CEREBRAL ICONICS: HOW ARE VISUAL STIMULI REPRESENTED CENTRALLY IN THE HUMAN BRAIN?

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Abstract. In the case of some sensory attributes (e.g. luminance), differential thresholds increase with the spatial separation between the stimuli to be compared, but in other cases (e.g. spatial frequency, hue) thresholds vary little whether the stimuli are close together or separated by 10 degrees of arc. To this latter class of sensory attributes, we here add two dimensions: Speed of motion and Chromatic purity. Stimuli were presented too briefly for an eye movement and could fall at any positions on an imaginary circle centred on the fixation point. What neural mechanisms underlie discrimination in such tasks? We doubt discrimination depends on a large array of dedicated 'comparator neurons', one for each possible pair of positions in the visual field and for each sensory attribute. Instead we suggest that information about local sensory properties is carried to the cortical site of comparison by neural connections that resemble the man-made Internet in so far as the same physical substrate from moment to moment carries different information in a symbolic code.

Introduction.

In this journal, twenty years ago, we raised an empirical question and a theoretical question regarding the human ability to compare the sensory properties of two stimuli briefly presented at two well-separated points in the visual field [1]. The empirical question was this: How precisely can such comparisons be made when the stimuli are well separated by up to 10 degrees of visual angle and even fall in opposite hemifields? The theoretical question – one seldom asked – was: What are the neural processes that underlie such comparisons? This simple psychophysical task raises fundamental questions about cerebral iconics, that is, about the representation of perceptual stimuli at central levels in the brain.

In the case of some sensory attributes, such as luminance [2], retinal disparity [3] and temporal phase [4], the precision of discrimination deteriorates rapidly as the discriminanda – the stimuli to be compared – are spatially separated in the visual field. In such cases, we can imagine that the observer's performance depends on dedicated comparator neurons at an early stage in the visual system. A paradigmatic example of a comparator neuron would be a retinal ganglion cell that draws excitatory and inhibitory inputs from spatially distinct regions of the local receptor array. Such a ganglion cell is sensitive to local contrast; and it is plausible, for example, that it is contrast signals from such cells that an observer uses in equating two abutting fields in a traditional visual photometer [5 pp 526-8].

In the case of other sensory properties, however, the observer's thresholds are similar whether the two targets are abutting or are spatially remote from one another; and this is the case even though the stimuli are presented so briefly that there is no time for an eye movement from one to the other. We have found that this is essentially the case for discriminating the spatial frequency of briefly presented gabors [6], for discriminating the contrast of gabors [6], and for discriminating each of the two cardinal dimensions of hue [7].

Human observers make such comparisons so effortlessly that it has seldom been asked how they do it. It is implausible that they rely on difference signals generated by a large array of dedicated comparator neurons, one for each pairing of positions in the field and one for each of several sensory attributes. Long-distance comparator neurons of this kind – 'dissociated dipole operators' – have sometimes been postulated [8], but at least three difficulties arise if

such dedicated comparator neurons are invoked to explain the results of our experiments on comparison at a distance [6]: (i) there is a combinatorial explosion in number of comparator neurons required if any two regions of the visual field are to be compared; (ii) the many long-distance connections will require a large bulk of white matter; and (iii) each action potential has a significant energetic cost [9] and, unless some extra apparatus is postulated, there will be an extravagant waste of energy if signals are continuously broadcast to the array of comparator neurons.

The present study. In this paper, we report exploratory data on two further sensory dimensions that resemble spatial frequency in that there is little or no deterioration in discrimination when the discriminanda are separated by up to 10 degrees of visual angle.   The two new dimensions – speed of motion and chromatic purity – are of interest because they are both what S. S. Stevens classically called *prothetic* dimensions [10, 11]: Along such a dimension, the sensation varies in strength, whereas on a metathetic dimension, such as hue, the sensation varies in quality. It is often supposed that prothetic dimensions are encoded at early sensory stages by the strength of response in a subset of neurons, whereas metathetic dimensions are encoded by place, i.e. by which neurons are active.

The case of speed. The perception of motion is an attractive example to study, since there is evidence of local comparators that identify relative motion in adjacent regions.

The most primitive motion-detector is itself a comparator, comparing the excitations at different retinal positions at different times [12], but there is evidence in mammalian visual systems for hard-wired detectors that respond to *contrasts* of motion. For example, in cortical area MT (middle temporal area) of the primate, many directionally-selective neurons exhibit a suppressive surround outside the classical receptive field, and their response is attenuated if motion of the centre-preferred direction is also present in the larger region [13]. Similarly, Ölvecsky and colleagues [14] recorded from directionally selective ON-OFF cells in the mammalian retina and found the response was reduced when motion was also present in the surround of the cell's receptive field. And there is also psychophysical evidence that suggests sensory channels sensitive to local contrast of motion: a recurrent, and remarkable, finding has

been that the after-effect of seen motion is essentially abolished if the adapting stimulus fills the entire visual field [15, 16, 17].

So motion offers a valuable test case. At short separations, comparison may depend on hard-wired comparators and the discrimination thresholds may be very low. When the stimuli are well separated in the field, a central comparison may be required and thresholds may be higher. However, the experimental outcome cannot be predicted in advance. The important role of bilateral optic flow in balance and locomotion suggests that the human brain may have specialised mechanisms for long-range comparison of speed. And it may also be relevant that cells with very large receptive fields, sometimes extending across the midline, have been reported in mammalian pre-striate and temporal areas, such as the lateral suprasylvian area of the cat [18], and the prelunate gyrus [19] and the medial superior temporal area [20] of macaque monkeys. Psychophysically, Nishida and colleagues have found good performance when observers must judge the phase relationships of motion in spatially separated regions [21].

Experiment 1. Speed of Motion. Methods.

Apparatus. The stimuli were presented on a 22-inch Mitsubishi Diamond Pro 2070 CRT monitor driven at a resolution of 1024 x 768 pixels and 100 Hz. The stimulus parameters were controlled by a VSG2/5 graphics system (Cambridge Research Systems Ltd, Rochester, UK). The system allows an output resolution of 15 bits per gun. The monitor outputs were linearized with an OptiCal photodiode (Cambridge Research Systems Ltd). The spectral power distribution for each gun at maximal output was measured with a JETI spectroradiometer.

[Figure 1 about here]

Stimuli. The stimuli were arrays of moving red and green dots displayed within sectors located on an imaginary circle of radius equal to 5 degrees of visual angle (see Fig.1a). The sectors had a width of 2 deg at their mid-points. Each dot consisted of a square of 4x4 pixels, which subtended 4.38 angular minutes at the viewing distance of 114 cm. Antialiasing was used to allow displacements of less than 1 pixel between frames. In order to construct the array of dots, we began with a regular array of dots separated by 25 pixels (27.4 ang min), but we then randomly jittered the position of each dot within the sector. The CIE (Commission Internationale de l'Éclairage) luminance of the dots was 38

cd/sq.m. The motion was always horizontal but was randomly to the left or to the right in both sectors. Stimulus duration was 180 ms: this duration is short enough that observers cannot move their eyes from one stimulus to the other during the presentation and it also makes it difficult for observers to rely on secondary cues such as the rate of disappearance of dots at the edge of the stimulus sector. Viewing was binocular.

Procedure. Eight spatial separations from 2 to 10 angular deg were tested in random order within each experimental run. On each trial, one of the two arrays, chosen randomly, was set to the referent speed of 5 deg/s and the other was set to a higher, variable speed. (The referent speed was chosen on the basis of preliminary measurements, which showed that thresholds were elevated at low speeds, as has been found for random dots by earlier investigators [22], while higher speeds produced visible streaking of the dots.) Thresholds were measured using a two-alternative forced choice procedure: the observer's task on each trial was to indicate whether the red or the green dots were moving faster. The colours were randomly assigned to the referent and variable speeds. The ratio of the variable speed to the referent was adjusted by a staircase procedure that tracked 79.4%. The step size was 10% of the difference between test and referent. Data from the first 5 reversals of the staircase were not used, and the subsequent 10 reversals were averaged to give an estimate of the threshold. Five independent estimates of each threshold were accumulated over different experimental days.

The experiments reported in this paper were approved by the Psychology Research Ethics Committee of Cambridge University, United Kingdom.

Observers. The observers were the two authors.

[Figure 2 about here]

Experiment 1. Speed of motion. Results and Discussion

Figure 2 shows that speed thresholds are rather similar over a large range of spatial separations. A repeated-measures ANOVA showed no significant effect of the separation of the discriminanda ($F[1]=1.842$, $p=0.404$, with Greenhouse-Geisser correction). Thus the discrimination of speed resembles the discrimination of spatial frequency [6] in that there is no systematic loss of sensitivity as the spatial separation of the discriminanda increases up to 10 degrees of visual angle.

In the present case, both observers in fact show the highest thresholds not when the discriminanda are furthest apart but when the two arrays of dots are touching (i.e. when there is 2 deg of visual angle between their mid-points). We have previously observed this tendency in the case of hue discrimination [23]. In both cases, the high thresholds for adjacent stimuli may be a result of spatial averaging between the target arrays.

A limitation of the present experiment is that we cannot formally rule out the possibility that our observers are making absolute judgements of one of the stimuli rather than making a true comparison. Ideally we must ensure that the observer does actively compare the internal representations of the two stimuli rather than simply making an absolute judgement with respect to one of the stimuli, comparing it to an internal standard. It is known that observers can establish rather precise internal standards of this kind [24]. In our second experiment, we formally demonstrate that the observers are actively comparing the two discriminanda.

Experiment 2. Chromatic purity.

In this experiment, we examined a further prothetic dimension, chromatic purity, which has a zero value at the white point and a maximal value for monochromatic lights. The subjective counterpart of this dimension is saturation or chroma, although sometimes there may also be secondary changes in hue as purity increases. (The latter is the 'Abney effect' [25].)

Ensuring a true comparison. To ensure an active comparison, we adopted a roving procedure in which there were 25 randomly-interleaved reference stimuli, closely spaced on the stimulus dimension [7, 26]. The observer did not know which stimulus was the referent, and so, if he took only one stimulus into account, he could not score more than 75% correct even if he never made an error on those trials where it was the variable stimulus that he compared to an internal standard. For the experiment to be manageable, however, there could not be separate staircases for each of the 25 reference stimuli. So we first made a preliminary estimate of how the Weber fraction varies along the sensory dimension. We then programmed a single staircase to adjust the factor – the percentage change – by which the variable stimulus differed from

the referent, scaling the factor according to the position of the referent on the dimension.

To check directly that observers could not achieve good discrimination by judging only one of the two stimuli, we also included blocks of trials where the computer program suppressed, on a random basis, either the referent or the variable stimulus, and observer was asked to respond as if both stimuli had been present.

Choice of stimulus region. We measured discrimination thresholds along a horizontal line passing through the white point in the MacLeod-Boynton diagram [27]. Along such a line the signal of the short-wave cones is constant and only the ratio of long- (L) to middle-wave (M) cone excitations is varying. We confined ourselves to increments in the L signal. One advantage of this range is that classical data suggest the Abney effect is minimal [25].

The brief increments in the L signal were presented on a large steady white field. Under such conditions, earlier work on purity discrimination has found that thresholds increase rapidly as the referent stimulus departs from the white point [28]. In exploratory work, we found that there is a range at moderate purities where discrimination thresholds change less rapidly for most observers; and we adopted this range as suitable for our roving procedure.

Experiment 2. Methods.

Apparatus. Experiments were carried out in both Cambridge and St. Petersburg using identical equipment and calibration procedures, with the only difference being that a VSG2/5 graphics system (see above) was used in Cambridge and a ViSaGe graphics system was used in St. Petersburg, allowing resolution of 14 bit per gun.

Stimuli. The stimuli were sectors of an annulus. Their centres were located on an imaginary circle of 5 deg radius (see Fig.1b). The width of the sectors was 2 deg of visual angle at their mid-points. The background was metameric to D65 with CIE luminance 10 cd/m^2, while the luminance of the sectors was 1.3 times higher that of the background. The stimulus duration was 180 msec. The chromaticities of the stimuli were specified in the MacLeod-Boynton chromaticity diagram [27]. Viewing was binocular from a distance of 57 cm.

Procedure. In a preliminary experiment, chromatic purity discrimination was measured for the range of L/(L+M) values from 0.69 to 0.73 along the horizontal axis of the MacLeod-Boynton diagram, while the S/(L+M) value of the stimuli was fixed at the same value as that of Illuminant D65. Measurements of chromatic purity thresholds were made at three spatial separations between the sectors (2, 5.5 and 10 angular deg). The goal of this experiment was to find the function relating thresholds to the L/(L+M) values of the test, as a preliminary to the roving procedure of the main experiment where this function could be used to scale the ratio between referent and variable chromaticities at different values of L/(L+M). Each separation was tested in a separate experimental run; within the run, different referent purities were tested in random order. At least 5 repetitions of each condition were accumulated on different experimental days.

The observer's task was to indicate whether the sector marked with a thin line (see Fig 1b) was of higher or lower purity than the other sector. Thresholds were measured using two-alternative forced-choice with a staircase procedure tracking 79.4%. The step size was 10% of the difference between test and referent. Data from the first 5 reversals of the staircase were not used, and the subsequent 10 reversals were averaged to give an estimate of the threshold.

In the main experiment, eight spatial separations from 2 to 10 angular deg were tested in random order within each experimental run; five repetitions were accumulated on different experimental days. In order to ensure that the observers attended to both the stimuli (rather than comparing only one patch to an internal standard), a roving procedure was used, in which multiple referent purities were tested using only a single staircase. On any given trial, the referent purity was not presented: the chromaticities of the two tests were obtained by adding or subtracting a delta value from the referent. The delta values for different referent purities were scaled according to the thresholds measured in the preliminary experiment. In other respects, the experimental procedure was the same as in the preliminary experiment.

We made a direct check that the observers took into account both of the spatially separated patches and did make a true comparison: in each experimental run, randomly intermixed with the true comparison blocks of trials, was a block in which only one patch was presented on each trial and the observer was asked to make an absolute judgement, judging the single target

with reference to the internal template built up over the course of the experiments. On these trials, the computer program randomly suppressed one or other of the two stimuli that would normally be presented. This block of trials could not be the first block in an experimental run, in order to ensure that observers were familiar with the range of purities in use.

Observers. Four observers (two males, two females) participated in the experiments. Two observers were the authors; the other observers were naïve as to the purpose of the experiments but were highly trained.

[Figure 3 about here]

Experiment 2. Results and Discussion.

Figure 3 (a) shows results for our preliminary experiment, in which thresholds were measured for a range of referents at intermediate levels of purity. Thresholds are plotted directly in terms of the difference between referent and variable stimuli in the value of L/(L+M) in the MacLeod-Boynton diagram [27]. For three observers there is little variation in threshold as purity increases, whereas for Observer 3 the thresholds increase with purity.

The data obtained for each observer were fitted with straight lines and the resulting functions were used to scale the values of referent and variable stimuli in the main experiment.   In Figure 3 (b), thresholds are shown separately for each observer as a function of spatial separation. The rightmost data points in the plot represent the case where the observer was asked to make an absolute judgement.

A repeated-measures ANOVA show a significant effect of separation after Greenhouse-Geisser correction ($F[1.976]=10.053$, $p=0.013$). However, as we have earlier observed for hue discrimination [7, 23], and (above) for speed discrimination, the comparison thresholds are highest not at the largest spatial separations but when the targets are juxtaposed; and here this effect is strong enough to give a significant result in the ANOVA. As we have previously suggested, the elevated thresholds when targets touch may be due to spatial averaging of these parafoveal stimuli. But for our present purpose, the interesting feature of the data is the small variation at larger separations.

Although observers differ in their overall sensitivities in this task, their thresholds when one of the discriminanda is suppressed (rightmost points in

the plot) are always substantially elevated. This confirms that in the comparison case, they are truly taking both stimuli into account.

General discussion.

The present study adds two prothetic sensory dimensions, speed and chromatic purity, to those dimensions where there is remarkably little deterioration in differential threshold as the targets are increasingly separated in the visual field.   The human ability to make such comparisons, easily taken for granted, requires an explanation.

Explanations in terms of dedicated neural comparators. For the reasons given in the Introduction, we doubt that comparisons at a distance are carried out by a battery of dedicated comparator units, one for each possible pair of local positions in the visual field and for each sensory attribute. It might be objected that receptive fields in the visual system become larger at higher levels of analysis in pre-striate cortex [18, 19, 20]. Could discrimination be based on the signals of large-field cells of this kind? This is unlikely. For if a cell is to subserve one of our comparison tasks, it is not enough that it should integrate inputs from a given sensory attribute over a large area. Rather, it must signal the difference, or the ratio, of the values of the stimulus attribute in two specific, local, and arbitrarily chosen regions of its receptive field; and it must preserve the sign of the difference. We are not aware that pre-striate cells of this type have ever been described. They would amount to the hypothetical dipole operators of Balas and Sinha [8].

Even if the results of a particular sensory comparison are represented by activity in a subset of a large array of dedicate dipole operators, another array of dedicated connections would be needed to deliver the results to the cortical site at which a motor response is generated. If any entity – a face, a word, a concept, the outcome of a sensory discrimination – is represented in the brain by the activity of a dedicated neuron (a 'gnostic unit' in Konorski's terminology [29]), then the information is 'frozen' in that cell: the only way the information can be delivered to other points in the brain is by innumerable long-range, dedicated connections.

Explanations in terms of an abstract code carried on a shared bus. At some cortical level, we believe, the use of dedicated neurons must be abandoned and there must be a transition to a stage where the brain operates with an

abstract code, in the way that the individual bits of a man-made computer represent different things – numbers, operators, characters, pixels – from moment to moment. This hypothesis recalls the literature on the 'global neuronal workspace' [30, 31], although the latter literature is primarily concerned with the explanation of human consciousness.

To account for our own particular concern – the comparison of sensory attributes when discriminanda are separated – we have postulated a 'cerebral bus' that delivers information from primary sensory cortex to the site of comparison [6]. We have suggested that the latter lies in the prefrontal cortex [32], and there is of course physiological evidence for this assumption (see for example the work of Pasternak and her colleagues [33]). The cerebral bus is to be identified with the great white-matter tracts of the brain (such as the inferior occipito-frontal fasciculus) and it would resemble the man-made Internet in that the same physical substrate carries different information from moment to moment. Successive messages on the bus may have different originating addresses and different destination addresses. It remains unknown whether this address information is carried on the cerebral bus by parallel fibres or is incorporated in the message itself, in the way that 'headers' in man-made networks carry information about the origin, the destination, and the format of the information being transmitted. The cerebral representations of the individual stimuli used in the present experiment might resemble the 'object files' of Treisman [34], where spatial position is just one attribute encoded among others. What the cerebral bus does do is avoid the need for hard-wired and dedicated connections between every transmitter and every receiver.

We have studied a very humble form of human decision making, but this simple psychophysical task raises fundamental questions about the representation of information at central cortical levels.

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Figure legends.

1. Examples of stimuli used in the experiments.

(a). Example of stimuli for Experiment 1. Two arrays of moving dots are briefly presented at a particular separation (here 5.5 degrees) on an imaginary circle of diameter 10 degrees of visual angle. The observer fixates centrally.

(b) Example of stimuli for Experiment 2. Two sectors of differing purity fall on an imaginary circle, as in (a). Here the separation of the midpoints is 10 degrees.

2. The two panels show results for the individual observers of Experiment 1. The y-axis represents the factor by which the speed of the variable stimulus differs from the referent at threshold. The x-axis represents the separation of the midpoints of the two stimulus arrays (see Figure 1a). Error bars are standard errors of the means. The functions fitted to the data are inverse second-order polynomials and have no theoretical significance.

3. Results for the Experiment 2: Purity discrimination.

(a) Results for the preliminary experiment on chromatic purity. Data are shown individually for observers 1–4 as indicated in the figure legend. The y-axis represents the difference in the value $L/(L+M)$ at threshold and the x-axis represents the $L/(L+M)$ value of the referent stimulus. Error bars are standard errors of the means.

(b) Thresholds for purity discrimination as a function of spatial separation. Data are shown individually for observers 1–4 as indicated in the figure legend. The y-axis represents the difference in the value $L/(L+M)$ at threshold, and the x-axis represents the spatial separation of the two stimulus patches (see Figure 1b). Error bars are standard errors of the means. The isolated, rightmost points correspond to blocks of trials in which one of the two stimuli was randomly suppressed and the observer was asked to make an absolute judgement.