry, not on the well-studied effects of attention on rivalry state. During binocular rivalry, contrast sensitivity is lower during suppression than during dominance in a detection task, but in a form or motion-discrimination task, contrast sensitivity is similar across rivalry states. During normal binocular viewing, transient (exogenous, involuntary) attention increases contrast sensitivity during both detection and discrimination tasks. In this study, on each trial, rivalry was established by the flash suppression technique. This was followed by either a transient cue adjacent to the target location (peripheral), or six cues, one at each possible location and four at other locations in the rivalrous regions (neutral), and then quickly followed by a tilted Gabor. The cues and Gabor were presented in the dominant or suppressed regions, and their locations were selected independently from one another, for a total of 4 cue–Gabor combinations. Data show that attention increases contrast sensitivity only when both the cue and Gabor are in the dominant region. This effect is maximal at 80 ms SOA, reduced at 140 ms, and no longer present by 220 ms. When both the cue and Gabor were in the suppressed region, at 220 ms, contrast thresholds were higher for the peripheral condition than for the neutral, which is consistent with the neutral cue bringing the cued region to dominance faster than the peripheral cue does; six transients disrupt rivalry more than a single transient. Unlike in a detection task, discrimination contrast thresholds did not differ between the suppressed and dominant regions. This is similar to observed thresholds for motion and form discrimination. [Supported by NEI Kirschstein-NRSA grant #5F32EY015988-02.]

◆ **How perceptual learning influences the subliminal priming effect**

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Perceptual learning—improvements in performance with training or practice—has been demonstrated in human observers in a wide range of perceptual tasks. We investigated the perceptual learning effect on metacontrast masking and subliminal priming to check if perceptual learning can improve recognition of masked stimuli and, if yes, whether it has an effect on priming. Participants were randomly assigned to an experimental and a control group. They participated in the experiment twice, in the pre-test and post-test (performed three days after the pre-test), in which reaction time (RT) was measured. Each RT part was followed by the prime-discrimination (PD) part. Two pairs of geometrical figures, square and diamond, were presented one after another (SOA = 50 ms) in each trial. The priming figures were small replicas of those used in the imperative stimuli and were masked by metacontrast. In the RT part, the diamond was defined as the target and the participants' task was to respond to the imperative stimulus by the hand on the target's side. In the PD part, participants had to respond to the prime stimulus with the left hand if they identified diamond in the prime figures or with the right hand if they did not. The experimental group was additionally trained for three consecutive days in identifying the priming figures (participants performed only the prime-discrimination task) with forced-choice judgment, with feedback about accuracy of performance. The experimental group showed significant improvement of performance with training. A straight priming effect was observed in groups. Furthermore, while the priming effect was equal in the pre-test, the effect was stronger for the experimental than for the control group after training. This result provides some evidence that perceptual learning improves recognition of the prime affects priming effect as well.

◆ **The effects of adaptation to a static stimulus on motion-induced blindness**

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Salient static stimuli disappear and reappear alternately for several seconds when they are surrounded by moving objects. This phenomenon is called motion-induced blindness (MIB). We examined the effects of adaptation to a static stimulus on MIB. The display contained a static stimulus (a yellow small dot) surrounded by rotating stimuli (a 7×7 array of equally spaced blue crosses rotated around the centre of array). To examine the effects of adaptation to the static stimulus, we manipulated SOA between the static stimulus and the rotating stimuli. Observers pressed a mouse button when the static stimulus disappeared and released it when the static

stimulus reappeared. The time between the onset of rotating stimuli and the button-press (disappearance latency), and the time between the button-press and release (disappearance duration) were measured. We examined the effects of adaptation time (experiment 1), dichoptic presentation (experiment 2), and positional change (experiment 3) on disappearance latency and duration. The static stimulus preceded the rotating stimuli by SOAs of 0, 5, or 10 s (experiment 1). The static stimulus was presented to one eye, and then both the static stimulus and rotating stimuli were presented to the same eye or the other eye (experiment 2). The static stimulus was presented in one position and then it was presented at the same position or different position with the rotating stimuli (experiment 3). Except for the condition in which the static stimulus was presented at different positions, disappearance latency was shorter in the 5 s and 10 s conditions than in the 0 s condition. We suggest that adaptation to the static stimulus reduces neural activity and therefore decreases disappearance latency. Our results also suggest that adaptation after binocular fusion affects MIB and that the location-based representation of static stimulus is involved in MIB.

◆ **The role of version and vergence in visual bistability**

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To investigate the role of version and vergence in visual bistability we exposed the visual system to four different stimuli. We used two perceptual-rivalry stimuli: slant rivalry and Necker cube rivalry and two binocular-rivalry stimuli: grating rivalry and house-face rivalry. For each of these stimuli, we studied the extent to which version and vergence are responsible for visual rivalry and vice versa. We compared conditions in which subjects were trying to hold one of the two percepts (hold condition) with conditions in which subjects did not try to actively influence the percept (natural viewing condition). We found that average gaze positions and average horizontal vergence do not change before the moment of a perceptual alternation for all stimuli in all viewing conditions. However, different voluntary control conditions can lead to different average fixation positions or different amounts of the scatter in fixation positions across the stimulus. We conclude that version and vergence do not by themselves determine the currently prevailing percept.

◆ **Motion-induced blindness as a kind of visual neglect**

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During motion-induced blindness (MIB), perceptually salient targets repeatedly disappear and reappear after prolonged viewing. Bonnef et al (2001 *Nature* **411** 798–801) attributed this effect to attention, and also suggested that MIB and visual neglect (simultanagnosia) may share some common mechanisms. It has been shown that deficits in neglect patients can be reduced (i) by regular perceptual grouping (eg by collinearity, shape similarity, connectedness, or common region), (ii) especially when it involves crossing the midline, and (iii) by perceptual grouping of elements into a subjective surface. Here, we examined these three ways of grouping in MIB of normal observers. We found that MIB was reduced when the upper left target grouped well with the other elements (experiment 1), especially when it grouped with other elements across the midline (experiment 2), and when it formed a subjective surface (experiment 3). These results suggest that perceptual grouping in MIB and in visual neglect function in a similar way, and they also suggest that MIB and visual neglect could share some common underlying mechanisms, like perhaps that of attention.

[Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE.]

◆ **Independence of visual awareness from selective nonspatial and spatial attention at early processing stages**

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According to a widely accepted idea, attention is the gateway to visual awareness. Only the results of attentional selection reach awareness, thus constituting the contents of subjective visual experience. A competing model postulates that awareness is independent of attentional selection: contents of subjective visual experience may also exist without attentional selection or outside the focus of attention. We tested the predictions of these competing models by tracking the independent contributions of attention and awareness to event-related brain potentials (ERPs) in two experiments. Awareness was manipulated by using short (33 ms) and long (133 ms) stimulus-mask onset asynchronies. Attention was manipulated by using a typical procedure in studies

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of selective attention: the participants were asked to respond to a target letter and to ignore nontarget letters. In experiment 1, the stimuli were presented to the centre of the visual field. In experiment 2, the stimuli were randomly presented to the left or right visual field, while the participants attended either to the left or the right visual field. The results showed that the earliest effects of visual awareness (visual awareness negativity) emerged regardless of the presence or absence of selective attention. Conversely, the early effects of attention (selection negativity) were elicited regardless of the presence or absence of awareness. Thus, the electrical brain responses reflecting visual awareness and attention are initially independent of each other. Only the later stages of conscious processing (after 200 ms from stimulus onset) were dependent on attention. The present study provides objective electrophysiological evidence that visual attention and visual awareness can be dissociated from each other at early stages of visual processing. We conclude that a stimulus may initially reach subjective visual awareness without selective attention, but the quality of subjective perception can be modified by attention at later stages of processing. [Supported by the Academy of Finland.]

◆ **Repetitive transcranial magnetic stimulation applied to MT+ attenuates object substitution masking in human brain**

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When the target is encoded in low spatiotemporal resolution, the detectability of a briefly flashed target may be reduced by a subsequent mask which does not touch it (object substitution masking: OSM). OSM has recently been interpreted to reflect information updating in object-level representation, with perception of the target and the mask belonging to a single object through apparent motion. We studied the issue by applying repetitive transcranial magnetic stimulation (rTMS) over MT+, the area in the human brain specialised in visual motion processing. Transient functional disruption of MT+ produced by rTMS attenuated OSM while sham stimulation did not. The results suggest that OSM would be mediated by normal functioning of MT+. We thus conclude that rTMS of MT+ impaired perceived object continuity and reduced OSM accordingly. [Supported by Grants #16203037 from JSPS and Nissan Science Foundation to NO.]

◆ **Unilateral versus bilateral experimental strabismus: Interhemispheric connections of single cortical columns in areas 17, 18**

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We have investigated the spatial distribution of retrogradely labelled callosal cells after microiontophoretic horseradish peroxidase injections into the single area 17 or 18 cortical columns in cats reared with unilateral and bilateral convergent strabismus. The eye deviation ranged from 10 to 70 deg in unilateral strabismic cats and from 10 to 40 deg in bilateral ones. The zone of labelled callosal cells was located asymmetrically in relation to the location of injected column in the opposite hemisphere. Some cells were found in the transition zone 17/18, and their retinotopic coordinates corresponded to the injected column coordinates, as was shown in the intact cats (Alexeenko et al, 2001 *Perception* 30 Supplement, 115). Other labelled cells were found in areas 17/18 in clusters located approximately 1000 µm away from marginal clusters of the transition zone. This distance approximately coincides with average width of cortical hypercolumns. Such clustered structure of the callosal cells zone was less pronounced in cats with unilateral strabismus. Analysis of labelling in the dorsal lateral geniculate nucleus has shown that most of the injected columns were driven by ipsilateral eye. These data may be interpreted as evidence for the eye-specificity of monosynaptic callosal connections. The origin and possible functional role of the expansion of such callosal connections in strabismic cats are discussed.

[Supported by RFBR grant 03-04-48258.]

◆ **Change blindness: Size matters**

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It is easy to detect a small change between two sequential presentations of a visual stimulus, but, if they are separated by a blank interval, performance is around chance. This change blindness (CB) can be rectified, or improved, by cueing the spatial location of the change either in the first stimulus or the interval; however, no advantage is conferred when the cue appears during the second presentation of the stimulus. This supports the idea that a representation of the first stimulus is formed and persists through the course of the interval before being 'overwritten' by the second presentation of the stimulus (Landman et al, 2003 *Vision Research* 43 149–164). We were interested

in the time course of the cueing effect during the interval. Following Landman et al, our first stimulus was an array of eight rectangles defined by texture and there was a 50% chance that one of the rectangles would change orientation in the second stimulus. Five cues were used, one within the first stimulus, three across the interval, and one in the second stimulus. Only one of these cues appeared in each trial. The cued rectangle was the one that would change between the first and second stimulus when a change occurred. The cue was a yellow line. Eighty-five observers showed the characteristic cueing performance supporting 'overwriting', but performance decreased over the duration of the interval suggesting that the initial representation of the first stimulus fades over time. However, when the size of the rectangles was increased, performance across the interval improved significantly. We consider two possible explanations: one is that simply by increasing rectangle size we raise the storage capacity for the number of rectangles in our representation, the other is that storage is related to task difficulty.

◆ **Is consciousness first-order?! Processing of second-order stimuli in blindsight**

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DB, an extensively studied blindsight case, has demonstrated the ability to detect and discriminate a wide range of visual stimuli presented within his perimetrically blind visual field defect. Previously, DB's ability for detection and discrimination of simple and complex luminance-defined forms has been investigated. Here, we report on psychophysical and pupillometric investigations, comparing performance for 1st-order and 2nd-order stimuli. Using a temporal 2AFC paradigm, we tested DB's ability to detect the presence of 1st-order and 2nd-order Gabor patches within his visual field defect. DB demonstrated significantly above chance detection of both the 1st-order and 2nd-order stimuli; however, he performed in Type II mode (with awareness) for the 1st-order stimuli but Type I mode (unaware) for the 2nd-order stimuli. These results suggest the importance of 1st-order stimuli for conscious awareness. It is also clear that DB's ability to detect stimuli within his field defect extends to 2nd-order stimuli. The use of 2nd-order stimuli rules out possible explanations of performance on the basis of local light-flux changes. Significant transient pupillary responses were elicited by the onset of both 1st-order and 2nd-order stimuli. The response amplitudes were attenuated in the blind field compared to the sighted field. The existence of pupillary responses in the complete absence of awareness in DB supports earlier reports of unaware pupil responses in another blindsight case, GY (Weiskrantz, 1998 *Consciousness and Cognition* 7 324–326).

◆ **Gamma phase synchronisation during perceptual rivalry in magnetoencephalography**

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Perceptual rivalry such as ambiguous-figure perception and binocular rivalry is an interesting perceptual phenomenon. It may reflect the flexibility of our brain, because it produces fluctuating perception though the stimulus does not change. Recent functional neuromagnetic resonance imaging (fMRI) studies suggest that multiple cortical areas are associated with perceptual alternation in ambiguous-figure perception, and large-scale integration of neural activity in such multiple areas is involved in perceptual rivalry. However, temporal relationships among these areas in perceptual alternation have not been elucidated. We conducted phase synchronisation analyses of magnetoencephalography (MEG) signals obtained from subjects' whole heads while they reported their percepts under two different viewing conditions: a rivalry condition in which they viewed an ambiguous figure (bistable apparent motion), and a replay condition in which they viewed an unambiguous stimulus consisting of two circles moving either horizontally or vertically. We calculated phase-locking value [Lachaux et al, 1999 *Human Brain Mapping* 8(4) 194–208] from unaveraged MEG channel signals using Hilbert transformation. As a result, we detected significant gamma-band phase synchronisations of MEG signals among the anterior channels, between the anterior and the posterior channels, and among the posterior channels, in several-hundred-milliseconds advance of subjects' reports of perceptual alternation. In particular, transient anterior–posterior synchronisations are significant in the rivalry condition. These results suggest that synchronised activities among/within cortical areas play important roles in perceptual alternation.

◆ **Implicit change detection: The fat lady hasn't sung yet**

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Can undetected changes in visual scenes influence subsequent processing? This issue—implicit change detection—is currently very controversial. Using a simple change detection task involving

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vertical and horizontal stimuli, Thornton and Fernandez-Duque (2000 *Visual Cognition* 7 323–344) showed that the implicit detection of a change in the orientation of an item influences performance in a subsequent orientation-change detection task. However, Mitroff et al (2002 *Journal of Experimental Psychology: Human Perception and Performance* 28 798–815) were not able to replicate this result after having corrected methodological biases, and thus took Thornton et al's findings as artifactual. We believe that Mitroff et al's failure to replicate might stem from several methodological differences between their study and that of Thornton and Fernandez-Duque. In this study, we offer a conceptual replication of Thornton and Fernandez-Duque's experiment in which we attempted to address all the methodological issues that we could identify. We found that implicit change detection does not appear to be artifactual, as we could replicate Thornton and Fernandez-Duque's findings after having corrected all the potential biases identified so far in a single experiment. We end by discussing the implications of this new evidence in the debate about implicit change detection.

[CL and AC are supported by the National Fund for Scientific Research (Belgium) and AD is supported by the Fysen Foundation.]

◆ **The role of verbal and visual representations in change identification**

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The purpose of this study was to explore the nature of the representations that underlie the identification of changes in visual scenes: specifically, whether the identification of items that disappeared, but not items that were moved within the scene, is mediated by verbal, rather than visual, representations. To test this hypothesis, fifty participants were asked to identify items that were either removed from, or relocated in, a visual scene. Half of the participants completed this task concurrently with a verbal task. Type of alteration to be identified (disappearance or relocation) was counterbalanced across participants such that half the alterations for each participant were of each type and if an item within a scene was repositioned for one participant, the same item disappeared for another. As expected, the concurrent verbal task impaired the identification of disappearances, but not of positional changes. However, this effect was found only in the case of items that were meaningful to the gist of the scene and those that were salient. The interference of a concurrent visual task with the identification of disappearances found in this study is consistent with previous findings that highlight the role played by verbal coding in the identification of some types of alterations to visual scenes (Pearson and Schaefer, in press *Visual Cognition*; Pearson et al, submitted *Psychonomic Bulletin & Review*; Simons, 1996 *Psychological Science* 7 301–305). This study confirms directly that verbal, rather than visual, representations mediate the identification of items that disappear, but not of items that are repositioned within a scene.

[Supported by a UW-CIHR grant to PMP and EGS.]

◆ **Time perception of near-threshold visual events**

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Is perceived duration (PD) of a perceptual stimulation contributed to by both the conscious and unconscious internal events this stimulation evokes? The PD of two successive Gabor patches, S1 and S2, was assessed via an adjustment technique whereby observers judged the total S1 + S2 duration relative to a variable duration probe. S1 had contrasts chosen to yield d' 's of about 1, 2, or 3, lasted 200 ms, and was presented 50% of the time; S2 was highly suprathreshold, lasted 300 ms, and was always presented. On each trial observers also decided whether or not S1 was present and PD was independently assessed for hits, fictitious events, misses, and correct rejections. PD of S1 + S2 did not depend on the sensitivity to S1, matched the duration of S2 (ie 300 ms) for misses and CR, and equaled 380 and 340 ms for hits and fictitious events, respectively. Hence, a near-threshold 200 ms physical event yielded a PD of 80 ms, whereas the equivalent imaginary event yielded a PD of 40 ms. We conclude that only consciously perceived mental events contribute to PD, whether they are evoked by physical stimuli (hits) or not (fictitious events). Accordingly, PD count is triggered by the internal responses exceeding the absolute decision criterion, c' , and is ended when these responses drop below it. The dependence of PD on c' combined with a leaky temporal integration of the internal response account well for the data. The inferred 40 ms PD of fictitious events can be understood as the average point in time when the random internal noise exceeds the criterion during the time window considered by the observer before the onset of S2.

◆ **Increased gamma synchronisation correlates with threshold of perception**

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It is assumed that coherent visual perception rests on the ability of the brain to generate a pattern of synchronised rhythmic activity. The so-called gamma oscillations and their synchronisation would be a general mechanism allowing a transient association of a neuronal ensemble that enables the perceptual binding of various features constituting a single object. Yet, what happens at threshold when the observer hesitates to make a decision? Recently, frequency changes in cortical activity have been reported while a subject looked at a progressively deformed Kanizsa square. The study showed that gamma oscillations are indeed related to the threshold of perception of illusory images. We examined the synchronisation of gamma rhythms between cortical areas at threshold of perceptual decision. Deformation of Kanizsa squares was achieved by a progressive misalignment of lower pacmen. Psychometric curves showed that a subject's perception of an illusory square was altered with a 0.20 deg displacement of lower pacmen (threshold). In parallel, visual responses were recorded in the right hemisphere in occipital (O2), parietal (P4), and temporal (T6) areas. The activity of single trials was analysed within a time window of ~200–512 ms with a wavelet transform method. We show that the induced gamma (30–40 Hz) synchronisation was transient and appeared in brief epochs. Perception of an illusory square (pacmen aligned) correlated with short latency episodes of gamma synchronisation (~180 and 350 ms). At threshold (square fades) we consistently observed powerful gamma synchronisation much later (~420 ms) between all areas. Altogether, the data indicate that synchronised gamma oscillations are related to perception of visual images.
[Supported by Conseil de Recherches en Sciences Naturelles et en Génie du Canada.]

◆ **The feedforward dynamics of response priming**

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Single-cell recordings indicate that a visual stimulus elicits a wave of rapid neuronal activation that propagates so fast that it might be free of intracortical feedback (Lamme and Roelfsema, 2000 *Trends in Neurosciences* **23** 571–579). In contrast, conscious perception is supposed to be possible only with recurrent processing. We traced the time course of early feedforward activation by measuring pointing responses to colour targets preceded by colour stimuli priming either the same or opposite response as the targets. Early pointing kinematics depended only on properties of the primes, independently of motor and perceptual effects of the actual targets, indicating that initial responses are controlled exclusively by feedforward information. Our findings provide a missing link between single-cell studies of feedforward processing and psychophysical studies of recurrent processing in visual awareness.

VISUAL SEARCH

◆ **On the role of texture disruption in within-dimension conjunction search**

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While the standard conjunction search is performed in a guided mode, the within-dimension conjunction search continues being serial and self-terminating. Here we explore the effect of perceptual grouping in within-dimension conjunction search through two experiments, differing in the organisation used to present the elements. In experiment 1, the elements appear randomly, dispersed throughout the visual area. In experiment 2, the elements presented are organised in patterns that lead to a regular perceptual texture. The results obtained differ greatly and clearly favour the presence of regular textures. They are interpreted in terms of the effect produced by the stimulus pattern generated in each case, which provides useful information for the visual processing. We conclude that these results are of interest for the processing models that include top-down operations into the guide mechanism since our data indicate that these guide operations can be determined also by aspects related to global display.

◆ **The 'encirclement effect' in an orientation search task**

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Visual search for a tilted line segment amongst a background of vertical line segments is very efficient, but the efficiency can be severely diminished when all line segments are encircled. We investigated how features of the circles, such as polarity and structure, affect the efficiency

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of detecting an oriented line segment. The stimuli were black (9.71 cd m^{-2}) vertical line segments (0.33 deg) on a gray background (29.2 cd m^{-2}), with one line segment tilted 30° from vertical, encircled or not depending on the experimental condition. The numbers of line segments in a display were 4, 8, 12, or 16. Observers were required to indicate as quickly as possible whether a tilted line segment was present in the display. We found that for line segments without encirclement the search was 'efficient', since reaction time remained largely unchanged as a function of set size. However, search became 'inefficient' when black circles surrounded all line segments, such that an additional 8 ms was needed for each extra line segment added to the stimulus. We tested the effect of polarity by placing white circles around black line segments. The efficiency of visual search did not change, and performance was almost the same as when black circles were used. However, adding white patches around black line segments, and replacing circles with broken circles, did affect search efficiency. In the latter condition, search efficiency was maximally affected when the broken circle was rotated to 30° . The results, in combination, suggest that masking may be the cause of the encirclement effect.

[Supported by Grant HKU7146/02H from the Research Grants Council of Hong Kong.]

◆ **Does central fixation account for medial letter facilitation in visual search?**

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Visual search tasks, in which a target letter is presented centrally, followed by a centrally presented five-letter array, show faster recognition of letter targets appearing in the initial, medial, and terminal positions of the array than those in other positions (eg Hammond and Green, 1982 *Canadian Journal of Psychology* **36** 67–82). Whilst facilitation of letter targets in exterior positions is thought to arise from specialised orthographic processes, it remains to be determined whether the same orthographic processes facilitate recognition of medial letter targets or whether more low-level visual processes, such as central fixation, are responsible. Conditions for written word recognition are thought to be optimal when initial fixation falls on the medial letter in words (eg Schoonbaert and Grainger, 2004 *Language and Cognitive Processes* **19** 333–367). This may account for the facilitation of medial letter targets found in visual search tasks, although this hypothesis has yet to be tested explicitly. We investigated the role of initial central fixation in medial letter facilitation in two experiments using visual search tasks. In experiment 1, target letters were presented noncentrally followed by centrally presented letter arrays. In experiment 2, target letters were presented centrally followed by letter arrays that were presented noncentrally. Results showed medial letter facilitation even when targets were presented noncentrally. However, facilitation of the medial letter was eliminated when letter arrays were presented off centre, as participants were required to shift initial fixation towards the displaced letter arrays. Interestingly, exterior-letter facilitation persisted in both experiments. These results suggest that, unlike exterior letters, medial-letter facilitation does not reflect specialised orthographic processes but arises from a tendency to initially fixate centrally on visually presented arrays. This finding lends support to recent models of letter-position encoding [Whitney, 2001 *Psychonomic Bulletin and Review* **8** 221–243; Grainger and Van Heuven, 2004, in *The Mental Lexicon* (New York: Nova Science)], and indicates that both bottom-up and top-down processes operate across different positions within written words to facilitate word recognition.

◆ **A reaction time model of self-terminating configural search in complex displays**

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Traditionally, researchers have studied visual search by asking observers to hunt for single targets defined by the presence or absence of one or more features (visual cues). Configural search requires observers to forage for a group of two or more targets defined by their mutual relationships. Remington et al (2000 *Human Factors* **42** 349–366) studied configural search using stimuli mimicking air traffic displays, and found that the time required to detect traffic conflicts was reduced by the addition of a redundant colour cue. We adapted Remington et al's paradigm to study the effect of multiple visual cues on search time. Observers viewed static, stereoscopic displays containing multiple arrowheads, which represented aircraft, and searched for the unique pair of arrowheads whose extrapolated paths formed the equal sides of an isosceles triangle. This geometric configuration, observers learned, signaled two aircraft with equal speeds on course for collision (a conflict). Each display contained 8, 16, or 24 aircraft distributed evenly across 0, 2, or 4 fixed flight altitudes, and conflicts could occur only between aircraft at the same altitude. Altitude was coded by: colour (modulated along an isoluminant R–G axis); horizontal binocular disparity; or both colour and disparity. When the respective cues were sufficiently

discriminable so that observers could segment the display into smaller altitude-defined sets of aircraft, we observed reductions in search time. We modeled changes in search time with a combinatoric, closed-form function of three parameters: the discriminability of the altitude cue(s), the total number of targets, and the number of altitudes in the display. Our model predicts the observed result that search time decreases as discriminability of altitude coding increases. Colour and disparity coding, respectively, were equally effective when matched for discriminability. When both cues were present, observers' search times were shorter than with either cue alone.

[Supported by NASA/Ames GSRP Fellowship (JLS), NYU GSAS Dean's Dissertation Fellowship (JLS), NASA AOS Project of NASA Airspace Systems (JBM), NIH/NEI EY08266 (LTM), Human Frontiers Science Program Grant RG0109/1999-B (LTM).]

◆ **A salience ripple in a homogeneous field: Evidence supporting the V1 salience model**

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In addition to a salience peak at the border of a homogeneous orientation texture field, Zhaoping's theory (2003 *Journal de Physiologie* 97 503–515) of visual salience by V1 activations predicts a secondary peak at a location several texture elements away from the border. This secondary ripple from the salient border is due to intracortical interactions in V1. The distance between the border and the ripple is determined by the length of the intracortical connections. The ripple is predicted to be strongest and weakest when the elements are parallel and perpendicular, respectively, to the border. A visual-search task for a target embedded in the orientation texture field was employed to test this prediction behaviourally. By independently varying the location of the target and the texture border, the border and ripple location are made task irrelevant. Consequently, an adverse effect of higher salience is expected for target at the location of the presumably more salient border or ripple (Lamy et al, 2004 *Journal of Experimental Psychology: Human Perception and Performance* 30 1019–1031). A longer reaction time was indeed observed at the border and the ripple location, ie 5th–6th element from the border, when the elements were parallel to the border only. In a separate experiment, we employed an orientation discrimination task of a central probe, superposed on a task-irrelevant texture whose border location was randomised. The discrimination performance, under limited presentation duration, is better when the border or ripple position fall on the probe than elsewhere. This may be caused by the more responsive V1 neurons to the border or ripple elements. These findings support the predicted ripple from the V1 salience model, suggesting that activities of V1 neurons correlate with salience.

◆ **Search behaviour in conjunctive visual searches with stereoscopic depth and colour**

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Visual search is often conducted in 3-D space. However, little is known about search behaviour in 3-D space. Two different hypotheses have been put forward as to how stereoscopic depth cues can be used to enhance search efficiency: either by splitting the visual scene into depth planes, which are subsequently searched in turn (Nakayama and Silverman, 1986 *Nature* 320 264–265), or by grouping of similar visual information (even across 3-D space) into 'kernels', which are then searched in turn (Chau and Yeh, 1995 *Perception & Psychophysics* 57 1032–1044). We contrasted these two hypotheses by studying two conjunctive searches with stereoscopic depth and colour. In experiment 1 this search was conducted across two depth planes and in experiment 2 across six depth planes. The six depth planes were subdivided into two triplets of depth planes, with the relative disparity 'within' a triplet being smaller than 'between' the two triplets, so that the two triplets appeared as two perceptually different kernels with similar chromatic and stereoscopic depth information. If the visual system splits up the visual scene into depth planes (as suggested by Nakayama and colleagues), search performance should be higher with six depth planes than with two. In contrast, if the visual system uses the chromatic and stereoscopic depth information to group similar visual information into kernels, visual-search performance should not differ appreciably between the two experiments (as suggested by Chau and Yeh, 1995 *loco cit.*), given that both displays consist of two perceptually different kernels. Our results indicate that search performance did not differ significantly between the experiments and search times were unaffected by the number of depth planes. Our data, thus, supports the hypothesis that the visual system groups similar visual information into kernels and then searches these kernels in turn.

[Supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Canadian Institutes of Health Research. The first author was supported, in part, by a Canadian Institutes of Health Research Training grant.]

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◆ **The effect of cast shadow for shape perception from attached shadow on visual search in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*)**

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Shadow information has been classified into attached and cast shadows. Previous studies show that an attached shadow is processed at early levels in the human visual system; however, little is known about the mechanism of processing cast-shadow information. We investigated the effect of cast shadows in four chimpanzees and four humans using a visual-search task from the comparative cognitive perspective. In experiment 1, we examined whether cast shadows facilitate the performance of visual search when they are attached to the congruent ('natural') directions of attached shadows. The task was to detect an oppositely shaded target among shaded disks (distractors). We compared the performances with the absence and presence of cast shadows attached to distractors. Furthermore, two attached-shadow directions were used: vertical and horizontal, and the effect of cast shadows on them was compared. The results suggest that three of the four chimpanzees and all four humans detected a target faster in the cast-shadow-present condition than in the cast-shadow-absent condition in both attached-shadow directions. These results indicate that a cast shadow has a facilitative effect on visual search both in chimpanzees and in humans. In experiment 2, we examined the effect of cast shadows attached to opposite ('unnatural') directions of attached shadows under the same visual-search task. In humans, performance was interfered with only in the vertical-attached-shadow condition, while it was facilitated in the horizontal-attached-shadow condition, suggesting that humans detected a target based on the absence or presence of 'feature', because shape discrimination under the horizontal attached shadow was difficult. In chimpanzees, however, there were no effects of cast shadows in both attached-shadow directions. Taking the results of experiments 1 and 2 together, for chimpanzees and humans cast-shadow information is informative only when the lighting direction is congruent with the attached shadow.

◆ **The principle of good continuation in dimension of a perceptual group of elements can guide visual search in the absence of spatial priming or contextual cueing**

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Previous research has shown that a consistent relationship between a given target and the features or spatial arrangement of the accompanying distractors can improve visual search. It has also been shown that repetition of the same target features or target spatial position over time can similarly improve target recognition. Thus, it seems that position and features of the target and/or of the distractors are somehow retained by the visual system and used to guide visual processes such as object recognition and search. Here, a paradigm for manipulating the sequential regularities of the dimensions of a perceptual group across trials 5 deg and 10 deg in width is introduced. Each perceptual group consisted of an array of 8 elements at equidistant positions along a virtual circle: 7 vertical bars acted as distractors and a tilted bar acted as the target. The relative position of the target with respect to distractors and the position of the perceptual group on screen across trials was randomised independently of target features and contextual information. Results showed that orientation discrimination of the target was improved or impaired (in terms of reaction times) when the target appeared at an implicitly expected or unexpected dimension of the perceptual group of elements on screen, respectively. These results suggest that the constancies in the dimension of the array of elements across trials facilitated its recognition, according to the Gestalt principle of good continuation in the attentional focus dimension. The results obtained are not merely due to bottom-up spatial priming, since facilitation occurs for positions far from those recently occupied by the target, nor due to contextual cueing, since the relative positions of the target and distractors are not kept constant. It is concluded that the principle of good continuation in attentional focus dimension can guide visual attention and facilitate search processes and object recognition.

◆ **Influence of binocular disparity changes on the crowding effect**

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Detection of a target stimulus would be more difficult when it is crowded with other distractors. This decrease of subjects' performance is a function of target–distractor distance, ie the 'crowding effect' (CE) would be stronger when the distractors are closer to the target. Using a dichoptic display, we showed distractors in two different conditions. In crossed disparity condition, subjects perceived distractors to be somehow closer in depth than the target. This depth cuing was implemented by adding horizontal disparity between locations of the two distractors. In without-disparity condition, disparity was zero and distractors were perceived in the same plane as the target. In both conditions, the target and fixation point were perceived in the same plane. Using this paradigm we tried to investigate the effect of perceptual depth cues on the CE. Subjects were asked to judge about the presented stimulus at the target location by pressing one of two response keys when target and the two distractor locations were filled randomly by either a 90° clockwise or counterclockwise rotated T as the target and a T or inverted one as the distractor. Stimulus size was 0.57 deg and target–distractor distance was 3 deg. The performance of subjects in crossed-disparity condition (55.0%) was significantly lower ($\chi^2_{20,2} = 4.242, p = 0.039$) than their performance in without-disparity condition (66.3%). Our results show that CE could be modulated by perceptual depth cues. It can therefore be concluded that the neural substrate of CE in the visual system lies after the areas in which the depth information is coded and probably beyond the primary visual cortex.

◆ **Feature-contrast response and additivity across dimensions**

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When targets contrast with the surround in more than one feature dimension they are usually perceived as more salient (Nothdurft, 2000 *Vision Research* **40** 1183–1201). We measured feature-contrast increment thresholds for a wide range of pedestals, and used targets with iso-salient orientation and spatial-frequency contrast as well as single-feature targets. Based on pedestal-versus-increment functions, the feature-contrast response function was estimated with a Naka–Rushton model, as done recently (Motoyoshi and Nishida, 2001 *Journal of the Optical Society of America* **18** 2209–2219). Our results show that the salience advantage for redundant targets is remarkable in the vicinity of the detection threshold, but rapidly declines over the next jnds and completely vanishes for highly salient pedestal contrasts. Interestingly, the feature-contrast response saturates for stimulus arrangements that allow grouping to simple figures but continues to rise for random-order spatial arrangements. Further, the saturation point on the feature-contrast response function coincides with the 82% correct point of the psychometric curve for a figure-discrimination task done with the same figures as for pedestal-versus-increment functions measurement. Our results indicate that higher-level processes of figure–ground segregation modulate early feature-specific pathways and the way they interact.

◆ **Human frontal eye fields and priming of pop-out**

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Priming of pop-out is a form of implicit memory which is believed to promote efficient search by facilitating saccades to targets that have been recently inspected (Maljkovic and Nakayama, 1994 *Memory & Cognition* **22** 657–672; McPeck et al, 1996 *Perception & Psychophysics* **58** 977–991; McPeck et al, 1999 *Vision Research* **39** 1555–1566). Repetition of a target's defining feature or its spatial position improves target detection speed. Pop-out priming has been well-characterised psychophysically, but little is known about its neurophysiological basis. The aim of these experiments was to investigate a potential role for the frontal eye fields (FEFs) or the angular gyrus (AG) in pop-out priming. 10 Hz repetitive-pulse transcranial magnetic stimulation (TMS) (500 ms) was applied over the left or right FEFs or AGs while subjects detected a pop-out target and made a saccade to the target location. To test the hypothesis that these areas play a role in short-term memory storage, TMS was applied during the inter-trial interval. To test whether these areas are critical when a saccade is being programmed to a repeated target colour or location,

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TMS was applied during stimulus processing. There was no effect of TMS over either of these sites in the inter-trial interval in either the spatial-priming or feature-priming task. TMS applied over the left FEFs during stimulus processing abolished spatial priming, but had no effect on feature priming. The data implicate a selective role for the left FEFs in the read-out, but not the storage, of a spatial memory signal that facilitates saccades to a repeated location. [Supported by the Wellcome Trust, the Medical Research Council, and the Royal Society.]

THURSDAY

POSTERS 3

COLOUR 1

◆ **Effects of feature pre-cueing in the conjunction search of colour and orientation**

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While we search for objects in our environment, we often have to combine information from multiple visual modalities such as colour or orientation. Previously, we (Hannus et al, 2004 *Perception* **33** Supplement, 13) found that despite matching the difficulty of colour and orientation discriminability, in conjunction search, subjects' first saccades went much more often to the correct colour than to the correct orientation. Thus, accuracy of orientation discrimination was found to be contingent on whether or not colour discrimination is required as well, suggesting that features are processed conjunctively, rather than independently. Here, we investigated this same issue by examining the effect of pre-cueing individual features on performance. We asked subjects to search for combinations of colour and orientation while their eye movements were recorded. We manipulated the temporal dissociation of feature processing in conjunction search: information about either colour or orientation was presented either 0, 20, 40, 80, 160, 320, or 640 ms before the other feature. Initial saccades were tracked to determine target selection. Pre-cueing of colour improved target-detection accuracy, whereas orientation pre-cueing did not. For the individual features, colour pre-cueing significantly improved colour-discrimination performance compared with orientation-discrimination performance. Pre-cueing orientation information had no effect on feature-discrimination performance. Current results suggest the existence of an asymmetry in the extent to which pre-cueing features can affect conjunction-search performance. Our findings are consistent with the idea that colour and orientation are not processed fully independently in conjunction search.

◆ **Existence and predictability of visual perception of chromatic Mach-bands effect**

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Perception of the colour and brightness of an object depends not only on the spectral composition of the light in its retinal image, but also on the context, which contributes to the object's appearance (induction effects). Several of the context's enigmatic effects on appearance, such as the well-known Mach-band effect, have been attributed mainly to brightness. Mach bands are visual illusory bright or dark bands, perceived adjacent to a zone where the luminance gradually increases or decreases. It has been claimed that chromatic Mach bands are not perceived under controlled conditions of isoluminance. Here we show that a variety of chromatic Mach bands can be clearly perceived under isoluminance conditions, from a novel Mach-band stimulus consisting of chromatic and achromatic regions separated by a saturation ramp. The chromatic Mach band is perceived on the achromatic side as colour that is complementary to the chromatic side. This effect has been shown significantly for six observers on 12 different chromatic Mach-band stimuli. A significant magnitude of perceived complementary colour has been found for the cardinal and non-cardinal colours of the chromatic Mach bands. Our previous computational model of colour adaptation (Spitzer and Rosenbluth, 2002 *Spatial Vision* **15** 277–302; Spitzer and Semo, 2002 *Pattern Recognition* **35** 1645–1659), which predicted colour induction and colour constancy, successfully predicted this variation of chromatic Mach bands, and its complementary perception. [Supported by Fred Chaoul generous donation and the Adams Super Center for Brain Studies grant.]

◆ **Modelling red – green and blue – yellow colour vision**

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The performance of human observers at discriminating between pairs of slightly different achromatic morphed images has been modelled by a simple (low-level) multiresolution model (Párraga, et al, 2000 *Current Biology* **10** 35–38). The model takes two slightly different pictures

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as input, analyses them in terms of the spatial information content at different resolution levels, and returns a measure of discriminability. We have expanded this model to work on full chromatic images by separating the stimuli into three physiologically meaningful 'channels' according to the McLeod–Boynton colour space and performing the multiresolution analysis in each channel separately. The model determines which of three channels gives the biggest discriminability measure. To relate the output values of the model to actual human discrimination thresholds we made two series of sequences of slightly different images of fruits (Párraga et al, 2003 *Perception* 32 Supplement, 168) that were designed to vary in shape, texture, and colour. The first series of stimuli varied their colour along the red–green axis (Párraga et al, 2004 *Perception* 33 Supplement, 118) and the second series varied along the blue–yellow axis to allow the two colour 'channels' of our model to be assessed independently. Once calibrated against psychophysical data from three observers, the colour model was tested against various results involving detection of coloured road and railways signs, fruit, etc.

[Supported by BBSRC and EPSRC/Dstl (UK).]

◆ **Multidimensional scaling of chromatic rivalry reveals red – green compression of colour dissimilarities**

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If two colours are sufficiently similar, visual processing can fuse them into a single percept when they are presented to the eyes separately as dichoptic stimuli. Other pairs are less compatible, and lead to chromatic binocular rivalry: the hue of the combined stimulus is unstable, lustrous, alternating, or shimmering. Conditions conducive to successful chromatic fusion, including the maximum tolerable dissimilarity between colours have been examined in several studies. However, little attention has been paid to the possibility that dissimilarity is more tolerable in some directions of the colour plane than in others, i.e. that chromatic fusion is in some sense 'colour-blind'. Moreover, the transition between fusion and rivalry is blurred by the existence of degrees of rivalry, forcing researchers to choose and enforce various criteria of 'tolerable dissimilarity'. This second issue is addressed here by presenting subjects with two dichoptic pairs at once, and asking them to indicate which colour combination was most stable or less rivalrous. Stimuli were printed on paper and combined with a stereoscope. The subjects' rankings of colour dissimilarity were analysed with multidimensional scaling, yielding a 'map' of the colour plane. Confirming an earlier single-subject study with CRT stimuli, this proved to be a distorted version of a map for the same stimuli based on direct dissimilarity judgments. The map was relatively compressed along a red–green axis, reducing red–green distances (and their rivalry) while blue–yellow differences remained large (an obstacle to fusion). There are implications for the underlying mechanisms of binocular fusion or rivalry.

◆ **Colour perception in peripheral vision**

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This study was conducted to assess the perception of colour at large visual eccentricities, because in previous studies on object recognition at large eccentricities subjects reported that they have seen the colour of the presented stimuli. This question seems important because the surface colour has been shown to improve object recognition [Tanaka et al, 2001 *Trends in Cognitive Sciences* 5(5)]. The stimuli were coloured geometrical shapes (blue, red, green, yellow, black, and grey) of equivalent luminance. In a categorisation task, eighteen observers indicated whether the stimulus was in colour or not (black or grey). In an identification task, eighteen other observers were instructed to name the colour of the stimulus. Eccentricities ranged from 0 to 80 deg left and right of fixation for the categorisation task and from 0 to 60 deg for the identification task. Eye movements were recorded. The exposure time was 80 ms. Observer response was given by response keys for the categorisation task and by voice response (verbal key) for the identification task. For categorisation, the results showed that observers were able to categorise colour up to 60 deg, except the green colour which was categorised up to 20 deg. At 80 deg, although well detected, the stimuli were not categorised. For identification, the results showed that colour was identified up to 60 deg, except again the green colour which was identified up to 20 deg. The lower sensitivity to green was reported in other studies (Newton and Eskew, 2003 *Visual Neuroscience* 20 511–521). These results suggest that colour can be perceived at large eccentricity and thus perhaps can improve object perception in peripheral vision as it does in central vision.

◆ **“Paint it black”: Hue and saturation shifts from spatially induced blackness**

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A chromatic stimulus in surface mode can be darkened by simultaneous contrast with an adjacent, more luminant subtend of the visual field. The consequences of spatially induced blackening are neurophysiological clues to its origin. Do these subjective shifts in the lightness of a colour also cause shifts in its hue and saturation? Are these comparable to those resulting from objective luminance changes? Published reports are few and contradictory. In this study, three normal trichromats were presented with monochromatic test fields ranging in wavelength from 425 to 675 nm. The chromatic stimuli were darkened with various levels of contrast-induced blackness by a broadband white surround, ranging in luminance in six steps across three orders of magnitude. Colour-naming descriptions were collected, allowing red, green, blue, yellow, white, and black responses, or their combinations. The resulting colour-naming functions were transformed and represented as a multidimensional space. As well as two chromatic axes, red–green and blue–yellow, this included two achromatic axes, to resolve separate qualities of whiteness/blackness and saturation contained within the data. Systematic hue and saturation shifts in the appearance of the test field were examined. Increasing levels of spatially induced darkening caused longer-wavelength colours to become redder in appearance while shorter-wavelength colours became greener. These subjective hue changes are similar to the Bezold–Brücke shift, which results from reducing the stimulus luminance, for colours seen in aperture mode. Contrariwise, any saturation changes caused by induced darkening did not follow the luminance-induced pattern. These results have implications for the stage of colour processing at which blackness is induced: it occurs prior to the locus of the chromatic-signal nonlinearities, which account for hue shifts, but subsequent to the nonlinearity in the achromatic opponent process, which affects saturation.

[Supported by a fellowship from Hanse Institute for Advanced Study, Germany, to GVP.]

◆ **An experimental study on colour assimilation on a CRT screen**

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Recent exact studies on colour assimilation relate to the locality of function, the retina, and the cortex (Cao and Shevell, 2005 *Vision Research* **45** 1031–1045; de Weert and van Kruijsbergen, 1997 *Perception* **26** 1217–1224; Hasegawa and Kondo, 2001 *Perception* **30** Supplement, 18). We examined the function determining appearance by adding interference patterns to inducing patterns. A test figure (TF) was 3 deg coloured (red, green, yellow, and blue) stripes on a gray ground whose ratios of width and luminance were 1 : 3 and 2 : 1, respectively. They were observed in a dark room haploscopically or under forced naked-eye fusion with and without interfering figures (IF) of stationary or moving slanted dark-gray stripes, or randomly set stationary lines. Three subjects matched induced colours to one of the colours (MF) set around TF. One set was composed of 9 colours, and 8 different sets were tested 3 times for each TF (+IF). The results showed mainly three points. (i) The difference between the two methods of observation had little effect. (ii) The randomness in the shape of IF made slightly reduced purity. (iii) Without IFs, perceived maximum purity was 4.5% on average for the same hue as the test colour. With IFs, when both TF and IF were perceived on the same plane, purity commonly decreased to 2.7% on average; and in the case of apparently floating IF, it was raised to around 3.5% (the ratio was 1 : 0.60 : 0.78). This variation was stressed in the moving IF; namely the ratio in the three situations was 1 : 0.77 : 0.88. The third point indicates that perceived segregation of the two planes (advancing and receding) makes us perceive the induced colour produced independently from the retinal image. This clearly means colour assimilation is originated mainly in the central system.

◆ **Measurement of chromatic adaptation affected by the relative luminosity levels**

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Thus far, it has been believed that chromatic adaptation occurs in the cells on the retina; however, in recent years it has been reported in many studies that various visual phenomena occur in the brain. Hence, studies are being conducted to prove that chromatic adaptation may be occurring in the brain in addition to the retina. Two experiments aimed at verifying the hypothesis that chromatic adaptation occurs not only in our retina but also after binocular fusion

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in human visual systems were conducted. First, the amount of adaptation was measured in subjects after the application of one of two adaptation conditions: the mutual condition and the simultaneous condition. A mutual adaptation condition was presented for 10 min to each eye alternately; in the simultaneous adaptation condition, both eyes were adapted simultaneously. The result of comparing the two adaptation conditions suggests that the mechanism following binocular fusion is also affected by chromatic adaptation; these results are not affected by subject choice, adaptation colour, dominant eye, and dark adaptation. Moreover, it is suggested that the process before binocular fusion is affected by the luminosity of adaptation stimuli, and the process after binocular fusion is affected by the luminosity contrast between adaptation stimuli and adjustment stimuli. In the second experiment, subjects adapted one eye and the effects of adaptation were measured for both eyes. The result showed that interocular transfer of chromatic adaptation occurred and suggests that the higher visual mechanism following binocular fusion is also affected by chromatic adaptation; however, it does not affect each eye. Since chromatic adaptation occurred, these results prove that the chromatic adaptation mechanism occurs after binocular fusion functions, and it is suggested that the shift due to interocular transfer of chromatic adaptation may affect the relative luminosity levels of the adapting stimuli and adjustment stimuli.

◆ **Men and women from ten language-groups weight colour cardinal axes the same**

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Bimler et al (2004 *Color Research and Application* **29** 128–134) compared men's and women's judgments of perceptual similarity on a triadic judgments task using desaturated stimuli. They found that men's perceptual judgments were more influenced by the lightness axis and less by the red–green axis than women's. Their subjects were all teenage or adult English speakers. Here we extend their investigation in several studies by testing for sex differences in colour perception across language groups over a range of tasks, with stimuli including more saturated instances. We included children from 4 years of age in some studies. In the main study with adults, we used a free-sorting task (grouping by perceived similarity) using 65 stimuli approximately evenly spread across colour space. Ten language groups were tested, including African, Caucasian, and European languages, with over 300 people overall. The probability of grouping each pair of colours together was correlated with their separations in the three dimensions of CIELab (lightness, red–green, and blue–yellow). Although there were significant differences across language groups in correlation sizes, there was no suggestion of any degree of sex difference across colour axes. Our developmental studies compared English speakers from 4–7 years-old with age matched rural children from Namibia sampled from several Bantu language groups (eg Ndonga and Kwanyama), with the use of a simplified grouping task and a triadic judgments task. Grouping and triadic performance was correlated with colour separation in CIELab, and, again, there was no hint of a sex difference, although there were marked cross-language differences: Namibian children were more influenced by lightness and less by hue differences than English children. Our results are inconsistent with Bilmer et al's, but this may be due to the differences in stimuli and tasks. Nevertheless, they suggest that there are no robust universal sex differences in colour perception.

◆ **Colour vision modelling for occupational vision requirements**

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Occupational vision standards typically include a colour vision test [Birch, 2003 *Diagnosis of Defective Colour Vision* 2nd edition (Edinburgh: Butterworth–Heinemann)] such as the Ishihara pseudo-isochromatic plate test. Such tests typically screen out individuals with some level of colour deficiency, primarily those with significant red–green deficits. Increasingly, organisations and employers require that vision standards be job-related and auditable, and yet the inability of an individual to pass a colour-vision screening test need not be an indicator of their ability to undertake a task in the real world. As part of a research programme investigating colour-vision requirements, we have developed a spatiochromatic model of human colour vision which simulates different types of anomalous and dichromatic vision. The model is an extension of the De Valois and De Valois model (1993 *Vision Research* **33** 1053–1065). Modifications to the model have included light adaptation, multiscale spatial representation, and a principal-components opponent-process mechanism. The model simulates colour discrimination tasks and allows a user to determine whether individuals with different levels of defective colour vision can carry out a particular task. Different types of anomalous vision are simulated by shifting the peak cone

sensitivity while dichromatic vision is simulated by deleting the relevant cone type. The model is reviewed and results of applying it to a range of real-world tasks are presented. These include a map-reading task and discrimination of colour-coded gas bottles, amongst others. [Supported, in part, by the Human Sciences Domain of the UK Ministry of Defence.]

◆ **Motion-based colour integration along S-cone modulation**

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Contradicting the conventional notion that human visual system separately analyses colour and motion, recent studies showed that L–M chromatic modulations could significantly affect luminance-defined motion perception. Although these findings suggest interactions between parvocellular and magnocellular pathways, similar effects were not generally found for S-cone chromatic modulations, for which the third, koniocellular, pathway is suggested to be responsible. Therefore, it remains an important open question whether the chromatic processing in S-cone modulations interacts with the luminance-defined motion processing. Recently, we found ‘motion-induced colour integration’, in which red and green colours presented at different locations on the retina, but along the trajectories of the same moving objects, are perceptually mixed into yellow (eg Watanabe et al, 2004 *Perception* 33 Supplement, 163–164). This phenomenon demonstrates a direct modulation of colour perception by luminance-defined motion. Here we tested whether the same effect was observed for S-cone modulated colours. In the experiment, the subjects were asked to evaluate the magnitude of subjective colour mixture for moving bars. The bars jumped every 6.25 ms in one direction with their colour alternating between pale purple and pale green, obtained by modulating S-cone contrast along a tritanopic confusion line that passed grey (CIE, $x = 0.33$, $y = 0.33$). As the jump size was equal to the bar width, different colours were not superimposed on the retina when the eyes were stationary. As in our previous observation with red/green stimuli, we found that the two colours on the trajectory of the moving bar were perceptually mixed more strongly than expected from spatial resolution of perceiving control chromatic gratings. This demonstrates that the chromatic processing in S-cone modulations also interacts with motion processing in motion-based colour integration.

◆ **Detection of colour change in a moving object**

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It is often assumed that moving stimuli are perceived in a facilitated way as compared to stationary or flashed ones. It is not always only motion (but sometimes also attention, etc) that discriminates presentation of stimuli between motion and stationary conditions. In the current series of experiments, we did detach motion of stimuli from some other possibly important properties of stimulus presentation (such as spatiotemporal or occurrence certainty of target event). We used a simple reaction-time (RT) task so that seven observers had simply to press a button as fast as they could when they had perceived the colour change (or a luminance change in a control condition) of a moving bar (with a constant velocity of either 6, 14, 20, 26, or 40 deg s⁻¹). As a result, we found that in the simple task of detecting the colour or luminance change of a moving or stationary (ie 0 deg s⁻¹) bar, the RT decreased with growing velocity. The repeated-measures ANOVA indicated that the effect of velocity on RT was significant ($F_{5,12} = 343.7$; $p < 0.001$). Even the slowest velocity (6 deg s⁻¹) showed some processing cost as compared to detecting the same change in a stationary stimulus. Thus, we demonstrated that kinematic properties of the stimuli influence the detection of other stimulus attributes (eg colour or luminance) that indicates much earlier interaction than usually thought between different processing streams.

[Supported by an ETF grant no.6244.]

◆ **The role of luminance and colour in categorising images**

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Our objective was to study the importance of luminance (L) and colour (C) in images, akin to Piotrowski and Campbell’s (1982 *Perception* 11 337–346) study on amplitude and phase.

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We used ten 512×512 face images, F_k , $k = 1-10$, most from Weber's Caltech dataset, and obtained their hue (H), saturation (S), and value (V) components. We obtained luminance images L_k by setting $H = S = 0$, and colour images C_k by retaining the H and S values for each pixel, and setting V to 127 (maximum is 255). We obtained low-pass (l) and high-pass (h) versions of the images using a Gaussian ($\sigma = 30$ pixels), with nine variants for each F_k : F_k , L , C components (L_k , C_k), and filtered versions, F_{lk} , F_{hk} , L_{lk} , L_{hk} , C_{lk} , and C_{hk} . For each variant in pair k and m , we created all possible composites with the C component of one variant and the L component of the other variant, pitting L against C in 2×9 such images for each pair. We displayed a composite image I_{km} , next to the originals F_k and F_m ; observers reported whether I_{km} resembled more F_k or F_m . We repeated this for all 810 $[(10 \times 9/2) \times 18]$ such composites. We report on averages of five observers, who displayed very similar patterns. We found that (i) L_k dominated C_m , C_{lm} , and C_{hm} at rates above 98%. (ii) L_{hk} dominated C_{lm} and C_{hm} at above 98%, and C_m at about 60%. (iii) L_{lk} dominated C_{lm} at about 98%, and C_{hm} at about 92%, but lost to C_m at above 62%; the latter condition is the only one that C dominated over L . We can conclude that luminance plays a stronger role than colour in perceiving images. In particular, high-frequency luminance components are more important than their low-frequency counterparts. The same trend appears to hold for colour. Additional experiments are in progress with a wider variety of images.

CONTEXT

◆ Illusory contour figures prime matching of real shapes

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Kanizsa suggested that discs with cutouts (pacmen) induce perception of overlying geometric forms with modal completion of their contours, and Kojo et al (1993 *Vision Research* **33** 897–901) demonstrated that such forms may be induced also by sequentially presented pacmen. Electro-physiological studies suggested that these effects may be low-level, though MEG and fMRI studies suggested high-level involvement. In parallel, numerous researchers analysed priming effects and looked for their cortical processing level. Beller (1971 *Journal of Experimental Psychology* **87** 176–182) proposed a primed matching paradigm, whereby the response that two letter shapes are the same is speeded by a previous exposure to this shape. This paradigm was extended to non-letter shapes in studies of the completion of occluded objects (Sekuler and Palmer, 1992 *Journal of Experimental Psychology* **121** 95–111). To extend the analysis of levels of perceptual processing, including modal completion and priming, we tested whether Kanizsa forms may lead to priming effects. We presented inducing pacmen either simultaneously or sequentially and compared their priming effect with that of real figures on a subsequent speeded same–different shape test. We found that Kanizsa modally completed figures prime real (ie complete) figures. It is not the pacmen themselves, but the more high-level-induced shapes that prime later perception. Rotated inducers do not prime real figures—thus it is neither the positions of the inducers, nor the missing sector from each inducer that cause the priming, but rather the possibility that, taken together, the inducers could induce an illusory surface. Even Kanizsa shapes that are induced by sequential presentation of their inducers prime later perception of real figures.

[Supported by 'Center of Excellence' grant #8009 from the Israel Science Foundation and the US–Israel Bi-National Science Foundation.]

◆ Contextual dependence of flash-lag illusion magnitude

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Recently, Jancke et al (2004 *Journal of Physiology* **556** 971–982) have shown that latencies for moving objects are shorter than for flashed objects (recording in vivo cells from V1). They postulate a pre-activation at the areas that would have been activated if the movement continued in the same direction. This mechanism potentially explains how the visual system compensates neural delays for motion and also offers a plausible 'low-level' explanation for the flash-lag effect (FLE). Also, it has been proposed (Seriès et al, 2004 *Journal de Physiologie* **97** 453–474) that adding two long-range laterally propagating cortical signals should result in a modulation of the latency of spiking responses. A corollary of this would be that two different moving stimuli appropriately 'synchronised' could join their pre-activation at the point where they would intersect. Therefore, a shorter latency for perception is expected when a second object moves to intercept a target moving object. Consequently, if we flash a line just before the potential collision between the target moving object and a second one, the FLE would be increased. We measured the FLE in this condition and found that the magnitude of the FLE was indeed

significantly increased. Control experiments with the second object fixed at the final position of its trajectory and with reversed motion (moving away from the trajectory of the first object) showed no effect. Interestingly, this magnification of the FLE also occurs when the second moving object is a barely noticeable thin ring, showing that summation of pre-activation is produced by motion itself rather than luminance effects. This suggests that higher perceptual processing (ie border integration into a moving object) is also involved. Results presented here link perceptual phenomena with described mechanisms at the cortical level allowing qualitative and quantitative predictions to be made and tested.

[Supported in part by a grant (number BSO 2001-2008) from the Ministerio de Ciencia y Tecnología of the Spanish government.]

◆ **Bistable perception of moving plaids in near absence of attention**

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Under certain conditions, the perception of moving plaids alternates between a coherent and a transparent percept (the two gratings either appear as one surface or as two distinct surfaces). We wished to establish whether visual attention alters the dynamics of this perceptual rivalry and, if so, how it does it. We presented a moving plaid briefly in the near periphery (duration 360 ms, eccentricity 5 deg) and, concurrently, two successive visual-search arrays near fixation. Compared to continuous displays, the brief and interrupted presentation of moving plaids prolongs mean percept duration approximately two-fold, consistent with Leopold et al (2002 *Nature Neuroscience* 5 605–609). The visual search reliably detains an observer's visual attention, ensuring near absence of attention from the moving plaid ('double-task situation'). Control experiments show substantially higher thresholds for direction discrimination with single patterns in the double-task situation. Successive trials were ~2 s apart, and observers reported the perceived direction of the plaid (thereby indicating the percept obtained on a given trial). The coherence coefficient [$F_{\text{coherent}} = N_{\text{coherent}} / (N_{\text{coherent}} + N_{\text{transparent}})$] differed by 10%–20% between single-task and double-task situations. However, the sign of this difference varied between subjects and/or sessions. Comparing successive trials, we also established 'dominance periods' for each percept, finding the gamma distributions typical for perceptual rivalry. In general, distribution parameters exhibited considerable variability between subjects and sessions. Interestingly, the mean dominance period and rate parameter of transparent percepts appeared to stabilise (ie become less variable) in the absence of attention. The distribution of coherence percepts did not show this effect. In conclusion, while attention dramatically alters thresholds of visual motion (eg in direction discrimination), it appears to have surprisingly little effect on perceptual multistability generated by the same class of stimuli.

◆ **Why is apparent tilt so large?**

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In the periphery, when vertical things are close to each other, a near-vertical target rarely appears near-vertical; it usually seems tilted one way or the other (Baldassi et al, 2004 *Perception* 33 Supplement, 41). We wondered whether this might be due to orientation-selective lateral inhibition. Inhibition of neurons preferring vertical might reduce the frequency with which the target is actually seen as near-vertical. To test this notion, we asked the observers to judge the direction of tilt (clockwise versus anticlockwise) of a parafoveal target surrounded by flankers varying in number (0 to 8) and in orientation with respect to vertical (-90° to 90°). Inhibition of neurons preferring non-vertical tilts should not reduce the frequency of vertical judgments. We used a magnitude-matching paradigm that required subjects to identify the target's tilt with a mouse click, recording both the direction and the perceived magnitude of the tilt. This technique allowed us to sketch the internal response distributions driving the observers' response in the presence of tilted distractors and to draw the relative psychometric function with a unique subject's response. Our results show that observers still rarely saw near-vertical targets as near-vertical. We conclude that lateral inhibition is not the primary reason for contextual effects on perceived tilt. Other models are considered.

◆ **Contextual effects on the perception of stimulus dimensions**

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A recent fMRI study has shown that the BOLD response to visual stimuli in human V1 is spatially nonlinear near the edge of the stimulated region (Shmuel et al, 2005, in *Proceedings of the 11th Annual Meeting of the Organization for Human Brain Mapping, Toronto, 12–16 June*).

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In particular, the activation extends significantly (ie about 1 mm) beyond the expected retinotopic mapping of the stimulus edge. However, it is unclear whether the corresponding increase in neuronal activity shows a similar nonlinearity and whether this nonlinearity biases our perception. Here, we have studied whether a visual stimulus that is spatially constrained by additional surrounding stimuli leads to a different percept than a stimulus that is presented on its own. We compared the perceived widths of bars with and without abutting flanks. High-contrast checker-bars flickering at 5 Hz were presented to four naive subjects. One bar flanked by bars flickering in counterphase and one non-flanked bar were shown simultaneously for 200 ms. The widths of both bars and flanks were varied randomly and the position jittered around an eccentricity of 6.8 deg. Subjects were instructed to fixate and to judge which one of the two bars had the larger width. A psychometric function was fit to the behavioural responses. Estimation of the point of subjective equality revealed that all subjects perceived the non-flanked stimulus as having a larger width. Over all subjects, the effect was about 0.3 deg of visual space, which corresponds to a cortical distance of about 1.3 mm (Brewer et al, 2002 *Journal of Neuroscience* 22 10416–10426). We conclude that the perceived dimensions of bars depend on the context of the visual stimulus. Whether this perceptual effect resembles previously found spatial nonlinearities in the BOLD response needs to be further studied.

◆ **Approach towards effective advertisement through consumers' eyes**

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In this project, the effects of beverage advertisement on consumers' minds were investigated. Consumers consciously or unconsciously are affected by the information they get from the advertisements. The role of an advertisement in decision making of consumers seems to be greater. As Japanese companies spent most advertising money on TV commercials, we focused on perception and recognition of TV commercials. In order to clarify where and how the subject's eye moved in each TV commercial, eye movements of subjects during watching of a couple of TV commercials were recorded with the eye tracking system 'FreeView'. The results showed some typical eye-movement patterns. Most striking was that female subjects frequently gazed at the faces of an actor or an actress in the commercial. Moving objects also attracted attention of the subjects. Within each object, subjects tended to move their eye towards the middle of the object (eg the labelling of a bottled drink). Following the eye-tracking experiment, we interviewed the subjects in order to ask how they felt and thought about each of the commercials shown. This allowed us to see which of the advertisements made good impressions on the subjects. Also in the interview records, comments about an actor or an actress were frequently observed. This suggests that a TV commercial using an actor or an actress can easily attract the attention of consumers and also give them a strong impression. Thus, the combination of eye tracking and interview is an effective way to investigate the perception and recognition of TV commercials by consumers.

◆ **For better or worse: Reconciling differences across lateral interaction tasks**

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The apparent contrast of a grating patch can be enhanced or reduced by the addition of an annular surround, depending upon the relative contrasts of centre and surround. The suppressive effect, found when surround contrast exceeds centre contrast, is widely attributed to gain control mechanisms involving lateral interactions across space. Similarly, performance on hyperacuity-level spatial-frequency and orientation-discrimination tasks can be enhanced or depressed by a surround of intermediate orientation or spatial frequency, again depending upon the relative contrast of centre and surround. Models based on lateral interactions over space can be easily modified to account for the spatial-discrimination results. These simple models, however, cannot account for results found with both apparent contrast and spatial discriminations indicating that masking effects are not reciprocal; a surround suppresses both apparent contrast and discrimination performance, but the centre has no effect on judgments made on the surround. These results suggest that higher-level mechanisms of figure–ground segregation play a role in centre–surround interactions. One glaring discrepancy between results found with apparent-contrast and spatial-discrimination tasks occurs when contrasts of centre and surround are equal. In the

apparent-contrast case, the suppressive effect is itself suppressed, leading to near-veridical perception of centre contrast. In the case of spatial discriminations, however, performance is maximally depressed when centre and surround contrasts are equal, leading to near-chance discrimination performance. The apparent-contrast and spatial-discrimination results may be reconciled if a mechanism that sums over centre and surround is activated when centre and surround are not clearly delineated as two separate parts of an object. We present two models that predict these apparently discrepant results by activating the same neural summing mechanism. The models differ in their decision stages, reflecting the difference in task demands.
[Supported by NIH EY13953 to LAO.]

◆ **Contextual modulation of bistable plaid motion perception**

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We investigated the effect of contextual surround on transparency decisions during plaid motion perception. Eight observers had to report whether they perceived transparent or non-transparent motion in a 5 deg central circular region of a moving square-wave plaid display (30% duty-cycle gratings, 1 cycle deg⁻¹ spatial resolution, 1 deg s⁻¹ velocity, 120° difference in movement direction). We defined 11 conditions with graded levels of transparency in the centre: 8 by varying the luminance of intersections and 3 by applying dynamic texture to the gratings. For the estimation of surround effects, we defined a centre-only and 5 different surround plaid conditions (20 deg diameter and 0.25 deg separation from the centre). Surrounds had the same spatiotemporal parameters as central stimuli, but were biased either towards transparent or non-transparent motion (2 by luminance and 3 by texture manipulations). Centre and surround conditions were randomised and presented in 10 s blocks. The proportion of transparent, non-transparent, and uncategorised percepts were measured and analysed with an ANOVA. We found significant perceptually graded response to the central stimulus depending both on luminance and texture manipulations, reflected not only in the proportion of transparent and non-transparent percepts, but also in the proportion of uncategorised responses. Contextual modulation caused a significant shift in the central percept, and showed a significant interaction with both luminance and texture manipulations in the centre, but only for the proportion of transparent-motion responses. The central transparent percept shifted towards the bias provided by the context by an amount contingent on the bias of the central stimulus itself. Future studies should further elucidate the dependence of contextual interactions on the length of presentation time and adaptation phenomena.
[Supported by FCT SFRH/BD/13344/2003, POCTI/NSE/46438/2002, BIAL15/02, Gulbenkian Program for Stimulating Investigations.]

◆ **Contour integration by cue combination**

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Contours are easily and effortlessly detected in Gabor fields when the local orientation of the stimulus elements is close to the global path angle of the contour (Field and Hess, 1993 *Vision Research* 33 173–193). However, recent studies show that contour integration is also mediated by other cues, such as disparity and depth (Hess et al, 1997 *Vision Research* 37 691–696). We let our subjects perform contour detection in Gabor fields with varying stimulus contrast and orientation. Our results show that contour salience is strongly correlated with the distance of the second-order parameter statistics of contour and the surrounding field. If orientation and contrast show sufficiently large statistical variation in the surround, and one of both features vary only a little along a spatial path, the elements along the path are perceptually grouped. Further, contour salience is strongly enhanced when the elements along the path show little variation in both feature dimensions. Our results support the notion that grouping is based on different features and their interaction and is presumably mediated by the same circuits in V1, V2, and LOC, as substantiated by recent fMRI studies (Altman et al, 2003 *Current Biology* 13 342–249).

◆ **Regulation of sensorimotor actions in conditions of open mountain space**

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The experiment was carried out on a team of students of Inter-regional Academy of Personnel Management who climbed mountain Elbrus (5642 m). The aim of the experiment was the study

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of space perception in the open space of high mountains. Individual perception of time and space depends on the height. Starting from 2000 m, an acclimatisation process takes place: students underestimate space and time intervals, and the size of the objects. Lack of experience results in illusions. Individual perception of objects differs from reality. Objects seem closer if they are observed either from a lying position or over a water basin or valley. Sunny weather and direct light also lead to visual illusions. Large and brightly-lit objects seem closer. The distance the students had to determine was divided into several segments. Each segment was determined separately and the results were summed up. Within 0.5 km distance, the students mistake was 10%; within 2–4 km, up to 20%; over 4 km, above 50%. Consequently, there was a tendency to underestimate the space interval. At the height of 3500–4000 m and higher, estimation of distance is harder. Snow that covers all points (the basis of visual perception) tampers with space determination. Personal energy potential rises with the height over the sea level.

◆ **Extraclassical receptive-field phenomena and short-range connectivity in V1**

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We suggest neural mechanisms for two extraclassical receptive-field phenomena in striate cortex (V1): surround suppression and contrast-dependent receptive field size. Extraclassical receptive field phenomena are commonly assumed, based on the cortical magnification factor, to result from long-range lateral connections and/or extrastriate feedback. Contrary to this common belief, we present large-scale simulations that provide rigorous computational support for the hypothesis that surround suppression and contrast-dependent receptive field size in V1 largely result from local short-range (< 0.5 mm) cortical connections within V1, and feedforward LGN input (arXiv:q-bio.NC/0504027). The large-scale spiking neuron model used to arrive at this conclusion is constructed from the basic established anatomical and physiological data for macaque. Surround suppression results from (A) direct cortical inhibition, or (B) suppression of recurrent cortical excitation, or (C) action of both these mechanisms simultaneously. When LGN surround suppression is not included, all mechanisms are about equally prevalent. When LGN suppression is included, mechanisms B and C are substantially more prevalent than A. We observe an average growth in the range of spatial summation of excitatory and inhibitory synaptic inputs for low contrast, as predicted by the phenomenological DOG and ROG models. However, this growth is neither sufficient nor necessary to explain receptive field growth for low contrast. Contrast-dependent receptive field size usually results from other or additional changes (with contrast) in the relative gain of these inputs as a function of stimulus size.

[Supported by grants from ONR (MURI program, N00014-01-1-0625) and NIMA (NMA201-02-C0012)]

◆ **Effects of visual context on the perception of collision events in chimpanzees (*pan troglodytes*)**

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The perception of collision events has been studied not only in investigations of the visual property of moving objects but also as a canonical example of causal perception [Michotte, 1946/1963 *The Perception of Causality* (London: Methuen)]. However, subjects of such studies have been exclusively humans, and causal perception has not been investigated in non-human primates. On the other hand, comparative cognitive studies on humans and human relatives have paid attention to the recognition of physical world, such as causality [Tommasello and Cal, 1997 *Primate Cognition* (Oxford: Oxford University Press)], and it has been a prime task to know the perceptual basis of such recognition in non-human primates. We investigated the causal perception of chimpanzees, focusing on the effects of visual context on the perception of stream/bounce motion events (Scholl and Nakayama, 2002 *Psychological Science* **13** 493–498). The contextual effects on the stream/bounce events can be described as follows: two objects moving across each other are often perceived to stream past one another but, when an additional context event, in which two objects bounce off, is temporally synchronised with the test event, the perception is biased toward bouncing. Two experiments were conducted on four chimpanzees, who had much experience of computer-controlled tasks. Prior to the experiments, the chimpanzees were trained to discriminate ‘bouncing’ and ‘streaming’ of the objects in an object-tracking task. In the first experiment, chimpanzees showed a significant increment of ‘bouncing’ responses depending on the addition of the context event. In the second experiment, the proximity parameter was varied. Effects of the context event were decreased with increased separation between test and context events as seen in previous research on humans (Choi and Scholl, 2004 *Perception & Psychophysics* **66** 926–942). These results suggest that chimpanzees perceptually organise the movement of multiple objects in the same manner as humans and that they perceive causality of collision events under the same constraint of visual property as that of humans.



A network model and its experimental test

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When both the centre and the surround of the receptive field of a neuron in the macaque striate cortex (V1) are stimulated, its response is suppressed compared to stimulation of the receptive field centre alone. This suppression has long been thought of as being mediated by long-range lateral connections within V1. However, recently it has been shown [Angelucci et al, 2002 *Journal of Neuroscience* **22**(19) 8633–8646; Bair et al, 2003 *Journal of Neuroscience* **23**(20) 7690–7701; Levitt and Lund, 2002 *Visual Neuroscience* **19** 439–452] that suppression can be evoked by stimuli far beyond the monosynaptic range of lateral connections. Moreover, the relatively short temporal latency of suppression arising from the far surround cannot be accounted for by the slow conduction velocity of lateral connections. In contrast, feedback projections from extrastriate cortex to V1 are commensurate with these large-scale suppressive effects in terms of spatial scale and conduction velocity. We set up a recurrent network model whose architecture is constrained to fit with recent anatomical/physiological studies (Angelucci et al, 2002, loco cit). In the model, the feedback connections from extrastriate cortex exert their suppressive influence arising from the far surround by targeting primarily excitatory neurons in the near surround, which in turn send V1 lateral connections to local inhibitory neurons in the receptive-field centre. The model can reproduce suppression from the far surround in a way consistent with currently available anatomical and physiological data regarding the static and dynamic effects of surround suppression. The model generates specific and easily testable predictions. One such prediction is that stimulation of the far surround can facilitate the centre response, when a high-contrast or low-contrast surround grating is presented together with a low-contrast centre grating. These predictions are compared with our recent physiological measurements, which support the model predictions and reveal that the suppressive influence of the far surround is not always suppressive.

[Supported by NSF Grants No. IBN 0344569 and DMS 020982, NIH EY 015262, RPB, Wellcome Trust 061113.]



Contextual influences in amodal completion: Evidence from magnetic brain responses

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In the process of perceiving partly occluded objects as whole objects, so-called amodal completion, there are two influences that can lead to qualitatively different sorts of completions. Global influences originate from the overall figural aspects of the shape, while local influences originate from parts of the shape. Here we measured the influence of these contextual aspects of partly occluded shapes using MEG recordings. Subjects were presented with a partly occluded shape, and after 1 s the occluder was removed, revealing a physical (possible) completion. There were two sorts of partly occluded shapes: one in which global and local influences result in different perceived completions, so-called ambiguous shapes, and another in which local and global influences result in the same perceived completion, so-called convergent shapes. We found an early left-occipital component, which was sensitive to both the figural aspects of the physical completion and the congruence between the physical completion and the perceived completion. In contrast, an early right-occipital component and a later anterior temporal component were sensitive only to the congruence between the physical completion and the perceived completion. We conclude that the left early component may reflect the figural aspects of the physical completion, modulated by the contextual aspects, whereas the early right-occipital component and the later component mainly reflect the violation of the expectancy of the perceived completion that was built up by the context.

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◆ (Con-)fusing contours

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We have created patterns in which illusory Kanizsa squares are positioned on top of a background grid of bars. When the illusory contours and physical contours are misaligned, the resulting percept appears to be rather confusing (van Lier et al, 2004 *Perception* 33 Supplement, 77). Observers often perceive a shift of the part of the grid that falls inside the illusory square, leaving the impression that the physical grid is indented at the positions of the illusory contours. All in all, these displays have a remarkably unstable and restless appearance. We have performed two experiments to study the strength and the direction of the illusory shifts. In the first experiment, an illusory square, induced by a pacmen configuration, was positioned at various positions on a grid of straight bars. After briefly flashing these stimuli, observers frequently reported illusory shifts (or indentations) of the background bars for those cases in which physical and illusory contours were slightly misaligned. In a control condition, the pacmen were replaced by crosses (that did not induce an illusory square). As expected, this time, no illusory shifts were reported. In the second experiment, observers had to judge the direction of the illusory shift. The results show that the perceived shifts, in fact, reflect a tendency to cancel the misalignment between physical and illusory contours in the display. We argue that these temporary relocations of physical and illusory contours reflect both competition and cooperation between the underlying contour mechanisms.

FACE PERCEPTION 1

◆ The accuracy of perceptual memory for personally known faces

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Recently, Ge et al (2003 *Perception* 32 601–614) reported a very high accuracy of memory for a highly familiar face. Their Chinese participants had to identify the most veridical appearance of Mao's face among unaltered and transformed (interocular distance was gradually increased or decreased) versions of his portrait. In the present experiment, the same facial transformations were applied to our participants' faces to evaluate whether this hyperfidelity for familiar faces is specific to famous individuals whose face is mainly known from a standard portrait, or if it could generalise to personally known faces (the own face and a close person's face). Results showed that performance was not different for the two familiar faces in the recognition task, or between the recognition task and a perceptual discrimination task. The high accuracy of memory previously shown for a very famous face generalises to personally known individuals for whom we have a varied visual experience.

◆ Electrophysiological correlates of translation-invariant and noninvariant components of facial adaptation

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Facial adaptation—induced by prolonged exposure to an individual face—can bias the perceived identity of a subsequently presented face. The goal of the present study was to isolate the translation invariant and noninvariant components of facial adaptation and to investigate their ERP correlates (ie the increase in latency and decrease in amplitude of the N170 component). Subjects performed a gender-discrimination task for peripherally (6 deg) presented facial morphs of upright or upside-down presented female and male faces. Each trial consisted of a 5000 ms adaptation period followed by a test face. During adaptation, two stimuli were displayed on the two sides of the fixation: within a block they were either both Fourier phase-randomised images (control condition) or one was a Fourier image and the other was a prototypical female face. This was followed by a test face (200 ms, morphed female–male face) presented randomly on either side of the fixation. ERP was recorded from 23 channels. Throughout the experiments, fixation was controlled by an infrared eye-tracking system. The psychophysical results showed strong adaptation effect both when the adapter and test images appeared on the same side of the fixation (SAME) as well as when they were presented in different hemifields (DIFF), compared to the control condition. However, the magnitude of adaptation was approximately twice as large in the SAME condition than in the DIFF condition. The adaptation effects on the N170 ERP

component followed a similar pattern to that found in the psychophysical data. Interestingly, the behavioural and electrophysiological results were very similar for upright and upside-down presented faces. Our results provide evidence that face-specific adaptation takes place simultaneously at different stages of visual processing, leading to translation-invariant and noninvariant facial aftereffects.

◆ **Hemifield-contingent face aftereffects**

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Recently, we have found [Kovács et al, 2005 *Vision ScienceS* (abstract)] that facial aftereffects consist of two components: one is translation invariant and the other is specific for the visual hemifield where the adapter has been presented. In the present study, we tested whether simultaneous adaptation to different faces in the two visual hemifields—a female and a male face, or a happy and a fearful face—might result in hemifield-contingent facial aftereffects. Subjects performed a gender-discrimination task (2AFC) with peripherally (separated by 12 deg) presented facial morphs of female and male, or happy and fearful faces. During adaptation (5 s) two face stimuli were displayed in the two hemifields: in the facial-gender adaptation experiments, a female and a male face; in the facial-emotion adaptation experiments, the two adapters were different expressions of the same face, one was happy and the other was fearful. Test faces were displayed for 200 ms randomly on either side of the fixation. In the control conditions—both in the facial-gender and facial-emotion experiments—the adapters were Fourier-randomised face stimuli that contained no figural information. Simultaneous adaptation to a female face in one visual hemifield and a male face in the other resulted in hemifield-contingent gender aftereffects. Test faces were perceived more masculine or more feminine—compared to the control—when presented in the hemifield with a female or male adapter, respectively. Similarly, adaptation with a happy and a fearful face resulted in strong hemifield-contingent facial-emotion aftereffects. Test faces were judged more fearful when they were presented in the hemifield with the happy adapter and happier when they were presented in the hemifield with the fearful adapter. Our results provide the first evidence for hemifield-contingent facial aftereffects and suggest that face processing involves hemisphere-specific mechanisms that can be adapted selectively.

[Supported by the Hungarian National Research and Development Program: 2/046 to ZV and 5/0079/2 to GK.]

◆ **The effect of rotation information on infant's recognition of unfamiliar faces viewed from different viewpoints**

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It has been suggested that 7-month-old infants can recognise unfamiliar faces viewed from a variety of viewpoints, such as the 3/4 view and the profile view (eg Fagan, 1976 *Child Development* **47** 627–638; Rose et al, 2002 *Infancy* **3** 435–455). However, in their experiment only a single static face image was used in both the learning and the test phase. In addition, some researches indicated that the motion information promoted infants' visual perception (eg Kellman and Spelke, 1983 *Cognitive Psychology* **15** 483–524). We examined the effect of the rotation information on face recognition in infants aged 3–7 months. Infants were first familiarised with a female face in two conditions: the smooth and the random condition. In the smooth condition, a movie of a female face rotated from the frontal view to the profile view was presented with regular frame order. In the random condition, the same movie was presented in random frame order. The familiarisation phase was two 30 s. After familiarisation, infants were tested with a pair of familiar and novel female 3/4 views for two 10 s trials. Each 3/4 view was viewed in the opposite direction to those of the familiarisation phase. If infants recognise the familiar face, they show a novelty preference for the novel female face. The results indicated infants' preference for novel female 3/4 view only in the smooth condition. This suggests that the rotation information facilitates learning unfamiliar face across the viewpoints.

[Supported by RISTEX, Japan Science and Technology Agency, and a Grant-in-Aid for scientific research (15500172) from the Japan Society for the Promotion of Science.]

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◆ **Analytical and configural processing in infants' gaze perception**

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Perceiving gaze direction is important for human adults and infants. Human adults process gaze direction by using the configural information of the face. In face cognitive developmental studies, 7–8-month-old infants showed configural processing in upright faces (Schwarzer and Zauner, 2003 *Vision Research* **43** 2783–2793), and analytical processing in inverted faces (Choen and Cashon, 2001 *Infant and Child Development* **10** 83–92). But until now, there have been no developmental studies about the interaction of gaze perception and configural information processing. We examined whether 6–8-month-old infants ($N = 96$) process gaze direction configurally or analytically. We used the face stimuli of schematic faces drawn by Wollaston (1824 *Philosophical Transactions of the Royal Society of London, Series B* **114** 247–256). In habituation period, a schematic illusion face was shown. In this face, human adults perceive direct gaze by analytical processing of only the eyes, and averted gaze by configural processing with facial contour. In the test period, two mirror images of this face were shown; one had a mirror image (eye-switch face), and the second had a mirror image except eyes (gaze-switch face). If infants process gaze direction configurally, they show novelty preference to a gaze-switch face. By contrast, if infants process gaze direction analytically, they show novelty preference to an eye-switch face. An upright face was used for experiment 1, and inverted faces were used for experiment 2. Results suggest that only 8-month-old infants could process gaze direction configurally in an upright face, and process gaze direction analytically in an inverted face.

[Supported by RISTEX, Japan Science and Technology Agency and a Grant-in-Aid (15500172) for scientific research from the Japan Society for the Promotion of Science.]

◆ **Adaptation to differences in 3-D face shape across changes in viewpoint and texture**

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Face-adaptation effects can provide clues as to the nature of underlying representations. Two experiments are reported in which an adaptation paradigm was used to test for adaptation to differences in face shape across changes in image properties. All experiments made use of synthesised 3-D face models based on principal components analysis of a database of laser scans of faces drawn from two distinct populations, Japanese and Caucasian. Participants were asked to make an ethnicity judgment. 3-D shape is known to be useful in this task and its variation can be captured by linear discriminant analysis to give a quantifiable variable. For both experiments the point of subjective equality (PSE) was measured before and after adaptation to a set of faces defined in terms of one of the distinct populations. The viewpoint and the texture map used for rendering the adapting faces were varied between subjects. For experiment 1, the pre-adaptation and post-adaptation PSE was measured for faces shown in 15° or 45° views, with adapting stimuli shown in one of these views. Adaptation, that is movement of the PSE in the direction of the adapting population, was found ($F_{1,8} = 20.1$, $p \ll 0.05$) independent of adapting or test view. In experiment 2, pre-test and post-test PSE was measured for 0°, 30°, and 60° views. Adaptation was always to the 30° view but the texture map used at adaptation varied between subjects. The texture used was an ethnicity specific average, either consistent or inconsistent with the shape information. Again, there was adaptation dependent on the shape defined ethnicity of the adapting stimuli ($F_{1,12} = 36.2$, $p \ll 0.05$). This was independent of texture map and test view. The results are interpreted as evidence for the high-level representation of 3-D face shape independent of view and surface reflectance.

[Supported by the National Institute of Information and Communications Technology as part of 'Research on Human Communication']

◆ **Linear functions of actual head and gaze angles predict the shift of perceived gaze direction for both 2-D and 3-D presentations**

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Perceived gaze direction of another person, the 'looker', can be affected by their head angle and the lighting. In order to measure these effects quantitatively, and to compare the effect of changes between real-life communication and the 2-D images used in telecommunications, we carried

out two experiments using: (i) a 3-D live condition, and (ii) a 2-D-image condition. Both involved two tasks: discriminating between 'directed' and 'averted' gazes and localising the actual point to which the looker's gaze was directed. In the 3-D live condition, participants judged the gaze direction of a looker seated 2 m in front of them. In the 2-D-image condition, an image of the same looker was presented on a display so that the apparent size of looker's face was the same as in 3-D live condition. Results showed that when the looker's head was rotated by 15°, people perceived a gaze averted 1.5° with the head rotation as 'directed.' Localisation results showed that the shift between perceived gaze and looker's actual gaze increased with head rotation and eccentricity of the looker's actual gaze, and could be approximated by a linear function of head angle and gaze direction. There was also a shift of perceived gaze in the opposite direction to the direction of lighting. Results for 2-D presentation revealed that perceivers were as sensitive as in the 3-D-live condition in discriminating directed/averted gaze, but the shift in localisation of gaze direction was larger than with 3-D presentation. As with 3-D, these shifts of location could be approximated by a linear function of head angle and gaze direction in the 2-D-image condition.

[Supported in part by the National Institute of Information and Communications Technology and Research and Development through Encouraging Researchers and their Collaborations for Strategic Information and Communications R&D Promotion Programme.]

◆ **The perception of facial expressions in children with autism spectrum disorders**

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A possible explanation for why people with autism spectrum disorders (ASD) have difficulty reading facial expressions is that they attend to a narrow range of features in the face when judging facial affect. Research on face identification found children with ASD to be better at recognising faces based on features in the lower part of the face (mouth) than on features in the upper part (eyes), while the reverse was found for normally developing children. We examined whether the same reliance on, or expertise in, mouth information could be found in emotion perception. Stimuli consisted of black-and-white photographs of male and female faces with five facial expressions each. We used one bottom-face emotion (happy, where the lower part is most important for recognition and discrimination), three top-face emotions (sadness, anger, and fear, where the upper part is most important), and a neutral expression. In addition to the original expressions, we made hybrid photographs where half of the face consisted of an emotional expression while the other half consisted of a neutral expression. High-functioning children with ASD and normally developing children aged 6–8 years were asked to judge the expressions of both the original and hybrid stimuli. For normally developing children we expected and observed more difficulties in recognising bottom-face emotions when the bottom part of the face was replaced by a neutral expression and top-face emotions when the upper part was replaced. If children with ASD were to rely mostly on mouth information, expressions (top-face and bottom-face) where the lower part of the face was replaced by a neutral expression would be more difficult for them to recognise. Contrary to this expectation children with ASD, like normally developing children, were found to recognise top-face emotions better when using eye information. No evidence was found for a reliance on, or expertise in, mouth information in children with ASD.

◆ **How age judgments increase by adding wrinkles to human faces**

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Owing to aging, the human skin loses elasticity, causing wrinkles to appear on it. We presented images of human faces to respondents and asked them to estimate the age of the persons to whom the faces belonged. Four types of wrinkles were manipulated on the faces: on the forehead (brow), ocular (crow's feet), nasal (rictus), and under the mouth. The analysis of the psychophysical judgments about the age reveals that our age perception depends on the type of wrinkles, their number, and also on the depth of the furrows. Thus, wrinkles on the forehead and on the mouth produce a greater increase in age judgments than those produced by ocular or nasal wrinkles. The depth of the furrows leads also to a significant increase of the age estimate.

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Also, the effects induced by the wrinkles on age judgments are not independent of the participants' age. As the age of the participants decreases (from middle age to adolescence), the age assigned to the faces increases. Adolescents (aged 12 years) believe that wrinkles appear roughly seven years earlier than do young adults (aged 21 years), and about nine years earlier than do middle-aged adults (aged 45 years).

◆ **The effects of perceptual load: Evidence for a face-specific attentional mechanism**

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Success in ignoring irrelevant distractors depends on the perceptual load in the relevant task when the distractor is a letter, or a picture of an object. For these classes of stimuli, failure to exclude a distractor from processing occurs only when perceptual load is low and attentional capacity that is surplus to the demands of the relevant task spills over to the distractor. When perceptual load is high, the consumption of all available attentional capacity by the relevant task precludes processing of the distractor. In contrast to letters and objects, faces appear to operate outside the constraints of perceptual load, with task-irrelevant faces processed for identity regardless of the level of perceptual load in a search task involving printed names (Lavie et al, 2003 *Psychological Science* **14** 510–515). This finding suggests that face processing is automatic and not dependent on general capacity limits, but leaves open the possibility that face processing may be subject to face-specific capacity limits. This possibility was investigated in the present studies. Participants decided whether a target presented in a circular array of one, two, four, or six task-relevant stimuli was a politician or a movie star. The identity of famous persons depicted by irrelevant distractor faces outside the target array was either congruent or incongruent with the target. When the target-relevant stimuli were letter strings and the target was a printed name, interference effects from the distractor faces were found at all set sizes. In contrast, when the target was a famous face set among unfamiliar faces, interference effects present at set sizes of one or two were eliminated at set sizes four and six. These results suggest a special role for faces in attention, consistent with the idea that faces may be processed by a dedicated system with face-specific capacity limits.

◆ **Angry faces are easier to identify than happy faces**

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Salient facial expressions, especially anger, are known to capture attention. Such faces should thereby receive better perceptual processing and their identification should be facilitated. Yet, an influential theory of face processing (Bruce and Young, 1986 *British Journal of Psychology* **77** 305–327) posits independent mechanisms for face expression and face identification, suggesting that face expression should not influence accuracy of person identification. To test this, with and without reduced attention, we used a sequential dual task (a skeletal attentional blink, AB) paradigm comprised of two targets, each followed by a mask. T1 was an abstract pattern composed of either many squares or many circles; its mask was another abstract pattern. T2 was a grey-scale Ekman face; its mask was another similar grey-scale face (both men). The first task was to report T1's texture (squares or circles), and the second task was to report if a pre-specified face (eg 'Bob') was present or absent. All stimuli were presented for 85 ms, but the interval between the offset of T1's mask and T2's onset was varied within each block so as to measure the AB effect. Within each block, T1 and its replacement stimuli always had the same expression (happy, angry, fearful, neutral), making face expression an uninformative cue to identity. Masks were always neutral. A significant AB effect was found in all conditions, indicating that both expressive and neutral faces are equally susceptible to dual-task costs and that both require attentional resources for identification. Interestingly, T2 performance was significantly better at all SOAs in the angry condition than in the happy condition, a finding that indicates that affective expression interacts with identification.

◆ **The influence of facial expressions on the other-race effect**

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It is well known that people remember faces from their own race better than faces from other races, a phenomenon reported as the 'other-race effect' or 'own-race effect' (Meissner and Brigham,

2001 *Psychology, Public Policy, and Law* 7 3–35). Many studies have shown that faces with positive expressions (happy) are also better remembered than those with negative expressions (sad, angry, fearful—Kottror, 1989 *Psychological Studies* 34 102–105; D'Argembeau et al, 2003 *Cognition and Emotion* 17 609–622; Putman et al, 2004 *Psychoneuroendocrinology* 29 953–960). However, the interaction between facial expressions and the other-race effect still remains to be clarified. Here, we investigated whether different facial expressions modulate the other-race bias. The experiment comprised three parts: learning, retention, and test. In the learning phase, Asian and Caucasian participants rated 64 faces (Asian-happy, Asian-sad, Caucasian-happy, Caucasian-sad) on distinctiveness without knowledge of a subsequent memory test. During the 10 min retention, participants were asked to rate the distinctiveness of English names. For the facial memory test, the task was to categorise 128 faces, 64 previously seen faces and 64 unseen faces, as 'seen' or 'not seen' during the indirect learning phase. Performance on the facial memory task showed significant interactions between the race and the expression of the faces, on both false-alarm rate and criterion. These results suggest that the other-race effect might be modulated by facial expressions. [Supported as a Brain Neuroinformatics Research Program sponsored by Minister of Commerce, Industry and Energy (Korea).]

◆ **The effects of distinctiveness on perceptual change detection for faces**

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The enhanced memorability of distinctive faces when compared to typical ones has been attributed to a greater familiarity increment for distinctive faces during learning (Vokey and Read, 1992 *Memory & Cognition* 20 291–302). Since typical faces are associated with higher general, pre-experimental familiarity, the greater increment in familiarity of distinctive faces leads to more accurate memory representations, producing higher 'hit' as well as lower 'false-alarm' recognition rates. Results from studies on perceptual and attentional processing suggest that familiarity enables more efficient processing of face stimuli (Tong and Nakayama 1999 *Journal of Experimental Psychology: Human Perception and Performance* 25 1016–1035). These previous findings lead to the hypothesis that, if typical faces are associated with higher general familiarity, then perceptual processing of these faces would be more efficient than that of distinctive faces. We examined the relationship between perceptual processing involving attention and distinctiveness. A modified change-blindness paradigm, similar to the one reported by Buttle and Raymond (2003 *Perception & Psychophysics* 65 1296–1306) was used. A pair of faces composed of distinctive and non-distinctive faces were briefly presented, followed by a second pair in which one of the faces from the first pair was changed. The presentations of both pairs were masked and participants were required to identify the location of change. Contrary to previous findings, changes involving distinctive faces were more easily detected than those involving non-distinctive faces, suggesting that greater attentional efficiency is involved in the processing of these faces. The results not only point to a nonlinear relationship between facial familiarity and distinctiveness but also suggest that distinctiveness may represent another dimension mediating processing efficiency. [Supported by the Canadian Institute of Health Research.]

◆ **Do infants use a generalised motion processing system for discriminating facial motion?**

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Previous research has shown that infants aged 4 to 8 months can perceive and discriminate facial motion (Spencer et al, 2004 *Perception* 33 Supplement, 56). Here we report a study in which we used an animated average face to test infants' ability to discriminate viewpoint invariance of biological facial motion. We familiarised infants with the animated face using one motion sequence of an actor telling a joke. The stimulus was either a full-face view (0°) or a face rotated 60° about a vertical axis (between full-face and profile). Once familiarised, infants were presented with two stimuli. One was the same as the habituation stimulus, shown at a different angle. The other was a novel motion sequence drawn from a different actor telling a different joke. Infants demonstrated a significant preference for the novel motion sequence, suggesting that they were able to encode the face-based motion in a viewpoint-invariant manner. However, in a parallel study of identical design but using inverted stimuli, infants did not demonstrate a face-inversion effect. This indicates that infants were using a general motion-processing system to discriminate between the sequences rather than a face-specific process.

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◆ **Memory for configural information of faces: The case of celebrity**

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Configural information is critical for face recognition. The conjunction effect has been taken as evidence to suggest that we only store in our memory explicit features of various faces, which sometimes can be erroneously combined to produce faulty recognition. This effect implies that our memory for facial configuration is fragile at best. However, to the extent that conjunction effect reflects memory for features that co-exist in the same face, it does not indicate whether or not we can memorise the relations among facial features. Here, we explored memory for configural information of faces. Faces of four public figures in Taiwan, including two politicians, a movie star, and a supermodel, were used. For each celebrity, nine versions of their faces, the original plus eight alternations of configuration information, were presented simultaneously on the display in each trial. Participants had to pick out the actual celebrity face from the nine alternatives. The alternations entailed minute changes in configuration such as the distance between eyes, and that between eyes and the mouth, etc. The mean accuracy was 0.71, which was significantly greater than the chance level. However, accuracy in identification varied substantially, from 0.49 to 0.92° among the four celebrities. In addition, accuracy was highly correlated with familiarity rating of the faces collected prior to the experiment proper. These results suggest that, contrary to the popular claim implied by the conjunction effect, we do store configural information of faces of celebrities, although the memory may be modulated by our familiarity with the celebrity. It would be interesting to investigate the mechanisms that enable people to detect minute alterations in facial configuration, which no doubt plays an important role in maintaining veridical memory for celebrity faces. To that end, we are currently investigating the capacity of visual working memory for configuration information of faces.

◆ **The effects of facial changes of time-series on the recognition of facial expression**

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We conducted two experiments to investigate the effects of facial changes of time series on the recognition of facial expression. Six participants took part in both experiments. A 2AFC task was employed to judge facial expression. Recognitions of morphed and actual dynamic images were compared between (experiment 1—smile or sad) and within (experiment 2—smile or wry smile) categories of facial expression. No difference was found in correct percentages between morphed and actual dynamic images in experiment 1, but there was a difference in experiment 2. It is suggested that the effect of facial motion information became greater because the within-expression task was more difficult in experiment 2. This indicates that facial changes of time series affect the recognition of facial expression.

SHAPE PERCEPTION

◆ **Curvature as an intermediate representation**

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Intermediate features such as curvature (convex versus concave) may play a critical role in global shape representation. It remains controversial whether the curvature of a stimulus (such as an hour-glass or diamond shape) is selectively encoded at a relatively local level (in area V4, for instance), or as a shape at a more global level (such as IT). We measured curvature aftereffects while varying the distance between the adaptor and test in two different conditions: with maintained fixation or across a 20 deg saccade. These parameters allowed us to investigate the properties of the neurons implicated in this task, including the size of their receptive fields and their spatiotopic and/or retinotopic properties. Our results showed that performance decreased when translation reached a maximum distance consistent with the intermediate size of receptive fields in V4, and aftereffect showed both retinotopic and some spatiotopic specificity. These findings suggest that curvature aftereffects may be located in an area where the receptive fields of cells have intermediate sizes, and visual area V4 would be a suitable candidate.

◆ **The interaction of motion and orientation in the perception of global structure**

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Research with moving frontoparallel Glass-pattern stimuli has shown that the apparent motion direction is influenced by the dipole orientation of the pattern (Krekelberg et al, 2003 *Nature* 424 674–677). We investigated how the motion and the orientation of a Glass pattern influences

the perceived direction of each. The stimuli were random-dot patterns (radius: 14.5 deg) consisting of 200 light increment oriented dot pairs (dot width: 5 min of arc) with signal pairs tilted at a common orientation. The dot pairs were drifted in a common direction at a speed of 4 deg s⁻¹ in a 1 s stimulus presentation. The task was to discriminate either the perceived direction of motion or dot-pair orientation, as a function of the angular difference between the orientation and motion direction of the dot pairs. We also examined perceived motion direction when the polarity of a dot within each pair was changed. Observers were required to determine whether the direction/orientation was to the left or right from a set of oriented reference lines superimposed on the pattern. The results showed that the apparent direction of motion was attracted by approximately 5 deg towards the dot-pair orientation for small (15 deg, 23 deg) angular differences, regardless of dot-pair polarity. However, under the same stimulus conditions, the apparent dot-pair orientation was much less affected. These results suggest that global form can be accurately extracted despite drifting motion and polarity difference, and that a later stage involved in the perception of global form may also be responsible for direction of motion perception. [Supported by Grant HKU7149/02H from the Research Grants Council of Hong Kong.]

◆ **Configural factors affect the bisection of visual size**

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Perception of visual size is affected by spatial arrangement. This is a well-known effect in size-distance interactions, in phenomena involving relative position along the vertical axis, and in Ebbinghaus-like illusions. Here, we demonstrate that bisection judgments are affected by relative spatial positions of the three objects (the two reference objects and the subjective middle), ie by the particular configuration defined by their centres of visual mass. Observers were shown two reference disks, a small one and a large one, and asked to judge, in a constant-stimuli experiment, whether a third disk appeared larger or smaller than their ideal middle disk. Several configurations were studied, including a baseline circular arrangement (three disks centred on the vertices of an equilateral triangle) and a linear arrangement (three disks with collinear centres and common tangents). The perceived mid-size disk obtained in the linear-configuration condition was smaller than the one in the baseline condition. To account for these differences we suggest that perception of middle size is influenced by intrafigural equilibrium, ie by an interaction between object sizes and interobject distances. Judgments of middle size do not depend on perceptual geometry only; they depend also on perceptual dynamics.

[Supported by MIUR-COFIN20]

◆ **Three-dimensional object shape from shading and contour disparities**

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We investigated how shading and occluding contours affect the perceived shape of globular objects during stereoscopic viewing. Both non-Lambertian shading, specularities in particular, and occluding contours have ill-defined binocular disparities. For example, the disparities of specularities depend not only on the position of a surface but also on its curvature. As a result, shading and contour disparities generally do not specify a point on the surface of an object. In four experiments, different observers adjusted numerous local surface attitude probes to a globular object with a substantial hyperbolic surface. The same object was displayed at three different rotation angles in all experiments. In experiment 1, the object was either Lambertian or Lambertian with added specularities. In experiment 2, we removed the Lambertian part of the shading; the objects were either black or black with specularities. In experiment 3, we reduced the disparity of the occluding contour to zero everywhere but retained about 95% of the shaded areas as well as the monocularly seen shape of the contour. In the fourth experiment, we removed both the Lambertian shading and the contour disparity, leaving just the specularities and the monocular contour. There was hardly any effect of shading condition or surface orientation on the perceived shape in experiment 1. Removing the Lambertian shading in experiment 2 rendered the sign of the surface curvature completely ambiguous (convex/concave) although all surfaces were perceived as being markedly curved. Reducing contour disparity to zero had no effect in experiment 3. Removal of both Lambertian shading and contour disparity made all surfaces appear flat. We conclude that shape perception is not a weighted sum of the cues nor does the perceived shape become more pronounced when more cues are available, as has been hypothesised before. Instead, these cues make qualitatively different contributions to the perception of three-dimensional shape in stereoscopic vision.

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◆ **Statistical adaptive potential for active contours**

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A very common problem in active contours (Kass et al, 1998 *International Journal of Computer Vision* 1 321–331) is the selection of suitable features for performing the best segmentation. The main problems in doing this are the resolution and the noise of the source images. Here, we present a statistical method to obtain a potential that automatically chooses and organises the best features from a set of images. The input image is first filtered with some feature-enhancer filters. This process detects all the relevant features: crests, valleys, and edges, and the use of different scales estimates the noise. Here, we have used a collection of Gaussian filters, but other filters can also be used. When all the features have been found, they are classified with a clustering algorithm. We have used *K*-means [Seber, 1984 *Multivariate Observations* (New York: John Wiley)], but other approaches are also valid [Suri et al, 2002 *IEEE Transactions on Information Technology in Biomedicine* 6(1) 8–28]. The resulting regions are divided into two groups, lineal clusters and block clusters. To do this we need to calculate the normalised second central moments of all regions for each cluster. The goal is to distinguish the lineal clusters with information about features of interest, and block clusters with information about objects or background. This clustering algorithm can be applied, if necessary, at other times to the lineal clusters in order to refine the features found. When the refined features have been found, a potential is devised. This potential gets the feature nearest to each pixel of the image; moreover, it stores the filter applied, and the direction to and the gradient values of that feature. This potential can be used in any active contour [Pulido et al, 2003 *International Congress on Computational Bioengineering, Zaragoza* (Zaragoza: C Copy Center) pp 654–657], and the algorithm can use the information on the features for high-level segmentation. The method has been applied to medical images.

◆ **Sign-dependent detectability of change in curvature as an empirical measure of perceptual closure**

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In 2-D image perception, changes in shape are more salient if they involve a change in a concavity than in a convexity. As the distinction between concavities and convexities is conditional on the assignment of figural status, this observation can be employed to measure figural status, and hence closure. Experiment 1 involved a temporal 2AFC change-detection task in which observers viewed two meaningless polygonal contours or silhouettes. They were either identical, or one vertex had been removed (or added). The size of the change was also manipulated. We confirmed the advantage for concavities found by Barenholtz et al (2003 *Cognition* 89 1–9). A strong effect of change size also emerged, with no difference between contours and silhouettes. In experiment 2, a ‘concavity effect’ was similarly obtained with spline-smoothed (non-angular) contour stimuli. In experiment 3, we used the same paradigm to disentangle two theoretical explanations for the effect: a local effect of ‘mere’ concaveness versus a global effect of part structure being dependent on the sequence of apexes (or curvature extremes) in the contour. In a new manipulation, we either removed (or added) a vertex, or we changed the extremity of a single vertex, thereby preserving part structure. It is concluded that both the local and the global components independently contribute to the concavity effect. In experiment 4, we applied the procedure to examine two traditional measures of closure. Using polygonal contours with a single gap, we manipulated gap size (corresponding to the *C* measure—Elder and Zucker, 1994 *Vision Research* 34 3361–3370) and the relative orientation of the terminating edges (corresponding to the reliability criterion—Kellman and Shipley, 1991 *Cognitive Psychology* 23 141–221). Only when both measures predicted closure, did the concavity effect emerge. We conclude that both measures indicate necessary conditions for closure.

◆ **Investigation of image structures important in shape perception from texture**

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Computational models of shape perception from texture often consider information contained in the Fourier amplitude spectrum but ignore phase. Recent research in our laboratory has shown that phase selectively affects shape perception from texture, implying that both amplitude and phase have to be considered. Here we report findings that shed light on possible conceptualisations of the joint contributions of amplitude and phase in shape from texture. Observers viewed optical projections of ellipsoidal cylinders and indicated the apparent cross section in depth of the depicted surface by adjusting the shape of an elliptical arc presented on a separate

monitor. Surfaces were covered with various textures presented with either their 'natural' Fourier phase or with their phase randomly 'scrambled'. We found magnitude and reliability of observers' depth judgments reduced by phase scrambling for some but not all textures, replicating and extending previous findings in our laboratory. To understand how phase and amplitude might jointly affect shape perception, we compared the local energy structures of our 'natural' and 'scrambled' stimuli. Local energy is a phase-sensitive and amplitude-sensitive measure of local image contrast and was computed from the outputs of a bank of even and odd symmetric filters tuned to 5 frequency \times 6 orientation pass-bands. Local energy structures of the 'natural' and 'scrambled' stimuli were very similar to one another ($r^2 > 0.80$) when phase scrambling did not affect depth perception, but differed considerably ($r^2 < 0.36$) when phase scrambling reduced depth perception. In conclusion, selective effects of phase on depth perception from texture can be accounted for by variations in local energy structure, but not by amplitude or phase information alone. The results suggest local energy as a psychologically plausible decomposition of image structure in shape from texture that seems promising for the future development of computational models.

◆ **Generative models and model selection for the perception of structure from motion**

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Previous studies have suggested that the human visual system can use a rigidity assumption in the recovery of 3-D structure from motion. However, counter-examples to the rigidity assumption have been reported. They demonstrate a nonrigid interpretation of moving images that are interpretable as rigid motion in space (Braunstein and Andersen, 1984 *Perception* **13** 213–217; Domini et al, 1987 *Journal of Experimental Psychology: Human Perception and Performance* **23** 1111–1129). We present a Bayesian framework for the perception of 3-D structure from motion. It builds on the concepts of a generative model and model selection. The rigidity assumption exhibits itself as a generative model of moving images due to rigid motion of objects. The model selection is carried out on the basis of relative likelihood of the generative models for rigid and nonrigid motion when a moving image is given. The selected model is exploited for the recovery of 3-D structure from the moving image. This framework leads to an empirically testable prediction: when planar surfaces rotate about a fixed axis toward the image plane, the resulting image sequences of expansion can be perceived as nonrigid if a frontoparallel bias is introduced in the initial images. This prediction is derived from an observation that rotating the frontoparallel plane shortens the width of the image projection, leading to a contracting image sequence; therefore the expanding image sequence is unlikely to be predicted by the generative model for rigid motion, whereby the process of model selection favours a nonrigid interpretation. We tested and confirmed the prediction in a psychophysical experiment using a discrimination task between rigid and nonrigid motion. We showed that our Bayesian approach can provide a good fit to the psychophysical results.

◆ **Effects of retinal painting on the phenomenal attributes of figures viewed through a narrow slit**

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When shapes are presented 'anorthoscopically' by passing them behind a narrow slit, observers often report that more of the shape appears to be visible at one time than is actually presented in the slit. In addition, if the motion across the slit is rapid, the figure shape is perceived as compressed along the axis of motion. These phenomena have been related to the painting of the stimulus on the retina by pursuit eye motions. We evaluated the effects of such painting by comparing figure percepts under normal free-viewing conditions and when retinal stabilisation was used to eliminate any pursuit-dependent painting. Two outline 5 deg wide Lissajous-like figures were moved back and forth across a 24 min of arc simulated slit at velocities of 4 and 8 deg s⁻¹ with and without retinal stabilisation of the slit. Observers adjusted a static reference figure to indicate both the shape of the perceived anorthoscopic figure and the proportion of the shape-adjusted figure that appeared to be simultaneously visible as the figure's centre crossed the slit. Without stabilisation, figures were perceived as compressed (to 83% of their actual width) at the fast speed and dilated (to 117%) at the slow speed. Stabilisation did not significantly alter these distortions. The percentage of figure visible at one time was overestimated at both velocities (39% at the fast speed, 30% at the slow speed, with 8% actually presented). The overestimation was not eliminated by stabilisation, but was significantly reduced (to 32% and 24% at the high and low speeds, respectively). Therefore, under the free-viewing conditions we employed, retinal painting does not account for or contribute to the perceived shape distortions. However, our

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data suggest a role for retinal painting in determining the amount of figure that is perceived to be simultaneously present at a moment in time.

[Supported by Land Sachsen-Anhalt Grant FKZ0017IF0000 and Bundesministerium für Bildung und Forschung Grant 01GO0202.]

◆ **Spatial and temporal constraints on form perception in dot patterns**

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We investigated the spatial and temporal constraints on form perception in dot patterns. The spatial constraint was defined as a density of pattern (the number of dots), and the temporal constraint as a duration of pattern exposure. The primed matching paradigm and the two-alternative forced-choice tasks were used. Test stimuli, square and 'ameboid', consisted of 24 collinear equidistantly arranged dots. Two groups of prime stimuli, squares and 'ameboids', were defined. Both groups included patterns of six density levels: 4, 8, 12, 16, 20, and 24 dots. The dots in the 24-dot pattern were equidistantly distributed. The less dense patterns were made by randomly eliminating 4 dots (eg $24 - 4 = 20$; $20 - 4 = 16$; etc), so that the dots were not equidistantly distributed along virtual contour. Primes were either positive for the congruent test figure or negative for the non-congruent test figure. The strength of positive and negative primes varied from maximum (24 dots) to minimum (4 dots). The primes with minimal strength played the role of neutral primes. The prime duration was varied (50, 100, 150, 200, 250, and 300 ms). The RTs were recorded. The results indicate the significant effects of prime density (the same profiles of results for both test figures, square and 'ameboid', were obtained): the greater the number of dots, the faster the processing of congruent test figures and the slower the processing of non-congruent test figures. The effect of prime duration was significant, but with the unexpected direction: the shorter duration of the prime, the greater the effect. This result shows that the percept of form in dot patterns generates early in the perceptual process and suggests that the standard concept of early vision cannot be used as a framework for the investigated phenomenon.

◆ **Background motion affects global shape perception**

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Local-motion can induce an apparent position shift in objects. We studied how motion affects the shape perception of a global structure generated by a group of moving random dots. Global dot-motion stimuli, which consisted of two overlaid groups of dots, were used in the reported experiments. One group of dots, the target, moved along an elliptical trajectory (1.21 deg s^{-1}), while the other group, the background, was divided into quadrants with dots alternately having expanding and contracting motion (1.21 deg s^{-1}). The apses of the elliptical trajectory lay either on the $45^\circ/225^\circ$ axis, or on the $135^\circ/315^\circ$ axis. A one-interval forced-choice paradigm was used; the observers were asked to judge in which direction the apses of the ellipse lay. Perceived circularity was found to be distorted, such that an ellipse, with an aspect ratio of 0.85, appeared to be more circular when its apses were located in quadrants with contracting motion. Similar results were found when the speeds of the dots were varied (from 0.25 deg s^{-1} to 5.10 deg s^{-1}), though a direct relationship between the shape effect and speed was not found. In further experiments, we examined the relative contribution of polarity and disparity to this shape distortion, and found that the distortion diminished if there were cues available that could effectively segment the figure from the background. We propose that veridical retinal positions are frequently not the sole information used by the visual system in shape perception.

[Supported by Grant HKU7149/02H from the Research Grants Council of Hong Kong.]

◆ **Modulation of V1 activity by shape: Intrinsic or feedback influences?**

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Recent neuroimaging studies have shown V1 modulations by shape manipulations, which is contrary to the current dogma that neurons in V1 are only interested in the local spatial information in scenes. Here we examine two possible explanations, one based on low-level intrinsic orientation contrast within the image; the other, based upon feedback influences from higher visual areas, which reduce V1 activation according to perceptual hypothesis of the scene. Functional and anatomical images were acquired with a Siemens Sonata 1.5T MRI. The stimuli consisted of an array of Gabors, whose orientation statistics were varied. Five different stimulus types were used. In two image categories, the Gabor array formed circular shapes, either one or ten circles. Also, a random array was presented to the subjects. The next two image types were random arrays where the local orientation smoothness or contrast was constrained to be similar

to the circular shapes. The fMRI data were correlated with two predictions: one based upon the local orientation contrast, and one based upon the shape information. Our results confirm that V1 is modulated by the degree of shape. Our correlation analysis indicates that this modulation is due to the local orientation contrast in images rather than overall global shape. We propose that decreased activity in V1 with increasing image structure does not reflect high-order perceptions of the scene, but rather signal changes in low-level image statistics generally correlated with shape. Thus, these modulations of V1 reflect the first steps in reconstructing shape information from the local V1 neuronal receptive fields.
[Supported by CIHR grant MOP-53346 to RFH.]

◆ **Müller-Lyer illusion with flickering wings**

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On the monitor screen, a pair of the inward Müller-Lyer wings was spatially superimposed with a pair of the outward wings. The shaft lines were not equal in length, and the wing vertices did not coincide. The two pairs were exposed one after another to produce a continuous flicker. The exposure duration varied in the 20–500 ms range but was the same for each wing pair. The subjects viewing the flickering stimulus monocularly manipulated the keyboard buttons to achieve the perceived equality of the shafts by changing one figure in length. The illusion was absent when exposure time was shorter than 80–90 ms but it appeared and augmented in strength with exposure increase reaching its saturation level at about 250 ms. In the experiments with an interleaving mask made of stripes of random orientation and position, the saturation value of illusion was achieved at exposures of 70–100 ms. The result was stable with the masking of 120–400 ms duration. The data obtained have shown the critical time—about 100 ms—of the Müller-Lyer illusion performance. Also, in experiments with a complete Müller-Lyer figure made of three pairs of synchronous flickering wings and masking, the critical time appeared to be 80–100 ms.

◆ **Perception of mirrored objects: A modeling approach**

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When we look at a polished metal kettle we get a remarkably strong impression of its 3-D shape. The question what are the underlying mechanisms to recover the shape of a mirrored object from a single static image (eg a photograph) remains. In general, this task is ill-posed since infinitely many possible combinations of the illumination pattern from the surrounding scene and surface properties can generate the same image. Here, we present a biologically motivated model for analysing images of mirrored objects to recover 3-D geometric shape properties. In order to constrain the space of possible solutions, we assume that the reflected scene contains isotropic contrast information. When the scene is isotropic, the distortions of the reflected image are related to the surface curvature of the object (second derivatives of the surface function) (Fleming et al, 2004 *Journal of Vision* 4 798–820). First, we use orientation-selective Gabor filters (V1 cells) to extract the raw orientation and strength of the local distortions that are caused by the mirrored surface. Next, we pool context information from the vector field of orientations (inspired by V2 cells with long-range lateral connections) and use this as a feedback signal (Neumann and Sepp, 1999 *Biological Cybernetics* 81 425–444). The recurrent feedforward/feedback loop enhances and smooths the flow patterns of image orientations to recover the characteristic curvature properties. Our simulations demonstrate quantitatively that the model can reliably extract surface curvature information even when the reflected scene is not isotropic (ie the model can withstand violations of the basic assumptions). Our investigations thus provide a simple, neurally inspired mechanism for the representation and processing of mirrored objects by the visual system.

◆ **Amodal perception of internal object contours**

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Perception of illusory contours and surfaces has been demonstrated on many occasions. These include examples as well known as the Kanizsa triangle and Ehrenstein illusion. Various researchers have proposed a variant of amodal completion of boundary contours (Peterhans and von der Heydt, 1991 *Trends in Neurosciences* 14 112–119) and filling-in of surface properties (Grossberg and Mingolla,

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1985 *Psychological Review* **92** 173–211) to account for the illusions. Amodal completion in pictorial space is thought to originate from reconstruction of the object boundary contour given a set of frontoparallel occlusion cues. The most dramatic demonstrations of illusory contours occur where inducers are orthogonal with respect to the completed contour, but orthogonality is not a pre-requisite for completion (Kellman and Shipley, 1991 *Cognitive Psychology* **23** 141–221; Tse, 1999 *Cognitive Psychology* **39** 37–68). Here we report a possibly overlooked case of amodal completion, namely that of illusory internal object contours. Here the shape of the object boundary contour functions as inducer. The effect is more convincing when the inducing object contour is itself an illusory contour. Completion is most vivid for rectilinear object shapes, with illusory internal contours appearing along the edges of planar facets on the object surface. Internal contours that would normally be visible given transparency or bistability are not perceived. Implications for models of amodal completion and rivalry are discussed.

[Supported by the Japanese Society for the Promotion of Science (JSPS.)]

ATTENTION 2

◆ Tracking transparent motion by attention and action

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The perception of two surfaces moving over each other transparently has provided an important tool for scientists who investigate motion integration and segregation. We required subjects to track one surface of a bivectorial transparent motion stimulus. In this case, the stimulus can be conceived as two objects competing for the observer's attention. Our objective was to manipulate the strength of the perception of one surface and examine if and how this affects perceptuo-motor performance. The stimulus consisted of two dot collections, moving back and forth horizontally in opposite directions. Observers tried to move a lever with their right arm in synchrony with one of these dot collections—the target surface. We manipulated the colours of the dot surfaces (both white versus green–red) and the coherence of the target surface (10%, 30%, 50%, or 100% coherently moving dots), while the distractor surface was always perfectly coherent. Implementing a colour difference between the two surfaces reduced synchronisation accuracy, ie the spatiotemporal difference between the arm position and the signal position. Synchronisation consistency, however, was only improved by a colour difference when the target surface was highly coherent. When the target surface was very noisy (10% and 30% coherence), performance was more irregular. Because colour provides an extra feature distinguishing the two surfaces, it helps to select the target surface and to maintain focused attention on it, which explains a more accurate synchronisation performance. Considering the results on synchronisation consistency, it can be argued that complicating the perceptual grouping of the target surface, by reducing its coherence, impedes these attentional processes. When both surfaces are white, participants tend to be distracted and the possibility for error detection and correction is limited.

◆ Splitting the beam? Evidence of divided visual attention assessed through a geostatistical method

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A long-standing debate has dealt with whether or not the spotlight of visual attention can be divided in noncontiguous spatially separated areas. In spite of much literature that supports the nondivision hypothesis, some recent electrophysiological evidence has indicated that attention may indeed be divided. Here we present a novel approach to investigate the distribution of visual attention in large continuous regions of the visual field by measuring simple reaction times. Ten participants were asked to press a button as quickly as possible as soon as they detected a target at one of 158 possible positions distributed in an area of 16 deg × 24 deg. While always fixating the centre, they were instructed to direct their visual attention to the centre of the computer screen (experiment 1), to the left (experiment 2), to the right (experiment 3), or simultaneously to both right and left, but not to the centre (experiment 4). In this novel approach, geostatistical methods were employed to analyse the data so as to emphasise spatial continuity patterns. The maps obtained via ordinary kriging (an interpolation method) show a general tendency towards shorter times (higher attentional allocation) either in the centre (experiment 1), or to the left (experiment 2), to the right (experiment 3), and most significantly clearly to both left and right, but not in the centre in experiment 4, thus confirming the possibility of a divided-attention situation. These encouraging results indicate the potential of this novel approach in

attentional studies. Clear evidence of divided attention could be obtained, confirming recent electrophysiological work by other authors.

[Supported by CNPq Grant # 141951/2002-8, FAPESP Grant # 04/07963-0.]

◆ **Effects of voluntary attention on negative afterimages during and after stimulus adaptation**

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Negative afterimages are known to oscillate in visibility before vanishing in awareness. It has been shown that the oscillation of afterimage visibility is influenced by voluntary attention (Lou, 2001 *Perception* **30** 1439–1448). It is less clear whether negative afterimages are also influenced by attention to the inducing stimuli during adaptation. In a recent study, Suzuki and Grabowecky (2003 *Journal of Experimental Psychology: Human Perception and Performance* **29** 793–807) reported that attention during stimulus adaptation delays and weakens the subsequent negative afterimage of the stimulus. In an attempt to confirm their findings, we conducted two experiments. In the first experiment, the onset and duration of the afterimages induced by attended and unattended stimuli were measured. On separate control trials, subjects responded to the offset of the attended and the unattended inducing stimuli. Contrary to Suzuki and Grabowecky, we found that negative afterimages appeared with nearly no delay at the offset of the inducing stimulus and were not affected by attention during stimulus adaptation. In the second experiment, we examined the effect of attention on the visibility of the afterimages. The inducing stimulus consisted of two overlapping outline triangles, one of them selected for attention. The visibility rating for the afterimage was higher for the part induced from the attended triangle than that induced from the unattended triangle. We suggest that a suppressive effect on a negative afterimage is due to the attention to the afterimages rather than the attention to its inducing stimulus.

◆ **Spatial scale of attention influences saccade latencies**

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We have discovered a phenomenon in which attention has a large and consistent influence on saccadic reaction time. When viewing two counterrotating concentric rings (0.8 and 8 deg diameter) that step together (< 8 deg), subjects make saccades at shorter latencies if they attend to the inner ring, whether the targets are stationary or being pursued. The difference in latency is so large (314 versus 158 ms) that the latency of a single saccade tells with 94% accuracy which ring had been attended. We tested several explanations for this latency difference. First, it might simply be an effect of stimulus eccentricity. It is not: the latency difference exists for stimuli at the same eccentricity. Second, subjects might divide their attention when instructed to attend to the large ring, causing an increase in latency. They do not: latencies are the same for a single large ring. Third, ring size alone may determine latency. It does not: latencies are short when attending large rings if the step is large. Finally, we asked whether this phenomenon was due to saccades being inhibited when smaller than the attended object, a motoric explanation; or because the ring size and step size both affect the detectability of the stimulus step, a visual explanation. When we systematically varied the size of the ring and the step size, we found that saccade latencies decreased as a function of the ratio of step size to ring diameter until the position error was larger than the size of the attended object. These results strongly support the motoric, rather than the visual, explanation. We propose that this latency effect arises from a tendency to inhibit saccades when the object of scrutiny moves but remains within the field of attention, to avoid unnecessary interruptions of vision.

◆ **Attention: Gain modulation or selectivity sharpening**

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Two different schemes have been proposed for modeling the adaptation effect. In the first scheme, adaptation reduces the response to the adapting stimulus and this reduction becomes smaller for other stimuli as a function of orientation difference between them and the adapted one. This model is called model of tuning repulsion and is congruent with observations in primary visual cortex.

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In the second model, adaptation attracts the tuning of neurons by a preferential reduction in responsivity for stimuli that are far from the adapting stimulus, rather than repelling the tuning, as reported by Kohn and Movshon (2004 *Nature Neuroscience* 7 764–772) for neurons in the middle temporal cortex. First, we made a simulation on the basis of these two adaptation schemes. At the next step, we investigated the effect of attention on tuning function of orientation-selective units, using two models of attentional modulation of neuronal responses. In the gain-modulation model, attention shifts the peak of the tuning curve of the neurons upwards by increasing their peak of firing. In the model of selectivity sharpening, attention reduces the bandwidth of the tuning function of neurons without any change in their base and peak of firing. Noudoost et al (2005 *Perception* 34 Supplement, this issue) showed that attention reduces the relative distance between orientation of the most effective adapting stimulus and the target orientation. Our computational results show that attention in the gain-modulation scheme does not shift the orientation of the most effective adapting stimulus with regard to the target one, but some other effective adapting stimuli appear in this condition. On the other hand, consistent with the psychophysical data, sharpening of tuning functions by attention only shifts the orientation of the most effective adapting stimulus toward the target one.

◆ **Visual field asymmetries and exogenous orienting of attention**

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Previous research has shown that there are visual processing asymmetries depending on the location of stimuli in some tasks. The attentional demands of the task should be taken into account when assessing processing differences between left and right and between upper and lower visual fields. He et al (1996 *Nature* 383 334–337) concluded that attentional resolution is greater in the lower than in the upper visual field. So our present research aims to check whether there are differences in processing between left and right and between upper and lower visual fields in a discrimination task judging ‘sameness’ or difference between two stimuli that appeared in one of eight locations with spatial uncertainty, and if it could be related to the orienting of attention. We manipulated attention directly through peripheral cues to oppose two different exogenous attentional states (diffuse versus specific orienting). Two discriminability conditions of the display were also considered. In case there are sensory factors affecting these asymmetries, a low-discriminability condition should exacerbate them. In case the only important factor is the attentional one, the differences as a function of location would be between the diffuse and the specific orienting condition. Our results do not show an interaction between type of cue and visual field, although the cue has had an effect. In the low-discriminability condition there are not any visual-field asymmetries. Only in the case of high discriminability is there an accuracy advantage for the upper visual field with respect to the lower one. There is no interaction between visual field and type of cue, nor between visual field and discriminability, nor among all three.

[Supported by the Junta de Castilla y León grant SA85/

◆ **Absence of biases in visual information processing**

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Several previous visual-search studies measuring both reaction time and response accuracy have demonstrated scanning biases across the visual field (ie a tendency to begin a serial search in a particular region of space). Specifically, one can observe a horizontal–vertical anisotropy (better performance on the horizontal than on the vertical meridian) as well as a vertical asymmetry (better performance in the lower than in the upper visual field). These effects can reflect ecological constraints: the most relevant visual information typically appears within the horizontal and lower dimension, rather than in the upper and vertical visual field. However, there are signs that indicate that these effects are not consistent throughout different visual-search tasks. In order to further investigate the possible existence of these asymmetries, we ran a series of experiments in which we tried to replicate these effects. The visual-search tasks that were used varied in terms of attentional requirements (detection of simple features and conjunction search) and the length of time of exposure to the stimuli. More specifically, we used one condition in which the display was short enough to greatly reduce the potential for serial search (ie scanning-limited), and another in which the display was present until response (ie not-scanning-limited). Our findings do not prove the existence of asymmetries in visual information processing as a result of the location of this element within the visual field.

◆ **Attention and feature integration**

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Visual features of nearby elements can strongly influence each other. Often it is assumed that these features are pooled in small spatial windows. Using the feature inheritance effect, we show that feature integration depends strongly on attention. In feature inheritance, a Vernier precedes a grating comprising five elements. Because of masking, the Vernier itself is largely invisible. Even though the Vernier was presented centrally, its offset is perceived at one of the edges of the grating to which observers pay attention (about a fourth of a degree of visual angle away from the Vernier presentation). If this attended grating element is offset, the offset is integrated with the one of the Vernier. For example, the illusory Vernier offset can be nulled when the grating is offset in a direction opposite to the Vernier. Hence, features of two different locations can be combined with each other. Surprisingly, if non-attended grating elements are offset, no such integration occurs. It seems that only features in the focus of attention are integrated—arguing against a simple spatial pooling mechanism. Focusing attention on one of the inner elements of the grating dramatically decreases performance compared to attending to the edges of the grating. Crowding or limited attentional resolution may account for this effect—and explain why observers attend spontaneously to the edges. Moreover, attention can be easily directed to either of the two edges if the edge to be attended is cued 180 ms before Vernier onset (ie too short to induce a saccadic eye movement). By varying the spacing of the grating, we show that feature integration depends crucially on the distance between the focus of attention and the location of Vernier presentation. Taken together, a spatial pooling mechanism without an attentional component cannot explain feature integration in the feature inheritance effect.

[Supported by the Volkswagen Foundation and by the NATO Science Program.]

◆ **Exogenous and endogenous attention shifts during smooth-pursuit eye movements**

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Studies on the interaction of visual attention and saccades argue in favour of a coupling of saccade goal and focus of visual attention (eg Deubel and Schneider, 1996 *Vision Research* **36** 1827–1837). Khurana and Kowler (1987 *Vision Research* **27** 1603–1618) proposed a coupling of visual attention and the target of smooth-pursuit eye movements. The current study investigated whether exogenous and endogenous attention shifts (Posner, 1980 *Quarterly Journal of Experimental Psychology* **32** 3–25) are possible during smooth pursuit. Subjects foveated a stationary fixation cross (fixation conditions) or a moving cross (smooth pursuit conditions). An exogenous or endogenous cue indicated the location of the upcoming discrimination target with a probability of 80%. The difference in discrimination performance between valid and invalid cue conditions was taken as a measure of visual attention. The discrimination target was either stationary or moved at the same velocity as the pursuit target. Stationary discrimination targets in space were stationary on the retina with eye fixation, but not with smooth pursuit, and vice versa for moving targets. Effects of exogenous and endogenous cueing were about the same size for fixation and pursuit conditions. It did not matter whether the discrimination target was stationary or moving. However, retinal motion of the discrimination target influenced smooth-pursuit gain. Pursuit gain decreased when the discrimination target was stationary in space and moved across the retina, but not when it moved with the pursuit target and was approximately stationary on the retina. The reduction of pursuit gain was present for exogenous and endogenous cues, but it occurred earlier in the exogenous than in the endogenous condition (~150 ms versus ~350 ms after discrimination target onset). The results suggest that the coupling of visual attention to the target of a smooth-pursuit eye movement is not as strong as has been proposed.

[Supported by the German Research Foundation Grants DFG KE 825/3-1 and 825/4-1,2.]

◆ **Inhibiting attention to objects and locations in 3-D displays: Additive effects**

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One of the processes thought to underlie visual selection works by biasing attention away from either recently examined locations or objects. The extent of this 'inhibition' is greatest when the inhibited object and the inhibited location coincide. In experiment 1, rectangles were presented

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stereoscopically at different depths but at similar positions horizontally and vertically. Here, any inhibition should have been based solely on a spatial code, as the objects, the rectangles, were clearly separate objects. In experiment 2, the corners of the rectangles were joined to produce a single cuboid that extended in depth space. Now inhibition based on both spatial and object codes should have been seen because, even when on different depth planes, the cue and target were associated with the same object. Consistent with our understanding of the additive effects of inhibition of space and object codes, the extent of inhibition in the second study was almost double that of the first. The results further suggest that space-based inhibition operates within a 2-D representation while object-based inhibition utilises a 3-D representation.

◆ **The effect of allocating spatial attention on contrast thresholds across the visual field**

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Spatial visual attention enhances information processing within its focus. Vision at an attended location is faster, more accurate, of higher spatial resolution and enhanced sensitivity for fine changes. But allocating attention to a location also affects perception outside this focus. Studies of this distribution of perception across the visual field could not unambiguously resolve its spatial structure. There is a facilitative effect in the main focus, followed by a gradual decrease either to baseline performance or a ring-shaped area of suppression in the surround. Our purpose was to investigate the spatial profile of attention across the visual field by probing contrast sensitivity at high resolution. Presenting a black disc on a computer monitor as a non-informative peripheral cue (0.25 deg diameter) on a grey background, we automatically drew the subjects' attention to one of two possible locations, either left or right from fixation (6 deg eccentricity). In a four-alternative forced-choice detection task, we quantitatively determined facilitatory and inhibitory effects of attention on contrast detection thresholds for stimuli at 12 different distances to the cued location. Detection thresholds below baseline were found at and near the cued location. With increasing distance, thresholds monotonically increased across the whole (12 deg) measuring range. We conclude that attending to a particular location enhances sensitivity for stimuli near the attended location and suppresses it at farther distances. This is inconsistent with reports that the spatial distribution of attentional influences follows a non-monotonic (ie Mexican-hat-like) distribution with reduced processing efficiency in the surrounding region and a recovery of processing efficiency at larger distances.

◆ **Human parietal cortex and attentional modulation of visual activities: A combined TMS and ERP study**

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Prior brain lesion and neuroimaging studies suggest that human posterior parietal cortex is engaged in guiding spatial attention. However, the precise function of the parietal cortex in attentional modulation of visual activities remains unclear. We applied repetitive transcranial magnetic stimulation (rTMS) to the left or right posterior parietal lobes of healthy adults before recording event-related potentials (ERPs) to the detection of targets in the left or the right visual fields in separate blocks of trials. Relative to a control condition with TMS over the precentral gyrus where sustained spatial attention did not modulate striate activity (C1) but enhanced extrastriate activities (P1 and N1) more in the attended than in the unattended conditions, TMS over the left parietal cortex resulted in enlarged C1 amplitude in the attended more than in the unattended conditions. TMS over the right parietal cortex, however, resulted in a reverse pattern of C1 modulation by attention. TMS over the left parietal cortex also reduced the P1 effect but increased the N1 effect relative to the control condition. The results provide direct evidence for the involvement of human parietal cortex in attentional modulation of the striate and extrastriate activities. Moreover, the role of human parietal cortex in attentional modulation of the visual activities varies as a function of the time courses of visual processing.

◆ **Working memory and the attentional blink**

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After identification of a first target (T1) in a rapid serial visual presentation (RSVP) task, identification of a second target (T2) is typically impaired for approximately 500 ms (the 'attentional blink', AB). Although several AB models exist, a common element is an attention-demanding stage where a durable representation of T2 in working memory (WM) fails to occur because of ongoing T1 processing. So what effect do WM processes have on the AB? Previous work (eg Akypurek

and Hommel, forthcoming *Memory & Cognition*) has shown that concurrent WM tasks impair overall performance; however, no modulation of the AB has been found. We investigated the effect of WM encoding processes on the AB using a hybrid WM/AB task. Subjects performed an AB task whilst maintaining two objects from a WM array: one coloured red, the other green (eg a car in red, flower in green). The WM task involved matching a grey-scale image (test image) to one of the items from the array. The test image was always one of the array items (eg the car). The item in the array to be matched against the test image was determined by a cue colour (red or green) that occurred either prior to the RSVP stream, or was coincident with T1. For example, an array with a car in red and an apple in green followed by a green cue means the apple (green item) is to be matched to the test image. Results show that, compared with presentation of cue colour outside the RSVP stream, concurrent presentation of the colour information with T1 increased the magnitude of the attentional blink. Follow-up experiments show that this effect is not simply due to a low-level perceptual change, eg altered target contrast.

◆ **Out of sight, out of object-based attention?**

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We used variations of the double-rectangle paradigm of Egly et al (1994 *Journal of Experimental Psychology: General* **123** 161–177) to examine whether object-based attention depends on instantaneous updating of object representations in iconic memory, or whether it uses memorised representations of objects. A cue was presented first, followed by two rectangles (objects), and then a target. Object-based selection gives rise to the same-object effect: faster RTs for invalid targets of the cued object than for invalid targets of the uncued object, even when their cue-to-target distance is held constant. We manipulated the way the objects were presented and the timing between the cue, the object, and the target. The same-object effect was found with a continuous presentation of objects that lasted until the emergence of the target. Discontinuous presentation of objects, however, diminished the same-object effect. Adding a task about the objects after their disappearance in order to increase the participants' incentive to hold the objects in memory did not bring back the same-object effect. Object-based selection thus seems to require fast on-line updating of representations of visual objects; memory representations of them do not suffice. [Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE.]

◆ **Mechanism of object-based attention: Spreading or prioritisation?**

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In the double-rectangle paradigm of Egly et al (1994 *Journal of Experimental Psychology: General* **123** 161–177), one end of two oblong rectangles is cued, and responses are faster when the target appears on the object that is cued than when it appears on the object that is not cued. This same-object effect is explained either by the spread of attention via sensory modulation, or by the assignment of a higher priority to the cued object. We first replicated the same-object effect in experiment 1. In two subsequent experiments, the rectangles were removed at several different post-cueing times and the target was presented beside the fixation sign on an otherwise blank display. The spreading hypothesis predicts attention to spread after cueing, and thus the same-object effect is expected when sufficient time is allowed for attention to spread. The prioritisation hypothesis predicts no such same-object effect when the target is presented alone, because in this case there is no object to assign any priority to. Results showed no same-object effect when the rectangles were removed either 100 ms or 200 ms after the cue display (100 ms). In a final experiment, the rectangles were removed during the 200 ms ISI and were presented again in the target display. The spreading hypothesis predicts no same-object effect because there is no object contour for attention to spread, while the prioritisation hypothesis does predict this effect because there are multiple objects during the target presentation which require attention to resolve the processing priority. The results show a significant same-object effect, and support the prioritisation hypothesis. [Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE.]

◆ **Electrophysiological correlates of attentional spreading over connected objects**

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Visual elements are perceived as a group if they are similar in properties such as colour or shape, or connected to each other. Visual grouping may be a phenomenon of attention such that attention

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obligatorily spreads over elements with grouping factors. We examined this hypothesis to elucidate neural bases on perception of visual grouping by using event-related potentials (ERPs) that have high temporal resolutions of brain activities. It was suggested that ERPs in response to bilateral stimuli had larger amplitudes at the contra-lateral than ipsi-lateral posterior electrodes relative to the attended visual hemifield (ERP attention effects for bilateral stimuli). If attention spreads over grouped elements by connectedness, ERP attention effects for bilateral stimuli would decrease when the stimuli are connected, compared with when they are unconnected. We recorded ERPs from twelve participants who were covertly attending to one hemifield and ignoring the other during rapid presentation of bilateral stimuli followed by a unilateral probe. The bilateral stimuli consisted of standard (both were rectangles) and target (one was square) presented in random order and the task was to press a button for the square at the attended hemifield. Half of the bilateral stimuli were connected by a line. ERP attention effects for bilateral stimuli were identified at P1 (80–130 ms post-stimulus onset), P2 (190–250 ms), and N2 (250–300 ms) latency ranges both for the standard and target stimuli. However, the attention effects at 190–250 ms decreased for the connected target stimuli. In addition, target effects, ie whether the square was presented at the attended or unattended hemifield, at 250–300 ms decreased for the connected stimuli. These results suggest that attention spread over the connected bilateral stimuli at 190–250 ms post-stimulus when the stimuli were task-relevant and affected following feature-matching processes.

◆ **Attentional enhancement along the path of a sequence of saccades**

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Attention during saccadic scanning is focused on the upcoming saccadic target, to the exclusion of other locations, in order to ensure accurate execution of the eye movement (Gersch et al, 2004 *Vision Research* **44** 1469–1483). In natural scanning, however, it may be valuable to be able to attend to locations other than the next target. To examine the nature and breadth of attentional allocation during the performance of saccadic sequences, a dual-task paradigm was used in which a visual test stimulus (Gabor patch) was presented briefly during selected intersaccadic pauses. The display was a 5×5 array of 1 deg coloured outline circles. Beginning at one of the 4 sides of the array, a sequence of 5 oblique saccades was made across the array to each of the 5 green circles that constituted the saccadic path. An oriented Gabor patch ($2.2 \text{ cycles deg}^{-1}$) with superimposed noise field appeared briefly (90 ms) in a pre-cued circle at a random time. Noise was presented in all circles. Contrast was chosen to obtain $\sim 75\%$ – 85% correct reports of orientation in a 2AFC discrimination task. Pauses between saccades were 215–315 ms, about the same as observed when saccades were made without the concurrent perceptual test. Orientation discrimination for Gabors on the saccadic path (including previously visited locations) was 19%–36% better than at off-path locations at equivalent eccentricities. Performance on the path varied, and was 5%–6% better at the target of the upcoming saccade than at the recently fixated location. These results show that attention during saccadic scanning serves multiple roles and can be allocated to more than just the immediate goal of the next saccade. Attention can also be used to enhance a set of task-relevant locations, while also guiding the saccade to the next target. [Supported by NIH Grant EY015522.]

◆ **Differences in attentional filtering between saccades and perception**

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The ability to aim saccades to selected objects is crucial for scanning natural scenes. Saccades made to objects in isolation land near the centre of gravity (COG) with a high degree of precision, implying that landing position is computed by spatial pooling across the target (eg Melcher and Kowler, 1999 *Vision Research* **39** 2929–2946; Vishwanath and Kowler, 2004 *Journal of Vision* **4** 445–458). In natural scenes, however, objects are not viewed in isolation. Saccadic accuracy thus depends on a selective filter that prevents irrelevant background details from influencing the pooling process. To understand the nature of the selective filter, we studied: (i) saccadic localisation of a cluster of 5 randomly-positioned dots, presented either by themselves or mixed with 5 distractor dots of a different colour; and (ii) perceptual estimation of mean dot size (Chong and Treisman, 2005 *Vision Research* **45** 891–900) on the same stimuli. Dots (diameter 0.5 to 1 deg) were generated randomly within a $4 \text{ deg} \times 4 \text{ deg}$ window located 7.6 deg – 8.4 deg to the left

or right of fixation. Display duration was 400 ms (same as mean observed saccadic latency). The perceptual results showed that mean dot size could be estimated accurately (difference between PSE and the standard size was $< 6\%$) and precisely ($JND = 10\%$ of mean size), with no effect of the distractors on the judgments. On the other hand, when saccades were directed to the cluster of target dots under instructions to ignore distractors, saccadic endpoints were displaced in the direction of the distractors by about 25% of the separation of target and distractor COGs. These saccadic errors indicate partial integration of distractor locations into the computed landing position ('leaky' filtering). The results argue against a single, early general-purpose selective filter. They show that, despite the otherwise strong links between saccades and perception, the two actually have different attentional filtering profiles.

[Supported by NIH Grant EY015522 and AFOSR Grant F4960-02-1-0112.]

◆ **Orienting in response to symmetric and asymmetric spatial precues: Implications for the distinction between endogenous and exogenous orienting**

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In three experiments, participants performed a simple response-time task with targets that could appear to the left or right of a central fixation marker. Visual precues informed participants of the likely location of the target object. In experiment 1, the cues comprised two coloured Xs presented on either side of the fixation marker. Covert orienting effects were larger and developed more rapidly in a condition with spatially asymmetric cues (red-left + green-right versus green-left + red-right) relative to a condition with symmetric cues (red-left + red-right versus green-left + green-right). In experiments 2 and 3, the cue was a single centrally presented letter. Effects of spatially symmetric (T, X, v, o) and spatially asymmetric (d, b) letter cues were compared. Validity effects were present for asymmetric cues, but entirely absent for symmetric cues. These findings are discussed in terms of the proposal that spatial correspondence learning plays a critical role in spatial precueing. In addition, implications of the results for the distinction between endogenous and exogenous orienting are discussed.

◆ **Cue summation and feature salience**

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The salience of an object is enhanced when it differs from the surround in more than one feature dimension (Meinhardt et al, 2004 *Vision Research* 44 1843–1850). However, the advantage of redundant target definition is strongly modulated by further aspects of the visual scene. We present data from various feature-contrast detection, discrimination, and identification experiments which elucidate side conditions of feature synergy. First, facilitation among features occurs only at lower levels of discriminability, in the vicinity of the detection threshold, but not for highly salient targets. Second, there is strong facilitation in stimulus arrangements that allow grouping to simple figures, ie cue summation enables figure detection in noisy environments when single cues are insufficient for stable figure-ground segregation. Experiments using an attend to/attend away paradigm show that feature and position certainty are not necessary for cue summation, but strongly enhance the amount of facilitation due to redundant target definition. Our results suggest that lower-level feature-contrast processing is in a functional hierarchy with global and higher-level processes signaling the presence of objects.

BINOCULAR VISION 2

◆ **Dynamic structural change of illusory surface with binocular stereopsis**

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A visual phenomenon, dynamic structural change, is demonstrated. In this phenomenon, changes of the shape of an illusory surface are perceived continuously by rotating the inducers. The illusory surface may even separate into two surfaces that fuse repeatedly when the inducers rotate synchronously. Dynamic structural change is perceived as if an illusory surface is pulled apart when a surface separates into two parts. In the present study, we investigated the perceptual property of illusory surfaces which have undergone dynamic structural changes. We measured the

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perceived positions of the separation. We used an adjustment method whereby observers could change the rotation angles of inducers for themselves in order to eliminate the effect of reaction time. Participants were asked to report the perceived position in which the illusory surface separated or fused by fixing the amplitude of the rotation angle of inducers. There were three illusory surface conditions: opaque, transparent, and half each. Four rotation speeds of inducers were used (5° , 15° , 30° , 35° s^{-1}). In all conditions, transition points from separation to fusion (or fusion to separation) in the dynamic structural change were not equivalent to the geometrically expected position of a rotation angle of 45° . The illusory surface was perceived as one, although each inducer's edge was not collinear in all stimulus conditions. Furthermore, the tendency became clear when the rotation speed of the inducers was sufficiently fast. These results provide evidence for the existence of Gestalt processes in dynamic structural change. We conclude that the dynamic structural change of illusory surface is useful for the investigation of the process of surface formation.

◆ **3-D illusory objects viewed with integrated prism glasses**

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Integrated prism glasses can produce binocular disparity owing to the difference of refraction in wavelengths (colours), and a stereoscopic display can be realised by coding the depth with colours: this is exactly the enhancement of colour stereopsis by prismatic effect in human optics (Dengler and Nitschke, 1993 *Perception & Psychophysics* **53** 150–156). We need not adjust both eyes in the direction of the pictures in this method, whereas both eyes have to be in the same horizontal direction in a normal stereoscopic display. Recently, this method has been used widely for producing 3-D visual effects and the glasses are commercially available. The picture can be generated easily according to the detailed description of ChromaDepth (<http://www.chromatek.com/>). However, 3-D illusory objects produced by this method have not been reported and are thought to be impossible. We investigated carefully the principle of this method and the mechanism of the 3-D illusory object perception [Idesawa, 1991 *Japanese Journal of Applied Physics* **30(4B)** L751–L754; **30(7B)** L1289–L1292; 1993 **32(1A/B)** L75–L78]; thereafter we developed a method for displaying 3-D illusory objects with integrated prism glasses. For realising the occlusion cues in the 3-D illusory object perception, one basic principle used is that the regions adjacent to the occluding object (which is the illusory object that is to be observed) on the occluded object should be depicted with a colour corresponding to the contour depth of the occluding objects and the other regions on the occluded object should be depicted with a colour corresponding to the greater depth than that of the contour of the occluding object. We realised the pictures successfully with opaque and transparent illusory surfaces and their interactions. However, a solid with volume and a transparent volumetrical object with mime effect [Zhang et al, 1998 *Japanese Journal of Applied Physics* **37(3B)** L329–332] were in principle difficult to realise, because of the difficulty of producing binocularly unpaired parts on an object.

◆ **Effect of the correlation between overlapping dot patterns on stereo transparency**

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In binocular vision, observers can perceive transparent surfaces by fusing a stereogram composed of two overlapping dot patterns with different disparities. When overlapping dot patterns are identical, the stereogram has potential matches that lead to transparency and non-transparency (or unitary surface) perceptions; these two perceptions are exclusive if the uniqueness assumption holds. Which surface is perceived in this ambiguous stereogram should depend on the property of the transparency detection mechanism in human stereopsis. This stereogram can be regarded as a random-dot version of the double-nail illusion and a stereo version of locally-paired-dot stimuli that was used to investigate the neural mechanism of transparent motion detection (Qian et al, 1994 *Journal of Neuroscience* **14** 7375–7366); we refer to the present stereogram as the locally-paired-dot stereogram (LPDS). Here we investigate the depth perception in the LPDS when the signs of contrast of two overlapping patterns are reversed; the contrast reversal could act as a segregation cue for overlapping surfaces, and it is considered that observers could easily perceive transparency if all corresponding dots have opposite contrast polarity. However, the result shows that the precision of the transparent depth discrimination when all corresponding dots had opposite contrast polarity (or overlapping patterns were anti-correlated) was worse than

when only 50% of corresponding dots had opposite contrast polarity (or overlapping patterns were uncorrelated). This result suggests that transparency perception in the LPDS does not simply depend on the proportion of opposite contrast dots but is affected by the global property of dot patterns, ie the correlation between overlapping surfaces. A model analysis shows that, assuming that the coarse-to-fine strategy is employed in the human visual system, this result can be naturally explained by the mathematical property of the disparity energy model.

◆ **Comparing stereopsis and apparent motion: The double-nail and Ternus phenomena**

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Some stereoscopic and apparent-motion displays can be obtained from one another by the manipulation of just one variable, namely stimulus onset asynchrony (SOA). Here, we investigate whether this close physical relationship also gives rise to a close psychological relationship. More specifically, we investigate whether the double-nail phenomenon in stereopsis, and the Ternus phenomenon in apparent motion, that seem so different at first sight, might nevertheless be lawfully related. The double-nail phenomenon is one in which two nails, placed right behind each other, appear side-by-side instead, and the Ternus phenomenon is one in which sometimes some shapes appear to move as a group (group motion) and sometimes one shape appears to hop over the other ones (element motion). Experiment 1 shows that, in fact, one and the same stimulus can give rise to Ternus group motion at some SOAs, and to the double-nail phenomenon at other SOAs. Experiment 2 shows that Ternus element motion also has its equivalent in stereopsis, despite earlier suggestions in the literature to the contrary. Finally, experiment 3 shows that order reversals of elements that block stereopsis also hamper apparent motion. On the basis of this and other evidence, we conclude that stereopsis and apparent motion are not only physically related, but psychologically too. The nature of this psychological relationship is in part explained by relating Ternus apparent motion to Korte's 3rd law, Korte's 3rd law to Panum's area, and Panum's area to the double-nail phenomenon.

[Supported by the National Science Council of Taiwan, NSC93-2413-H-002-017 and NSC94-2413-H-002-019.]

◆ **Surface perception detecting method by using the Poggendorff illusion in binocular viewing**

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Surface perception is an essential function of the visual system. In the Poggendorff illusion, two collinear diagonal lines obliquely abutting the inducing element are perceived as shifted. We observed this illusion binocularly; then we devised a Poggendorff configuration without physical contact between the line element and the inducing element. By using the newly devised configuration, we proved, by controlling the perceptual depth of the inducing element without any changes of the conventionally considered factors in this illusion, that the nearer perceptual depth of the inducing surface is crucial for perceiving the illusion. In addition, we proved that the nearer opaque-surface perception of the inducing element is indispensable to perceiving the illusion in the configuration without physical contact. On the basis of these facts, we developed a probing method for opaque-surface perception, in which the condition of opaque-surface perception could be detected from the occurrence of the Poggendorff illusion. We tested several concrete examples confirming the effectiveness of this probing method, and showed that the opaque-illusory-surface perception could be detected effectively with the proposed method. Furthermore, we used this method to investigate opaque and transparent properties of the surface; then we demonstrated the capability of this method by applying it in the transition area of opaque to transparent. We believe that the developed probing method of opaque-surface perception with Poggendorff configuration without physical contact could be a way of achieving better understanding of the surface-perception mechanism of the human visual system.

◆ **The role of horizontal disparity in depth judgments from relative size cues in 3-D and 2-D scenarios**

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The removal of horizontal disparity with a synopter has been shown to be detrimental to perceiving depth in real 3-D scenes (Koenderink et al, 1995 *Perception* **24** 115–126) and to enhance the perception of pictorial 2-D relief (Koenderink et al, 1994 *Perception* **23** 583–594). We conducted a study to test both of these assertions. We constructed a novel stimulus consisting of thin cylindrical bars at different depth planes. The stimulus was viewed from a fixed

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position through an aperture so that neither motion parallax nor linear-perspective cues were available. This produced a 3-D real scene containing only relative size as a monocular cue. A photograph of the real scene was used for the 2-D pictorial scene. Both configurations subtended a horizontal visual angle of 24.5 deg and were viewed at a distance of 0.5 m. Forty participants made distance judgments in centimetres between 25 pairs of bars in both scenes using either binocular or synoptic viewing conditions. Results showed that synoptic viewing caused participants to underestimate distances in the 3-D condition, and to overestimate distances in the 2-D condition compared to binocular viewing. We conclude that synoptic viewing facilitates the visual interrogation of images with ambiguous or absent depth cues.

◆ **Binocular rivalry and clinical suppression assessed with MEG**

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In binocular rivalry, different stimuli are presented to either eye of the subject and the stimuli cannot be merged into one percept. Subjectively, the stimuli alternate over time, ie only one particular stimulus is visible at a particular time. The aim of this experiment was to investigate what happens to the stimuli when they are not visible, ie suppressed. The data were acquired on a 151 channel CTF omega system at a sampling rate of 312 Hz. The two stimuli consisted of square-wave gratings, and differed in their orientation and temporal frequency. Three different conditions were tested. In two conditions, the stimuli were physically alternated over time (non-rivalrous), either regularly or in a semi-random alternation identical to a rivalrous perception rate. In the third case, the two stimuli were presented to different eyes, producing binocular rivalry. In all cases the subjects indicated which stimulus was perceived. The MEG data were analysed with synthetic aperture magnetometry (SAM), a beamformer technique that constructs a set of weights that links each voxel in the brain to the MEG sensors. Once this filter is established, the time course is extracted at the voxel maximally responding to the physical regular alternation of the stimuli. The energy at the stimulus frequencies was then compared relative to reported stimulus dominance for all conditions. Region-of-interest analysis in primary visual cortex indicated significant power changes at the stimulus frequency when the stimulus was physically alternated, both regularly and semi-randomly. In the rivalry condition, no such changes were found, neither in healthy subjects nor amblyopes. Binocular rivalry is thus shown to produce MEG patterns distinct from physical alternations. This may suggest that the site of suppression associated with binocular rivalry and amblyopia occurs after our cortical recording site.

[Supported by CIHR grant MOP-53346 to RFH.]

◆ **Stereopsis, rivalry, or superimposition?**

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When two very dissimilar images are projected to our left and right eyes simultaneously, the two images cannot be fused into a single object; instead of producing the impression of depth, the two patterns alternately access conscious perception; this is known as binocular rivalry [Levelt, 1968 *On Binocular Rivalry* second printing (The Hague: Mouton)]. In spite of great progress in this research area, the mechanism remains poorly understood. In order to explore how binocular fusion works, I designed an experiment: the special stereograms used in the experiment include two images, one is the Shanghai Xianyang Park landscape, the other one is a plate picture in which all pixels have same grey level, eg white or black; in other words there is no contrast in these plate images. The instrument is a hand stereoscope, the subjects are undergraduates and teachers in the Computer Science Department at Wuhan University of Technology. Subjects observed through the stereoscope these stereograms and wrote down their perceptual experience. All subjects reported that they saw only the landscape in binocular viewing, brighter or darker depending on whether the corresponding plate image was white or black; no rivalry was observed. The experimental investigation indicates that the two images superimposed with weighting instead of rivalry. This results cannot be explained by the fusion theory or the suppression model, but is well known in ophthalmology. This indicates that the theory of the binocular mechanism should be deeply studied. [See also Hayashi et al (2004 *Vision Research* 44 2367–2380) “An integrative model of binocular vision: a stereo model utilizing interocularly unpaired points produces both depth and binocular rivalry”].

[Supported by NSFC No. 60275040.]

◆ **Distance perception during binocular viewing via stereo-goggles at different display distances**
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We investigated how the visual system combines vergence and disparity information to arrive at estimates of distance to an object. Judgments of distance to a target, based solely on binocular vergence, are often inaccurate. Placing a fixed object in the visual environment distorts judgments even further. Foley (1985 *Journal of Experimental Psychology: Human Perception and Performance* **11** 133–149) found interactions between distance judgments to target and reference points in a sparse visual environment. We ran an experiment in which observers were presented with two target points via stereoscopic goggles and a computer screen, and were asked to verbally estimate the distance to each point. One point could vary (across trials) in distance away from the observer (from 12 to 38 cm), while the other point remained fixed at 25 cm but could lie either 3 or 9 deg below the variable point. Observers ran the experiment twice, at an observer-to-screen viewing distance of 35 cm, and also at 50 cm. We found that distance judgments were rarely veridical and that, unlike in Foley's results, there was little interaction between judgments of the variable and fixed target points. In spite of individual differences, results were very similar per observer for the two vertical separations used between the target and reference points. Because the screen itself provides an accommodation cue to distance, we expected an interaction between screen distance and perceived target distance. Screen distance either systematically increased or decreased judgments for some, but not all, observers, and there was no systematic effect across observers. This suggests that the interaction of accommodation and binocular parallax is difficult to predict for a display system with a fixed viewing distance.

[Supported by the EPSRC.]

◆ **The dependence of reaction time on RDS spectrum**

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The reaction time (RT) of depth detection was investigated with black-and-white random-dot stereograms (RDSs) (12 deg × 15 deg) with a coded rectangle (3 deg × 6 deg) having crossed or uncrossed disparity near D_{\max} with different blurring ($\sigma = 0 - 2$ pixels) in seven observers (one female and six males, aged 25–34). Their mean RT to such stimuli behaves in one of two ways: (a) RT increases with blurring increase or (b) RT has minima at intermediate blurring values. The effect is more evident at uncrossed disparity: the difference between minimal and maximal mean RTs was significant ($p > 0.97$) and varied between 80 ms (experienced observers) to 1220 ms (naive observers). The type (a) dependence can be easily explained by using the model of depth selection of Lyakhovetskii et al (2002 *Perception* **31** Supplement, 139–140), whereas the type (b) dependence needed more detailed investigations. The simulation results allow us to assume that the increase of image gradations leads to faster RTs. Therefore in an additional experiment we compared the mean RT for blurred ($\sigma = 1$ pixel) and multigraded (32 intensity gradations) RDSs. In most cases the difference between mean RTs for such stimuli is not statistically significant ($p < 0.5$). Thus the dependence of RT on the RDS spectrum may be due to the increase of intensity gradations and lack of point-by-point correspondence between RDS half-images.

◆ **Fixational convergence patterns reflect perceived depth in perspective surfaces**

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Fixation convergence performance was investigated in twenty-two subjects by recording movements of both eyes simultaneously under unrestrained head posture (EyeLink system). Fixation had to be directed to 10 spatially distributed targets in a predefined order within acoustically timed periods of 10 s. Three display types were compared: (i) a perspective grid with volumetric target elements that were graded in size, hence resulting in a strong depth impression; (ii) a 2-D grid with elements of constant size, but with systematically arranged locations so as to converge on a common vanishing point, producing a weak (ambiguous) perspective representation; (iii) a 2-D grid as in (ii), but with randomly located elements, producing a definite plain, coplanar, percept. Successive fixations from 'near' to 'far' targets in (i) resulted in accumulative vergence drifts, whereas a significant drift correction occurred when fixations returned from 'far' to 'near'. This performance was typical for all subjects. A similar behaviour was observed for ten subjects in (ii), with almost no vergence drifts in the remaining subjects. All subjects showed the lowest vergence drift magnitudes during fixations in the coplanar pattern (iii). Moreover, in display (ii),

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nine subjects perceived a coplanar pattern, whereas the remaining subjects perceived a perspective depth representation. 'Coplanar' perceivers performed similarly in (ii) and in (iii), whereas 'perspective' perceivers performed in (ii) more similarly to (i) than to (iii), implying that, at least to some extent, vergence eye movements actually reflect perceived depth.
[Supported by a grant from C E Smith Foundation, Jerusalem.]

◆ **Contrast influence on binocular fusion limits**

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Panum's area in the foveal region was examined with paired three-dot stimuli organised in right-angle patterns displayed separately to each eye. The length of the sides of the stimuli was 20 or 30 min of arc. In the experiments, subjects manipulated by the panel keys and pushed one end-dot of the test stimulus horizontally to the left or to the right and vertically up or down in 0.3 min of arc steps until reaching the fusion limits. The background luminance was 10 cd m⁻²; the luminance of the reference dots was 50 cd m⁻²; and the test-dot luminance was varied from 20 to 50 cd m⁻². Panum's area was found to have an ellipsoidal shape with the ratio of diameters roughly constant, 1 : 2 for all luminance values tested. The size of the area did not vary with the test-dot luminance changes within the 35–50 cd m⁻² range and it increased regularly with luminance decrease below 35 cd m⁻² until reaching the dot-detection threshold at about 22 cd m⁻². The test-dot luminance below the background level made the test-dot appear black and disabled binocular fusion. According to Herring's law, variability of Panum's area size with luminance changes may be interpreted as a weighted averaging of monocular visual directions.

◆ **Unilateral versus bilateral experimental strabismus: Long-range connections of ocular dominance columns in striate cortex**

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To evaluate changes produced by manipulations of binocular vision, the long-range connections of ocular dominance columns (ODCs) were investigated in striate cortex of cats reared with convergent unilateral (U-cats) or bilateral (B-cats) strabismus. Tangential distribution of retrogradely labeled cells in area 17 was assessed after micro-iontophoretic horseradish peroxidase (HRP) injections into the single ODCs of area 17 or 18. Eye preference of injected ODCs was evaluated by analysis of labeling in dorsal LGN laminae. All HRP injections in B-cats have revealed labeled cells in area 17. Approximately 50% of injections located in hemisphere ipsilateral to deviated eye in U-cats did not show such labeling. Length of horizontal connections of ODCs receiving inputs via uncrossed visual pathways varied from 1–8 mm in B-cats and 3–6 mm in U-cats (for intact eye ODCs) along the projection of visual field horizontal meridian. Connections of ODCs receiving inputs via crossed pathways (~25% of ODCs in B-cats and U-cats) were relatively short (1–3 mm). Though the reduced probability of HRP labeling of 'crossed ODC' connections was found in normal cats too, the length of crossed and uncrossed ODC connections in them was equal (about 4 mm both). Thus early-onset unilateral and bilateral strabismus produces different effects on the horizontal connections of 4 types of ODCs, more pronounced (suppressive) for ODCs driven by ipsilateral deviated eye in U-cats. The revealed neuromorphological changes raise the question about their relation to adaptive reactions directed to overcome diplopia, such as alternating fixation, and suppression of the deviated eye.
[Supported by the RFBR grant 03-04-48258.]

COLOUR 2

◆ **Reaction time distribution with near threshold S-cone increments and decrements**

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In a previous experiment, we measured detection threshold using S-cone selective increments and decrements with ramped onset or offset. Stimulus duration was 100 ms. At both stimulus polarities, blurring the onset increased the threshold more than blurring the offset. We concluded that a duration of 100 ms of S-cone selective stimuli is short enough for preferential stimulation of ON and OFF neurons depending on stimulus polarity (Racheva and Vassilev, 2004 *Perception* 33 Supplement, 58). The aim of our present experiment was to check the effects of S-cone selective stimulus onset and offset by using the reaction-time paradigm of Tolhurst (1975 *Vision Research* 15 1143–1149) and Schwartz (1992 *Vision Research* 32 2087–2092) at longer stimulus durations. In the main experiment, simple reaction time (RT) for near-threshold blue light increments and decrements of long durations on a yellow background was measured. In two

control experiments, we obtained RT for blue-on-blue and red-on-red near-threshold increments and decrements. The stimuli and background occupied the whole field of the monitor (28 deg \times 21 deg). Different stimulus magnitudes were used, yielding a percentage of missed stimuli between 0% and 50%. RT distributions for the same percentage of missed stimuli were compared. In the main experiment, the distribution was unimodal regardless of the percentage missed and followed stimulus onset. RT distribution was bimodal in both control experiments at high rates of misses, the peaks being separated by an interval equal to stimulus duration. The results suggest that, compared with the control experiment, near-threshold offset of S-cone selective stimulus is ineffective or less effective than stimulus onset in evoking sensation. This asymmetry is present with both stimulus polarities. Together with the differences in spatial summation for increments and decrements found previously by us, the present findings support the existence of separate S-cone ON and OFF pathways.

◆ **Psychophysical investigation of the role of photochemical bleaching in chromatic afterimages**
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Two hypotheses for the mechanism of chromatic afterimage are examined: one is photochemical bleaching which causes the deterioration of sensitivity of three cones of our retina, and the other is adaptation of the higher neural mechanism which changes our chromatic perception. Exact measurement of chromatic afterimages was carried out by 'the blank rotation method', which made it possible to see afterimages sequentially by using blinking inducers (Sakata, 2004 *Perception* 33 Supplement, 62). It was found that a given inducer colour could produce different chromatic afterimages with different peripheral colour. This result suggested that neural mechanism adaptation could affect the colour of afterimages. But this was not an explicit evidence on the chromatic afterimage mechanism. To elucidate this, in the first experiment the colours of a chromatic afterimage on a black background with a black peripheral background were measured in a dark room, with 15 min dark adaptation, in order to examine the two hypotheses. The results showed that no subject could see a chromatic afterimage on a black background in the dark room after dark adaptation. Since higher neural mechanisms are affected by colours of peripheral background, the colour of the afterimage would be affected by peripheral colours if higher neural mechanisms took the main part in causing chromatic afterimages. In the second experiment, the effect of chromatic peripheral background was measured on a black background, and the results also showed no afterimages in this experimental condition. The absence of a chromatic afterimage on a black background with a chromatic peripheral background showed that a light source was needed to yield chromatic afterimages. This fact suggests that the deterioration of sensitivity by photochemical bleaching of cones causes chromatic afterimages. Colours of chromatic afterimages seem to be caused by photopigment bleaching and are affected by higher neural adaptation. A determinant of three-cone photochemical bleaching was estimated from these and earlier results.

◆ **Effects of chromatic content and temporal frequency on the BOLD response in different visual areas**
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We investigated the effect of temporal frequency on the BOLD response to stimuli defined by luminance or colour. A rotating radial sinusoidal grating was presented in an annulus (inner radius \sim 0.5 deg, outer radius \sim 10 deg) centred about a fixation marker. The grating was modulated in the L - M (colour) and the L + M (luminance) direction at a fixed contrast of 14% and at three different temporal frequencies (1, 4, and 10 Hz). The cone contrast stimuli were calculated with the 10° Stockman and Sharp sensitivity functions and the spectral properties of the displays were characterised with a pr650 Photoresearch spectroradiometer. The temporal stability of the display was established by means of a photodiode. In the fMRI, a balanced blocked stimulus presentation was used (30 s blocks; all conditions have the same history), and subjects performed an attention-binding task at the fixation spot. Responses in area V1 tended to be larger for the colour stimuli, especially at the lowest temporal frequency. For area MT, no clear preference was found between the contrast-matched colour and luminance stimuli. In a ventral occipital area (presumably V4), responses to luminance exceeded those for colour at the medium temporal frequency. In terms of temporal frequency, luminance responses tended to be highest at 4 Hz, while in the ventral occipital area colour responses reached their peaks mostly at 1 Hz. Most of the visual areas investigated here change their colour preference with temporal frequency. The colour selectivity of a visual area measured with fMRI appears to be a

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complex mixture of different temporal-response profiles in the neuronal population of the area. [Supported by Bundesministerium für Bildung und Forschung CAI: 01GO0202 and Land Sachsen-Anhalt FKZ0017IF0000.]

◆ **Different colour contrast stimuli perception in fog**

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Visual acuity VA for colour stimuli and colour contrast sensitivity CS, treated as the main visual performance parameters, were determined in the Clermont-Ferrand artificial fog chamber at fog densities corresponding to the visibility range of 6–15 m. Red, green, blue, and yellow on white background Landolt-C optotypes served as stimuli for visual-acuity studies. Stimuli for colour contrast sensitivity were red, green, and blue Gabor gratings with spatial frequencies of 5–30 cycles deg⁻¹. Two factors were examined as the main causes of differences in the effect of fog on visual perception. First, different distributions of 'blue', 'green', and 'red' cone photoreceptors within the eye retina in central and peripheral vision. Second, the stronger scattering of short-wavelength (blue) light in fog. The lowest contrast sensitivity was found for blue gratings (CS decreasing in fog from 50 to 2 compared to 100 to 15 for red). However, visual acuity in fog for blue Landolt-C optotypes was higher than for red and green optotypes. The colour intensity of Landolt-C optotypes presented on LCD screen was chosen to correspond to the blue, green, and red colour contributions against an achromatic white stimulus. Thus, the blue stimuli had the greatest intensity contrast. Also, blue stimuli on a white background correspond to uniform distribution of blue stimuli within the whole stimulus area, both within the white background and within stimulus C optotype area, and consequently the greater shorter wavelength scattering does not alter the perception of blue stimuli. Search times of stimuli with different colour and dynamic visual acuity (up to stimulus velocities of 30 deg s⁻¹) were also determined in simulated fog conditions by using scattering obstacles with controllable degree of light scattering. These experiments also revealed the smallest increase of visual search times and better dynamic visual acuity in fog for blue–white colour contrast stimuli than for red–white and green–white combinations used in road and traffic signs.

◆ **The role of random wiring in chromatic selectivity of parvocellular neurons**

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The receptive field centre of parvocellular (PC) ganglion cells in central retina is thought to be driven by a single (M or L) cone. The random wiring model of PC receptive fields states that their receptive-field surrounds can be composed of different mixtures of M and L cones, which should give rise to varying degrees of chromatic opponency. Here, we studied the signals carried by central (up to 15 deg eccentricity) PC neurons ($N = 60$), using single-unit electrophysiology in the lateral geniculate nucleus of anaesthetised and paralysed trichromatic marmosets ($N = 3$). Stimuli were drifting (4 Hz) black–yellow (LUM), red–green (RG), or M- or L-cone isolating sinusoidal gratings. Spatial-frequency tuning functions were obtained for these four conditions. For most neurons (92%), the LUM response was in-phase with either M- or L-cone modulation (dominant cone) and opposite-phase with the other cone type at low frequency (0.01 cycle deg⁻¹). At low frequency, 55% of the cells were RG opponent (ie RG response > LUM response). Modulating the dominant cone alone often resulted in band-pass spatial-frequency tuning, as expected if the dominant-cone type contributes to both the receptive field centre and surround. This effect was quantified by calculating the attenuation ratio $AR = 1 - (\text{low-frequency response}/\text{maximum response})$ for the dominant cone. The AR values ranged between 0.2 and 1. Chromatically opponent cells showed less contribution of the dominant cone to the surround (opponent AR: 0.90 ± 0.12 , $N = 32$; non-opponent AR: 0.50 ± 0.22 , $N = 23$), suggesting that colour opponency is strengthened by spatial segregation of the M and L cones. We conclude that the variability of chromatic properties of PC receptive fields in central retina is compatible with random cone connections in the receptive-field surround.

[Supported by the Australian NHMRC, grant 253621.]

◆ **Dissociation of colour and figure–ground effects in the watercolour illusion**

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Two phenomena can be observed in the watercolour illusion: illusory colour spreading (Pinna et al, 2001 *Vision Research* 41 2669–2676) and figure–ground organisation (Pinna et al, 2003 *Vision*

Research 43 43–52). We performed two experiments to determine whether the figure–ground effect is a consequence of the colour illusion or due to an independent mechanism. Subjects were tested with displays consisting of six adjacent compartments delineated with purple/orange double lines on a light background. The order of purple and orange lines alternated so as to produce watercolour illusions in one set of compartments but not in the others (null compartments). In experiment 1, the illusory colour was measured by finding the matching physical colour in the null compartments. ‘Figure-ness’ (probability of “figure” responses, 2AFC) of the watercolour compartments was then determined with and without the matching colour in the null compartments. The colour match reduced figure-ness, but did not abolish it. There was a range of colours for which the watercolour compartments dominated as figures over the null compartments, although the latter appeared more saturated in colour. In experiment 2, the effect of tinting the null compartments was measured in displays without watercolour illusion (no orange lines). Figure-ness increased with colour contrast, but its value at the equivalent contrast fell short of the figure-ness value obtained for the watercolour pattern. Thus, in both experiments, figure-ness of the watercolour pattern was stronger than expected from the colour effect, suggesting independent mechanisms. We conjecture that part of the figure–ground effect of the watercolour pattern results from the double lines stimulating neurons that are selective for asymmetric edge profiles. Such neurons may signal border ownership (Zhou et al, 2000 *Journal of Neuroscience* 20 6594–6611) and thus contribute to figure–ground segregation. [Supported by NIH grant EY02966.]

◆ **Measurement of averaged luminance of two colours by flicker photometry and its application to determine the relative gamma characteristics of CRT phosphors**

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Simple flicker photometry allows us to obtain an equal luminance between different colours. We examined whether this could be used to obtain averaged luminance of two colours of different luminance, and developed a convenient psychophysical method for measuring the averaged amounts of luminance of two colours. As an application of this method, we measured the relative gamma characteristics of CRT phosphors. The stimulus was a checker pattern in which two types of coloured elements with different luminance on the identical phosphor were embedded. We prepared two patterns in which the arrangements of the element colours were reversed, and flickered them alternately with the temporal insertion of a uniform field between them. The uniform field had the phosphor colour identical to the pattern elements and its luminance could be changed by observers. As in flicker photometry, observers adjusted the luminance of the uniform field to get the luminance at a minimum flicker. We confirmed that the luminance of the uniform field determined for certain combinations of luminance of the elements was almost of an average of them, by comparing the results with an averaged luminance measured with a spectrophotometer. Applying this method to measure the relative gamma characteristics of phosphors of CRT colour displays, we obtained successively the luminance of the middle range for each of three phosphors over the range from the minimum to the maximum luminance. The shape of the gamma characteristics agreed well with those measured with a spectrophotometer. This method allowed us to obtain the relative amounts of luminance and the gamma characteristics of three phosphors, although it might still be difficult to obtain their absolute luminance.

[Supported in part by a Grant-in-Aid for the 21st Century COE Program ‘Design of Artificial Environments on the Basis of Human Sensitivity’, Kyushu University, Japan.]

◆ **Colour difference thresholds for discrimination of colour distributions**

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A coloured texture pattern with a certain colour distribution is distinguishable from surrounding coloured texture patterns by the differences in colour distributions. We investigated the discrimination thresholds in terms of the differences in the mean and the standard deviation of the colour distributions. We examined the thresholds of differences in each direction of three axes (L^* , u^* , and v^*) for 3-D normal distributions in the CIELUV colour space. The stimulus patterns consisted of 900 disks of 0.28 deg diameter presented in the square region of 6.8 deg side in the centre of a colour CRT display. The region was divided into four regions (2×2), and the colours of the disks presented in one of these regions (the test field), which was chosen randomly, had a different distribution from that in other regions (the background field). The mean and the standard deviation of the test field were varied from those of the background in the sixteen directions on the plane made by the mean and the standard deviation. We used a standard

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deviation of 5 and three kinds of means for the background distributions: $(L^*, u^*, v^*) = (40, 0, 0)$, $(40, 53, 0)$, and $(40, 0, -60)$. We found that the points of the thresholds plotted in the sixteen directions laid an almost elliptical shape, and the thresholds for the background $(40, 53, 0)$ and $(40, 0, -60)$ increased in the direction of u^* and v^* , respectively, in comparison with those for the $(40, 0, 0)$ background, although the thresholds in the other directions were almost unchanged. These results suggest that the discrimination thresholds are affected by the means of the background colour distributions.

[Supported in part by a Grant-in-Aid for the 21st Century COE Program entitled 'Design of Artificial Environments on the Basis of Human Sensitivity', Kyushu University, Japan.]

◆ **Categorical colour perception for multi-coloured texture patterns**

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Objects in our visual environment have multi-coloured surfaces. We are frequently able to call the surface colour by a single-colour name when non-uniform colour surfaces consist of similar colours. It is possible that we get a single-colour impression from the multi-coloured scene. Here, we examined the chromatic mechanism producing such a single-colour impression. We measured hue differences of colours in multi-coloured texture patterns in which we could sense a single-colour impression, and the categorical colour of the impression. We presented a random-dot texture pattern consisting of square dots (4 min of arc in size) with two kinds of colours, which had different Munsell hues and a constant Munsell value ($V = 5/$) and chroma ($C = /6$) on a CRT display. Observers judged whether a single-colour impression overall was perceived in the pattern or not. If they perceived a single-colour impression, they named the perceived colour by the colour-naming method. We found that the extent of hue difference in which the single-colour impression was perceived depended on the hue combination in the pattern. When the hues of the colour combination in the pattern existed on an identical tritanopic confusion line, the single-colour impression was easily obtained. In addition, the single-colour impression could be perceived even when the two colours belonged to different categories of so-called categorical colours. Observers seemed to be able to integrate the multi-colours in non-uniform colour surfaces into a single-colour impression even when the extent of the hue difference exceeded the colour category. We conclude that the colour information perceived as a single-colour impression is extracted on the way from the receptor level to the level categorising colours in the chromatic pathway.

[Supported in part by Grants-in-Aid for the 21st Century COE Program 'Design of Artificial Environments on the Bases of Human Sensibility' and the Strategic Research Center Developing Program 'Integration of Technology and Sensitivity', Kyushu University, Japan.]

◆ **Steady-state misbinding in one colour**

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We conducted 5 experiments on an illusion which was first reported by Wu et al (2004 *Science* **429** 262). The display consisted of two sheets of random dots. In one sheet, dots in the centre were red and dots in the periphery were green. In the other sheet, dots in the centre were green and dots in the periphery were red. One sheet was moving up, the other sheet was moving down. When observers were asked to report the direction of moving dots in the periphery, while gazing at the centre of the display, they showed a higher error rate than the chance level (experiments 1–5). That is, observers illusorily perceived dots in the periphery to move in the same direction as those of the same colour in the centre. The illusion (ie high error rate) occurred regardless of density or luminance of dots, but was strongly affected by the speed of dots (experiment 1). The illusion disappeared when dots in the centre moved in a random manner, or did not move (experiment 2). Moreover, when the luminance (experiment 3) or speed (experiment 4) of dots in one colour (eg green) became higher, which made the direction of moving dots in the one colour salient, the illusion occurred only in the other colour (eg red). Similar results were seen when green dots in the centre were replaced with blue (or yellow) dots (experiment 5). The results of experiments 3–5 indicated that observers illusorily perceived most of the dots (both red and green) in the periphery moving in the same direction. Given that the illusion reflects illusory conjunction in feature-integration processes (Wu et al, loco cit.), these findings suggest that not all features are necessarily preserved in feature-integration processes.

◆ **Substitution of visual signals**

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We analysed two strategies of the visual system: (i) the independent and hierarchical processing of information on colour and movement in the early stages, and (ii) the 'silent substitution' of signals at higher levels, which is indicative of the high interactive power of the visual system. The experimental material consisted of two short sentences in Arial Bold, presented on a PC monitor in chromatic and achromatic versions. Different levels of contrast and speed were analysed. At certain time intervals, the observers reported greater or lesser legibility of the texts. Taking the static and achromatic situation as a reference, the following observations were made: (i) the need for contrast is compensated for by the exclusively top-down cognitive effects; (ii) the frame in static texts was of no importance; but (iii) the frame was important for moving texts owing to the frame-distance relationship established between letters (24 frames were needed as opposed to the 10 used in the static texts). This fact, which follows Korte's laws, is usually analysed by filters sensitive to changes in luminance between letter and background. This would explain why we believe that purely chromatic contrast does not contribute to the legibility of texts in general, although colour helps to initiate and weigh up attention processes. Summing up, in tasks of recognition we noted that movement exceeds the contribution of colour, while the latter, in turn, exceeds legibility. If a text is familiar, these two factors may decrease but not be annulled. Lastly, the experimental situation chosen allowed the alternative confrontation of two neural areas, the inferotemporal and the parietal which, as is known, analyse colour and movement respectively, to be visualised. The interaction between bottom-up and top-down processing, where attention is important, has also been analysed.

◆ **Colour constancy is as good as colour memory allows—A new colour constancy index**

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In the natural world, colour constancy relies on colour memory: to perceive that an object's colour has remained the same under a change in illumination, we would naturally refer to its remembered colour under the previous illumination. Here, we quantify this dependence by investigating colour memory shifts for real paper samples under constant and changing illumination. On each trial, the observer ($N = 7$) pre-adapts to the reference illumination (D65) for 60 s, then views and memorises the reference paper under the reference illumination for 10 s. The observer then adapts to the test illumination while performing a distracting task, for 60 s, after which he selects the best match from an array of 16 test papers under the test illumination. The test papers are systematically varied between trials; the test illumination is either the same as the reference (the constant illumination condition) or one of four distinct sources (D40, D145, 'red' or 'green'). We find that colour memory is not, in general, perfect; there are small but significant colour differences between the reference colour and the selected match. But changes in illumination appear to affect neither the size nor direction of the colour memory shift. We therefore developed a new colour-constancy index that explicitly compares the memory shift under changing illumination with the shift under constant illumination. An index value of 0 indicates the worst possible constancy (memory deteriorates under changing illumination); 1 indicates perfect colour constancy (the shifts are identical under changing and constant illumination); and values above 1 (to a maximum of 2) indicate improved memory under changing illumination. For this task, and for every condition, the mean colour-constancy index is close to 1. Therefore, we conclude that, for the human visual system, colour constancy is as good as colour memory allows it to be.

◆ **Late stages of photolysis: Cone vs rod visual pigments**

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Slow stages of the photolysis of visual pigments play a crucial role in the process of recovery of photoreceptor sensitivity (dark adaptation) after bleaching. Ten-times-faster dark adaptation of cones (diurnal vision), as compared to rods (nocturnal vision), may imply correspondingly faster decay of the photolysis products of their pigments. However, there is no information on the kinetics of photolysis of visual pigments in intact retinal cones. The aim of the present work was

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to study the late stages of photolysis of visual pigments in intact cones and rods. Visual pigments of goldfish rods and red cones were studied with a fast-scanning dichroic microspectrophotometer. We found that the basic products of photolysis of the cone visual pigment are similar to those of rod porphyropsin but decay substantially faster. Immediately after fast bleaching, metapigment-II in equilibrium with metapigment-I appears both in cones and in rods. Further, they decay to 3-dehydroretinal and opsin. However, no metapigment-III can reliably be detected in goldfish photoreceptors. In cones, metapigment-II decays to 3-dehydroretinal and opsin with a half-time of 4 s, while in rods the photolysis proceeds almost 90 times slower. Kinetic analysis of the decay of metaproducts and 3-dehydroretinal to 3-dehydroretinol conversion indicates that the limiting stage in 3-dehydroretinol production in rods is the decay of metapigment-II to 3-dehydroretinal and opsin, while in cones the enzymatic reduction of 3-dehydroretinal is rate-limiting. The two features of cone visual pigments, fast quenching of the residual activity of cone metaproducts due to fast hydrolysis of 3-dehydroretinal/opsin Schiff base, and correspondingly fast appearance of the substrates for dark visual pigment regeneration (free opsin and 3-dehydro-retinol) are essential conditions for faster dark adaptation of cones as compared to rods. [Supported by the Russian Foundation for Basic Research 03-04-49713.]

SPATIAL VISION 2

◆ Selective mechanisms for complex visual patterns revealed by compound adaptation

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It is well documented that the visual system has a number of neural mechanisms (or channels), each responding selectively to particular Fourier energies in the visual world. We wanted to know whether there are subsequent mechanisms responding selectively to particular combinations of those energies such as plaids. We used a novel form of selective adaptation to compounds of sinusoidal gratings (plaids), where two areas of the visual field were simultaneously adapted to the same four sinusoidal components, combined to form two different sets of patterns. The point of subjective equality was then determined for a plaid probed simultaneously in the two locations. In one location the plaid had itself been used as an adaptor, whereas in the other its components had been used, combined into other plaids. In all observers, for a variety of patterns, the degree of adaptation to the compound was greater than the degree of adaptation to the components. The data are consistent with the existence of neural mechanisms responding selectively to particular conjunctions of Fourier energies.

[Supported by grants from the Royal Society (2003/R2), the BBSRC (BB/C50289X/1), and by a Wellcome Trust Vacation Scholarship (VS/04/NOT/AA23).]

◆ Limited spatial-frequency range of peripheral channels

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The spatial-frequency channel structure has been a difficult topic to study (i) because channels are not likely to be uniform across the visual field, and (ii) because of inadequacies of the probe techniques. In the present study, several improvements have been made: (a) to achieve channel uniformity, the visual periphery was studied; (b) in further push to uniformity, local Gaussian stimuli were used as a probe; (c) we employed the Stiles near-threshold masking sensitivity paradigm, which is insensitive to transducer nonlinearities. The results show that the lowest-frequency channel is tuned to much higher spatial frequency than previously thought (3 cycles deg^{-1} at 2 deg eccentricity, 1 cycle deg^{-1} at 8 deg). The peak frequency of the lowest channel scaled with eccentricity according to the cortical magnification. The highest channel was tuned to 3 to 4 times higher spatial frequency than the lowest channel, and, therefore, the range was constant across eccentricities from 2 to 8 deg. Additionally, the masking curves for different test contrasts indicate that the channel structure within this range is discrete (although the full measurement of its structure remains to be carried out). These results suggest that human spatial channels are produced by a few types of neurons in the visual cortex whose receptive fields are constant in cortical units.

[Supported by NEI Grant 13025.]

◆ Visual reaction times to compound gratings

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Simple reaction times (RTs) show a strong relationship with contrast when first-order stimuli are used (eg simple gratings; Plainis and Murray, 2000 *Neuropsychologia* **38** 1555–1564). We investigated

the link between RTs and suprathreshold contrast using second-order structures, such as compound gratings. Stimuli were presented on a Sony GDM F-520 CRT display by means of a VSG2/5 stimulus generator card (CRS, Rochester, UK). They were Gabor patches (plaids and compound gratings containing sinusoidal components of two frequencies), measured 100 pixels in diameter at half height in the centre of the display, subtending 1.15 deg at a 2 m distance. Spatial frequencies of 1, 4, and 16 cycles deg⁻¹ at 8 different orientations were tested. Monocular RTs were measured over a range of suprathreshold Michelson contrasts. Contrast detection thresholds were also assessed by the methods of adjustment. Three subjects participated in the experiments. We found that RTs to complex grating patterns increase exponentially with contrast, with higher spatial frequencies producing steeper functions. Sensitivity, as derived from the RT versus contrast functions, varies with orientation of the gratings similarly for both first-order and second-order stimuli. However, compound gratings are in all conditions less visible than their sinusoidal components. These values agree with sensitivities derived by the contrast detection thresholds. The results support the hypothesis that second-order stimuli are better defined by a change in higher-order image statistics, such as local contrast. Moreover, orientational tuning seems to precede the detection of second-order stimuli.

◆ **Perceptual span for navigation increases at low contrast**

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How much visual information in a single glance is required for efficient navigation? We addressed this question by measuring the perceptual span in a goal-directed walking task. Clinical research has shown that peripheral visual-field loss and reduced contrast sensitivity (CS) are associated with severely impaired navigation performance. These findings, together with the fact that CS declines with eccentricity, led us to hypothesise that perceptual span will increase with reductions in image contrast. Using an immersive virtual environment, we assessed navigation performance in twenty normally sighted subjects as they walked to a target tree within a virtual forest consisting of trees, boulders, and holes in the forest ground. Subjects' field of view (FOV) was restricted to 10, 20, or 40 deg and image contrast levels were high, medium (50% of high contrast), and low (25% of high contrast). Navigation performance was assessed as time to reach goal, which was divided into two phases: latency (time from display onset to commencement of walk) and a walking phase (from latency until reaching goal). Perceptual span was defined as the smallest FOV at which subjects could navigate the course with no more than a 20% increase in time from baseline. Perceptual spans determined for the medium and high contrast levels were not significantly different from each other (14.2 versus 13.3 deg for latency and 16.3 versus 15.9 deg for walk time). However, perceptual span for both latency and the walking phase was significantly increased at the lowest contrast level (21.2 and 23.1 deg). These findings suggest that the size of the FOV required for navigation remains fairly robust against reductions in image contrast until it reaches very low levels.

[Supported by US Army Grant #W911NF-04-1-0059]

◆ **Differences of the grouping effect of fovea versus parafovea centred targets**

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Differences between the brain grouping processes when the target was centred at the fovea or at the parafovea were investigated. The stimulus consisted of a chessboard with black and white squares. Fixation localised in the centre of the target or at its border at different eccentricities. The observer got an instruction to organise in his imagination the separate squares of the chessboard target as the St Andrew diagonal cross or the upright St George cross. If the observer fixated a dot in the centre of the target the grouping of the rectangular squares as the St George or the St Andrew cross was perfect. It was possible to organise mentally the crosses from a large number of squares for a short time. The well-known alternation effect of the upright and oblique crosses appeared. The crosses can be destroyed and left and right diagonals (vertical versus horizontal strips) begin to alternate. The grouping was possible if the target was centred at the point of fixation. If the target was centred but the area corresponding to the fovea had no squares, the grouping was still possible at the periphery, this being the case of radial symmetry. If the fixation point was displaced laterally from the target and the chessboard was presented asymmetrically, to one side of the parafovea area, the observer's performance was dramatically weak: the observer could not effectively carry out grouping of the cross. This weak performance was not the result of bad peripheral resolution, as the observer saw perfectly each of the squares of the board we used. The observer can organise the squares in horizontal, vertical, or diagonal strips, but not generate the cross. These grouping-effect differences consist in symmetrical and

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asymmetrical target presentations to different points of view, but not in differences between the centre and periphery.

[Supported by the Russian Foundation for Basic Research.]

◆ **Perceived size and perceived distance of targets seen from between legs: Evidence for proprioceptive theory**

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Perceived size and perceived distance of targets seen from between legs was investigated in three comparisons. Five targets 32 to 163 cm high were presented at viewing distances of 2.5 to 45 m, and a total of ninety observers verbally judged the perceived size and perceived distance of each target. In comparison 1, fifteen observers inverted their heads upside down and saw the targets through their own legs, and another fifteen observers saw the targets while being erect on the ground. The results were that inverting the head lowered the degree of size constancy and compressed the scale for distance. To examine whether these results were due to an inversion of retinal image or of body orientation, two further comparisons were performed (comparisons 2 and 3). In comparison 2, fifteen observers stood upright and saw the targets through prism goggles that rotated the visual field 180°, and another fifteen observers stood upright but saw the targets through hollow goggles lacking the prisms. The results were that, in both goggle conditions, size constancy prevailed and perceived distance was a linear function of physical distance. In comparison 3, fifteen observers wore the 180° rotation goggles and saw the targets bending their heads forward, and another fifteen observers saw the targets wearing the hollow goggles and lying on their bellies. The results showed a low degree of size constancy and a compressed distance scale. It is, therefore, suggested that perceived size and perceived distance are affected by an inversion of body orientation, not of retinal image. When path analysis and partial correlation analysis were applied to these data, perceived size was found to be independent of perceived distance. These results support the direct-perception model.

◆ **Facilitation and inhibition in the spatiotemporal template for ring target detection**

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Using the classification image technique (Beard and Ahumada, 1996 *Proceedings of SPIE* 3299 75–85; Murray et al, 2002 *Journal of Vision* 2 79–104), Neri and Heeger (2002 *Nature Neuroscience* 5 812–816) derived spatiotemporal facilitatory and inhibitory templates for vertical-bar detection. We investigated more closely the nature of such templates using a ‘ring’ target to determine the relative strength of inhibitory responses from inside and outside the target region. Our stimulus consisted of fifteen temporal frames of five spatial elements: one central disk and four surrounding concentric rings, termed the innermost, inner, middle, and outermost elements, respectively. The width of each ring was the same as the diameter of the central disk, and, when a target was present, the middle ring always served as the target location. The target element was brighter than the screen background and the remaining elements were darker than the background. Random luminance noises were assigned independently to each element’s luminance, and assigned noises changed in every stimulus frame. On a non-target trial, the non-target pattern was presented across all fifteen frames. On a target trial, the target pattern was presented in the middle three frames (frames seven to nine), and the non-target pattern was presented in the remaining frames. Four observers judged whether a target was presented on each trial. Results showed that observers’ templates had a peaked and transient facilitatory response at the target ring location during the target presentation. Moreover, an inhibitory response was found from the outer and the outermost elements, and inhibition remained even after the actual target presentation. An inhibitory response from the innermost and inner elements was not found, except in one observer. These results suggest that observers’ spatiotemporal templates are not simple copies of the spatio-temporal target pattern, shedding light on detailed visual information processing that could not be revealed by other psychophysical methods.

[Supported by JSPS Research Fellowship for Young Scientists (No. 200201154), NSERC Discovery grants (42133 and 105494), and the Canada Research Chair Program.]

◆ **The model of perceived space**

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The aim of this research was to check whether elliptic shape of the perceived space is a consequence of an unequal distribution of depth cues in the direction of the horizon and zenith, or is an inherent characteristic of our visual system. If elliptic shape of the perceived space is a consequence of an unequal distribution of depth cues, estimates of the distance towards the horizon and zenith should be identical in conditions of equal distribution of depth cues. Otherwise, elliptic shape of the perceived space would be an inherent characteristic of the visual system. In order to solve this dilemma, an experimental field research was performed with forty-six participants, who were asked to equalise the distances of two circles towards the horizon and zenith. The experiment was conducted in a dark room (uniformly reduced distribution of depth cues) and in an open field (unequal distribution of depth cues). Participants estimated distances from two positions (body orientations)—standing and lying down. The results showed that estimated distances towards the horizon are longer than estimated distances towards the zenith in a dark room and in an open field, when participants were standing. When participants were lying down in an open field, estimated distances towards the horizon were also longer than estimated distances towards zenith, but in a dark room estimated distances in the two directions were identical. These findings confirm that perceived space has an elliptic shape and that this is an inherent characteristic of our visual system. However, this shape can be modified, depending on contextual information (observer's position and distribution of depth cues). The ratio of estimates of distances towards the horizon and zenith was 3/4 in most situations.

◆ **Functional roles of intracortical connections for the integration of visual features:**

An intrinsic optical imaging study

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How layer II/III horizontal networks integrate different features inherent to visual information for orientation and direction of motion discrimination has been the focus of many theoretical and experimental studies. It has been suggested that each neuron receives horizontal inputs from a large variety of neurons with different properties. On the other hand, histochemical studies have demonstrated that the horizontal networks link neurons of similar orientation preferences. We have previously proposed a simple analysis method that could functionally extract the patterns of intracortical connections by optical imaging of intrinsic signals. Each stimulus is presented three times, to each eye separately and to both eyes simultaneously. The model is based on the intrinsic signal modulation between the response to binocular stimulation and the sum of the monocular responses. Pixels sending excitatory and inhibitory connections to reference pixels are typically clustered into patchy domains. In this study, we examined the reconstructed, functional patterns in detail. Orientation, direction, direction selectivity, and ocular dominance at individual pixels were systematically compared to response properties of the pixels they were connected to. We confirmed some of the properties relative to orientation and direction that have been reported in electrophysiological experiments, and present some evidence for the influence of direction selectivity and ocular dominance at selecting the appropriate connections. We conclude that this new method is a useful tool to identify the intracortical connections based only on optical imaging data.

◆ **Influence of perceptual magnification on visual acuity**

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Horizontal symmetrical prisms are known to modify the perceived size of a visual scene (Drobe and Poulain, 2004 *Perception* 33 Supplement, 174) while retinal image size stays unmodified. Base-in prisms increase, while base-out prisms decrease perceived size (SILO effect). In this experiment, the influence of a 6% perceptual magnification induced by two base-in prisms (4 prismatic dioptres) on visual acuity was analysed. High- and low-contrast visual acuity was measured for fifteen observers with randomly chosen prisms or plane lenses at 40 cm. Perceptual magnification had no influence on high-contrast visual acuity ($p > 0.35$). Low-contrast visual acuity was slightly, but not significantly, reduced with prismatic lenses ($p > 0.08$), probably owing to the transverse chromatic aberration induced by the prisms [Granger et al, 1999 *Optometry and Vision Science* 77(12s) 181]. These results suggest that retinal image size and not perceived image size is used for visual acuity.

Thursday

◆ **Filling-in of texture information from feature conjunctions**

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The masking procedure introduced by Paradiso and Nakayama (1991 *Vision Research* 31 1221–1236) was used to demonstrate filling-in processes for brightness and texture information. We briefly presented textures constructed from Gabor patches that were followed by a rectangular frame. If the texture was homogenous, subjects usually perceived the texture inside the frame as scattered fractions of the texture. If the texture contained another texture (eg with changed element orientation) of the same size as the frame, subjects described the inside of the frame as darkened but homogeneous in texture. The amount of darkening is smaller for higher feature contrasts between target and background texture. These results substantiate the findings of Caputo (1998 *Vision Research* 38 841–851) of distinct filling-in processes for brightness and texture. Frames of different sizes were further used to systematically decrease the amount of region information in textures while keeping the texture border constant. Subjects had to detect quadratic textures that differed from the surround in orientation, spatial frequency, or the conjunction of both. They signalled whether a masked texture contained a target or was homogeneous. We found that the degree to which the texture region is masked does not affect detection performance for targets defined by a single feature. It does affect detection performance for targets defined by conjoined features: the smaller the mask, the better the detection performance. The finding is interpreted in terms of region-based feature-integration mechanisms: a complete texture region enables synergistic feature processing, whereas texture borders do not. The decline of synergy from complete to incomplete regions is slower for higher feature contrasts. This is in line with our earlier findings that feature synergy is negatively correlated to feature contrast (eg Meinhardt et al, 2004 *Vision Research* 44 1843–1850).

◆ **Top – down information from the figure – ground assignment process to the contour-integration process**

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We investigated the relation between the two processes of contour integration and figure–ground assignment in the visual system. Psychophysical experiments were performed to clarify whether these processes are arranged simply in the one-way cascade manner, or in the interactive one. Each stimulus included a lot of small equilateral triangles with equal size, whose position and orientation were randomly determined. One trial was composed of two frames of stimuli presented sequentially. One frame included only randomly arranged triangles, the other frame had a path represented by a set of regularly arranged triangles embedded in randomly arranged triangles. The paths can be classified into two types. (a) Each triangle is placed so that one of its three edges was on a tangential line of a smooth curve, and all triangles constituting the path were on the same side against the smooth curve. (b) The same as (a), except that the side of the triangles against the smooth curve alternated. The task for the subject was to answer which frame contained the path represented by edges of triangles. The correct rate of type (a) was high compared to the type (b). The result indicates that (i) line segments that provide information about figural side can be integrated into a long curve, and (ii) when figural sides of such line segments alternate, integration tends to be weak. Additional experiments were performed to confirm that subjects did not integrate the triangles themselves, but integrated line segments constituting the triangles. In conclusion, the top–down information flow from the figure–ground assignment network to the contour integration network exists in the visual system, and figural sides of edges must be identical along the path in order to be integrated.

◆ **Partial modal completion theory cannot explain occlusion illusion**

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Kanizsa (1979) reported a size illusion in which a figure bounded by an occluding edge looks larger than the same figure not bounded by an occluder. Brooks et al (2004 [Abstract] *Journal of Vision*) 4(8) 722a, <http://journalofvision.org/4/8/722/> showed that partial modal completion theory might explain this illusion. According to this theory, the occluded region appears larger because the visual system fills in a thin strip along the occluded border. Earlier studies of the time course of perceptual completion showed that modal completion occurs within 100–200 ms, and shorter presentations leave the fragmented figures uncompleted (Ringach and Shapley, 1996 *Vision Research*

36 3037–3050). On the basis of this finding, modal completion theory predicts that occlusion illusion should be perceived better in presentations longer than 100–200 ms when completion has almost occurred rather than presentations shorter than these times. In the present study, this prediction is evaluated by estimating occlusion illusion in different presentation times. In each trial, after fixation-cross presentation, the occluded semi-circle (the occluder was a square) and unconcluded semi-circle were shown for 80–280 ms (in steps of 40 ms) and then immediately a mask was presented [it has been shown that masking can interrupt perceptual completion (Rauschenberger and Yantis, 2001 *Nature* 410 369–372)]. Observers then had to report which semi-circle was bigger. Contrary to modal-completion-theory prediction, observers were more likely to report the illusion in shorter presentations. This finding is not in agreement with modal completion theory and implies that the modal completion mechanism cannot properly explain the occlusion illusion. Current results point out that faster mechanisms must be in operation for occlusion illusion perception.

◆ **Grouping-based feature transportation**

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One of the major questions in the cognitive and neuro sciences is how features are integrated to create a unique percept. Usually, features are perceived at the spatial location they were displayed at. Here, we present a new illusion—repetitive metacontrast—which demonstrates that features can be transported from one location to any other location in a spatial region of at least half a degree in diameter. A single Vernier, offset either to the left or right, was briefly presented and followed by a pair of straight flanking lines rendering the Vernier invisible (classical metacontrast). Surprisingly, the Vernier offset was perceived at the flanking lines even though these were in fact straight. We successively presented further pairs of flanking lines with increased spacing. Such sequences create two ‘streams of lines’ expanding from the Vernier. The Vernier itself remained invisible but its offset was perceived in the streams. We called this effect repetitive metacontrast since not only the Vernier but also most of the flanks—except for the last pair—were only barely visible individually. Subjects attended to one stream and reported the perceived Vernier offset. If one of the flanks in the attended stream was offset itself, this offset was combined with the Vernier offset. However, this feature integration occurred only in the attended stream. We presented complex displays with more than two streams which, for example, could coincide. As with two streams, offsets were only integrated when attention was paid to a stream. We conclude that, in repetitive metacontrast, features can be freed from their physical carriers and ‘transported’ to other spatial locations.

◆ **An upper lower asymmetry in foveal bias**

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Foveal bias refers to a distortion in visual memory for which observers reproduce the location of a transiently visible peripheral target closer to the fovea. We compared the magnitudes of foveal bias between upper and lower visual fields employing an absolute localisation task. The target stimulus was a 1 deg diameter black dot presented at 40 locations comprising 5 eccentricities and 8 directions on a frontoparallel plane, 48 cm apart from the observer’s eye level. Observers were asked to memorise the location of the target that appeared for 1000 ms while maintaining their fixation binocularly at a designated mark centred on the screen. 150 ms after target offset, a mouse cursor appeared 3 deg away from the target at one of the same 8 directions mentioned earlier and disappeared after the trial was over. The observer’s task was to point to the remembered location of the target with the mouse cursor and to press the left button of the mouse to record the coordinates of the screen. A two-way (2 visual fields × 5 target eccentricities) repeated measures ANOVA with six observers showed a significant main effect of visual field ($F_{1,5} = 8.868, p < 0.05$), with larger magnitudes of foveal bias being at the upper visual field. A significant interaction between visual field and target eccentricity was also observed ($F_{4,20} = 4.051, p < 0.05$), showing that the magnitudes of foveal bias at upper visual field were significantly larger only at 9, 12, and 15 deg eccentricities. We interpret these results as suggesting that there might be some association of asymmetry between upper and lower hemi-retina in receptors and ganglion-cell density (Curcio and Allen, 1990 *Journal of Comparative Neurology* 300 5–25) with the frame of reference guiding our localisation behaviour.

Thursday

◆ Contrast discrimination with simultaneous monocular and dichoptic masks

D H Baker, T S Meese, M A Georgeson (Neurosciences Research Institute, School of Life and Health Sciences, Aston University, Birmingham B4 7ET, UK; e-mail: bakerdh@aston.ac.uk)

In experiments reported elsewhere at this conference, we have revealed two striking results concerning binocular interactions in a masking paradigm. First, at low mask contrasts, a dichoptic masking grating produces a small facilitatory effect on the detection of a similar test grating. Second, the psychometric slope for dichoptic masking starts high (Weibull $\beta \sim 4$) at detection threshold, becomes low ($\beta \sim 1.2$) in the facilitatory region, and then unusually steep at high mask contrasts ($\beta > 5.5$). Neither of these results is consistent with Legge's (1984 *Vision Research* **24** 385–394) model of binocular summation, but they are predicted by a two-stage gain control model in which interocular suppression precedes binocular summation. Here, we pose a further challenge for this model by using a 'twin-mask' paradigm (cf Foley, 1994 *Journal of the Optical Society of America A* **11** 1710–1719). In 2AFC experiments, observers detected a patch of grating (1 cycle deg^{-1} , 200 ms) presented to one eye in the presence of a pedestal in the same eye and a spatially identical mask in the other eye. The pedestal and mask contrasts varied independently, producing a two-dimensional masking space in which the orthogonal axes (10×10 contrasts) represent conventional dichoptic and monocular masking. The resulting surface (100 thresholds) confirmed and extended the observations above, and fixed the six parameters in the model, which fitted the data well. With no adjustment of parameters, the model described performance in a further experiment where mask and test were presented to both eyes. Moreover, in both model and data, binocular summation was greater than a factor of $\sqrt{2}$ at detection threshold. We conclude that this two-stage nonlinear model, with interocular suppression, gives a good account of early binocular processes in the perception of contrast.

[Supported by EPSRC Grant Reference: GR/S74515/01.]

FRIDAY

POSTERS 4

FACE PERCEPTION 2

◆ **The effect of orientation and feature inversion on the perception of face expression:****Support for a dual-mode theory of face processing**

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In the Thatcher illusion, a face with inverted eyes and mouth ('thatcherised') looks bizarre when viewed upright but looks normal when inverted. This perceptual change is thought to reflect different processing mechanisms for faces, with upright-face processing relying on configural information, and inverted-face processing relying on features. Support for this dual-mode view comes from demonstrations of a discontinuity in the function relating face orientation and responses to faces (ratings, recognition), in particular after rotations of $\sim 90^\circ$. A loss of configural information following inversion is also thought to affect identification of emotional expressions, but it is unclear how changes in orientation affect the perception of expression. We investigated the effect of the Thatcher illusion on the detection of the emotional expression in rotated faces. Observers viewed photographs of unfamiliar happy and angry faces in normal and thatcherised versions at 7 orientations (separated by 30°) from 0° (upright) to 180° . In two experiments, they made expression or thatcherisation judgments. Expression judgments showed nonlinear decreases in performance ($\sim 90^\circ$ – 120°) for thatcherised faces, and weaker nonlinearities for normal faces. Thatcherisation interacted with expression: thatcherised happy faces were judged as angry up to 90° while thatcherised angry faces appeared more angry than normal faces. Orientation effects on thatcherisation judgments showed nonlinearities too, but no effects of expression. These results suggest that expression detection relies on configural coding of critical face parts; the nonlinear effects of rotation further support the dual-mode view of face processing. In a separate study, we also investigated the ability of a prosopagnosic patient (HJA) to make expression and thatcherisation judgments with upright face stimuli. While HJA was unable to make thatcherisation judgments, his expression judgments were affected by thatcherisation. We suggest that face processing in HJA is feature-based rather than configuration-based, allowing expression judgments but impairing thatcherisation judgments.

[Supported by the Economic and Social Research Council]

◆ **Decomposition of EEG oscillatory activity by the categorisation of features driving facial expression**

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A fundamental problem in vision is to determine the specific visual information correlated with the perception of a stimulus, and to understand how the brain extracts and integrates this information to arrive at a conscious perception. To address this issue in the context of visual representations we have developed a new method, based on 'bubbles' (Gosselin and Schyns, 2001 *Vision Research* **41** 2261–2271; Smith et al, 2004 *Psychological Science* **15** 753–761), to relate the information-processing states of the brain to its electrical oscillatory behaviour as measured by EEG. In this study, we have explored the time course of processing of four of the basic facial expressions of emotion (surprise, fear, disgust, and anger), directly relating EEG oscillatory activity to the facial features driving it. In the experiment, we instructed naive observers to categorise, by expression, sparsely presented pictures of expressive faces as revealed by randomly located Gaussian apertures in 3-D space (2-D image space \times 5 spatial scales). We found that EEG oscillations in theta, alpha, and beta bands support discrete information-processing epochs, corresponding to a modulated sensitivity of the brain to both expression-specific and non-specific facial features (including the eyes, eyebrows, nose, mouth, etc). These sensitivity curves (one for each spatial scale considered) effectively project EEG activity into the space of the scale information associated with perception. Furthermore, we computed phase-locking factors between pairs of sensitivity curves to find the time points of highest information integration and thus establish when brain activity is most sensitive to the information driving each expression perception.

[Supported by a BA grant (SG-37881) to MLS and by an ESRC grant (R000239646) to PGS.]

Friday

◆ **Perceptual validation of facial animation: The role of prior experience**

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Facial expressions play a complex and important role in communication. A complete investigation of how facial expressions are recognised requires that different expressions be systematically and subtly manipulated. For this purpose, we recently developed a photo-realistic facial animation system that uses a combination of facial motion capture and high-resolution 3-D face scans. In order to determine if the synthetic expressions capture the subtlety of natural facial expressions, we directly compared recognition performance for video sequences of real-world and animated facial expressions (the sequences will be available on our website). Moreover, just as recognition of an incomplete or degraded object can be improved through prior experience with a complete, undistorted version of that object, it is possible that experience with the real-world video sequences may improve recognition of the synthesised expressions. Therefore, we explicitly investigated the effects of presentation order. More specifically, half of the participants saw all of the video sequences followed by the animation sequences, while the other half experienced the opposite order. Recognition of five expressions (agreement, disagreement, confusion, happiness, thinking) was measured with a six-alternative, non-forced-choice task. Overall, recognition performance was significantly higher ($p < 0.0001$) for the video sequences (93%) than for the animations (73%). A closer look at the data showed that this difference is largely based on a single expression: confusion. As expected, there was an order effect for the animations ($p < 0.02$): seeing the video sequences improved recognition performance for the animations. Finally, there was no order effect for the real videos ($p > 0.14$). In conclusion, the synthesised expressions supported recognition performance similarly to real expressions and have proven to be a valuable tool in understanding the perception of facial expressions.

◆ **Is symmetrical face always more attractive than a non-symmetrical face?**

M Oda (Department of Psychology, College of Letters, Ritsumeikan University, 56-1 Tojiin Kitamachi, Kita-ku, Kyoto 603-77, Japan; e-mail: oda@lt.ritsumei.ac.jp)

High correlation between the symmetry and attractiveness of faces has been reported in many studies. On the other hand, it has also been known that larger eyes increase attractiveness of the face. Because the intensities of these effects have not been compared, we could not judge which feature is more effective for attractiveness. We conducted a questionnaire and an experiment for comparing the attractiveness of symmetrical faces with that of non-symmetrical faces with larger eye(s). Subjects had to evaluate not only attractiveness but also beauty, because attractiveness and beauty could have a different meaning for evaluation. Important cues for attractiveness/beauty were investigated by using a questionnaire. About 70%/80% of subjects described larger eyes as an important cue for judging the attractiveness/beauty, but no subject referred to the symmetry of a face as a cue for attractiveness and about 10% of subjects did so for beauty. These results showed that the eye size was more important in consciousness than the symmetry in judging the attractiveness/beauty of a face. For the experiment, symmetrical faces were created by morphing the intact faces and producing mirrored faces of these. Modifying the eye size of the symmetrical faces created non-symmetrical faces. The stimuli used were the intact and symmetric faces, faces with the left or right eye enlarged, and faces with both eyes enlarged. The subjects rated attractiveness/beauty on a seven-point scale. The symmetrical faces were rated as more attractive/beautiful than the intact faces. Not only faces with larger eyes than the original symmetrical faces were rated more attractive/beautiful, but also faces with one larger eye were rated more attractive/beautiful than the symmetrical faces. These results indicate that an asymmetrical face can be rated as more attractive/beautiful than a symmetrical face.

◆ **Face distinctiveness in self-organising neural networks**

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Distinctiveness is the ease with which a particular exemplar can be recognised among similar ones. In humans, face distinctiveness is related to a facilitation in recognition: in particular, atypical faces seem to be recognised better and faster than typical faces (Light et al, 1979 *Journal of Experimental Psychology* **5** 212–228; Valentine and Bruce, 1986 *Perception* **15** 525–535). Distinctiveness and related phenomena can be accounted for by considering faces as points of a multidimensional hyperspace whose dimensions define their own characteristics (Valentine, 1991 *Quarterly Journal of Experimental Psychology* **43A** 161–204). As a consequence, the greater is the

distance between two faces in this hyperspace, the greater is the perceived difference between them. This so-called 'face space' is characterised by a higher exemplar density in the central part and a normally decreasing concentration moving from the centre toward the edge along the different dimensions. According to this conceptualisation, typical faces are supposed to be located closer to the centre of face space whilst atypical faces are supposed to lie in more external areas of face space; moreover, typical faces would be, because of their location, more similar to each other than atypical faces. We employed a self-organising neural network architecture to model both exemplar distribution in face space and the influence of distinctiveness on recognition accuracy and reaction time.

◆ **View-dependent face recognition in human and monkey**

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Several lines of evidence indicate the existence of view-tuned units in inferotemporal cortex of macaque monkeys. We hypothesised that, if face-view dimension exists in IT cortex, a repulsive shift of perception along view dimension would be expected, caused by adaptation to a singular view as previously found for other dimensions, eg orientation (TAE). We used a set of 14 face views (in steps of about 7°) changing from left profile (a face looking to 0°) to front view (looking to 90°). We asked seven naive human subjects to judge whether presented stimuli had been rotated less than 45° (profile selection) or not (front selection). Subjects received feedback about their response by different beeps at the end of each trial. After reaching 90% performance, subjects performed the same task after 5 s of adaptation to one of the 14 views without any further feedback. We found that adaptation to front view biases this categorisation toward profile selection and, also, profile adaptation biases toward front-view selection (binary logistic regression, $p < 0.05$). In the next step, we demonstrated the same effect in a macaque monkey. The monkey was trained to categorise the 14 face views as in the paradigm used for human subjects. Response selection was performed by saccade to one of the two response points. Correct trials were rewarded. Adding 5 s of adaptation led to shifts in response selection similar to those with human subjects. For both humans and monkeys, the amount of this bias correlates with distance between view angle of the adapting stimulus and the categorisation criterion (45°) (Pearson correlation, $p < 0.05$). This is the first psychophysical evidence to support a view-dependent face-recognition mechanism in monkey brain.

◆ **Perception of local configural changes in own-race and other-race faces**

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We studied the effects of expertise on processing of local configural information in a simultaneous paired-comparison paradigm using faces in which interocular distance either remained unaltered or had been distorted by 10%. Decision accuracy for own-race and other-race faces was compared in whole and partial (a strip with the eyes and eyebrows) face conditions at upright and inverted orientations. Higher accuracy for own-race than for other-race faces in both whole and partial face conditions supported the hypothesis that expertise with a class of faces affects sensitivity to local configural changes. The presence of this advantage at both upright and inverted orientations provided further evidence for the notion that local encoding of configural information can occur relatively independent of orientation. Finally, consistent with the idea that the effects of expertise are perceptually driven, discrimination was more accurate for own-race than for other-race faces irrespective of whether participants were explicitly told that they were to see their own-race faces in one block and other-race faces in another block (experiment 1) or whether both own-race and other-race faces were intermixed in a block (experiment 2). Overall, present results suggest that expertise with a class of faces modulates encoding of local configural information in faces.

◆ **Inter-hemispheric interaction for bodily emotional expressions: Is the right-hemisphere superiority related to facial rather than emotional processing?**

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Earlier studies on functional hemispheric asymmetries for the perception of emotions have consistently shown an advantage of the right over left hemisphere. However, to date only affective

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facial expressions have been used to study emotional laterality. In the present study, we used the redundant target paradigm on healthy subjects to investigate functional hemispheric asymmetries and interhemispheric cooperation in the perception of emotions from bodily expressions. Happy or fearful bodily expressions were briefly presented according to the following conditions: (i) an emotional expression only in the left visual field (LVF); (ii) same only in the right field (RVF); (iii) two emotionally congruent expressions simultaneously projected to both hemifields (BVF); (iv) two body pictures, one showing happiness and the other, in the opposite hemifield, showing fear. A go/no-go task was used requiring subjects to react when a bodily expression (regardless of its position or number) conveyed the target emotion. The target expression (happy or fearful) was fixed for each block of trials and counterbalanced. Latency and accuracy analyses showed no significant difference in reaction times or errors between the two unilateral conditions either for happy or for fearful expressions. This indicates no hemispheric specialisation in the perception of bodily emotional expressions. Simultaneous presentation of two congruent fearful, but not of happy, bodily expressions led to shorter latencies for stimulus detection that exceeded the limit for a probabilistic interpretation supporting interhemispheric cooperation and neural summation. No such effect was present with BVF incongruent expressions. The present study supports earlier findings on inter-hemispheric cooperation in emotional processing from facial expressions but fails to show any functional asymmetry. This latter finding contrasts with previous data showing preferential engagement of the right hemisphere in the perception of emotions and suggests that the right-hemisphere superiority is likely to be related to facial rather than emotional processing per se.

◆ **Judgment of gaze direction is affected by the looker's head silhouette**

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Determining the view direction of socially interacting partners is an indispensable human capability (Symons et al, 2004 *Journal of General Psychology* **131** 451–469; Bock et al, 2005 *8th Tübingen Perception Conference*, 25–27 February). Many investigations (models and experiments) focus on how facial features, such as pupils, eyebrows, or lips, influence social behaviour (Allison et al, 2000 *Trends in Cognitive Sciences* **4** 267–278). Investigations by Gibson and Pick (1963 *American Journal of Psychology* **76** 386–394) suggested that mutual gaze is determined by the head orientation together with the pupil's direction. It remains unclear how global and local features interact to generate the representation of perceived gaze. We used a synthetic 'looker' head (perspective projection; OpenGL). In a first experiment, subjects adjusted the looker's gaze for different horizontal head orientations using an adaptive method (Best PEST). We compared these conditions with displays in which pupil and sclera were the only visible facial features. Results demonstrate that information about the head orientation helps in detecting the true gaze direction. In a second experiment, we focused on the influence of the head silhouette (filled surface/outline) without facial features but with the eye posture left intact. The head orientations generating the silhouette were either coherent or incoherent with the head orientation casting the eyes. The results demonstrate that the silhouette and the relative position of the eyes significantly influence the perception of the looker's gaze. Our investigations show that silhouette, pupil gaze, and spatial eye-position information together contribute to the formation of an ambient invariant for social interaction. Rather than the pupils' direction alone determining gaze direction (Anstis et al, 1969 *American Journal of Psychology* **82** 474–489), we conclude that the gaze invariant is built by the eye-form relative to the face-form (Gibson and Pick, loco cit.) and is further influenced by the spatial configuration of facial parts.

[Supported by a grant from the Ministry of Science and Arts of Baden-Württemberg, Germany (Az.: 23-7532-24-13-19/1) to HN.]

◆ **Removing the own-race bias in face recognition by shifting attention**

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The own-race bias (ORB) in face recognition can be interpreted as a failure to generalise expert perceptual encoding developed for own-race faces to other-race faces. Further, black participants appear to use different features to describe faces than white participants (Shepherd and Derogowski, 1981 *British Journal of Social Psychology* **20** 125–133). An experiment is reported where the size of the ORB was assessed by a standard face-recognition procedure before and after a 1 hour training regime. This regime involved training white participants to distinguish faces that varied only on their chin, nose, and mouth. The ORB, present prior to training, was removed after training. It is concluded that the ORB is a consequence of a failure of attention being directed to those features of other-race faces that are useful for identification.

◆ **Dorsally mediated face and object recognition**

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Complex object recognition has been largely thought to be mediated by ventral-stream regions that process form and shapes. The role of motion as mediated by dorsal-stream regions in the recognition of complex objects has been largely ignored. This is because of the difficulties inherent in creating complex objects that are defined solely by motion cues. Here, we report robust recognition of unfamiliar faces defined solely by motion. Subjects were able to reliably recognise unfamiliar faces defined by classic structure-from-motion cues as well as unfamiliar faces defined by second-order phi-like motion in a simultaneous 1:8 matching task. We subsequently tested several brain-damaged patients with motion impairments, prosopagnosic, and control patients on this task and a series of structure-from-motion and shape-from-shading tasks. Our results suggest that: (a) motion-defined faces and complex objects can be reliably recognised, and (b) that high-level motion processing mechanisms must be intact for successful recognition of these complex stimuli. These results suggest that high-level motion processes and thus dorsal-stream processing can empower robust recognition of complex objects, such as faces. [Supported by CIHR, FRSQ, and NSERC.]

◆ **An analysis of face properties by principal component analysis**

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Faces have multiple properties based on which they can be categorised at different levels of specificity, such as gender, ethnicity, age, identity, and so on. In the seminal paper on the cognitive processes involved in face perception, Bruce and Young (1986 *British Journal of Psychology* 77 305–327) proposed that identity-specific properties and visual-specific properties such as gender, age, and ethnicity are handled at different levels of face perception. This implies that the features required for the identification task are to a large extent different from the features required for categorising gender, ethnicity, and age. However, recent research suggests that identity and gender are not completely parallel (Bruno and Rossion, 2002 *Visual Cognition* 9 1003–1020) and are derived mostly from the same features (Calder et al, 2001 *Vision Research* 41 1179–1208). In this study, from a computational perspective, we investigated whether identity-specific and visual-specific properties of faces are derived from entirely different features or from entirely similar features, or from a set of different and common features. We used a principal component analysis as a feature extractor and a linear discriminant to categorise faces based on different properties. Our findings are as follows. (i) Very few features are required to encode information related to the visual-specific properties, while a large number of features is required to encode identity information. (ii) Many of the important features of a property are also found to be important for other properties. However, a strong correlation is found only for visual specific properties. For example, when gender-important features are removed, categorisation of gender and the other visual-specific properties is degraded to a large extent, while the identity task is degraded to a much smaller extent. This suggests that identity is derived from a large number of features which also include features that encode visual specific properties.

◆ **The effect of framing position in photography on the viewers**

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In portrait photography, people can generate certain emotion by choosing the position from which the photograph is taken. The variation of emotion depending on position of the camera and the distance between the camera and the subject was investigated. The photographs were taken in standard setting, varying three parameters: (a) distance: short, middle, long; (b) vertical position: high, central, low; (c) horizontal position: right, front, left. Observing the photographs, people rated their emotion on positive–negative, static–dynamic, light–heavy dimensions with 7-point scales. The results show that long distance tends to produce light feeling, high camera position produces positive feeling, and frontal view makes the feeling static.

◆ **Idiosyncratic exploration strategies for neutral faces—when schizotypy prefers left**

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Visual attention deficits in psychosis have been related to left as well as to right hemisphere impairment. To disentangle possible contributions of medication effects on attentional preferences

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from illness-related effects, we studied in healthy volunteers whether idiosyncratic biases in the first saccade toward the left or right half of face images depend on the degree of schizotypy, a thinking style reminiscent of the one presented by psychotic patients. Participants performing a visual scan path experiment for neutral faces filled in standardised positive (magical ideation, MI) and negative (physical anhedonia, PA) schizotypy scales. We grouped individuals according to their median scale scores into four groups; either they had high (hiMI–hiPA) or low (loMI–loPA) scores in both scales, or they were only high in one or the other scale (hiMI–loPA, loMI–hiPA). Results for classic visual scan path parameters, such as number of fixations, saccade latencies, total scan path length or saccade amplitude per image did not show differences between the four groups. However, subjects in the hiMI–hiPA group depicted the most pronounced left-face preference for the first saccade, while subjects in the loMI–loPA showed the least left-face preference. Subsequent analysis indicated that high scorers on MI but not PA accounted for a pronounced left-face preference. These findings support a leftward hemispacial bias and, by inference, a right hemispacial inattention as a function of positive psychotic-like thought in normal individuals. This study would also suggest that earlier reported right-face preferences in patients resulted from medication or related secondary side-effects.

[Supported by the British Academy (SG-38465).]

◆ **Affective impressions and recognition performances for upright and inverted faces**

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It has been suggested that affective impressions can generally be summarised as three factors (activity, potency, and evaluation) by using the semantic differential method [Osgood et al, 1957 *The Measurement of Meaning* (Urbana and Chicago, IL: University of Illinois Press) pp 71–75]. In this study, we considered the effect of impression factors on recognition of inverted faces, focusing on the specific influences of the evaluation factor. It has been reported that people have difficulty in recognising inverted faces (eg Yin, 1969 *Journal of Experimental Psychology* **81** 141–145). We assumed that, when faces are inverted, the impression judgment would also be more difficult, especially on evaluation, which is based on affective or subjective judgment. At first, we measured various impressions of inverted faces and compared them to those of upright faces (Sakuta and Gyoba, 2003 *Tohoku Psychologica Folia* **62** 75–85). As a result, it was shown that most of the impressions of the inverted faces were weakened and the factor scores moved toward zero, which is assumed to indicate neutral property of the affective impression. In particular, the impressions related to evaluation were largely weakened in the inverted faces. Then, we also examined recognition performances on the inverted faces and compared them to the recognition data for the upright faces (Sakuta and Gyoba, loco cit.). When the faces were inverted, the recognition performances were significantly decreased, especially in the faces with low potency or low evaluation. These results have been discussed in terms of components or configural information processing of face recognition. Carey and Diamond (1977 *Science* **195** 312–314) suggested that the face inversion effect is caused by a disruption of encoding the configural information. According to this view, it is highly likely that facial impressions related to evaluation are mainly based on the configural information, rather than the component information.

◆ **Others-based motion: Stabilising ambiguous motion**

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In two experiments, we examined whether the gaze of others had effects on the perceived direction of motion of observers. In the first experiment, we used a pictorial face with either a static gaze at the centre or a dynamic gaze shifting from the centre to left or right. A luminance sinusoidal grating having its phase shifted by 150°, 160°, 170°, 180°, 190°, 200°, or 210° every 200 ms was presented across a screen; shift by 180° indicates that no net motion signal is at work. Slightly after the initiation of the phase shift of the grating, the eyeballs in the face started smoothly moving. After the gaze shift had finished, the stimuli were replaced with a grey blank field having a fixation symbol only. Observers were asked to observe the stimuli, maintaining their fixation on the designated symbol lying between the face and the grating, and to judge the perceived motion direction. The results showed that judgment was biased towards the dynamic gaze direction. In the second experiment, in which we eliminated the face except the eyeballs from stimuli, such a bias was not observed. This latter result indicates that the outcome in experiment 1 was not due to motion capture between the eyeballs and phase shift of grating. The results suggest that the human visual system is endowed with a function that can extract meaningful information from dynamic shift of the gaze of others.

LIGHTNESS, BRIGHTNESS, AND CONTRAST 2◆ **Masking nonlinearities emerge from local-linear independent component analysis (ICA)**

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A number of experimental results show the following linear and nonlinear facts about the early pattern analysers in V1. (i) The linear receptive fields of the sensors are narrow band-pass functions organised in a log-polar wavelet-like way. (ii) Auto-masking: contrast incremental thresholds of sensors tuned to specific frequency bands increase with the amplitude of the stimulus. This is equivalent to saying that the sensitivity of the mechanisms decreases with the contrast of the stimulus, or that the response of the mechanisms is a saturating nonlinearity. (iii) Cross-masking or Gain Control I, General behaviour: the sensitivity of a particular sensor to its optimal stimulus decreases when this stimulus is superimposed on a high-contrast background of different frequency content. This effect increases with the contrast of the background. (iv) Cross-masking or Gain Control II, Relative influence between frequencies: the above effect (or perceptual interaction between frequencies) decreases as the distance between the frequencies increases. It has been argued that the aim of the nonlinearities in the visual mechanisms may be removing the relations between the coefficients of the signal after global linear ICA-like stages (Schwartz and Simoncelli, 2001 *Nature Neuroscience* 4 819–825); specifically, that the above strategy, ie removing the bow-tie like dependences between wavelet coefficients, was appropriate to obtain the parameters of a particular nonlinearity (the divisive normalisation) that reproduces masking effects. Here, we present a different result that supports the same efficient encoding hypothesis: instead of assuming a particular functional form for the nonlinearity (eg divisive normalisation), we show that when using a novel local-to-global nonlinear ICA, masking-like behaviour is reproduced as well. This result is an additional indication that Barlow's efficient encoding hypothesis (with no additional constraint) may explain not only the shape of receptive fields of V1 sensors but also their nonlinear behaviour.

[Supported by projects TIC2003-01504 (CICYT-FEDER), Grupos04-08 (GV), and the Program DN 8644.]

◆ **BOLD responses to luminance defined figure – ground discriminations**

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Figure–ground segregation is a crucial early step in visual scene analysis. We measured the BOLD response to checkerboard stimuli of varied contrast to investigate the cortical correlates of contour-based segregation. BOLD responses to contrast reversals of checkerboards were compared with both the response to 'full field' flicker of the same frequency and the response to a homogeneous stationary grey field. The contrast of the checkerboard (and between the two states of the homogeneous field) varied between 100% and 1.25%. Seven cortical areas (V1, V2v, V2d, VP, V3, V3a, MT) were identified for each of the nine observers in separate experiments. For each observer, two regions of interest (ROIs) were defined in each of these cortical areas: one in the central, the second in the peripheral visual field. The BOLD response as a function of stimulus contrast was measured in each ROI. BOLD amplitudes increase rather linearly with the logarithm of stimulus contrast, but at different positions (ROIs) for the homogeneous versus checkerboard stimuli. Amplitudes are highest for checkerboards near the centre of the visual field in V1, decreasing in higher areas. The highest signal change for the homogeneous field stimuli, on the other hand, occurs in the peripheral visual-field representation, partially outside the area stimulated. Surprisingly, stimulus contrast does not markedly influence the BOLD signal for the homogeneous stimuli at the central ROI nor for the checkerboard stimuli at the periphery. The peripheral representation even shows a negative BOLD signal when checkerboard stimuli and homogeneous field stimuli of high contrast are compared, mimicking a long-range inhibition. Thus, the exact form of the transducer function relating contrast to cortical BOLD response depends strongly on the position in the visual field, on the type of baseline used for comparison, and on the cortical area investigated.

◆ **Does the brain generate representations of smooth brightness gradients? A novel account for Mach bands, Chevreul's illusion, and a variant of the Ehrenstein disk**

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Sasaki and Watanabe (2004 *Proceedings of the National Academy of Sciences of the USA* 52 18251–18256) provided evidence that surface representations are generated in V1. Given the observation

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that lightness constancy is also observed in V1 (MacEvoy and Paradiso, 2001 *Proceedings of National Academy of Sciences of the USA* **101** 8827–8831), these findings can be interpreted such that surface representations do not depend on, for example, illumination gradients or specular highlights (since lightness constancy is preserved in the presence of specular highlights—see Todd et al, 2004 *Psychological Science* **15** 333–339). Accordingly, we argue that surface representations in general do not contain smooth luminance gradients, since it is a priori not clear whether such gradients would interfere with, or aid, downstream processes for object recognition. However, because we know from introspection that smooth luminance gradients are not lost to perception, we furthermore argue that gradients are explicitly represented in V1, in addition to surface representations. Here, we present a neuronal architecture, the gradient system, which clarifies how spatially accurate gradient representations can be obtained by relying only on high-resolution (ie foveal) retinal responses. Although the gradient system was designed and optimised for segregating and generating representations of luminance gradients with real-world images, it quantitatively predicts many psychophysical data on the perceived strength of Mach bands as a function of, for example, the spatial frequency and blur of a trapezoidal luminance profile (Ross et al, 1989 *Vision Research* **29** 699–715), or an adjacently placed stimulus (Ratliff et al, 1983 *Proceedings of National Academy of Sciences of the USA* **80** 4554–4558). The gradient system furthermore predicts that Chevreul's illusion is perceived as a consequence of an 'erroneously' triggered gradient representation, and it also accounts for a modified Ehrenstein disk. Given the successful prediction of those data, and the capability of real-world image processing without changing parameter values, the gradient system strongly favours the hypothesis of explicit representations of smooth luminance gradients in the primate visual system.
[Supported by the 'Juan de la Cierva' grant from the Spanish government.]

◆ **Signal-to-noise ratio as a crucial determinant of vertical symmetry detection**

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Two experiments were conducted to test the hypothesis that the perception of noisy symmetry is crucially determined by signal-to-noise ratio. The number of dots (n) in dot patterns and the signal-to-noise ratio (S/N , ie, the ratio of the number of symmetry pairs S and the number of noise dots N) were varied systematically. Participants had to discriminate symmetric patterns from random patterns, and d 's were calculated from the data. In experiment 1, pattern size varied to maintain a constant dot density across all conditions. The results comply with the hypothesis (ie same d 's for same S/N values, even though n varies)—except for the highest level of n (384 dots), which was probably due to the eccentricity of the implicit pattern contour. In experiment 2, dot density varied to maintain a constant pattern size across all conditions. This time, the participants' criterion varied but the d 's did not, which again complies with the hypothesis. Hence, experiments 1 and 2 both suggest that the S/N ratio and, for a part, pattern size determine the detectability of vertical symmetry, whereas numerosity and dot density do not.

◆ **Flash-induced perceptual fading: Dependence on colour and shape similarity**

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We investigated the effects of perceptual grouping by colour and shape similarity on flash-induced perceptual fading. This flash-induced fading effect (Kanai et al, 2003 *Journal of Cognitive Neuroscience* **15** 664–672) is considered as a time-locked variant of the Troxler effect. In the original experiment by Kanai, a short circular flash surrounding an object in the peripheral visual field causes the object to temporarily disappear from visual awareness. In the present study, two objects (which could either be similar or different both in colour and in shape) were presented at an eccentricity of 2.6 deg from a fixation cross. After 2 s, a short flash (40 ms) was presented around one of the objects. The two objects remained on the screen for 2.5 s after the flash. Participants were instructed to report which objects disappeared from awareness for a short period after the flash. Significant effects of both colour similarity and shape similarity were found. For colour as well as for shape the percentage of mutual disappearance was higher in trials containing similar objects as compared to those containing dissimilar objects. The results suggest that the flash-induced perceptual fading effect is influenced by grouping by colour and shape similarity.

[Supported by NWO grant.]

- ◆ **Illusory contours due to the depiction of apparent causal agents and their projected shadows**
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Illusory contours are also described as 'experimental hallucinations', given that physically non-existent objects are grasped at the reality level of perception. Among the recent varieties, one must include the 'causality illusory contours' (Bonaiuto et al, 1988 *Rassegna di Psicologia* **5** 73–79; 1991 *Perception* **20** 243–252), where hallucinatory objects appear if we depict groups of people acting in a coordinated manner on areas of the field. An oldest known process results from depictions of chiaroscuro effects, aiming to represent solid wholes illuminated slantwise (letters, numbers, or other objects: Coren, 1972 *Psychological Review* **79** 359–367). However, the psychological literature did not have examples of analogous phenomena obtained by depicting 'projected shadows': shadows not belonging to the highlighted objects but projected by other bodies, and able to reveal presences otherwise not distinguishable. Some of my drawings depict groups of hurdle-race runners: their shadows are coordinated and systematically shaped as if there really were barriers in front of the runners, or behind them. These barriers stand out quite strongly although they are not actually drawn, and thus act as a fairly new type of illusory contour situation. I have obtained other similar figures, together with further evidence of the causal role of the figures 'responsible' for the shadows. In fact, if just the textures consisting of black elements (as the 'shadows') are presented, the average subjective clarity of the illusory objects, tested with eleven-point evaluation scales, drops sharply. If the actors are visible and maintain the same graphic density, but do not have coherent and meaningful relations with the shadows (because they are upside-down or fragmented), the illusory contour clarity again falls sharply. I present several examples of these experimental demonstrations, together with diagrams illustrating the collected data, and a discussion of the relevant mechanisms.

- ◆ **Does surround size matter in contrast-gain control?**
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When a texture patch is embedded in a similar texture surround, the contrast of the centre patch typically appears to decrease. The apparent contrast reduction is known to increase monotonically (and saturate at some point) as a function of the surround size. Intuitively, this is straightforward: the bigger the suppressive surround, the bigger the effect. Typically, this has been explained by assuming a spatially extended contrast-gain control mechanism that incorporates some simple weighting function for spatial pooling. Currently, however, there are few systematic empirical studies about properties of the weighting function. We measured the apparent contrast of a circular (0.8 deg diameter) sinusoidal centre grating patch (vertical, spatial frequency = 3 cycles deg⁻¹, contrast = 0.15) in the presence of a similar but higher contrast surround (contrast = 0.3) separated by a 12-min-of-arc-wide unmodulated gap in most conditions. Three experiments were performed: (1) the diameter of the surround was varied from 1 deg to 16 deg; (2) the unmodulated gap was extended from 1 to 15 deg, holding the surround outer diameter constant at 16 deg; and (3) the gap was expanded from 12 min of arc to 15 deg, holding the annulus width constant at 1 deg. As expected, suppression increased and saturated with the expanding surround. Suppression decreased as the gap increased and surround width decreased in experiment 2. Surprisingly, holding the annulus width constant while increasing gap size in experiment 3 yielded a function virtually identical to that in experiment 2. We demonstrate that these results, while not intuitive, can be explained by gain control models that integrate surround contrast using a Gaussian-like weighting function over space.

- ◆ **The effect of glare on simple reaction times**
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We investigated the effect of glare on reaction times (RTs) to achromatic sinusoidal gratings, for a variety of spatial frequencies and contrasts. Stimuli were generated on a PC and displayed on a CRT monitor through a video attenuator to achieve higher contrast resolution. Glare was generated by using an incandescent lamp located 10 deg away from the line of sight. Horizontal gratings were presented in a circular patch subtending 6.77 deg, with a mean luminance of 0.142 cd m⁻². Viewing distance was 1.5 m. The experiment was performed for spatial frequencies of 1, 2, 4, and 8 cycles deg⁻¹ and for a wide contrast range. Two levels of glare were used in addition to the no-glare condition: 15 and 60 lx measured between the two eyes. The experiment was performed in blocks containing all contrast values for each spatial frequency and glare level.

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Thirty measurements were carried out for each contrast to determine the average RTs. The stimuli were presented for 340 ms, with an inter-trial time randomly varying between 1000 and 3000 ms. During this time, the subject had to report, by pressing a mouse button, whether the stimulus had appeared. RTs shorter than 100 ms and longer than 2000 ms were discarded. Results show that RTs increase with decreasing contrast for all conditions. When RTs are plotted as a function of the inverse of contrast, they present a linear relationship. Interestingly, for all conditions, glare produces an increase of the slope of these lines, which means that, in presence of glare, RTs increase more rapidly with decreasing contrast.

◆ **Does brightness sum? An axiomatic psychophysical approach**

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Whether, and the degree to which, brightness sums over the two eyes has remained controversial, contrary to loudness summation, ever since Fechner proclaimed that it did not sum. The well-known Fechner's paradox of brightness perception involves stimulus conditions in which less intense signals produce brightness percepts that are greater than those of some more intense signals. Yet, outside of those stimulus bounds and depending on experimental conditions, brightness perception has been found to be anywhere from an average of signal inputs to the two eyes to a perfect summation of those signals. Recently, Luce (2002 *Psychological Review* 109 520–532; 2004 *Psychological Review* 111 446–454) proposed a psychophysical theory concerning the global percept of subjective intensity in which a psychophysical function ψ maps pairs of physical intensities onto the positive real numbers and represents, in an explicit mathematical way, subjective summation and a form of ratio production. The theory has been well sustained in the auditory domain (Steingrimsson and Luce, in press *Journal of Mathematical Psychology*). Here, we show that under given stimulus conditions, the necessary and sufficient Thomsen condition is met ensuring that brightness perception has the quasi-additive form $\psi(x, u) = h^{-1}[f(x) + g(u)]$, where (x, u) represents the joint presentation of light intensities x and u to the left and the right eye, respectively. Additionally, the necessary and sufficient conditions have been formulated and empirically verified that give rise to the specific additive representation $\psi(x, u) = \psi(x, 0) + \psi(0, u) + \delta\psi(x, 0)\psi(0, u)$, $\delta \geq 0$, where the data are consistent with $\delta = 0$. This representation, with $\delta = 0$, was previously sustained in binaural loudness. Current data show that binocular brightness sums in a fashion consistent with a particular additive representation, one that is identical to that for binaural loudness summation.

◆ **Estimations of light-source direction depend critically on material BRDFs**

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We investigated in what way the bidirectional reflectance distribution function (BRDF) of an object influences the perception of light-source direction. Previously, we have shown that participants make consistent errors in their judgments of whether the light-source direction on materials with different BRDFs is the same or different. Here, we investigate the nature of such errors. We rendered spheres, using four physics-based BRDFs representing matte, glossy, pitted, and velvety surfaces under collimated illumination from various directions. Participants were asked to set the illumination direction of an interactively rendered matte test sphere until they were satisfied that it equalled that of the illumination direction of a reference sphere of one of the four BRDFs. The results show that participants estimate the light-source direction on the velvety surface to be very similar to the light-source direction on the matte surface. In these two materials, the location of the shadow edge is similar under the same illumination, although the shading is completely different. Participants consistently underestimate the angle between the light-source direction and the viewing direction on the glossy compared to the matte sphere by a factor of 0.6. On glossy spheres there is a strong highlight. If participants (falsely) base their judgments of the light-source direction solely on the location of the highlight, we would predict the underestimation to be 0.56. Surprisingly, participants also consistently underestimate the angle between the light-source direction and the viewing direction on the pitted surface compared with the matte surface. In this case, the location of the rather blurred 'highlight' on the surface cannot fully explain the participants' settings. We conclude that participants use the position and strength of the highlight and the geometry of the shadow edge to make their judgments.

[Supported by the Netherlands Organisation for Scientific Research (NWO) and a High Potentials Grant from Utrecht University.]

◆ **Factors of metallic appearance perception analysed by subjective evaluation**

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Seeing object surfaces in a visual scene, we can easily distinguish surfaces having metallic appearance from those having other appearances. One of the main factors producing metallic appearance is known to be metallic lustre, which depends mainly on specular reflectance of the surface, the highlight, luminous contrast, and so on. Such physical properties are also used as cues for the reproduction of metallic surfaces in computer graphics, for example, in the Cook–Torrance lighting model. However, these are the physical properties causing the sensation of metallic surface, but the perceptual properties and the visual mechanisms producing them are not yet well-known. We examined the relationships between the strength of metallic-lustre perception and the physical properties of light reflected from various surfaces. We made stimulus images by taking digital pictures of ten metallic sheets and one piece of gray paper, which had different properties of surface reflection. Subjects observed two of them simultaneously on a colour CRT display and judged which appeared more metallic by the method of alternative forced-choice paired comparison. By applying Thurston's method to the results, we obtained rating scores for the evaluation of metallic appearance. We found that the largest fluctuation range of the rate of luminous contrast over the surface, in other words, the largest range of the second derivative of low-spatial-frequency components of the luminous modulation, was highly correlated with the resulting rating scores. This suggests that we perceive metallic quality sensations by integrating spatially the change of luminous contrast over the surface.

[Supported in part by a Grant-in-Aid for the 21st Century COE Program 'Design of Artificial Environments on the Basis of Human Sensitivity', Kyushu University, Japan.]

◆ **Retinal and cortical patterns of spatial anisotropy in simple contrast-detection tasks**

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We explored retinal (naso/temporal) and cortical (left/right) patterns of anisotropy of visual contrast sensitivity under selective conditions that allowed us to study the relative contribution of the magnocellular/parvocellular and rod/cone pathways. Normal participants were selected in two age groups: children ($N = 97$) and adults ($N = 99$; $N = 48$; $N = 81$; $N = 30$; and $N = 15$ for different test configurations spanning at least 17 visual locations). Magnocellular-biased test stimuli were sinusoidal gratings of $0.25 \text{ cycle deg}^{-1}$, vertically oriented and undergoing 25 Hz counterphase flicker. Contrast sensitivity tasks with a significant parvocellular contribution used grating stimuli at $3.5 \text{ cycles deg}^{-1}$ and 0 Hz temporal frequency. In this case, both photopic (mean background luminance, 51 cd m^{-2}) and mesopic (0.8 cd m^{-2}) conditions were tested. A prominent pattern of anisotropy was found when test conditions favoured the contribution of the parvocellular system. In this case, a significant nasotemporal asymmetry (better performance in the temporal field) was found both under photopic and mesopic conditions. A significant cortical hemifield effect (the left field being significantly better than the right visual field) was also found. A more subtle but very significant perceptual disadvantage of the superotemporal visual field was found when performance was assessed in a way that probed the magnocellular system. The nasotemporal and left/right patterns of anisotropy obtained with the more parvo-biased stimulus was found to be consistent with the known retinal asymmetries of photoreceptor and ganglion cell distribution. The surprising left/right asymmetry observed for this task suggests an additional cortical origin for anisotropies in contrast-sensitivity tasks. The pattern of magnocellular disadvantage cannot be explained simply in terms of cell density differences and is probably related to nasotemporal size differences of dendritic arborisations at the retinal ganglion cell level, as well as to electrophysiological anisotropies.

[Supported by Projecto Bial 15/02; FCT/POCTI/46438/2002; FCT/SFRH/BD/11828/2003.]

◆ **SLC with static and dynamic backgrounds**

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Surfaces covering the majority of a visual scene qualify for the role of an anchor—the value used by the visual system to compute the lightness of all other surfaces in the scene. In natural scenes, such surfaces can be a composition of different shades (eg sky, water). However, the visual system often treats such surfaces as having a single shade for lightness computations. In three

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experiments we used surfaces composed of gray shades as a background in a simultaneous lightness contrast display (SLC). We investigated the articulation of the background, and the duration of the stimuli. The observers' task was to judge the lightness of a comparison patch relative to a target patch in SLC, either by adjusting the comparison patch (experiments 1 and 2) or in a forced-choice task (experiment 3). In experiment 1, we placed the target patch on either uniform backgrounds—static, spatially filtered noise backgrounds; or dynamic noise backgrounds. Both types of noise background strengthened the SLC illusion. The effect was measurable as increased lightness of the target patch, indicating stronger articulation. This articulation effect was further tested in experiment 2 by increasing the spatial frequency of the noise. Although we found the usual SLC trends for the manipulation of target and background luminance levels, the size of the illusion was reduced in comparison to experiment 1. The spatial frequency did not simply change the articulation but also enhanced constancy. Finally, we manipulated the stimulus duration in experiment 3. We found that the illusion was weaker for short duration (320 ms) than for long durations (960 ms or more). This was the case for static and dynamic backgrounds, suggesting that the number of different frames does not play a role in lightness computations.

◆ **Relative effect of luminance ratio and texture on appearance of transparency**

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We experimentally reconfirmed the appearance of transparency from the viewpoint of the relation between figural features determined by Adelson and Anandan (1990, paper presented at the AAAI-90 Workshop on Qualitative Vision; quoted from Anderson, 1997), the categorisation of appearance by Anderson (1997 *Perception* 26 419–453), and the attaching of texture, adapting them mainly to the figure adopted by Gerbino et al (1990 *Journal of Experimental Psychology: Human Perception and Performance* 16 3–20). This figure has eight partitions, four X junctions, and four different-luminance parts. α (refraction rate : luminance factor), absolute luminance in each part, and contrast polarity were controlled with and without dots. The task of the seven observers was to indicate their impression of the depth position of the inner field in each figure and to respond to the receding or advancing of individual parts by a category scale. When three contrast polarities were set, the result of the oral response (figural unity and degree of depth impression) can be summarised as follows: the modes of Anderson's category were adaptable even to the Gerbino pattern, while the bistable mode included more complicated features, tri-layer and others. Under five levels of α and two conditions of luminance difference (constant and variable) between the outer part and the inner part of each quarter, when single-reversing polarity was retained, the unique mode appeared in both conditions, but the bistable mode could be seen only in the variable condition and depended on α level. Furthermore, only the luminance dots different from those of any surfaces produced change in depth. The above suggests that not only α and contrast polarity but also luminance difference bring about various changes in the appearance of transparency, and that texture, as long as it is regarded as a part of the other surface, has less effect.

◆ **Spatial summation and inhibition in human visual contrast processing**

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We measured the perceived contrast of a grating patch in various conditions to tackle the mechanisms of centre–surround interactions in visual contrast processing. In the first experiment we measured the perceived contrast of a circular sinusoidal grating patch (spatial frequency 4 cycles deg⁻¹) while varying its diameter (0.25–8 deg) and contrast (0.025–0.4). In the second experiment, the perceived contrast of a centre patch (diameter 1 deg, contrast 0.1) was measured while varying the contrast of a surround (diameter 4 deg, contrast 0.0–0.4). Perceived contrast was always measured by matching the contrast of a 1 deg comparison stimulus to that of the target. In the first experiment, at low contrasts, increasing the stimulus size caused the perceived contrast first to increase and then to reach a plateau. At higher contrasts, initial increase in perceived contrast was always followed by a subsequent decrease. We interpret the increase in perceived contrast with increasing stimulus size as spatial summation and the subsequent decrease as spatial inhibition. In the second experiment, the perceived centre contrast decreased as the surround contrast was increased, with one exception: when surround contrast was equal

to the centre contrast (the stimulus was a large uniform contrast patch), the effect of the surround was greatly reduced, even compared to the condition where the surround contrast was only half of the centre contrast. We conclude that perceived contrast is influenced by both a summation and an inhibition process, and that the balance between summation and inhibition in human visual contrast processing is strongly contrast-dependent. Further, the inhibition acts more strongly on a separate centre than it does within a uniform contrast stimulus.

◆ **Polarity specific reduction of the brightness of Gaussian blobs in the presence of flankers**
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Sharp luminance borders can trigger brightness spreading along the adjacent surface. Some V1 simple and complex cells are known to respond to the brightness of an unmodulated luminance field much larger than the classical receptive field of the cell: the response of the cells correlates negatively with the temporally modulated luminance border contrast. These cells could either actively carry the brightness signal mediated by simple cells responding to the luminance border, or the cells might have a large extra classical receptive field directly activated by the far away luminance border. Instead of sharp-edged luminance patches, we measured the effects of Gabor flankers, mimicking odd- and even-symmetric type of V1 simple cells, on the brightness of a circular Gaussian luminance blob (flanker spatial frequency = 1 cycle deg⁻¹, SD = 0.3/1 deg, contrast = 1; luminance blob SD = 0.5 deg, contrast = 0.1). The blobs were either incremental or decremental. The flankers had either the same polarity as the luminance blob or opposite to it. The distance between the blob and the flanker centre was 2 deg. The brightness of the blobs was measured with a 2IFC staircase method. In all conditions, the flankers reduced the brightness of the luminance blob (incremental and decremental); we never saw enhancement of brightness. Surprisingly, the strongest reduction (20%–30%) was observed with even-symmetric flankers of opposite polarity to that of the luminance blob. The odd-symmetric flankers and the even-symmetric flankers of same polarity as the blob reduced the brightness significantly less. The reduction was more pronounced for incremental blobs than for decremental blobs. The results imply that brightness processing is more complicated than has been assumed and the conclusions are not straightforward. However, the mechanism we measured is phase and polarity specific and the effects we observe resemble brightness assimilation.

◆ **A surround-induction function unifying assimilation and contrast in a computational model of colour appearance**

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Since the colour perceived from an image point depends on its surround and observing conditions, any visual task computed on a digital image should be performed on the corresponding perceived image. Building perceived colour images requires computation of an image representation in which the effects of induction mechanisms of the human visual system are included in the chromaticity of the image points. Assimilation and contrast mechanisms induce colour changes depending on spatial-frequency properties of images, which depend on the image content in itself and on observer's parameters. These two induction mechanisms can be simulated by a unified computational model based on a wavelet framework. We propose a surround-induction function as a key in the construction of the perceived image. The surround-induction function combined with multiresolution decomposition makes it possible to recover a modified colour image. The parameters of this perceptual function are given by the image content and the observer's conditions. So far we have focused on assimilation and contrast effects but the model possesses interesting properties allowing a general unified approach including other induction mechanisms. The perceived images can be useful for representing colour appearance in digital images for colour assessment or semantic image analysis.

◆ **Illuminance flow over Utrecht oranges**

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In many scenes, the light field is similar at different positions in the scene because it comes from a single distant source. This induces similar structures in the illuminance of objects at different positions in the scene. In this respect, the illuminance flow (the 'flow of light over the surface') can be compared to optic flow: the optic flow of stationary objects is due to a common motion, namely the motion of the observer, and the illuminance flow is due to a single light source. Light vectors can be decomposed into normal and tangential components with respect to a surface. Lambertian 'shading' of the surface depends upon the normal component only.

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The surface illuminance flow is defined as the vector field of directions of the tangential light vector components. Texture gradients over rough objects depend upon the tangential components and reveal the illuminance flow. We studied illuminance flow over rough spherical objects (allowing sampling of a complete hemisphere of viewing directions in one image), such as an orange, rough candles, a golf ball, and objects painted matte white. The objects were photographed under collimated, hemispherical diffuse, and Ganzfeld illumination (similar to direct sunlight, an overcast sky, and a polar whiteout, respectively). We named the image collection the 'Utrecht oranges database'. Using the finding that patches of roughly uniform texture reveal the local orientation of the illumination, we were able to map the global structure of the illuminance flow. We found that it is a robust indicator of the light field and an important entity for many subsequent inferences from the image such as shape from shading.

[Supported by the Netherlands Organisation for Scientific Research (NWO).]

◆ **'Suppressed-by-contrast' cells in the lateral geniculate nucleus of the macaque**

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Rodieck (1967 *Science* **157** 90–92) described a rarely encountered class of cat retinal ganglion cell that was 'suppressed-by-contrast'—a cell's response to any effective visual stimulus was a reduction in the maintained discharge. In fortuitous extracellular recordings from the lateral geniculate nucleus (LGN) of macaque we encountered 5 such cells, all of which were located at the transition from parvocellular (P) to magnocellular (M) layers; their receptive fields were parafoveal, in positions consistent with those of P-cells and M-cells found in the same penetrations. Each of these cells responded to any stimulus with a reduction in the high (average $\sim 45 \text{ imp s}^{-1}$) maintained discharge rate to a monitor on which the screen was refreshed at 200 Hz (at a refresh rate of 60 Hz the maintained discharge was substantially suppressed). These responses were independent of contrast polarity, and cone-isolating stimuli revealed inputs from all cone types. The receptive fields were small and, like those of nearby P-cells and M-cells, were able to resolve drifting gratings of at least $7 \text{ cycles deg}^{-1}$; temporally modulated uniform fields were as effective as drifting gratings. Counterphase flickering gratings elicited responses modulated weakly at twice the frequency of stimulation; no null spatial phase could be found at any spatial frequency. Temporal-frequency tuning curves were bandpass: for uniform fields, 25 Hz was the most effective modulation frequency, but the neurons could resolve at least 50 Hz. Flashed stimuli brought about transient reductions in discharge rate. Neurons with these properties have not previously been found in the primate thalamic pathway. Their presence in LGN suggests that they might have some relatively direct role in perception.

[Supported by grants EY13079 and EY04440.]

MULTISENSORY INTEGRATION 2

◆ **Comparison of audiovisual temporal synchrony perception with visual motion perception suggests a general feature-matching model for cross-attribute binding**

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Temporal synchrony is a critical cue for binding audiovisual information. To understand the sensory mechanism responsible for audiovisual synchrony detection, we compared its properties with those of visual motion detection, since extensive investigation has been made of this computationally analogous task (either task bears the correspondence problem). It is suggested that at least two mechanisms contribute to visual motion detection. One is low-level 'motion-energy computation' that is fast and pre-attentive, while the other is high-level 'salient-feature tracking' that is slow and post-attentive. Our study suggests that the audiovisual synchrony detection is similar to 'salient-feature tracking' in that it is slow [since audiovisual synchrony is detectable only for temporally sparse signals such as repetitive pulse train lower than 4 Hz: reported partly by Fujisaki and Nishida (in press *Experimental Brain Research*)], and post-attentive [since visual search for an audiovisually synchronous target is serial, and precueing about the location or feature of synchronous signals improves synchrony detection: reported partly by Koene et al (2005, paper presented at Vision Sciences Society Meeting)]. This resemblance is unlikely to be coincidental, considering that cross-attribute apparent motion requires 'feature tracking', and that temporal-synchrony perception between different visual attributes (eg colour and motion) is also slow and post-attentive (eg Nishida and Johnston, 2002 *Current Biology* **12** 359–368). These results suggest that similar high-level salient feature-based mechanisms are generally responsible for signal

matching between separate sensory channels, including audiovisual synchrony detection. To be more specific, the representation used for cross-attribute bindings is attribute-independent markers of salient features, and these markers are extracted from low-level signals through stimulus-driven segregation processes or top-down attention.

◆ **Auditory salience defined by frequency difference captures visual timing**

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In the perceived world, information from different modalities is integrated together. However, it is not easy to decide correctly which information in one modality should be integrated with which one in the other modality, because the world consists of too many objects and events. The cues and the mechanisms for correct integration of information from different modalities remain unclear. In this study, the effect of salience of the auditory information defined by frequency difference between element sounds in a tonal sequence on judgment of synchrony between auditory and visual stimulus was investigated. In the experiment, point light on a CRT display was presented simultaneously with the 2nd or 3rd element sound in an auditory sequence which consisted of four brief sine waves. Subjects were required to respond which element (2nd or 3rd) in the auditory sequence was heard when the point light was presented. Subjects could judge correctly which auditory element was heard at the same time as the point light was seen when the frequencies of the elements of the auditory sequence were the same, although when the frequencies of the 2nd and 3rd element of the auditory sequence were different from other elements of the sequence, the auditory element with different frequency captured the point light 'timing', and subjects could not judge the correct auditory element synchronised with point light. These results suggest that the integration of information from different modalities might not be achieved by static cues or mechanisms such as mere timing between modalities, but may be achieved by some dynamic manner depending on the structure of information in one modality.

◆ **Representation of visual – auditory integration effectiveness in event-related potentials**

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Event-related potential mismatch is widely used in the investigations of heterosensory integration. This index makes it possible to determine spatial and temporal patterns of the integrative processes (eg Giard and Peronnet, 1999 *Journal of Cognitive Neuroscience* **11** 473–490). Our aim was to determine how mismatch amplitude depends on heterosensory integration effectiveness. We used natural images having both the visual and auditory expressions. The visual and auditory stimuli were presented either unimodally or jointly. Mask parameters (superposition of all stimuli) were previously selected for each subject so that the identification probability for the unimodal stimuli was 10%–15% above random guessing. The evoked potentials were recorded for unimodal (EP_v and EP_a) and bimodal (EP_b) stimulation. Then the mismatches were calculated for each registration point [$EP_b - (EP_v + EP_a)$] and their verification was computed. Moreover, each experiment yielded identification probability values for visual (P_v), auditory (P_a), and bimodal (P_b) images. Then we calculated a theoretical identification probability for the bimodal images ($P = P_v + P_a - P_v P_a$) and rated the difference between the theoretical and the experimental probabilities ($\Delta P = P_{bt} - P_b$): the smaller this difference, the higher is the subject's integration effectiveness. We compared the integration effectiveness with the mismatch amplitude in different areas. We found that the most pronounced mismatch appears in 150 ms and has a duration of 60–80 ms. The mismatch was higher in the specific areas (especially in visual) with subjects who had relatively poor integration effectiveness. On the contrary, it was higher in nonspecific areas with subjects who had relatively high integration effectiveness. The highest correlation between the mismatch amplitude and the integration effectiveness takes place in the left frontal cortex.

◆ **Change of the temporal-order judgment of sounds depending on the direction of concurrent self-motion perception**

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We examined the effect of self-motion perception on the perceived temporal order of auditory events. Our previous study revealed that the perceived temporal order of 'visual' events was

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altered depending on the direction of visually induced self-motion (Teramoto et al, 2004 *IEICE Transactions on Information and Systems* **E87-D** 1466–1476), but it was not clear whether the same phenomenon was observed with events in a non-visual modality. In experiment 1, a pair of white-noise patterns was presented at various SOAs to different ears through headphones, while large-field visual motion was continuously presented and compelled observers to perceive self-motion (yaw-axis circular vection). The results revealed that the perceived order of auditory events was modulated by the direction of visually induced self-motion in much the same way as in our previous study. In experiment 2, to reduce response bias (the observers might simply report the side on which they perceived self-motion), we used the method in which a pair of different pitched sounds was presented and observers were requested to judge which kind of sound they perceived first (high or low pitched sound), not its side (left or right). In experiment 3, to clarify whether this phenomenon was specific to ‘apparent’ self-motion or not, we examined the effect of concurrent real self-motion on the perceived temporal-order of auditory events. We discuss how the information on self-motion was used to reconstruct the temporal order of visual/auditory events in the brain.

◆ **Improvement of visual contrast sensitivity by auditory cueing signals**

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Neurophysiological and psychophysical studies have demonstrated that vision and audition can be integrated (Calvert, 2001 *Cerebral Cortex* **11** 1110–1123), yet the way they interact and the mechanisms involved are currently unknown. We studied the cross-modal interaction using a Gabor detection paradigm. Temporally primed visual signals are known to enhance contrast sensitivity in human vision (Tanaka and Sagi, 2000 *Vision Research* **40** 1089–1110). Here, a simple auditory cue (pip, 1000 Hz, duration = 30 ms) was used to examine the effect of auditory–visual interaction on contrast detection of a Gabor visual signal (exposure time = 100 ms). We found that (i) detection threshold was reduced up to 45% (facilitation effect, four subjects) when the auditory signal was presented within a window of ± 100 ms from the visual target, and (ii) there was no facilitation outside the ± 100 ms window. These results demonstrate that visual and auditory systems interact in a rapid manner within the time window of ± 100 ms of asynchrony, resulting in improvement in contrast detection, suggesting a direct connection between early levels of visual and auditory processing. Considering the findings of human MEG study that auditory signals reach the cortex more rapidly (30 ms: Pellizzone et al, 1987 *Neuroscience Letters* **82** 303–307) than visual signals (75 ms: Nakamura et al, 1997 *Cognitive Brain Research* **6** 9–22), the result suggests that auditory signals were preserved for about 145 ms [= SOA (100 ms) + initial V1 activity (75 ms) – initial A1 activity (30 ms)] in the neural system before the two signals were integrated. This auditory–visual interaction may be a basis for high-level integration such as revealed in the McGurk effect.

◆ **Contour interpolation in the dorsal visual system: Accurate grasping with Kanizsa squares**

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In agreement with the two-visual-systems hypothesis (Goodale and Milner, 1992 *Trends in Neurosciences* **15** 20–25), several investigators have found that a number of visual illusions do affect perception to a greater extent than action. These findings are in agreement with the proposal that the ventral and dorsal visual systems independently mediate visual processing for perception and object-directed action, respectively, and that the latter processes the absolute, retinally specified, metrics of the target. More recently Dyde and Milner (2002 *Experimental Brain Research* **144** 518–527) proposed that visual illusions that are largely processed in areas that precede the anatomical chiasm between the two systems should affect both perception and action. We tested this claim by measuring whether the scaling of grip aperture in grasps with Kanizsa illusory contours, a phenomenon thought to be modulated by early visual cortex (Peterhans and von der Heydt, 1989 *Journal of Neuroscience* **9** 1749–1763), is accurate. A comparison of the maximum grip apertures from grasps with 3-D, 2-D-luminance-defined, 2-D-Kanizsa, and 2-D-control stimuli revealed significantly larger apertures for the 3-D condition, but, crucially, no differences between any of the other conditions. Differences between grasps with the 3-D and 2-D stimuli could be accounted for by the additional haptic feedback available from 3-D targets. More notably, however, grasps with the Kanizsa or control stimuli were as accurate as with the luminance-defined stimuli, clearly suggesting that information about the interpolated contours

was available to the dorsal pathway. These results are in agreement with the claim that the dorsal visual system does not process only the retinally specified properties of the target, but that it can use other signals when these are generated in early visual cortex.

◆ **Consonants in the takete – maluma phenomenon: Manner and place of articulation**

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In our previous studies we evaluated phonetic–iconic congruency in the Takete–Maluma phenomenon using the naming task, choice method, and visual semantic differential scales. The results have shown that the distribution of phonemes and consonant–vowel patterns in pseudo-names of abstract visual patterns strongly depends on some physical characteristics of visual patterns (Janković and Marković, 2001 *Perception* 30 Supplement, 29). In the present study, we analysed the connection of physical characteristics of visual patterns with consonant types, considering the manner and place of articulation. Subjects were asked to produce pseudo-words corresponding to presented monochromatic abstract visual patterns. The patterns were varied according to dimensions: sharp–oval, dark–light, simple–complex, irregular–regular, and compact–disperse. By cluster analysis and multidimensional scaling procedure, the two clusters of visual patterns were extracted: taketes (sharp, dark figures) and malumas (oval, light figures), and corresponding sets of takete-like pseudo-words and maluma-like pseudo-words. The results show that, as regards the manner of articulation, takete-like pseudo-words have significantly more trill /r/, plosives /d/t/g/k/, and affricates /ts/dz/; while maluma-like pseudo-words have significantly more laterals /l/L/ and nasals /m/n/. As regards the place of articulation, takete-like pseudo-words have more velar /g/k/h/ and dental /t/ts/z/s/ consonant types. High and significant positive correlation has been detected between visual pattern dimensions oval and light with lateral consonants; and also the dimensions sharp and dark with trill, velar, and dental consonant types.

◆ **Accuracy of perception of being pointed at**

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Pointing is an important form of nonverbal communication, but little is known about its perceptual characteristics. In this study, we measured the accuracy of a person's perception of being pointed at in the situation where the person pointing (the pointer) and the perceiver (the subject) are directly facing each other. In our experiments, the pointer pointed an extended index finger at one of 15 targets positioned within a range of 6 deg to the right and left of the subject's nose. Subjects were asked to judge whether the finger was pointing at them or not (2AFC) to determine the range within which subjects feel that they are being pointed at (self-range). Average self-ranges obtained for each of the three viewing distances used (188, 288, and 388 cm) were 3.42, 3.89, and 4.18 deg. The self-range increased slightly as the viewing distance increased, but the effect was relatively small. These results indicate that pointing perception is based on the (distal) angle of the finger or hand shape rather than the pointed at (proximal) position around the subject's face, and that the critical angle is relatively independent of distance. This tendency is similar to that which has been found for gaze perception (Sato and Matsuzaki, 2001 *Perception* 30 Supplement, 34). In addition, the values of self-range for pointing are very similar to those found for gaze perception. In the present experiment, the pointer was looking at the target while she was pointing. Thus, it is possible that the performance of pointing perception was affected by gaze. To evaluate this possibility, we conducted another experiment where the pointer's eyes were closed. The obtained self-range was significantly larger when eyes were closed, regardless of the viewing distance. These results indicate the importance of gaze in pointing perception.

[Supported by the Ministry of Education, Grant-in-Aid for Scientific Research (B) to TS. YT is a JSPS post doc. fellow.]

◆ **Flash-lag anisotropy for movement in three domains**

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A flashed object presented in alignment with a moving object is seen as trailing behind the moving object. This flash-lag effect (FLE) (Nijhawan, 1994 *Nature* 370 256–257) is asymmetric and considerably stronger for movement toward the fovea than for movement away (Mateeff and Hohsbein, 1988 *Vision Research* 28 711–719). Three experiments were designed to test this

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anisotropy for movement in different domains. In experiment 1, we confirmed ‘visual–visual flash-lag’ (FLEv-v) anisotropy by asking subjects to fixate a central point on a CRT and compare the position, relative to a visual flash, of a visual target moving away from or toward the fixation point. In experiment 2, subjects moved their invisible forearm, either away from or toward a fixation point, and compared the position of a finger to that of a visual flash (motor–visual flash-lag task; FLEm-v). In experiment 3, subjects were stimulated on their invisible forearm, by a tactile stimulus moving away from or toward a fixation point. Subjects compared the location of the tactile stimulus with that of a visual flash (tactile–visual flash-lag task; FLEt-v). The subjects showed a FLEm-v anisotropy, in which finger movement toward the fovea produced a strong flash-lag effect, while movement away from the fovea produced almost no effect. Results from FLEt-v task gave evidence of a much larger anisotropy than that for FLEm-v and FLEv-v tasks. These findings show flash-lag anisotropy in three domains, revealing analogous mechanisms for spatial localisation in vision, action, and touch. These findings reinforce previous suggestions that different sensory systems, and the visual and the motor systems, function along similar principles (Sperry, 1952 *American Scientist* **40** 291–293). Bimodal neurons, eg ‘vision + action’ and ‘vision + touch’ neurons, reported by Graziano et al (1994 *Science* **266** 1054–1057) and ‘vision + action’ neurons (Gallese et al, 1996 *Brain* **119** 593–609) found in the pre-motor cortex and other parts of the brain, may mediate the interaction between domains.

TEMPORAL VISION

◆ Perceived time is not (only) time’s child

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The perception of time enjoys a peculiar status in experimental psychology and cognitive sciences: time does not have receptors and information about the timing of real events has to be conveyed by the timing at which neurons fire. For this reason some authors have argued that any perceived delay is the phenomenological counterpart of a physiological delay and have conceived time-order judgments as a window onto the physiological level of the brain (Moutoussis and Zeki, 1997 *Proceedings of the Royal Society of London, Series B* **264** 393–399). In a series of experiments that we are carrying out in our laboratory, we are aiming at demonstrating, however, that physical time is not the only factor which determines the perceived order of events. We present here a study of the effect of the configuration of visual stimuli upon perceived synchrony. We projected on a computer screen 4 wedges (circular sectors of 90°, radius 1 deg) which were placed at the edges of a virtual square (side: 5.4 deg). In one condition they were oriented such as to form the vertices of a Kanizsa square (and thus belonged to a figure); in the control condition they were oriented randomly. After 1 s of presentation 3 of them changed colour, the fourth one could change colour either before, at the same time, or after the other 3 (ISI from –210 to +210 ms). Subjects ($N = 20$) had to state whether the change was synchronous or asynchronous. Statistical analysis revealed that the interval for perceived synchrony depends on the configuration and is larger when the 4 elements belong to a figure. Our data demonstrate that perceived synchrony does not depend only on the timing of the stimuli and support the idea that experienced time does not belong to the dimension of simple neural activities.

◆ The effect of acceleration on localisation of starting and vanishing points

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Judgments of moving target position are typically displaced for both onset starting point (SP) and offset vanishing point (VP). Absolute target velocity has always been reported as a crucial factor for both mislocations (eg Hubbard, 1995 *Psychonomic Bulletin and Review* **2** 322–338; Kerzel and Gegenfurtner, 2004 *Vision Research* **44** 577–590). Five experiments are presented, aimed to test the influence of the modulation of target velocity on SP and VP. A dot moved on a 12.5 deg path: the length of the path was virtually divided into three sections and the velocity was modulated in (a) the first section (experiment 1); (b) the central section (experiment 2); and (c) the last section (experiment 3). The velocity profile could be linear (experiments 1 and 3) or sinusoidal (experiment 2). In each experiment, 5 levels of velocity modulations (ranging from 2 to 10 deg s⁻¹) were used, with 2 accelerated, 2 decelerated, and a constant velocity profile. Consistent with previous results, a backward SP displacement and a forward VP displacement were obtained: the average errors in pixels were 28.96 (SD = 43.27) for SP ($t_9 = 4.76$, $p < 0.001$) and 22.43 (SD = 21.19) for VP ($t_9 = 6.62$, $p < 0.000$). Results showed an effect of velocity modulation on VP but not on SP. A control experiment was performed, in which target constant velocity (4 levels) corresponded to the instantaneous velocity it had at VP in experiment 3. The trend of results was the same as in experiment 3, thus supporting the hypothesis that a low-level

mechanism is responsible for the forward displacement of VP, based on the local, ongoing motion trajectory and not on the representation of a higher-level structure of the motion event as a whole, as previously suggested (Verfaillie and d'Ydewalle, 1991 *Journal of Experimental Psychology: Learning, Memory, and Cognition* **17** 302–313).

◆ **Spatiotemporal dynamics of figural aftereffects and figure–ground segregation: A revised theory of simultaneous illusion and figural aftereffects of concentric circles**

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Figural aftereffects were studied by numerous researchers in the ten years after the publication by Gibson of “Adaptation of the perception of curved lines” (1937 *Psychological Review* **44** 222–244)—the temporal theory—and Kohler and Wallach’s “Figural after effects” (1944 *Proceedings of the American Philosophical Society* **88** 299–357)—the spatial theory. But the systematic experiment by Wilson (1965 *Quarterly Journal of Experimental Psychology* **17** 1–13) demonstrated that the phenomena are not produced by one factor. The phenomena are not merely the effect of the line figure, but the whole of its surrounding field. In this field, the spatial and temporal effects are not independent of each other, but act as a complex process, as in a stroboscopic movement. Considering the theory of the figural aftereffects, one might take notice of figure–ground segregation as a fundamental process of the organisation of a figure. In this research, the following two hypotheses have been selected: (a) the size of a region seen as the figure is smaller than that of the ground; (b) when a region is reversed, the figure-like property of that region turns to ground. In both propositions, the converse is true. The simultaneous illusion of concentric circles is explicable by hypothesis (a) and also the figural aftereffects are explained by (a) and (b). The observation of Takagi’s contour effect (1927 *Japanese Journal of Psychology* **2** 217–261) and also of the difference in the increment threshold between inside and outside of the contour line by Nozawa (1958 *Japanese Psychological Research* **5** 22–27) justify the application of two hypotheses of the illusion and figural aftereffects of concentric circles.

◆ **The role of represented direction of gravity force in time perception: Which is more important, physical or phenomenal direction?**

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Time interval is not only inferred from actual time passed, but also perceived by spatial distance (the kappa effect). Wada and Noguchi (2000 *IEICE HIP* **99-70** 33–38) suggested that time perception is affected by the representation of physical forces such as gravity. We examined which direction of gravity, physical or phenomenal, would influence the perceived time interval. Three targets were successively presented on a slope: the first target was displayed in a fixed position; the second target was displayed in three different positions with respect to the first one—near, middle, and far; the third target was displayed in a fixed position. The duration between the second and third targets was varied in three steps (300, 500, and 700 ms). Participants were asked to judge this duration in comparison with the duration between the first and second targets. In experiment 1, the test target cast a shadow, and was seen to proceed along the ground in 3-D space. In experiment 2, the experimental setting was very similar to experiment 1 except for the way the shadow was cast which was accompanied by the target mounted sideways. In this setting, the target seemed to rise from the ground in the 3-D space. The implications of these phenomena for time perception are discussed.

◆ **Temporal illusion called ‘kappa effect’ in event perception**

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The ‘kappa effect’ is a temporal illusion which is caused by spatial distance. The effect occurs when subjects judge the duration spanned by a series of successive stimuli along a straight line. If the temporal separation between stimuli is constant and the spatial distance is variable, the perceived temporal separation tends to increase as the spatial distance increases. We examined which representation of physical force (eg gravity) that is included in event perception would influence the kappa effect. Three circular stimuli were sequentially presented on a slope on a computer display. The first and second stimuli were successively displayed at fixed positions to show a slipping event, and the third stimulus was displayed in different positions in order to manipulate time intervals, spatial distances, and directions of traverse (slipping and climbing). Participants estimated the perceived duration between the second and third stimuli. In experiment 1, the third stimulus was presented below the first one; whereas in experiment 2, the third stimulus was the same as or above the first one in the climbing event. These experiments consistently

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demonstrated the presence of kappa effects when stimuli were perceived to traverse the slope. In experiment 1, the perceived velocity of climbing tended to be slower than that of slipping, but in experiment 2, the trend was opposite. These results suggest that temporal perception is affected by ecological events coping appropriately with given stimuli, and confirm the validity of the hypothesis.

◆ **The screen edge as an occluder: Expectation of existence constancy during spatiotemporally discontinuous motion**

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When an object gradually moves behind another object in the visual scene (occlusion), the occluded object is perceived as continuing to exist (existence constancy) and to continue moving in the same direction and with the same speed (spatiotemporal continuity). However, when the occluder is the edge of a television screen, the object is not expected to reappear outside of the screen. Instead, conventional film technique would relocate the object to the opposite screen edge as a 'cut' is made to an adjacent camera, violating the normal expectation of spatiotemporal continuity during occlusion. The goal of this study was to investigate whether viewers expect the object to continue to exist after leaving the screen by showing preference for gradual occlusion over sudden disappearance. This would suggest a dissociation of existence constancy and spatiotemporal continuity. Subjects were required to respond to a binary-decision reaction time (RT) cue overlaid on an object as it moved across the screen, relocating from one edge to the other on exit. The RT task was used to estimate visual attention. When the object relocation is predictable, a saccadic eye movement will occur that coincides with and mirrors the object relocation. Preparation for the saccade can be observed as a ~ 100 ms withdrawal of attention prior to the saccade. In this study, it was found that subjects only withdrew attention in preparation for a relocation that occurred after the object was fully occluded by the screen edge. If relocation occurred when the object was touching the edge or only half occluded, no preparation was observed and recovery of full attention following the relocation took significantly longer. These results indicate that viewers expect an object to satisfy the requirements for existence constancy (gradual occlusion) even though the occluder, the screen edge, violates assumptions of spatiotemporal continuity. This suggests a dissociation of existence constancy and spatiotemporal continuity.

◆ **Temporal dynamics of texture segmentation**

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In line textures, large orientation discontinuities pop out as a result of instantaneous early detection mechanism (Nothdurft, 1992 *Perception & Psychophysics* **52** 355–375). However, perception of overall orientation contrast by either grouping (Casco et al, 2004 *Neuroscience Letters* **371** 18–23; Casco et al, 2005 *Vision Research* **45** 2384–2396) or orientation averaging (Parkes et al, 2001 *Nature Neuroscience* **4** 739–744) also involves early processing level and contributes to texture segmentation. To address the issue of temporal dynamics of these mechanisms, we analysed texture boundary segmentation based on fixed orientation contrast in a matrix of oriented Gabors. In the matrix, the overall local orientation in the background was either parallel or orthogonal to the texture boundary, which was placed in the most eccentric row (column). Using 2AFC task, in different experiments we measured sensitivity to either presence (d') or the orientation (% correct) of the texture boundary. We found that, at short durations, observers perceived overall local orientation but did not detect the presence ($d' = 0.2$) and did not discriminate the orientation of the texture boundary in either parallel (55%) or orthogonal condition (39%). At durations larger than 40 ms, texture boundary was detected ($d' > 0.8$) and its orientation discrimination was facilitated by overall local orientation if it was 'orthogonal' to the texture boundary (63% versus 79%). Results suggest that individual orientation is not filtered out, as predicted by most texture segregation models [Landy and Graham, 2004, in *The Visual Neurosciences* Eds L M Chalupa, J S Werner (Cambridge, MA: MIT Press) pp 1106–1118], but contributes to the dynamic processing of textures: at first, overall (not individual) orientation in a full spatial region is represented (may be mediated by early-cortical, long-range lateral interactions), and wins for salience over the texture boundary; further on, the texture boundary wins for salience but its detection/discrimination is mediated by overall (not local) orientation contrast.

[Supported by Ministero dell'Istruzione dell'Università e della Ricerca, grant PRIN 2005.]

◆ **The flash-lag effect and subjective confidence**

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We examined the flash-lag effect (FLE) by subjective confidence ratings, and dealing with the possibility of disentangling temporal and spatial aspects of behaviourally and introspectively measured FLE. Thirteen observers participated in an experiment where they had to localise a colour-change of a horizontally moving bar (6.4 or 25.6 deg s⁻¹, in separate blocks) in space or time and to give a subjective confidence rating about the choice. The colour-change was compared to a 5 ms flash under the moving trajectory by the method of constant stimuli. In the localisation task, the flash appeared once in seven different points (-1.44, -0.96, -0.48, 0, +0.48, +0.96, +1.44 deg), and in the timing task the flash onset time was varied (-150, -100, -50, 0, +50, +100, +150 ms). Observers were asked to give a discriminative response about the relative temporal or spatial position of the colour change and the flash. The confidence was allowed to vary from 50% (the answer was random) to 100% (absolute confidence about the given discriminative choice). The results show that the confidence ratings follow the pattern of the FLE showing a similar but smaller shift. It was possible to explain the spatial offset in terms of temporal delay and vice versa, especially for the higher-velocity condition, and the correspondence between time and space was better for confidence ratings. According to the discriminative ability and respective confidence ratings, the relative overconfidence and underconfidence was calculated (Runeson et al, 2000 *Psychological Review* 107 525–555). Generally, the pattern indicated a considerable cognitive contribution in the FLE. The task difficulty effect was also present, showing a transition from overconfidence in easy task displays to underconfidence as the judgment difficulty increased. We found that applying confidence ratings carries independent meaning in case of the FLE.

[Supported by an ETF grant no. 6244.]

◆ **Temporal dynamics of contrast gain control in macaque V1**

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Contrast gain control in primary visual cortex (V1) is typically characterised by two nonlinearities: contrast saturation (and its associated latency advance) and cross-orientation suppression. If the two phenomena are mediated by the same mechanism, we would expect them to have a similar temporal signature. To test this, we compared the temporal evolution of the response of V1 neurons to stimuli designed to isolate these two different nonlinearities. We measured the response of V1 neurons to a probe presented at different times relative to the onset of a pedestal ($t = -200$ ms, 0 ms, 25 ms, 50 ms, 75 ms, 100 ms, 300 ms). The probe was a brief (50 ms) stationary sinusoidal grating optimised to the preferred orientation, spatial frequency, and spatial phase of the neuron. The pedestal was a static grating of optimal spatial frequency presented for 150 ms, the phase of which was randomised every 10 ms. In separate blocks of trials the pedestal was either presented at the preferred orientation of the neuron to evoke contrast saturation, or orthogonal to the preferred orientation of the neuron to evoke cross-orientation suppression. While all the neurons from which we recorded exhibited contrast saturation, only half of them exhibited cross-orientation suppression. Both types of nonlinearities were quite fast, starting within the first 25 ms of the onset of the pedestal and peaking by 50 ms. However, the two pedestals exerted different effects on response latency to the probe. As expected, the response latency to the probe was decreased when the pedestal was at preferred orientation. Conversely, the response latency to the probe increased when the pedestal was at the orthogonal orientation. These results suggest that the two nonlinearities, contrast saturation and cross-orientation suppression, arise from different mechanisms.

[Supported by EY 04440.]

◆ **Temporal integration of speed in perceived causality**

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Causal relation between two movements is evident in the launching paradigm [Michotte, 1946/1963 *The Perception of Causality* (London: Methuen)], in which the first moving object (S1) appears to cause the motion of the second object (S2). The causal relation requires a short delay between S1 and S2 (40 ms, launching) and fades when it is long (1040 ms, non-launching). We recently showed that in the launching condition the speed of S2 is overestimated by 34% with respect to the non-launching condition (Parovel and Casco *Vision Research* submitted). Here, we demonstrated the general properties of the spatio-temporal integration mechanism underlying speed

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overestimation in the causality phenomenon. We manipulated the trajectory-to-trajectory alignment [4 experiments], the spatio-temporal coincidence between S1 and S2 [3 experiments], the duration of the whole event [1 experiment], and the speed ratio [2 experiments]. A two-interval forced-choice task was used to measure the point of subjective equality between S2 speeds in launching versus non-launching conditions. Data support an integrative mechanism with different properties than motion averaging, motion trajectory integration, and sequential recruitment; indeed, S2 speed overestimation also occurs when S1 is slower than S2, independently from the trajectory-to-trajectory alignment or the spatial coincidence. The mechanism underlying perceived causality specifically relies on two temporal factors: it requires a short interval between S1 and S2 movements, and also it increases with their short durations. Moreover, we found that S2 speed overestimation in launching determines a displacement of psychometric functions rather than a change in slope, demonstrating a perceptual rather than a decisional effect, in agreement with Michotte's interpretation that the relationship of causality in launching events is directly perceived, without the mediation of high-level processes.

◆ **Visual sensitivity to changes in acceleration of gravity tested with free-falling objects**

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The laws of physics determine the movement of the objects in our visual environment. How sensitive are humans to violations of the fundamental physical parameters determining real-object movements? This question was addressed by measuring the visual sensitivity to changes in the acceleration of gravity for free-falling objects. An RGB colour-graphics system (VSG 2/3, Cambridge Research Systems, UK) controlled by a laboratory computer was used to simulate objects in free-fall with an adjustable acceleration of gravity. The experiment was carried out for simulations with a range of horizontal and vertical initial velocities. In each trial, a sequence of images simulating the fall was projected by an LCD projector on a large area of a wall. The task of each observer was to adjust the acceleration of gravity such that the resulting movement of the free-falling object looked natural. It was found that observers adjusted the value of the acceleration of gravity with different precisions depending on the initial conditions of the velocity but within about 10% of the corrected value, corresponding to a precision of the order of 30 ms in the time of the fall. These results suggest that observers are moderately sensitive to changes in the value of the acceleration of gravity for free-falling objects.

◆ **Absence of flash-lag when judging global shape from local positions**

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When a flash is presented aligned to a moving stimulus, the former is perceived to lag behind the latter. This mislocalisation error is known as the flash-lag effect (FLE). Here, we examined whether the FLE also drives shape perception. To do this, we used Glass patterns (GP) made of 400 paired dots. One dot of the pair moved along a specific direction, while the other served as a flash (10 ms.). All the moving dots had the same direction and this was varied randomly across trials. We set the GP in a way that a global spiral shape could only be physically available when the flashed dot of each pair was aligned with the moving dot. In one condition, observers were shown stimuli with different offsets between the two paired points on a trial-to-trial basis. Subjects had to report whether they saw a clockwise or counter-clockwise spiral shape. If a FLE drove the percept we would expect the maximum of correct responses to be displaced with respect to the point of perfect physical alignment. The results show that the peak of correct responses is not significantly shifted away from the point of alignment (zero offset). This distribution is similar to that obtained in a control condition with static dots. A significant FLE (~50 ms) is found when a position judgment is required between the two dots of a given pair. We conclude that the absence of FLE is due to the fact that it is unnecessary to ascertain an object's position after a temporal marker.

[Supported by grant TIN2004-04363-C03-02 from the Spanish Ministry of Education.]

DEVELOPMENT AND AGEING

◆ **Time-dependent adjustment of disparity fixation after a glare exposure**

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After a glare, a time-dependent adaptation is observed followed by recovery of normal vision. Most studies concerning recovery have been carried out on monocular alterations of vision but few on binocular alterations. We have shown earlier that, in a steady visual environment,

binocular vergence depends on the luminous level (Bourdy et al, 1991 *Ophthalmic and Physiological Optics* **11** 340–349), but we do not know what changes may occur in disparity fixation during the readaptation period. We used the same experimental set-up as Ogle [in Ogle, 1950 *Binocular Vision* (Saunders Co.) chapter 8, p. 73], with the stimulus displayed on a screen. Fixation disparity was first measured for three steady luminous levels (photopic, mesopic, scotopic); then, using the thousand-step-staircase method [Mollon, in Bourdy et al, 1987 *Lighting Research and Technology* **19**(2) 35–44], the fixation disparity was measured after the glare every 10 s in a 2 min experiment. The glare luminance was 25 cd m^{-2} with durations of 2 s and 10 s or 50 cd m^{-2} with durations of 1 s and 5 s, corresponding respectively to $L \times T$ values of 50 and 250. Results show that changes in fixation disparity can be observed during recovery. These changes are not correlated with the $L \times T$ factor. Two groups may be distinguished according to age: young observers (under 30 years of age), for whom the return to steady values depends on the intensity of the glare and occurs after an 80 s delay; and older observers (over 60 years of age) for whom there is no return to a steady position during the whole of the experiment. It is well known that the effects of dazzling depends, in a significant way, on the age of the observer. During glare, young observers were submitted to an equivalent veil brightness lower than older people (Vos, 2003 *Clinical & Experimental Optometry* **86** 363–370), which may explain their greater ability to return to the state of balance of their vision.

◆ **The effects of ageing on processing load in feature and conjunction search: A pupil-size and eye-movement study**

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The pupil of the eye dilates with processing load. We have previously shown that this measure is sensitive to subtle difficulty manipulations during performance in an inefficient feature-search task (eg Porter et al, 2004 *Perception* **33** 757). Here, to investigate ageing effects on load during search, we compared a conjunction with two feature-search tasks for younger (age 18–30 years) and elderly (age 60–85 years) participants, matching tasks as well as possible for response speed and accuracy. For both age groups, the patterns of pupillary dilation during performance were indistinguishable for the three tasks, suggesting similar processing load for the different searches. Moreover, pupillometry measures seemed unaffected by minor differences in eye-movement indices between tasks. Conjunction search involved more saccades and longer overall scan paths than feature searches, mirroring slightly longer reaction times. Additionally, conjunction-search-based saccade amplitudes were reduced and fixation durations increased, the latter for elderly subjects only. On directly comparing results for younger and older participants, a general slowing of both performance and pupil response was evident in the elderly. Older participants showed delayed pupil reflexes on stimulus onset and slower recovery from these compared with the young. Fixation durations were also longer, with more saccades made per search trial by the older group. However, the pupils' dilatory patterns towards response were equivalent in shape and amplitude for both age groups. Given that pupil dilation patterns were identical for the different tasks, they cannot have been influenced by response speed, number of eye movements, or fixation duration. Taken together, these data indicate that the essential processing nature, as measured by pupillary indices of processing load, is preserved for both feature- and conjunction-search tasks in healthy ageing. This processing nature seems unaffected by the occurrence of search-type specific and age-specific changes in strategy as implied by eye-movement data.

◆ **Chromatic induction in infancy**

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The colour perception of an embedded field is affected by the surrounding colour. This phenomenon is known as chromatic induction. We investigated whether 5- and 7-month-old infants ($N = 64$) were affected by surrounding colour by using a familiarisation–novelty preference procedure. In experiment 1, infants were shown a chromatic induction stimulus. The stimulus consisted of six coloured squares in tandem. The six squares had the same chromaticity coordinates (dull green or dull pink), and the surrounding field was divided into two regions: the upper region was green, the lower region was pink. For adults, the upper three squares were perceived as different in colour from the lower three squares owing to chromatic induction. At first, infants were familiarised with this stimulus. After familiarisation, the infants were tested on their discrimination between the uniform colour display and the two-colour display. If infants' colour

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perception was affected by surrounding colour, they would show a novelty preference for the uniform colour display. The result showed that 5- and 7-month-olds showed a novelty preference for the uniform colour display. This suggests that the colour perception of 5- and 7-month-olds could be affected by surrounding colour. In experiment 2, infants were shown a different chromatic induction stimulus. The configuration and surrounding of the stimulus was same as in experiment 1, but chromaticity of the upper three squares was different from the lower three. All six squares were perceived the same colour owing to chromatic induction. If infants' colour perception was affected by surrounding colour, they would show a novelty preference for the two-colour display. The results showed that 7-month-olds, but not 5-month-olds looked significantly longer at the two-colour display than at the uniform colour display. Our results suggest that 7-month-olds could be affected by surrounding colour as adults are.

[Supported by RISTEX, Japan Science and Technology Agency, and a Grant-in-Aid for scientific research (15500172) from the Japan Society for the Promotion of Science.]

◆ **Children's understanding of spatial relation and orientation of the observer's frontal plane**

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The object of this research was to examine how the reference frame works on the spatial relation and orientation during development. The researchers conducted two space tasks at the frontal plane on 178 children aged 4 to 12 years. In this study, the researchers performed an object-rotation task (ORT) to measure the participants' understanding of spatial relations. The researchers rotated a specific stimulus element by 0°, 45°, 90°, 135°, or 180°, and asked children to construct original whole stimulus elements with rotated cue elements. The researchers also performed a body-rotation task (BRT) in which children were asked how the view of an astronaut doll changed as it rotated by the same amount as the ORT to measure the participants' spatial orientation. The results of this study show that the performance in the ORT improves linearly with age, but the results of the BRT depicted a complicated U-shaped curve in which performance decreased especially among children aged 4 to 6 years and then increased among children aged 8 to 12 years. The BRT measurement contained both angle and orientation of the view from the doll. The contra-orientation error increases with 10-year-old children yet decreases with 11-year-old children. There may be substantial developmental change in the understanding of orientation. The researchers postulate that viewer-centred and object-centred frames of reference produce these changes.

◆ **Early development of velocity sensitivity to radial motion**

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Radial expansion/contraction is a crucial cue of motion-in-depth perception. The radial motion sensitivity emerges very early in life. Earlier studies reported that about 1-month-old infants showed defensive motor responses to a large field expansion (eg Nanez and Yonas, 1994 *Infant Behavior and Development* **17** 165–174). Although these earlier works showed an early onset of radial motion sensitivity, recent PL/FPL studies reported dramatic changes of radial motion sensitivity in older subjects. For instance, asymmetric sensitivities to radial expansion/contraction emerge between 2 and 3 months (Shirai et al, 2004 *Infant Behavior and Development* **27** 315–322), and sensitivity to speed-gradient of expansion flow increases between those ages (Shirai et al, 2004 *Vision Research* **44** 3111–3118). These studies suggest that radial motion sensitivities increase at around 2–3 months. For the other type of relative motion, increases of velocity sensitivities have been reported after 2 months of age (eg Bertenthal and Brudbury, 1992 *Developmental Psychology* **28** 1056–1066). However, development of velocity sensitivity to radial motion has not been examined. In the present study, we investigated radial motion velocity sensitivity of infants aged 2 and 3 months. We used two dynamic random-dot patterns (RDPs) placed side by side. One RDP was a radial expansion/contraction and the other was translation (up, down, right, or left: counter-balanced across infants). Two RDPs had the same velocity value and we set two velocity conditions (for 2-month-olds, low = 5.31 deg s⁻¹, high = 7.97 deg s⁻¹; for 3-month-olds, low = 2.66 deg s⁻¹, high = 5.31 deg s⁻¹). We measured infants' looking time for two RDPs and calculated the preference rate for an expansion/contraction. We found that the 3-month-olds preferred expansion/contraction over translation only in the high-velocity condition. No 2-month-olds showed significant expansion/contraction preference. These results suggest the radial motion velocity sensitivity increases between 2 and 3 months.

[Supported by RISTEX, Japan Science and Technology Agency, and a Grant-in-Aid for scientific research (15500172) from the Japan Society for the Promotion of Science.]

◆ **The effect of occlusion information on motion integration in infants**

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Owing to the aperture problem, local motion signals must be integrated across space. However, not all motion signals should be integrated. Accurate interpretations of image motion depend on both the integration of motion signals produced by the same object and the segregation of those produced by different objects. To perform this task, the human visual system evidently makes use of form information such as occlusion (eg McDermott et al, 2001 *Perception* **30** 905–923). We examined the effect of occlusion information on motion integration in infants aged 3 to 8 months. We used the diamond stimulus of McDermott et al (2001, loco cit.), in which an outline diamond translates with a circular trajectory, its corners hidden by occluders (occlusion condition). For adults, the occluded diamond generally seems to move coherently in a single circular path. However, if the occluders are removed (bar condition), the line segments of the partial diamond seem to move separately from each other in the direction normal to its orientation. Infants were first familiarised with the diamond stimulus either in the occlusion condition or in the bar condition. After familiarisation, they were tested on the discrimination between two types of test displays: a global-motion (GM) test display and a local-motion (LM) test display. Both test displays were composed of four moving dots. In the GM test display, the movement of the four dots simulated the coherent motion of the diamond behind the occluders. In the LM test display, the movement of the four dots simulated the local motion of the line segments (local motion). The results showed that preference for the LM test display was significantly greater in the occlusion condition than in the bar condition. These results suggest that occlusion information influences the occurrence of motion integration in infants as well as in adults.

[Supported by RISTEX, Japan Science and Technology Agency and a Grant-in-Aid for scientific research (15500172) from the Japan Society for the Promotion of Science.]

◆ **Dipole source localisation from motion/goal-directed action perception in infants**

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Previous studies have shown a rapid development of the MT/V5 area between 2 and 5 months of age. At 5 months, this area is activated bilaterally for rotational motion, with an earlier onset in the left hemisphere. There is also frontal and parietal activation. This development might be related to the corresponding development of smooth pursuit, motion perception, binocularity, and reaching (Rosander et al, 2005, submitted). In this study, the previous ERPs have been localised by independent component analysis and dipole source analysis (by using EEGLAB). A second experiment was conducted that showed goal-directed actions in infants of 5 months of age. The components found from rotational motion have been used as control for the activation elicited from goal-directed action perception, which is believed to engage mirror neurons (Rizzolatti and Craighero, 2004 *Annual Review of Neuroscience* **27** 169–192). Preliminary results show that at least two different areas in the frontal lobe are more engaged in the goal-directed action condition than in the mere motion condition.

◆ **Mesopic light levels reveal a deficit in reflexive optokinetic nystagmus in older people**

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Available data suggest that peripheral motion sensitivity in reduced illumination declines with age. OKN data can discriminate glaucoma patients from normals (Severt et al, 2000 *Clinical and Experimental Ophthalmology* **28** 172–174). Here, we report age-related rather than disease-related differences in OKN. Vertical gratings of either 0.43 or 1.08 cycles deg⁻¹ drifting at either 5 or 20 deg s⁻¹ and presented at either 8% or 80% contrast were projected onto a large screen viewed at 1.5 m. Gratings were presented as (i) full field stimulation, (ii) central stimulation with gratings presented within a central Gaussian-blurred window of 15 deg diameter, and (iii) peripheral stimulation with gratings presented outside the central 15 deg. All conditions were randomly presented at two light levels: ‘mesopic’ (1.8 cd m⁻²) and ‘photopic’ (71.5 cd m⁻²). Each trial lasted 20 s, followed by a 25 s period spent viewing a uniform grey field. Observers were required not to track specific stripes but rather to maintain central fixation. Eye movements were recorded with a 250 Hz SMI Eyelink system and slow phase velocities (SPVs) of the OKN in the

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last 15 s of each trial were collected. Participants were ten observers in each group: 'young' (mean = 32.3 years, SD = 5.98 years) and 'old' (mean = 65.6 years, SD = 6.53 years) with normal vision and free of ocular disease. There was no overall difference in SPV between the groups. However, for low-contrast, full-field, and high-velocity conditions, there was a significantly larger drop-off in SPV for the older group (photopic mean = 8.9 deg s⁻¹ versus mesopic = 0.36 deg s⁻¹) than the younger group (photopic mean = 5.6 deg s⁻¹ versus mesopic = 2.14 deg s⁻¹). Taken together, such conditions favour M-pathway sensitivity as determining the reflexive OKN response, suggesting a clear diminution in M-pathway sensitivity in the healthy ageing eye.
[Supported by Australian Research Council RIEF Grant R00002374.]

- ◆ **The effects of eye torsion on long-range neuronal connections in cat striate cortex**
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Experimental strabismus, surgically induced early in postnatal life, was found to change the length of long-range neuronal connections (Alexeenko et al, 2005 *Perception* **34** Supplement, this issue). We assessed the contribution of eye rotation to such changes. In 6 strabismic cats (3 cats with unilateral strabismus and 3 with bilateral strabismus), a torsional deviation of eye was also detected. The angle between pupil slits, when viewed frontally, was 22–30 deg, while in normal cats it averages 14 deg (Olson and Freeman, 1978 *Journal of Neurophysiology* **41** 848–859). Spatial distribution of retrogradely labelled cells in area 17 following micro-iontophoretic horseradish peroxidase injections in area 17 or 18 cortical columns was investigated. The length changes of long-range neuronal connections in area 17 along the representation of visual-field horizontal meridian occurred both in cats with and without eye torsion. However, the enlargement of these connections along the representation of the vertical meridian of the visual field was found only in cats with torsional eye deviation. We suggest that the revealed reorganisation of neuronal connectivity may explain the changes in cell orientation preference (Isley et al, 1990 *Journal of Neurophysiology* **64** 1352–1360), which compensate for eye torsion.
[Supported by RFBR grant 03-04-48258.]

MOTION 2

- ◆ **Global-motion perception is governed by a single motion system**
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Global-motion perception was probed by measuring signal-to-noise dot ratios (ie thresholds) necessary for evoking coherent motion perception. To this end, small sets of coherently moving signal dots were embedded in fields of noise dots moving at equal and constant speeds in random directions. Previous research (Edwards et al, 1998 *Vision Research* **38** 1573–1580; Khuu and Badcock, 2002 *Vision Research* **42** 3031–3042) showed that global motion perception was impaired (ie thresholds increased) when the noise dots moved at similar speeds as the signal dots, but not when they moved at substantially different speeds. High-speed noise did not elevate thresholds for low signal speeds, and vice versa. The results prompted the conclusion by the aforementioned researchers that global motion perception is governed by two independent speed-tuned systems: one for slow and one for fast motion. We measured thresholds for more than two signal speeds, and found identical results for all signal speeds: noise speed only influenced thresholds if it was near the signal speed. Considerable overlap of the threshold curves was found between conditions. These results speak against a bipartite global motion system. Model simulations indicate that the experimental results can result from a single motion system.

- ◆ **Reversed phi with random-dot kinematograms under luminance-contrast and colour-contrast reversal**
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Apparent movement is sometimes reported to be seen in the opposite direction if luminance contrast of successive frames is reversed (reversed phi: Anstis, 1970 *Vision Research* **10** 1411–1430). This phenomenon is less mysterious than it might appear at first glance: reversed phi is compatible with many low-level theories of motion perception (eg Adelson and Bergen, 1985 *Journal of the Optical Society of America A* **2** 284–299). Moreover, Lu and Sperling (1999 *Perception & Psychophysics* **61** 1075–1088) showed that reversal of perceived direction in contrast-changing stimuli is in many cases a physical property of the stimuli rather than a perceptual phenomenon.

In our experiments, using 2-frame random-dot-kinematograms (RDKs) with four different directions, we found the reversed motion signal to be much weaker than the (unreversed) signal without contrast reversal [contrary to the data reported by Sato (1989 *Vision Research* **29** 1749–1758)]. Experiments with isoluminant red–green RDKs showed similar results, but without any evidence for contrast reversal: exchanging the colour code in the second frame appears to erase the motion signal completely.

◆ **Spatial integration in apparent and real motion induced by Glass patterns**

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A succession of independent Glass patterns comprised of dipoles with dots of the same contrast polarity gives way to a strong perception of global motion with ambiguous direction (Ross et al, 2000 *Current Biology* **10** 679–682). Conversely, sequences of independent Glass patterns, where each dipole is made of a black and a white dot, convey perception of global motion in the direction from the black to the white dot of the pair. This effect is due to a delayed perception of black dots with respect to whites [Del Viva and Gori, 2004 *Journal of Vision* **4**(8) abstract 850]. These observations suggest that the perception of motion induced by these two similar stimuli is generated by different neural mechanisms. We compared spatial integration properties of these two stimuli. We measured coherence thresholds as a function of stimulus area in circular Glass pattern sequences of both kinds. Glass patterns fell within a 26 deg circle notionally divided into radial sectors of varying aperture. Signal dots were confined to one or more sectors, with the remaining part of the circle set to average luminance. Sensitivity for detecting patterns with same-polarity dots was higher than for detecting patterns with opposite-polarity dots for all tested conditions. The lowest sector aperture allowing perception was about 10 deg for same polarity and 60 deg for opposite polarity. These results suggest global integration mechanisms with different receptive field size that operate at this level. For the discrimination task, sensitivity for Glass patterns with opposite-polarity dots was found to be very similar to sensitivity for real motion, supporting a common integration mechanism. Overall, our data indicate that different spatial-integration mechanisms operate in Glass patterns with same-polarity and opposite-polarity dots.

◆ **Perceptual binding and surface segregation based on motion**

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We used a visual search paradigm to investigate whether attentional mechanism in feature-binding (colour, motion, orientation, etc) was involved in the surface segregation based on coherent motion. In the experiment, a couple of superimposed stimulus patterns were presented each in four quadrants on a screen. The stimuli were composed of either random dots or lines. One of the patterns in each quadrants moved; the other remained as a background of the moving one. One of the four quadrants (the target) had different elements from the other three quadrants. Without the motion, observers could not find the target because all quadrants had both target and distractor elements when two patterns were superimposed. The task was to locate the target quadrant. Instead of using the number of distractors as a task variable, we controlled the duration of the motion (40–160 ms). The dependent variable was the percentage of correct answers. We used a coherent-motion condition where elements moved in the same direction and a random-motion condition where each element moved in a random direction. There were two search conditions: (i) double-conjunction search for motion and colour or motion and orientation, (ii) triple-conjunction search for motion, colour, and orientation. If the elements with the coherent motion are grouped together as one surface, visual search will be performed in parallel and the target will be immediately detected. However, if the perceptual binding of features is unrelated to the grouping, the search performance will be serial and we will not find any difference between motion conditions. We also found that, when the motion duration was short, the coherent motion facilitated target detection significantly as compared with random motion. We also found higher performance in the triple-conjunction search than in the double-conjunction search. It is suggested that surface segregation based on coherent motion precedes perceptual binding for particular features.

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◆ **Post-adaptive changes in the perceived speed of radial motion flow**

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Adaptation studies provide strong evidence for specialised motion mechanisms sensitive to meaningful global patterns of motion (eg radiation, rotation). Despite much interest in this topic, research on speed perception in complex motion is scarce. We explored global velocity adaptation in coherent versus 'scrambled' patterns of radial flow. We measured the velocity aftereffect (VAE)—ie the decline in perceived speed with adaptation to motion—a phenomenon well described at the local level (see Thompson, 1981 *Vision Research* **21** 337–345). The stimulus extended up to 50 deg in the periphery from a central fixation. Luminance-defined concentric sine waves were scaled with eccentricity to represent a perspective view through a tunnel. Temporal modulation of this pattern creates the impression of linear motion-in-depth, at a constant speed. In separate blocks, observers adapted to segmented versions of this stimulus, or to a motionless background (baseline). In the test phase, observers compared motion speed in adapted regions to that in non-adapted regions of the display. Test and comparison stimuli reversed directions randomly from trial to trial and had random relative phase. We found that adaptation to a single segment or to incoherent flow replicates all aspects of the VAE at the local level. By contrast, adaptation to juxtaposed segments of coherent flow markedly reduces the magnitude of the VAE across all test speeds and ensures veridical perception of the adaptation velocity. We conclude that the global speed of a looming stimulus is encoded more accurately than the speed of its local 2-D components. [Supported by NSERC, FQRSC.]

◆ **Velocity discrimination thresholds for flow-field motions with moving observers**

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Locomotion-produced optic flow is used by the visual system to compute heading direction, obstacle avoidance, time of impact, etc. While walking or running, vertical sinusoidal-like oscillations of the head are contaminating the optic-flow information. We measured velocity discrimination thresholds when the observer was stationary, walking, or running at 4.6 km h⁻¹ on a treadmill. We compared this to the situation when the flow-field was bobbing at low, medium, or high amplitude while the observer was stationary. Results showed that velocity thresholds were not impeded by the observer's movement, with running even resulting in the lowest thresholds. Oscillating the flow-field systematically increased the thresholds. Preliminary results of threshold estimates when observers followed an oscillating fixation point with either a stationary flow-field or an in-phase oscillating flow-field, showed that availability of eye-movement information reduced the detrimental effect of flow-field oscillations. The present results demonstrate that the detrimental effects of locomotion-induced oscillations are removed by the availability of non-visual information about the source of the oscillations. [Supported by NSERC, FQRSC.]

◆ **Anisotropy of motion sensitivity at the temporal margin of the visual field**

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The temporal visual field extends to 90 degrees or more from the line of sight. Despite the biological importance of this far peripheral region, it has been little studied experimentally. It is known that only moving objects are detectable at the edge of the temporal field, and that contrast sensitivity is maximal at a very low spatial frequency, close to 0.1 cycle deg⁻¹ (Mollon and Regan, 1999 *Perception* **28** Supplement, 28). In the present study, we measured contrast sensitivity for drifting Gabor patches at extreme eccentricities on the horizontal meridian. The spatial frequency of the stimulus was 0.55 cycle deg⁻¹, and it was turned on and off with a Gaussian temporal profile. The drift direction was orthogonal to the orientation of the Gabor and a two-interval temporal forced-choice procedure was used to measure contrast sensitivity for different directions of drift. Subjects received feedback on each trial. Thresholds were obtained by a single staircase, which converged to 70.17% correct. A marked anisotropy of sensitivity was found: contrast thresholds were lowest for directions of drift close to the vertical axis and were as much as three times higher for other directions. For this region of the visual field, there may be only a limited number of neural analysers. In the corresponding retinal region, there is known to be only a single sparse layer of ganglion cells [Polyak, 1941 *The Retina* (Chicago, IL: University of Chicago Press) page 218]. [Supported by NSERC, Canada; C T Taylor Fund, Cambridge.]

◆ **Anticipated velocity slow-down in anticipation of the position of a free-falling object after occlusion in virtual environment**

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A series of experiments on the anticipation of position of a free-falling object after occlusion was carried out. A ping-pong ball was launched, freely fell down, and was occluded by a board in a virtual-space experimental environment. Subjects were required to indicate the position of the ball after the occlusion with five levels of delays marked as the colour change of the board. The anticipated velocity was calculated from the indicated position of the ball and the stimulus delay. This represents the occluded object's velocity imagined by the subject. Interestingly, all the subjects underestimated the object's falling distance from the top of the board. It was suggested that the subjects could imagine that the object's velocity after occlusion was considerably smaller than the actual. In order to investigate the cause of this unexpected slow-down of anticipated velocity, two series of experiments were performed based on various hypotheses. In experiment 1, the subjects were required to indicate the anticipated position of the object moving, at 1 m s^{-1} or 3 m s^{-1} , in the occluded task. In experiment 2, they were also asked to indicate the position of the free-falling object in the same occluded task, in the disappearance task, and in the unoccluded (visible-object) task. After the visible-object task the occluded tasks were performed again. We found that the anticipated velocities in all tasks were smaller than the actual. Thus, the anticipated velocity slow-down appears to be independent of the acceleration, the object's velocity, the psychological condition, and the inexperience in the task. Interestingly, the indicated position was in obvious error even in the visible-object task, similar to that in the anticipation task. The judgment error was in the upward direction again; that is, opposite to the direction of motion of the object. The cause of this phenomenon, opposite to the flash-lag effect and the Fröhlich effect, will be studied.

◆ **Illusory motion induced in rotating gray-scale textures of varying luminance**

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Vertical gratings whose luminance profile corresponded to a set of periodic triangular impulses were created. Plaids with the same minimum and maximum luminance were also generated by using different combinations of orthogonal gratings. Depending on the skewness of the triangular impulses and the component gratings in the plaids, the resulting textures appeared as a set of objects with different geometrical and material properties (metallic cylinders, spherical or ellipsoidal objects of semi-transparent glass, metal elements of irregular shape, or matte corrugated surfaces). When these textured surfaces were slanted and rotated about a vertical axis, an illusory motion of the brightest strips was perceived for textures with glossy appearance. To evaluate this effect, two experiments were performed. In both experiments a slanted textured surface rotated over a range of -25° to $+25^\circ$ and was replaced by a gray background at the end of the rotation cycle. The experimental variables were the texture type, the slant of the surface, and the direction of rotation. The subject's task was to adjust the orientation of a line, presented on a separate screen, so that it coincided with the orientation of the brightest strips (experiment 1) or of the darkest strips (experiment 2) in the textures at the final moment of surface motion. The results showed that the texture type had significant effect on the task performance only for the brightest strips in the textures. For textures that appeared glossy, the adjusted orientation of the brightest strips deviated less from the vertical than the adjusted orientation of the darkest strips, indicating that the apparent gloss of the texture induced non-rigid motion of the surface.

[Supported by NIH Grant TW-05753.]

◆ **The effect of isoluminant adaptation upon the velocity aftereffect**

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We investigated the effect of adaptation to monochromatic and isoluminant red-green gratings upon the perceived speed of subsequently presented monochromatic gratings for a range of adaptation and test speeds. Stimuli were horizontally oriented sinusoidal gratings ($0.4 \text{ cycle deg}^{-1}$), which drifted upwards at 2, 8, or 16 deg s^{-1} and were situated 1 deg to the left and right of a fixation spot. All combinations of adapt and test speeds were tested, each in a separate session.

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All sessions began with 60 s of adaptation (to the left of fixation), following which 40 test trials were presented for 1 s, each followed by 5 s of top-up adaptation. On each test trial, participants judged which was slower, the test stimulus (presented to the left) or a simultaneously presented matching stimulus (presented to the right), the speed of which was controlled by a modified PEST procedure. For monochromatic adaptation, perceived speed was always reduced when the speed of the adaptation pattern was equal to, or greater than, that of the test pattern. However, lower speed adaptation resulted in an increase in the perceived speed of higher test speeds. For isoluminant adaptation, the pattern of adaptation effects was different. At higher test speeds, adaptation never resulted in a reduction in perceived speed as observed for monochromatic adaptation, but increases in perceived speed were present for low adapt speeds. The results are consistent with a ratio model of perceived speed, whereby speed is taken as the ratio of two temporally tuned mechanisms. The difference in adaptation effects between monochromatic and isoluminant conditions provides limited support for a scheme whereby magnocellular and parvo-cellular signals may form the substrate of such a ratio mechanism.

◆ **Tuning for temporal interval in human apparent motion detection**

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Motion detection in apparent motion of random-dot patterns (RDPs) requires correlation across space and time. It has been difficult to study the temporal requirements for the initial correlation step because temporal measurements jointly depend on temporal filtering, delay-tuning, and successive temporal integration. Moreover, it has been difficult to construct a stimulus containing a single delay only. To measure delay tuning independently of temporal integration, we constructed a motion stimulus containing a single delay value only, and with constant motion energy, irrespective of delay. The stimulus consists of a sparse RDP with a two-frame, single-step dot lifetime. It is constructed by generating a dynamic RDP on each stimulus frame, and showing this pattern once again after a delay of n frames, superimposed on the newly generated RDP. Each frame thus consists of 50% of new random dots and 50% displaced random dots. The delay between corresponding dot patterns can be chosen freely, without affecting the number of steps per second, steps in total, and temporal-frequency content. We measured left–right coherence thresholds for direction discrimination by varying coherence levels in a Quest staircase procedure, as a function of both step size and delay. Highest sensitivity was found at a temporal delay of 12–30 ms. Sensitivity decreased for lower and higher temporal delays. The fall-off at higher delay values was much sharper than previously described. The data allow us to describe to what extent delay tuning in coherence detection is independent of step size.

◆ **Time course of perceived direction of rotation in the Enigma figure and a possible bias produced by motion adaptation**

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In 1981, Leviant devised Enigma, a figure that elicits spontaneous perception of rotary motion in the absence of real motion. This figure consists of concentric sets of narrowly spaced radial lines interrupted by three moat-like coloured annuli. In experiment 1, we asked how the perceived rotation on the three rings changed during a 30 s observation period. Specifically, we measured the duration for clockwise versus counterclockwise rotation by recording the time of motion reversal from one to the other. Seven naive subjects served as observers. The task was to fixate on the centre of the Enigma figure and press a key each time the perceived motion changed direction. In this way, we obtained the duration of rotation in a given direction. Measurements were done five times for each of the three rings in random order. The mean number of reversals for clockwise and counterclockwise rotation was 6.4 (SD = 0.3) for each, and the mean duration 4.7 s (SD = 0.4 s), uniformly distributed over the entire 30 s. No significant difference was found between the inner, middle, and outer rings. However, there was a significantly higher frequency (64.8% versus 35.2%) for seeing clockwise rotation at the beginning of each observation period. In experiment 2, we studied whether adaptation to a black-and-white sector disk rotating either clockwise or counterclockwise would bias the perceived direction of motion in the Enigma figure. Informal results for one subject suggest a large effect of the direction of real motion on the direction of illusory motion.

[SG was supported by a DFG-grant SP67/8-2 and the Padua-Freiburg Program, KH by a DFG graduate program ‘Brain and Behavior’ (885/1).]

◆ **Perceived position in depth: The role of local motion**

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A well reported finding is that the perceived 2-D location of a stationary object is affected by local motion within the object. Here, we report a similar positional effect with motion in depth produced by changes in binocular disparity. We measured the position in depth of a 3-D stationary cylinder whose shape was defined by a group of dots (cylinder: radius = 2.8 deg, depth = 3.3 cm, dots: radius = 0.055 deg). Dots in the cylinder were animated in depth in three motion conditions: (i) one-directional motion, (ii) random motion, and (iii) static. We measured the apparent position of the cylinder by asking observers to align two reference frames with the near and far ends of the cylinder. When the dots moved either away from or towards an observer, the apparent positions of the near and far planes of the cylinder were shifted (around 0.08–0.17 cm) in a manner consistent with the cylinder being displaced in depth in the direction of motion, as compared to the position of the cylinder defined by static dots or randomly moving dots. The positional shift induced by dots moving away from an observer was stronger than that induced by dots moving towards an observer. Our findings suggest that local motion in depth induces misperception of position in depth in a similar way to frontoparallel local motion which induces a misperception of the 2-D position of an object. However, the effect is asymmetric with respect to the different directions of local motion in depth.

[Supported by Grant HKU7149/02H from the Research Grants Council of Hong Kong.]

◆ **Representational momentum and the line-motion illusion**

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If appearance of a horizontal line is cued by prior appearance of a stimulus at one end of the line, that line appears to unfold or extend from the cued end toward the uncued end; this has been referred to as the line-motion illusion (eg Hikosaka et al 1993 *Vision Research* **33** 1219–1240). Memory for the final location of a previously viewed moving target is often displaced in the direction of motion; this has been referred to as representational momentum [eg Thornton and Hubbard, 2002 *Representational Momentum* (New York: Psychology Press/Taylor and Francis)]. Whether displacement consistent with representational momentum occurred for illusory line motion was examined. In experiment 1, a visual cue was presented (0.83 deg × 0.83 deg) 250 ms before a horizontal line (8.17 deg × 0.83 deg) appeared, and the cue was slightly to the left or right of the line. The line was presented for 250 ms, there was a retention interval of 250 ms, and then a probe similar to the initial line appeared. Observers judged whether the probe was the same as the initial line. Memory for the edge of the initial line most distant from the cue was displaced in the direction of illusory motion, and this is consistent with representational momentum. In experiment 2, memory for a line preceded by a cue (as in experiment 1) was compared with memory for a line not preceded by a cue, and lines preceded by a cue were remembered as longer than were lines not preceded by a cue. Experiment 3 was a control study that confirmed the line-motion illusion occurred with the stimuli used in experiments 1 and 2. The results suggest representational momentum can result from illusory motion (see Hubbard et al, 2005 *Psicologica* **26** 209–228) and reflect higher-order processing.

◆ **Crossed barber-pole illusion under barber-pole effect**

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I report here a new illusion and perceptual switching caused by the barber-pole effect. The illusion and the switching can occur even in the case of classical plaid patterns. The intersection of constraints (IOC) and other models of motion integration have assumed that superimposed plaid patterns would resolve the 'aperture problem' of single gratings since local ambiguity would disappear. However, the aperture problem accompanies the classification of terminators (extrinsic or intrinsic) at aperture boundaries. Thus, we cannot suddenly ignore the effect of the terminators even in the case of superimposed plaid patterns. Experiments were designed such that a drifting plaid of gratings formed the stimulus; it was windowed by a rectangular frame with the same luminance as that of the background. With an appropriate ratio for the elongated aperture, the perceived motion successively switches between two alternatives: coherent motion or component motion. The former can be predicted by the classical IOC, whereas the latter differs substantially from the 'component motion' in the context of plaid pattern analysis. In the latter, each grating is perceived to move parallel to the longer axis of the rectangular aperture and not perpendicular to its orientation; each grating moves in the opposite direction on a different depth plane. Then the terminators on the longer edge are intrinsic. I have called the perception of the latter a

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'crossed barber-pole illusion'. The illusionary perception increased with the ratio of the elongated aperture. The 'crossed barber-pole illusion' and perceptual switching are under barber-pole effect.

◆ **Anisotropy of velocity perception during pursuit eye movements**

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We found anisotropy of perceived velocity during pursuit eye movements. Previous studies have established that pursuit eye movements affect perceived velocity (eg, Turano and Heidenreich, 1999 *Vision Research* **39** 1177–1187; Turano and Massof, 2001 *Vision Research* **41** 385–395), showing that the extra-retinal velocity signal derived from pursuit eye movement biases the perceived velocity. We measured, by using the method of magnitude estimation, the perceived velocity of a moving stimulus as a function of direction of pursuit movement. The stimulus was either a dot or a dot and a checkerboard pattern moving at a constant velocity within a fixed distance of 20 deg. Eye movements were monitored by the limbus-tracker technique. Three independent variables were the viewing condition (pursuing or fixating), the direction of motion (horizontal or vertical), and the velocity (5, 10, 15 deg s⁻¹). The results with six observers showed that the vertical movement was perceived faster than the horizontal one (anisotropy) in the pursuing condition, but not in the fixating condition. We discuss whether the anisotropy of velocity perception is caused by different extra-retinal velocity signals between horizontal and vertical pursuit movements.

◆ **Integration of motion signals to second-order chromatic and luminance patterns**

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To investigate motion signal integration between second-order chromatic and luminance patterns, we tested perception of coherent and component motion in plaid patterns. Plaid motion stimuli consisted of second-order isoluminance and luminance patterns, in which spatial frequencies of envelope and carrier component were 0.2 cycle deg⁻¹ and 1 cycle deg⁻¹, respectively. Contrast of both isoluminance and luminance second-order motion patterns was twenty-fold of each detection threshold. We measured probabilities of coherent-motion perception at a temporal frequency of envelope component of 0.05–6.4 Hz. When the temporal frequency of the isoluminance motion is the same as that of luminance motion, the probability functions reach maximum for all three normal colour subjects. And the probability functions decrease as temporal-frequency difference between the isoluminance and luminance motion stimuli increase. These indicate that second-order motion signals produced in luminance and chromatic domain can be integrated in a specific neural site and that its temporal tuning could be determined by physical parameters but not by perceived speed. This result corresponds with previous studies, which reported motion correspondence between nonlinear chromatic and luminance random Gabor patterns in a two-frame motion, but their subjects did not see motion between linear chromatic and luminance patterns (Baker et al, 1998 *Vision Research* **38** 291–302; Yoshizawa et al, 2000 *Vision Research* **40** 1993–2010). We conclude that the second-order chromatic motion signal can be treated by a different process from that for first-order chromatic motion.

[Supported in part by a Japanese MEXT grant 15530479 to TY.]

◆ **Retinotopic magnocellular impairment with preserved motion-coherence perception: Evidence for functional segregation of medial and lateral visual dorsal streams**

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We applied psychophysics as well as structural and functional imaging in a patient with a unilateral parieto-occipital lesion, to study his visual dorsal stream processing. Using standard perimetry, we found deficits involving the periphery of the left inferior quadrant abutting the horizontal meridian, suggesting damage of dorsal retinotopic representations beyond V1. Retinotopic damage was much more extensive when probed with frequency-doubling-based contrast sensitivity measurements, which isolate processing within the magnocellular pathway: sensitivity losses now encroached on the visual central representation and did not respect the horizontal meridian, suggesting further damage to dorsal-stream retinotopic areas that contain full hemi-field representations, such as human V3A or V6. Functional imaging revealed normal responses of human MT+ to motion contrast. Taken together, these findings are consistent with

a recent proposal of two distinct magnocellular dorsal stream pathways: a latero-dorsal pathway passing to MT+ and concerned with the processing of coherent motion, and a medio-dorsal pathway that routes information from V3A to the human homologue of V6. Anatomical evidence was consistent with sparing of the latero-dorsal pathway in our patient, and was corroborated by his normal performance in speed, direction discrimination, and motion coherence tasks with 2-D and 3-D objects. His pattern of dysfunction suggests damage only to the medio-dorsal pathway, an inference that is consistent with structural imaging data, which revealed a lesion encompassing the right parieto-occipital sulcus. Unlike other developmental and ageing models of dorsal stream dysfunction, in which posterior cortical damage is non-selective, the observed retinotopic magnocellular impairment with preserved motion coherence perception provides evidence for functional segregation of medial and lateral visual dorsal streams.

[Supported by FCT-Portugal/FEDER/POCTI/NSE46438 and Fundação Bial Projecto 15/02.]

◆ **Spatial and temporal frequency properties of the neurons in the tecto-thalamo-cortical visual system of the cat**

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The existence of extrageniculate tecto-thalamo-cortical visual system in the feline brain has been demonstrated in a number of morphological and physiological studies. Despite the large number of reports on these structures, the behavioural role of this extrageniculate visual system has not yet been clarified. The aim of this study was to estimate and compare the spatiotemporal characteristics of the visual cells in this visual system of the cat. Single-unit activity has been recorded in the superior colliculus, in the suprageniculate nucleus of the thalamus, and in the visual cortical areas along the anterior ectosylvian sulcus. Sinusoidal grating stimuli were used with 8 spatial frequencies between 0.05 and 0.54 cycle deg⁻¹. They were drifting at velocities between 0.6 and 9.6 deg s⁻¹. The majority of the units in the structures preferred rather low spatial frequencies and high temporal frequencies. Their spatial tuning was characteristically rather coarse. The receptive fields of the thalamic and cortical units were extremely large covering most of the contralateral and the ipsilateral visual hemifields. Summing up these results, we can suggest that the extrageniculate visual system may play a role in the perception of self-motion and thus it may participate in the adjustment of sensorimotor behaviour to environmental challenges. This is in agreement with morphological connections of this system to the substantia nigra and the caudate body in the feline brain.

THEORY AND MODELS

◆ **Classification images and ecologically ideal observers**

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Ideal observer theory is the normative baseline to which human or animal performance can be compared. Different normative theories can be developed depending on the assumptions made on the stimulus and the task. The power of a normative theory is dependent on how realistic its assumptions are. Some recent work has more or less explicitly used the hypothesis that conventional ideal-observer theory lacks an important property of biological visual systems: adaptation to the statistical structure of ecologically valid input, ie natural images. For example, the statistical correlations of the input variables (eg correlations between input pixels) imply that the optimal strategy for detecting a target may take into account variables that are not in themselves the target of detection; they can still provide information on the target because they are correlated with it. At the same time, classification image methods have been developed to estimate linear templates used by human observers. Typically, the results are compared against conventional ideal observers and the properties of ecologically valid input are ignored. Here, the implications of the hypothesis of the importance of ecological statistics in the fundamental case of linear classification images are considered. The task is detection of a stimulus masked by Gaussian noise with a linear template. The question what the optimal linear template is like when statistical structure of natural images is taken into account is investigated. This leads to a simple model which is likely to be applicable to many other cases as well.

◆ **A biologically inspired spiking retina model for the encoding of visual sequences**

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A 'biologically-plausible' model for the magnocellular pathway of a retina is presented. It consists of units representing ganglionar cells, modeled as 'integrate' and 'fire' neurons with three ionic channels.

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The first channel is a depolarising conductance, driven by the bipolar cells connected to the ganglionar, who are assumed to behave as spatiotemporal linear filters on the input sequence. The second channel is a constant leakage conductance, while the third one corresponds to some optional horizontal inhibition between neighbouring cells in the biological retina, that can allow redundancy removal. Thus our retina can perform an interesting alternative to such greedy algorithms as the 'matching-pursuit'. Besides, our model is foveated: the receptive fields of the ganglion cells grow larger with eccentricity while the cell density decreases, as in mammals, according to a highly parametrisable log-polar sampling scheme. Furthermore, the front end of the mechanisms integrates intrinsic calibration parameters of a camera and can simulate a rotation of the eye, allowing saccadic displacements or eye tracking as possible developments. At the implementation level, the neurons' spiking is computed through an event-orientated formalism and its related software, 'mvaspike', is very useful as all equations become coupled through lateral connections. This software will allow the connection of the retina to higher-level, spike-based, treatments. Experimental properties and comparisons with biological data are presented. Study of this retina has two goals. First, we propose a time-continuous to event-driven representation of a dynamic visual sequence, to be used as input of other neuronal simulators or computer vision systems requiring a sparse encoding of the visual information. Second, this model provides an integrated view of the real neural encoding taking place in the magnocellular pathway, and very likely in the parvocellular pathway, when considering smaller receptive fields and saccadic displacements. [Realised within the scope of the European FACETS project.]

◆ **Is the early visual system optimised to be energy efficient?**

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A neural representation which balances natural image encoding with metabolic energy efficiency shows many similarities to the neural organisation observed in the early visual system. A simple linear model was constructed that learned receptive fields by optimally balancing information coding with metabolic expense for an entire foveated visual field in a two-stage visual system. The model consists of a space variant array of photoreceptors; natural images were then encoded through a bottleneck such as in the retinal ganglion cells that form the optic nerve. The natural images represented by retinal ganglion cell activity are then encoded by many more 'cortical' cells in a divergent representation. Qualitatively, the system learns by optimising information coding and energy expenditure and the results match (i) centre-surround organisation of retinal ganglion cells, (ii) Gabor-like organisation of cortical simple cells, (iii) high densities of receptive fields in the fovea decreasing in the periphery, (iv) smaller receptive fields in the fovea increasing in size in the periphery, (v) spacing ratios of retinal cells, and (vi) aspect ratios of cortical receptive fields. Quantitatively, however, there are small but significant discrepancies between density slopes, which may be accounted for by taking optic-blur and fixation-induced image statistics into account. In addition, the model cortical receptive fields are more broadly tuned than real cortical neurons; this may be accounted for by the computational limitation of modelling a relatively low number of neurons. This work shows that retinal receptive fields can be understood in terms of balancing coding with *synaptic* energy expenditure and cortical receptive fields with *firing rate* energy expenditure, and provides a sound biological explanation of why 'sparse' distributions are beneficial.

◆ **Detection in correlated noise**

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The common assumption of additive, white (delta-correlated) Gaussian noise employed to interpret data from detection experiments represents an approximation, since in a rigorous sense white noise does not exist. Here, the probability of detection of a stimulus is derived starting from the more realistic assumption that the noise is not white. The derivation is based on results from the theory of extreme values. Psychometric functions are defined in terms of approximations to a first-passage time distribution, with the second spectral moment $R''(0) = \lambda_2$ (less than infinity) and the internal threshold S as free parameters. For λ_2 close to 0, the random fluctuations become negligible; for λ_2 approaching infinity, white noise is approximated. It is shown that (i) psychometric functions based on the assumption of white noise (eg Watson, 1979 *Vision Research* **19** 515–522) for detection by temporal probability summation (TPS) are inconsistent with the very notion of TPS, and (ii) approximations with λ_2 less than infinity do not turn into expressions for psychometric functions based on the assumption $\lambda_2 = \text{infinity}$ for a start. Moreover, it is shown that the estimates of impulse and step responses (Roufs and Blommaert,

1981 *Vision Research* **21** 1203–1221) are incompatible with the assumption of additive, stationary noise for whatever value of λ_2 less than infinity. This result is discussed with respect to the finding of slow activity fluctuations in the visual cortex (Leopold et al, 2003 *Cerebral Cortex* **13** 422–433).

◆ **The SET game as an interface to perceptual mechanisms**

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The SET® game is a visual-perception game. It includes four different dimensions (colour, shape, number, and filling), each including three values. The goal is to identify a set—3 cards which are all different or all alike within each dimension, independently from the other dimensions. We implemented the SET game with an interactive computer program, allowing us to record subject moves and response times. We call the number of dimensions fulfilling the demand of difference (ie spanning all the values in that dimension), the class of the set. As a first step, we wanted to check if sets of lower classes are perceived more easily. Preliminary results indicate that, indeed, sets from lower classes are found faster, and are recognised first when more than one set is present. Learning curves stabilise after a few games, with class-dependant characteristics. As an initial step towards modeling set perception, we designed a simple neural network based only on similarity judgments. It succeeded in identifying sets in certain circumstances. We generated a novel paradigm for determining the order of dimensional salience. We asked subjects to judge which of two test cards seemed more similar to a reference card. The outcome of all possible comparison combinations leads to a DAG (directed acyclic graph), with a path indicating dimensional ordering. This ordering may facilitate detecting the influence of salient dimensions on the perception of sets. This paradigm may be generalised to other cases.

◆ **Cross-modal relations in early-cognitive vision**

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We describe a novel image representation in terms of local multimodal primitives that is motivated by human visual processing. The primitives can be seen as functional abstractions of hypercolumns in V1, and are applied within an artificial visual system modelling early-cognitive vision. The primitives carry multimodal information: different aspects of visual information such as orientation, phase, colour, local motion, and depth are coded as separate sub-parts. The primitives also carry information about the structural quality of the local visual sub-structure (ie the likelihood that they represent edges, homogeneous patches, or junctions). It is known that the above-mentioned visual modalities are also processed within the hypercolumnar structures in spatially distinct sub-regions (eg different layers or sub-areas). Recent biological work suggests a closer interaction between these sub-regions than has been assumed in the past. In this work, we intend to shed light on the interaction of visual modalities from the perspective of an artificial visual system. The design of such a system leads in a natural way to requirements of cross-modal processing. For example, the coding of colour depends on the local structure: for step-edges, the colour information on the left and right side of the edge must be kept separated, while for a homogeneous image patch this distinction is not relevant. Furthermore, the quality of optic flow depends on the ‘edgeness’ or homogeneity of the local structure (eg aperture problem). Also the depth distribution varies with the local structure. For example, there is low likelihood for depth discontinuities at homogenous image structures. The multi-modal primitives allow us to investigate these relations and we present qualitative and quantitative results for cross-modal dependences for optic flow, depth, colour, and phase information.

[Supported by the European project ECOVISION.]

◆ **Interval bias in discrimination tasks**

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In a 2IFC discrimination experiment, two stimuli are presented consecutively and the subject has to report which stimulus was perceived as higher in a given magnitude, guessing when uncertain. According to signal detection theory (SDT), the probability of a stimulus being selected as higher should not be affected by the order of presentation, but empirical data systematically reveal an effect of presentation order that has been referred to as ‘interval bias’ (Klein, 2001 *Perception & Psychophysics* **63** 1421–1455). We have elsewhere presented a model based on conventional SDT that explains this effect as a combined result of (i) temporary changes in

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sensitivity caused by the presentations themselves, and (ii) response strategies that make subjects use one of the response keys more often than the other across trials in which they are forced to guess. The model predicts that there is a single underlying psychometric function in the absence of these factors but, when they come into play, the observed psychometric function varies location with presentation order. We set out to test these predictions in a series of experiments in which the amount of sensory change was manipulated by varying presentation duration as well as the length of the inter-stimulus and inter-trial intervals, and in which response strategies were manipulated by having subjects either always respond 'interval 1' when forced to guess, always respond 'interval 2', or always use a third response key that ensures the balance of correct guesses across intervals. The results collected thus far show that the location of the observed psychometric function actually varies as expected with the order of presentation, the response strategy, and the trial timing. These results offer guidelines for the design of 2IFC discrimination experiments that reduce or even eliminate order effects.

◆ **Modeling of simple cells through a sparse overcomplete Gabor wavelet representation based on local inhibition and facilitation**

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We present a biologically plausible model of simple cortical cells as (i) a linear transform representing edges, and (ii) a nonlinear stage of inhibition and facilitation between neighbouring coefficients. The linear transform is a complex log-Gabor wavelet transform which is overcomplete (ie there are more coefficients than pixels in the image) and has exact reconstruction. The inhibition consists in diminishing the coefficients which are not at local maxima along the direction normal to the edge filter orientation, whereas the facilitation enhances the collinear and co-aligned local-maximum coefficients. After the inhibition and facilitation stages, the reconstructed error is iteratively projected on facilitated coefficients. Such a process keeps exact reconstruction and concentrates the signal energy on a few coefficients situated along the edges of the objects, yielding a sparse representation. The rationale for such a procedure is: (a) the overcompleteness offers flexibility for activity reassignment; (b) images can be coded by sparse Gabor coefficients located on object edges; (c) image contours produce aligned and collinear local maxima in the transform domain; (d) the inhibition/facilitation processes are able to extract the contours. The sparse Gabor coefficients are mostly connected with each other and located along object contours. Such layout makes chain coding suitable for compression purposes. Specially adapted to Gabor wavelets features, our chain coding represents every chain by its end-points (head and tail) and the elementary movements necessary to walk along the chain from head to tail. Moreover, it predicts the module and phase of each Gabor coefficient according to the previous chain coefficient. As a result, redundancy of the transform domain is further reduced. Used for compression, the scheme limits particularly the high-frequency artifacts. The model also performs efficiently in tasks the human visual system is supposed to deal with, such as, for instance, edge extraction and image denoising.

◆ **The dialectical architecture of visual intelligence where every activity is available as a tool for the next activity**

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Automatic implementation of decoders for visual perception is achieved as follows. The action described by a production rule is realised by means of the decoder in which a pattern of connections corresponds to that of the stimuli. According to Karasawa (2004 *Proceedings of CCCT'04: Computing, Communications and Control Technologies, Austin, Texas, August 5* 194–199), each programmable controllable connection among inputs is realised by a floating-gate avalanche-injection MOS FET, where inverted signals are used for writing, and the detection of matching between inputs and connections is carried out by using the signal source in which low-level signal is provided via comparatively smaller resistance than the high-level signal. An example of a dialectical operating system is the surveillance system in which the view area is controlled by visual perception. The processes of segmentation of a view field are programmed according to the object of surveillance. Positions of things to be checked in detail must be listed through rough analyses. The area of secondary analyses is directed towards a selected thing and the calculation of function similar to a zoom lens is carried out for the normalisation of number of pixels. A decoder unifies results of analyses. The action of the machine is triggered by a cognitive activity of top priority. The surveillance system must interact frequently with the outer world. Each operation

ends at its output. The causality makes prediction possible. Although original causalities of the image are obtained heuristically, the checking list for a machine is implemented via a human. Moreover, the visual intelligence is obtained without language use, but a linguistic expression is available as a symbol of integrated activities.

◆ **A statistical explanation of visual and kinesthetic space with a learning restriction: Independent scalar learning for each summation (ISLES) model**

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Human perceptual space shows various distortions of the physical space. The various phenomenal deviations are known as illusions. We propose a statistical learning model for an integrated explanation of the deviations. The model is a neural network model with a scalar learning rule. The model can explain not only distortions of visual space, but also distortions of kinesthetic space and sensory motor coordination. The spatial deviations in the model after sufficient learning are explained on the hypothesis that the model can learn only a part of the input signal space because the samples of input signals are limited as human developmental experiences by the human physical embodiment. The shapes of Helmholtz's horopter are explained as the limitation of effective learning area in vergence. The difference between the parallel alley and the distance alley is explained as the difference of whether the constancy of ordinal scale or interval scale is kept under the learning. The asymmetrical inclination of the vertical horopter is explained as the asymmetrically visual experiences obstructed by the presence of ground. Not only the shape of haptic horopter and alley, but also the shape of auditory horopter and alley are explained similarly. The deviations in the reaching movements to visual targets when using a hand are explained as the bias of hand reachable area and the nonlinear transformation under the eye–hand coordination during reaching. In particular, the difference between the active reaching and the passive reaching is explained as the difference between input/output signals on each reaching motion: “from the eye to the hand” and “from the hand to the eye”. This model not only explains them but also predicts other phenomena of spatial correspondences in space perception. The ISLES model is useful for modeling the integration of space perception.

◆ **Colour constancy as Bayesian inference on scene statistics**

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The problem of colour constancy is formulated as Bayesian inference on scene statistics to recover the colour of incident illumination. We begin with the data-rendering equation describing the relation between the illuminant and statistics of surface colours, and statistics of the observed scene. We focus here on the first-order and second-order statistics (mean and luminance–colour correlation) of the scene which are likely to be cues for the illuminant colour as suggested by recent psychophysical observations. Then, we construct prior distributions for statistics of the illuminants and a set of surface colours as the probability density describing particular illuminants and surfaces existing in the world. Simulation results show that Bayesian estimates for the illuminant colour which maximise a posteriori probability computed with a given scene are robust across hue distribution changes of surface colours. To evaluate the performance of the model, we first tested it for scenes similar to stimuli used by Golz and MacLeod (2002 *Nature* 415 637–645). The estimated luminance colour systematically depends on the luminance–colour correlation of the observed scene. This simulation result resembles the observation by Golz and MacLeod: more reddish illuminant is estimated for higher luminance–redness correlation. Furthermore, our model predicts that luminance–blueness correlation also affects the estimated illuminant colour in a similar fashion to luminance–redness correlation. Also, we compared the performance for illuminant colour estimation with the gray-world algorithm, the proposed Bayesian model, and the Bayesian model without luminance–colour correlation. Although no models achieved perfect colour constancy, performance of the proposed model seems to be superior to that of the other two models because estimates tend to be clustered according to illuminant colour despite the hue distributions of surfaces. The proposed Bayesian framework for the problem of the colour constancy using scene statistics provides clues for understanding how the visual system uses scene statistics to solve vision problems.

[Supported in part by the 21st Century COE Program ‘Intelligent Human Sensing’]

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◆ **Modelfest and contrast-interrelation-function data predicted by a retinal model**

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Information is coded by isotropic filters (retinal ganglion cells) and anisotropic ones (cortical simple and complex cells). A retinal detection model was studied by du Buf (1992 *Spatial Vision* 6 25–60). Recently, cortical detection models were explored (du Buf and Bobinger, 2002 *Perception* 31 Supplement, 137). All models are based on nonlinear summation of filter responses (frequency and/or orientation channels) over (local) neighbourhoods and can, after some optimisation, predict detection data of many stimulus patterns. The fact that both retinal and cortical models can be made to predict data leads to the fundamental question: where exactly are spatial patterns detected? This revived our interest in retinal models, and we tested the simplest one: in the case of Modelfest data, nonlinear summation with exponent 3.2 over a ‘foveal’ area of 4 deg within each channel, and summation over eight frequency channels (0.5 to 20 cycles deg⁻¹) with exponent 2. Channel gain factors were calibrated, for each subject, by using the first 10 stimuli (Gabor patches). After excluding three subjects (overall worst predictions) and 4 stimuli (Gaussian blobs, all predictions too low; noise and town, all predictions too high), excellent predictions were obtained for 62% of the remaining 29 stimuli and thirteen subjects. The same model, but with spatial summation with exponent 3 and after calibration with data of Bessel-type stimuli, gave excellent predictions of contrast-interrelation-function data obtained by subliminal summation of two stimuli: radial Bessel on disk and on double disk (Meinhardt and Mortensen, 2001 *Biological Cybernetics* 84 63–74), and linear but windowed gratings (Meinhardt, 2001 *Biological Cybernetics* 85 401–422). Results suggest that basic detection takes place in the retina and that more effort should be devoted to optimising retinal models.

[Data produced by U Bobinger while supported by POCTI/36445/PSI/2000 and FEDER, and FCT/POSI framework QCA III.]

◆ **Multi-scale keypoint hierarchy for focus-of-attention and object detection**

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Hypercolumns in area V1 contain frequency- and orientation-selective simple and complex cells for line (bar) and edge coding, plus end-stopped cells for keypoint (vertex) detection. A single-scale (single-frequency) mathematical model of single and double end-stopped cells on the basis of Gabor filter responses was developed by Heitger et al (1992 *Vision Research* 32 963–981). We developed an improved model by stabilising keypoint detection over neighbouring micro-scales. Because of the many filter scales represented by simple and complex cells, it is likely that, apart from a multi-scale line/edge representation, the visual cortex also constructs a multi-scale keypoint representation over multiple frequency octaves. Simulations with many different objects showed that, at very coarse scales, keypoints are found near the centre (centroid) of the objects. At medium scales, keypoints are detected at important parts of objects, for example the ‘fingers’ of plant leaves, whereas at finest scales they are found at points of high curvature on the contour. In other words, the multi-scale keypoint representation offers a hierarchical structure in terms of object, sub-objects, and contour. In addition, a retinotopic summation of all detected keypoints over all scales provides one map with peaks caused by keypoints that are stable over many scales, and this map can be used as a salience map for focus-of-attention (FoA). Further experiments showed that, for example, face detection can be achieved by grouping keypoints at expected positions (eyes, nose, mouth), taking into account symmetries and distances, and by combining suitable scales. Hence, position-, rotation-, and scale-invariant face detection may be achieved by embedding the multi-scale keypoint representation, in addition to the line/edge representation, into feedforward and feedback streams to/from higher areas V2, V4, and IT (what, or parvo system), whereas the salience map for FoA interacts with short-term memory via areas PP and MT (where, or magno system).

[Supported by PRODEP III Medida 5-Açção 5.3.]

◆ **Control of chaos in the visual system**

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Though chaotic dynamics have been much studied with respect to the activity of the brain and the heart, only very few reports can be found that are related to chaotic trends in the eye; some studies have been published relating to the vertebrate eye but data can be easier to obtain and

interpret by investigating the insect model eye. Here, we study the response of the visual system to intermittent light stimulation by electroretinographic (ERG) recording. We studied stimulus transduction using the model eye of *Drosophila melanogaster* provided with a highly developed visual system, though with a more limited set of neurons than the human eye. The ERG signal can provide information from three main types of visual cells located in the retina and in the first optical ganglion. Various computational tests have been applied in order to carry out a diagnosis of the dynamics of the visual system. At a relatively low frequency of intermittent light illumination, a dominant quasi-periodic trend as well as a chaotic overlapped component have been revealed in the ERG data. At higher frequencies, a significant change occurs in the ERG signal: the hyperpolarisation component is smaller for every second signal in every pair of consecutive signals, while the depolarisation component remains the same for all consecutive signals. Simultaneously, the chaotic trend of visual system dynamics is obviously enhanced. Only small differences in the critical frequency are noticed when passing over from the wild *Drosophila* type to the white, eye mutants. One could therefore control the chaotic dynamic component by adjusting the intermittent light frequency. The physiological explanation is based on the peculiarities of the photoreceptor and the neural cells that are involved in the generation of different ERG components. The hypothesis of resonant oscillators identifiable with the two main cells from the first optic ganglion is discussed.

◆ **Effectiveness of the sensitivity measures in relation to the stimulus range**

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Our research group, in different investigations, has studied the comparison between different sensitivity measures in psychophysical tasks [eg Garriga-Trillo, 1987 "Olfactory psychophysics: sensitivity measures", in *Progress in Mathematical Psychology 1* Eds Roskam and Suck (Amsterdam: North Holland) pp 343–349; Fontes, 1988 *Psicofísica de la Estimación de Distancias entre dos Rectas Verticales y Paralelas* PhD thesis, UNED, Madrid; Villarino, 1994 *Medidas de la Sensibilidad Gustativa: Una Aplicación para la Discriminación de Vinos* PhD thesis, UNED: Madrid], using always the same methodology: to calculate the relationship between different measures derived from several theoretical models. In this work, we continue that line of investigation, centring us in the sensitivity measures derived from Stevens's model [1975 *Psychophysics: Introduction to Its Perceptual, Neural and Social Prospects* (New York: John Wiley)]. Applying the magnitude estimation technique to visual stimuli (lines and squares), we created two experimental conditions for each stimulus pattern: (i) wide stimulus range, and (ii) narrow stimulus range. Our goal was to study the performance of each sensitivity measure in relation to the response bias under the influence of this stimulus range. Our results suggest that it would be useful to study the factors that cause response bias in psychophysical tasks from an individual perspective.

◆ **Efficient representation of natural images by local cooperation**

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Low-level perceptual computations may be understood in terms of efficient codes (Simoncelli and Olshausen, 2001 *Annual Review of Neuroscience* **24** 1193–1216). Following this argument, we explore models of representation for natural static images as a way to understand the processing of information in the primary visual cortex. This representation is here based on a generative linear model of the synthesis of images with an over-complete multi-resolution dictionary of edges. This transform is implemented with log-Gabor filters and permits an exact reconstruction of any image. However, this linear representation is redundant, and since different representations may correspond to any image, we explore more efficient representations of the image. The problem is stated as an ill-posed inverse problem, and we compare first different known strategies by computing the efficiency of the solutions given by matching pursuit (Perrinet, 2004 *IEEE Transactions on Neural Networks* **15** 1164–1175) and sparse edge coding (Fischer, in press *Transactions on Image Processing*) with classical representation methods such as JPEG. This comparison allows us to provide a synthesised approach with a probabilistic representation which would progressively construct the neural representation by using lateral cooperations. We propose an algorithm which dynamically diffuses information to correlated filters so as to yield a progressively disambiguated representation. This approach takes advantage of the computational properties of spiking neurons such as integrate-and-fire neurons, and provides an efficient yet simple model for the representation of natural images. This representation is directly linked with the edge content of natural

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images and we show applications of this method to edge extraction, denoising, and compression. We also show that this dynamical approach fits with neurophysiological observations and may explain the nonlinear interactions between neighbouring neurons which may be observed in the cortex.

VISUOMOTOR CONTROL

◆ **Frame of reference effects in a video-controlled reaching task**

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We showed previously (Huber and Hellmann, 2003 *Perception* 32 Supplement, 121–122) that rotations of camera perspective in video-controlled reaching tasks reduced movement accuracy and lengthened the time needed to carry out these movements. The movement error suggested a bias towards the pictorial target point (PTP). We carried out new experiments to confirm this hypothesis. Participants in our experiments carried out a reaching task using visual input from a real-time video display. Direct vision of hand and workspace was precluded. In experiments 1 and 2, participants ($N = 28$ and $N = 24$) carried out reaching movements towards 6 target points in a randomised design, resulting in a systematic directional error towards PTP. In experiment 3 ($N = 17$), we attempted to modify frame-of-reference effects by means of large arrows indicating what in a cartographic map would be up-north. Contrary to expectations, this manipulation had little effect on the angular direction, although performance (speed, spatial accuracy) slightly improved. In experiment 4 ($N = 12$), we replaced the rotation of the camera by turning the display monitor instead, aiming to test whether the monitor would provide a more effective frame of reference. While, as expected, the effects of the monitor rotations were smaller than those due to camera rotations, the effects of rotation did not disappear. The pattern of results was similar to that found in the earlier experiments. In addition, we investigated practice effects. Even within a short number of trials, significant learning effects could be shown. In a separate experiment, participants carried out a large number of trials. While general improvements could be shown, the differences between the unrotated (0°) and the rotated conditions remained stable. We conclude that the directional error towards PTP is likely to be due to transformations between different frames of reference. Attempts to reduce these effects have been so far of limited success.

◆ **Adaptive strategies for perception – action coupling**

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The detailed characteristics of perception – action coupling have been studied with a sensorimotor pointing task. Using a graphical pen, subjects ($N = 6$) had to point to the final location of the invisible centre of simple geometrical shapes—cross, diamond, chevron—after their movement along a circular—clockwise or counter-clockwise—trajectory ended. The target shapes could be fully visible, thus yielding a highly coherent motion percept, or presented behind vertical rectangular masks. In these latter conditions, perceived global coherence was dependent upon the visibility of the masks. Constant and variable errors and the spatial distribution of pointing responses indicate the following. (i) Accuracy of pointing responses is better at high than at low motion coherence. (ii) With fully coherent shapes, pointing accuracy is similar for a cross and a single spot—ie baseline condition—and worse for the diamond and chevron for which the profiles of the spatial distribution of pointing responses are different. In addition, pointing responses are biased in the direction of motion—representational momentum—an effect which disappears with decreasing coherence. (iii) At low coherence, the location of the target centre is overestimated and many pointing errors occur. Overall, observers appear to adapt their motor strategies to the specific context—ie shape and coherence—within which they have to deploy their action. These results, showing comparable, although slightly different, biases for perception and action, are discussed in the light of the proposed dichotomy of dedicated functional processes through the ventral and dorsal pathways.

◆ **The influence of the Brentano illusion on saccades and pointing movements**

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When making an eye and hand movement towards the same target, the eye and hand can either use the same source of visual information to perform the task or a different one. Using the same information is efficient; however, if this information contains an error, this causes the eye as well as the hand to be incorrect. In this study, we tried to find out whether saccades and

pointing movements use the same source of information when eye and hand movements are performed either in the same or in separate trials. Three experiments were performed with the Brentano illusion, which primarily influences judgments of length, but not those of position. A task will only be influenced by this illusion if the task requires a visual estimate of length. In an earlier study (de Grave et al, 2004 *Experimental Brain Research* **155** 56–62), it was found that the hand uses illusory length information when pointing to a visual target. If the eye uses the same information to perform a saccade, we expect a similar effect of the illusion on saccades as on pointing. In the first experiment ('combined'), subjects were required to make saccades as well as pointing movements in the same trial from one end vertex of the Brentano illusion towards the middle vertex. In the other two experiments ('separate'), the same stimuli were used but now subjects had to make either only pointing movements while keeping fixation or only saccadic eye movements. The Brentano illusion influenced eye and hand movements in all three experiments (saccades combined: $26\% \pm 3\%$; pointing combined: $27\% \pm 2\%$; saccades separate: $27\% \pm 2\%$; pointing separate: $31\% \pm 2\%$). No difference in illusion effect was found between the different experiments, which favours the interpretation that similar sources of information are used in eye and hand movements.

[Supported by a grant from the Deutsche Forschungsgemeinschaft (DFG: FR 2100/1-1) and by the European Research Training Network: Perception for Recognition and Action (PRA).]

◆ **Vision of the thumb as the guide to prehension**

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Prehension involves transporting the hand to the target location and then applying an appropriate grasp to secure and lift the object. Considerable debate surrounds the role of vision in the implementation of these actions. The 'two-digit' hypothesis (Smeets and Brenner, 1999 *Motor Control* **3** 237–271) argues that both thumb and finger are transported under visual control to simultaneously pincer optimal grip-points on the object, whereas Wing and Fraser (1983 *Quarterly Journal of Experimental Psychology* **35** 297–309) presented evidence that the thumb is the primary visual guide, at least during the pre-contact phase of hand transport. A 'third-way' hypothesis (Mon-Williams and McIntosh, 2000 *Experimental Brain Research* **134** 268–273), however, proposes that the particular digit chosen as the guide may be influenced by specific task conditions. Using motion-capture cameras, we tracked subjects' thumb and finger as they made precision grasps to pick up cylindrical objects [(2 sizes, 4 locations), under normal (binocular) and reduced-cue (monocular)] viewing. We found that the thumb made first contact with the target object on $\sim 80\%$ – 90% of trials, with little influence of the objects' spatial properties or the visual information available. These findings suggest that the consistently preferred strategy in visually guided prehension is to transport the thumb to a selected point on the target object and then close the grip by moving the finger in behind. This was supported by a second experiment, in which subjects reached and grasped cylindrical objects with either the thumb or finger selectively occluded from view. Inability to see the thumb caused major disruptions, mainly to the transport phase of prehension, while the no-vision-of-the-finger condition resulted in just a single grasping-related deficit. This suggests that the thumb is important to the on-line control of prehension for basic symmetrical objects, perhaps serving as a reference for 'disparity nulling' between the approaching hand and the target.

◆ **Motor preparation in top-level marksmen**

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The effect of motor experience on the brain activity was investigated in a special population: high-level rifle marksmen. Movement-related cortical potentials (MRCP) to self-paced movement of the left and right index fingers were recorded in two groups of subjects: marksmen and controls. All subjects were right-handers. The following MRCP components were considered: Bereitschaftspotential (BP), negative slope (NS'), motor potential (MP), and re-afferent positivity (RAP). The BP and NS' components, which emerged prior to movement onset, are associated with motor preparation. For right-finger flexion (but not for left-finger flexion) differences were found between groups. BP and NS' latencies were longer for marksmen than for controls; amplitudes were smaller. In contrast, no difference was found between groups for MP and RAP amplitude or latency. Sources analysis, based on a realistic model of the brain, showed with high reliability (97% of variance explained) that the BP (time window: -1500 to -400 ms), NS' (-400 to -50 ms), MP (0 to $+100$ ms), and RAP ($+100$ to $+200$ ms) components were generated in the supplementary motor area, pre-motor area, primary motor area, and somatosensory area, respectively.

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No difference was found between groups regarding the localisation of generators of all components. The results are discussed in terms of economy of motor preparation due to the specific practice involved in shooting. Results are relevant for the interpretation of previous data on saccadic latencies collected in the same athletes (Di Russo et al, 2003 *Vision Research* **43** 1837–1845).

◆ **Regulation of sensorimotor actions in conditions of closed space**

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Research on closed-space perception has been conducted by students who visited caves for the first time. The results show that light adaptation and perception of closed space are individual. People experience various fears and sensuous illusions. Visual information inside a cave is poor. Perception of directions, intervals, and objects becomes complicated. Orientation in closed space leads to intensification of all senses. The research proves that stress in the extreme conditions of closed space raises the energy potential of a person. Muscle sense plays an important role in closed-space orientation. The experiment shows an interesting fact: students with a leading right eye had a vulnerable right side and those with a leading left eye were consequently injured from the left.

◆ **Constant effects of the rod-and-frame illusion on delayed perceptuomotor tasks**

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Task-dependence is an important topic in the search for neural correlates of perception–action relationships. The present study focuses on the extent to which the rod-and-frame illusion (RFI) is task-dependent. In three experiments, participants were asked to perform different visuomotor tasks with responses that consisted either of (i) replicating the orientation of the stimulus rod by rotating a line on a computer screen through a series of key presses, (ii) making a perceptual judgment about the rod orientation in a forced-choice paradigm, or (iii) rotating and propelling a hand-held cylinder in order to replicate the orientation of the stimulus rod. The effects of the RFI proved robust and constant, irrespective of whether the task required perceptual or motor processes. Our findings add to the generality of the claim that visual illusions are task-dependent. The task-independence of the RFI with delayed responses reported here refines the results of Dyde and Milner (2002 *Experimental Brain Research* **144** 518–527), who found task-dependent effects of the RFI under no-delay conditions.

◆ **Reference-frame effects on postural compensation during visual vehicle control**

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The optokinetic cervical reflex (OKCR) is a visually mediated postural movement in which a pilot tilts the head in synchrony with the horizon when the aircraft banks. One explanation for OKCR is that it helps the visual system maintain a world-based reference frame. This suggests that, if the pilot were induced to adopt an alternative reference frame (eg that of the vehicle), OKCR would change or weaken. We performed experiments in a model cockpit to measure OKCR with different flight displays, among which the reference frame was varied. Experiment 1 recorded OKCR with traditional ‘inside-out’ flight displays, where the aircraft symbol remained stationary and the external world moved around it, as in a periscope view. Curves mapping head tilt against horizon tilt had positive slopes. In experiment 2, we compared the inside-out display against two other configurations, which incorporated ‘outside-in’ feedback. A fully outside-in display depicted pitch and bank manoeuvres with a moving aircraft symbol while keeping the horizon stationary. An intermediate ‘frequency-separated’ display depicted steady-state aircraft bank with an inside-out moving horizon, while indicating transient manoeuvres with an outside-in aircraft symbol moving in synchrony with the joystick. Positive head-tilt slopes were recorded in inside-out and frequency-separated conditions, indicating that posture was yoked to the external horizon. Notably, however, the outside-in condition brought about slightly negative head-tilt slopes; furthermore, in both the frequency-separated and outside-in conditions, subjects made transient movements in synchrony with the moving aircraft symbol, not the horizon. This indicates that, while pilots adopted the external-horizon reference frame most of the time, some pilots were orienting to their own vehicle some of the time. This transient adoption of the local reference frame might result from the control link between joystick and aircraft symbol. Further investigation can determine why the adoption of the external reference frame by moving viewers can falter.

◆ **Visuo-motor interactions in the flash-lag effect**

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The flash-lag effect (FLE) is a visual illusion that consists in perceiving a flashed stimulus behind an aligned moving target. In this study, we investigated whether the motor system interacts with the visual system in this illusory perception. Subjects ($N = 24$) performed a visual judgment task in two visuo-motor conditions and in a control visual condition: they had to state whether a flash appeared behind or ahead of a small disk (diameter 0.27 deg) moving on a computer screen along a circular trajectory (diameter 5.12 deg). Fixation was held during the task. In the control condition, the computer controlled the movement of the disk along the trajectory. The moment at which the flash was presented and the position of the moving stimulus at the time of the flash were random. A double staircase algorithm controlled the position of the flash relative to the moving disk. The first visuo-motor condition was similar to the control condition except for the fact that subjects controlled the movement of the disk by moving a robotic manipulandum (Phantom 1.5, Sensable Technology). The robot produced a force field that maintained the manipulandum on the circular trajectory. The instantaneous velocity was monitored to ensure that subjects moved the disk at a similar speed in all conditions. The second visuo-motor condition was the same as the first one, but subjects had to produce a constant force (203.9 g force) against the robot to move the manipulandum along the trajectory. The flash-lag effect was observed in all conditions. A repeated-measures ANOVA and a Duncan a posteriori test revealed that it was significantly greater in the visuo-motor conditions than in the control condition. This finding demonstrates that the motor system interacts with the visual system while perceiving moving objects.

◆ **Knowing where, but not getting there: Visual navigation in adolescents with early periventricular lesions**

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Visual navigation in familiar and unfamiliar surroundings is an essential ingredient of adaptive daily-life behaviours. Brain imaging helps to reveal the neural network subserving visuospatial navigation that involves several cortical regions and the right hippocampus (Grön et al, 2000 *Nature Neuroscience* 3 404–408). Recent work suggests that interrelations and connectivity between brain structures, rather than integrity of each structure per se, are of importance for successful navigation (Holscher, 2003 *Reviews in Neurosciences* 14 253–284). Here we ask whether the ability to navigate is impaired in adolescents who were born premature and suffer congenital bilateral damage to periventricular brain regions. Performance on a 2-D labyrinth task was significantly lower in patients with periventricular leukomalacia as compared with premature-born controls without lesions and term-born adolescents. The ability of visual navigation inversely relates to the severity of the motor disability, leg-dominated bilateral spastic cerebral palsy. This agrees with the view that navigation ability substantially improves with practice (Maguire et al, 2000 *Proceedings of National Academy of Sciences of the USA* 97 4398–4403), and might be compromised in individuals with restrictions in active spatial exploration. Visual navigation is negatively related to the volumetric extent of lesions over the right parieto-occipital and frontal periventricular regions. Whereas impairments of visual processing of point-light biological motion are associated with bilateral parietal periventricular lesions (Pavlova et al, 2003 *Brain* 126 692–701; Pavlova et al, 2005 *Cerebral Cortex* 15 594–601), navigation ability is specifically linked to the frontal periventricular lesions in the right hemisphere. We suggest, therefore, that more anterior periventricular lesions might impair the interrelations between the right hippocampus and cortical areas leading to disintegration of neural networks engaged in visual navigation. A further step toward uncovering the functional neuropathology of visual navigation would be an analysis of the time course and dynamic topography of brain activity.

[Supported by the DFG and by the Medical School of the University of Tübingen.]

◆ **Using a Kalman filter to predict visuomotor adaptation behaviour**

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The sensorimotor system recalibrates when the visual and motor maps are in conflict, bringing the maps back into correspondence. We investigated the rate at which this recalibration occurs.

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The Kalman filter is a reasonable statistical model for describing visuomotor adaptation. It predicts that the rate of adaptation is dependent on the reliability of the feedback signal. It also predicts that random trial-to-trial perturbation of the feedback signal should have little or no effect on the adaptation rate. We tested these predictions using a pointing task. Subjects pointed with the unseen hand to a brief visual target. Visual feedback was then provided to indicate where the pointing movement had landed. During the experiment, we introduced a constant conflict between the pointing and feedback locations, and we examined the changes in pointing as the subject adapted. From the change in pointing position over trials we determined the adaptation rate. In experiment 1, we tested whether the reliability of the feedback affected adaptation rate by blurring the visual feedback and thereby reducing its localisability. Six levels of blur were used and spatial discrimination measurements confirmed that the blur was effective in altering stimulus localisability. We also constructed a Kalman filter model of the task. We found that adaptation rates of the filter and of the subjects decreased when blur was increased (ie with less reliable feedback). In experiment 2, the reliability of the visual feedback signal was manipulated by randomly perturbing the feedback signal on a trial-by-trial basis. Again, in good agreement with the prediction of the Kalman filter, we found no significant effect on adaptation rate as we manipulated the amount of perturbation. Taken together, these results provide evidence that human visuomotor adaptation behaviour is well modeled by a Kalman filter that uses weighted information from previous trials, including the reliability of the information, to update the visuomotor map.

[Supported by the 5th Framework European Project Touch-HapSys (IST-2001-38040).]

◆ **Visual strategies when catching a ball**

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Prediction is important for positioning gaze in tasks requiring sensorimotor coordination (Flanagan et al, 2003 *Current Biology* 13 146–150; Land and McLeod, 2000 *Nature Neuroscience* 3 1340–1345). We asked subjects to catch a tennis ball thrown by them against a wall, ensuring that it bounced on the floor prior to contact with the wall. Our aim was to see if there was a greater reliance on prediction when subjects received additional information from the throw, compared with subjects who simply caught the ball in an earlier study. Specifically, we were interested in differences in eye-movement strategies at the time of the bounce. On average, the ball bounced 175 ms and 339 ms after release. Subjects looked at the first bounce point less frequently (20%) than at the second (80%). They pursued the returning ball from the second bounce point. Fixations were significantly closer to the second bounce point (wall) than to the first (7° vs 13°). Arrival of gaze on the wall preceded the ball by 324 ms. This was much earlier than for subjects who caught the ball thrown by another person (53 ms prior to bounce). This implies that knowledge of the throw allows a greater use of prediction, and that different strategies can be used when catching a ball. Fixating the wall when bouncing the ball off the floor suggests we can rely on internal models of the properties of the ball and the environment in tasks such as throwing and catching.

[Supported by NIH Grants EY05729 and RR09283.]

◆ **Biomechanical costs and grip planning: A model**

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When grasping an object with a precision grip, the best positions to place one's fingertips depend on the object's shape. The grip axis should pass through the centre of gravity to prevent the object from rotating when lifted. The grip force should be perpendicular to the object's surface so that the fingertips don't slip. The forces applied by the two fingertips should have the same size but opposite directions so that the net torque is zero. For circular cylinders, these constraints still leave an infinite number of suitable grip orientations, but cylinders with an elliptical circumference can best be grasped along one of their principal axes. Cuijpers et al (2004 *Journal of Neurophysiology* 91 2598–2606) found that such cylinders are indeed grasped near their principal axes, but with systematic 'errors'. They showed that these 'errors' were planned in advance. The question is whether these errors are partly due to distortions of the visually perceived shape or only due to biases towards more comfortable grip postures. To find out, we modelled the data as a trade-off between an optimal and a comfortable grip using a biomechanical cost/gain function that considers the influence of the object's shape on the stability of the grip. We found

differences between the model and the data that depended systematically on the cylinder's aspect ratio and orientation. Thus, perceptual errors do contribute to the motor errors.

[Supported by NWO MaGw 410-203-04.]

◆ **Dissociation between the use of vergence and binocular disparity information in the control of reaching and grasping movements**

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Binocular information provides important advantages for controlling reach-to-grasp movements. To investigate the source(s) of the binocular advantages, we examined the effects of independently altering vergence or disparity cues on the performance of these manual actions. Four viewing conditions were created by randomly placing a plano lens (control), a prism lens (8 D base-in or base-out), or a low-power (+2 to 4 D) spherical lens over the eye opposite to the subjects' preferred hand prior to each movement trial. The prism lenses were designed to selectively interfere with vergence-specified distance (VSD) information, while the spherical lens reduced disparity sensitivity in each subject to 480 s of arc. Following a brief adjustment to the given lens (3 s preview), subjects reached and picked up cylindrical objects (2 sizes, 3 locations) with a precision grip, while their hand kinematics were recorded with the ProReflex 3-D-motion capture system (Qualisys, Sweden). Key-dependent measures of the movements made under each viewing condition were analysed from the mean and quartile data obtained. Subjects produced the shortest times to establish initial object contact, and they made contact at the highest velocity and with the widest grip under the base-in prism condition. These effects are mutually consistent with uncorrected over-reaching of the objects based on their VSD as being further away than they actually were. Conversely, subjects produced the longest times to object contact under the spherical lens condition. This occurred because they specifically prolonged the period of grip closure, consistent with uncertainty about the positions of the optimal grasp points on the objects relative to the approaching digits. Our results suggest that, under normal binocular conditions, vergence information contributes to the efficient programming of the reach, whereas binocular disparity cues provide advantages for executing the grasp.

[Supported by the Wellcome Trust.]

◆ **Change of the contribution of head movement for gazing target associated with different tasks**

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Our object was to investigate whether the contribution of head movement for gazing target changes depending on the task. In the experiment, subjects were required to gaze at a single-word target displayed 7 to 40 deg vertically or horizontally from the centre by naturally moving their eyes and head. Each trial was associated with either of two tasks: target recognition or pointing movement. Subjects' head movements were recorded with a head-movement tracker, and fixation on the target in each trial was confirmed by an eye-tracking system which could impose eye position on the video output of the camera mounted on the subject's head. We found that proportions of head movements were largely varied between subjects, but relatively less varied within each subject. Pointing movements increased the proportions of the head movement, and reduced the variance in these proportions within each subject. However, the latency of the head movement was not significantly changed between the tasks. In an additional experiment, recognition task was performed with target words flanked by distractors. The latter had similar effects to pointing movement. These results suggest that the proportion of head movement in gazing at a target varies with attentional demands required by the tasks.

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