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Integration and Disintegration of Human Visual Awareness

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Declaration

I, Barrie Roulston, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

The neuronal underpinnings of visual awareness has recently become the primary question of interest for many researchers, with many theories suggesting distinct mechanisms. The aim of this thesis was to test predictions of the low-level modular theory of visual awareness. This modular view is encapsulated in the 'microconsciousness' framework (Zeki & Bartels, 1999) in which each visual processing system, such as that for colour, is capable of generating a conscious correlate autonomously in parallel across space, within each of the different functionally specialised areas of the visual brain, and across time, with different attributes perceived at different times. Given the scope of this topic, we approached it from three diverse angles: (1) Two psychophysical experiments investigated temporal aspects of visual perception – in particular these addressed the issue of whether the timing of awareness is an 'online' phenomenon rather than integrated into a temporal buffer zone prior to awareness. We measured the relative perceptual times of different magnitudes of direction changes and investigated the 'flash-lag' effect (Nijhawan, 1994) and related illusions of positional localisation. (2) The first two fMRI experiments examined the necessity of frontal and parietal areas for visual awareness in the context of bistable figures, combined with dynamic causal modelling (Friston et al., 2003), and perception outside the focus of attention. (3) We looked to extend the concept of modularity of awareness to that of 'access consciousness', that is the ability to give a report of a conscious experience (Block, 1996), in addition to the previous studies on phenomenal consciousness. To this end, we combined psychophysics with fMRI to investigate the interaction between report modality and visual perception. We conclude that the low-level modular theory of stands up to direct tests of its predictions and remains a viable theory of visual awareness.

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PAPERS

Roulston B.W., Self M.W., Zeki S. (2006) Perceptual compression of space through position integration. *Proc Biol Sci.* **273**, 2507-2512

Introduction

1.1 Overview

The route from a visual stimulus to explicit conscious perception has become of great interest to neuroscientists in the last decade or so. The neuronal underpinnings of what Bertrand Russell (1921) referred to as 'pure sensation' has moved from an interesting footnote to the primary question of interest for many researchers. However, there is no agreement on what constitutes the necessary and sufficient neural conditions for visual awareness; in other words, the 'easy' problem of consciousness (Searle, 1993) is a misnomer. Our knowledge of this phenomenon is both primitive and, more often than not, contradictory, which necessarily means that current theories of what constitutes brain states capable of producing visual awareness are composed of broad strokes.

Low-level theorists posit that visual awareness arises in the cortex where visual attributes are processed. The predominant thinking in this camp is the theory of 'microconsciousness' (Zeki & Bartels, 1999), which argues that visual awareness for a percept, such as colour, is generated in the area that processes the attribute, such as V4. While visual processing in a particular area may occur without awareness, an increase in activity leads to conscious perception independently of any other area(s) (Moutoussis & Zeki, 2002). Implicit in this assumption is that conscious perception may occur in a feed-forward manner, without feedback to earlier areas, or top-down influences from higher areas such as the parietal or frontal cortices. Furthermore, it also implies that if the processing of visual information takes different times for different attributes, visual awareness for these shall occur at different times (Moutoussis & Zeki, 1997a), leading to perceptual asynchrony. In direct opposition to this account, advocates of the high-level camp argue that for visual awareness to arise, there needs to be activity in 'higher' areas such as the frontal and parietal cortices, in tandem with activity in the visual cortex (e.g. Dehaene et al., 2003; Rees & Lavie, 2001). This type of theory has multifariously been referred to as 'the global neuronal workspace' (Dehaene et al., 1998), the 'fronto-parietal network' (Rees et al., 2002) and the 'central executive' (Shallice, 1988).

The conceptual motivation for this thesis is to empirically test the idea that visual awareness can occur in a low-level manner, generated autonomously in the visual cortex. To do this, we have used two lines of attack: (1) use psychophysical studies to measure the timing of visual perception, (2) fMRI to measure brain activity whilst tracking subjective reports of perception.

1.2 What is consciousness?

'Consciousness' is a nebulous term with a wide spectrum of meanings, depending on whom you happen to be talking to. Much of the debate on this topic seems to get lost in a quagmire of semantics; therefore it is important to provide at least a general working definition for this thesis. Synaptic transmission was not defined in a rigid way before its basic workings were unveiled, as it was not known how neurons pass on electrical signals; the analytic definition came after the mechanisms were discovered. This is the goal, not the starting point of science and the same principle applies consciousness (Searle, 1998). Thus 'consciousness' in the present context simply refers to phenomenal subjective experience and will often be used interchangeably with 'visual awareness', referring to purely subjective visual phenomena that are perceived. This is a reflection of the fact that vision is the system adopted by most neuroscientists to study consciousness. It is important to note that this definition is distinct from self-consciousness, which refers to a complex self-referential awareness, and knowledge, in that you may be aware of the colour red, but have no knowledge of its history, associations and so on. It is also important to consider the notion that there may be more than one type of consciousness. Block (1996; 2005) has previously argued that there are two definitions of consciousness: phenomenal or p-consciousness, and access or a-consciousness. P-consciousness can be taken to mean the definition described above, the pure qualia, whereas a-consciousness refers to the availability of this information for voluntary report.

1.3 Is consciousness a neurobiological problem?

"The body is our medium for having a world."

— Maurice Merleau-Ponty, The Phenomenology of Perception (1962)

What relation does consciousness have to the brain? Before we can even begin to find the neurobiological mechanisms for awareness, it is important to ask if this is possible at all. This is the modern formulation of the classic mind-body problem, which in Western thought can be traced back at least as far as Plato, although the best-known formulation is that of Rene Descartes (1641). He argued from a staunchly dualist position, by distinguishing the mind, including consciousness, from the brain, thereby reflecting the two fundamental properties of the world, mental and material. In direct contrast to this view, an implicit assumption of modern neuroscience, and of this thesis, is that every mental operation, including consciousness, has a neural underpinning. Perhaps this is most elegantly demonstrated by examples from the neuropsychological literature, such as in the case of akinetopsia, the loss of ability to perceive visual motion (Zeki, 1991). This syndrome was reported in a patient with bilateral lesions of the extrastriate cortex (Zihl et al., 1993), over V5, an area known to process visual motion (Zeki et al., 1991). Furthermore, in macaques it was shown that by stimulating the analogous visual area with microelectrodes, the animals' perception of motion could change (Salzman et al., 1990). Therefore there is both correlational and causal evidence that neural activity in V5 underlies the perception of motion.

However, even if consciousness is completely dependent on the physical brain, it is not clear that a scientific study of these processes can explain consciousness. To be able to give a scientific account of consciousness, one must be able to make an intelligible connection between subjective states like perceiving motion and objective phenomena such as the firing of neurons in V5. Thus the problem of consciousness can be divided into two parts (Chalmers, 1995): the easy problem - the relation between consciousness and brain states, and the hard problem - how third-person objective neurobiological phenomena give rise to subjective, first person states. The former is essentially an empirical endeavour and is already some way to being solved as illustrated by the work on V5 described above. However the latter is more problematic.

A typical scientific explanation for a phenomenon is reductionistic i.e. it is reduced to a cause. Thus the heat of a gas is reduced to the mean kinetic energy of the molecule movements. A neurobiological reductionist account of consciousness would reduce consciousness to neural activity. There is nothing but neural activity. However, it should seem obvious that this sort of explanation fails. Unlike the case of the heat of the gas, this explanation fails as it leaves out precisely what we are trying to explain i.e. subjective experience; in other words 'the theory has left out the mind' (Searle 1992). To know everything about neural activity would take us no closer to knowing what it is like to have, for example, an echolocatory sense such as bats do (Nagel, 1979). In short, there is an 'explanatory gap' between subjective experience and objective brain activity (Levine, 1983).

The mistake that a reductionist account of consciousness makes is that it assumes neural activity and conscious processes share ontological identity. When I see the colour blue of my pen it is ontologically subjective, in the sense that it is only experienced by me. In this sense, all conscious states and perceptions are ontologically subjective. However, the neuronal activity in my area V4 which occurs when I experience colour is ontologically objective, in the sense that it does not need to be experienced by myself or any other being, in order for it to exist. Furthermore, this activity can be verified by anyone with the appropriate instruments to do so. The reductionistic account fails to recognise these as distinct phenomena. Therefore to get round the hard problem of consciousness, one has to accept that brain activity and subjective experience are simply two different irreducible perspectives of the same phenomenon (Velmans, 2000), and do not share the same ontological identity. A scientific account of consciousness is possible and can progress by mapping the subjective aspects of experience with the objective measurements of neuroscientific techniques such as functional brain imaging. Subjective experience may be measured by introspective reports such as verbal or button presses in humans, and, arguably, behaviour in higher primates, going on the assumption that these are conscious beings. While equating reports with subjective experience is in itself problematic, especially when considering a- and p-consciousness (this issue is addressed in detail in chapter 3.3), the broad scientific framework has been established to solve the 'easy problem'. In the next sections we review the experiments that have utilised such paradigms and the corresponding neurobiological theories inspired from this.

1.4 Neural Basis of Visual Perception

The modern study of perception has its roots reaching into 17th century British empiricist philosophy, with philosophers such as John Locke and David Hume. This doctrine stressed that knowledge about the world is the result of experience provided by the senses. However, not until the early 19th century was perception considered to be a candidate for objective scientific investigation. Key in this development were the seminal works of the German scientists Gustav Fechner, and Hermann von Helmholtz, both credited with establishing modern psychophysics. This new scientific field forged a method by which the relationship between the physical aspects of the stimulus and the subjective percept could be objectively measured. It provided a clear framework in which to understand the mechanisms of subjective perception.

In 1912 Max Wertheimer published 'Experimental Studies of the Perception of Movement', a paper on stroboscopic motion, and launched the highly influential Gestalt movement of psychology. The central tenant of this school was the role that context plays in perception; thus stimuli do not remain insulated from each other, they interact so that visual awareness is the sum of these separate 'sensations'. This is perhaps best illustrated by multistable figures, such as the Necker cube, where observers perceive such stimuli to be in one of two states, which periodically 'flip' from one state to another, despite the retinal input remaining constant. This demonstrates the Gestalt emphasis on the holistic form creating processes of our perception. Although the movement was relatively short-lived, many of its ideas form the basis of contemporary vision research, including the present thesis.

Independently of psychophysical studies of visual perception, neurological evidence was already providing keen insights into the neural mechanisms of visual awareness. Indeed, the window into perception offered by brain damage had been known since a least ancient Greek times, with early physicians such as Hippocrates, who stated that the 'brain is the seat of sensation'. However, it was not until the 19th century that real progress was made. One of the most insightful papers came from a Swiss ophthalmologist named Louis Verrey, who published the paper entitled 'Hemiachromatopsie droite absolue' (1888). It describes the case of a 60-year-old woman who had suffered a stroke resulting in damage to the occipital cortex of the left hemisphere. This resulted in total blindness in her upper-right hemifield, and the selective inability to perceive colour in the lower-right hemifield. Thus not only does this demonstrate that a certain area of the brain is necessary for colour vision; it shows that this area is functionally specialised for the representation of colour. More substantial evidence for the retinotopic organisation in the human visual cortex came in the following century from case studies of individuals suffering from gunshot wounds, head trauma, or stroke (Holmes & Lister, 1916; Holmes, 1918). During World War I, the neurologist Holmes conducted a series of studies on cases of gunshots or other war-related brain damaged patients. In some cases, a very confined area of the brain was damaged due to gunshot from which Holmes estimated the anatomical locations of the brain lesions and measured the resulting visual-field defects. Holmes (1918) drew a retinotopic map of the visual cortex by putting drawings of the occipital lobe and visual field side-by-side and indicated the correspondence between different regions on each map. These studies demonstrated that the left visual field projects to the right hemisphere and *vice versa* for the right visual field. Therefore he was able to demonstrate a vital role for V1 in visual awareness and its retinotopic specificity.

However, many of these neurological findings, especially achromatopsia, were not to gain much credence or clarity until the introduction of electrophysiological methods in the middle of the 20th century, when it became possible to objectively measure the responses of individual neurons to controlled visual stimuli (Hartline 1938; Kuffler 1953; Hubel and Wiesel 1959; Werner and Mountcastle 1963). The most important early discoveries studied the neuronal properties of the mammalian visual system. Using single-cell recording Kuffler (1953) established the receptive fields of retinal ganglion cells by describing the area of the retina on which stimuli can either excite or inhibit the cell. Figure 1.4.1a illustrates two types of cells found: on-centre, off-surround cells and off-centre, on-surround cells. The latter is maximally active when less photons fall on the centre, but more fall on the surround. The former has the opposite response profile. However, the major advance in our understanding of the properties of neurons in the visual cortex came from Hubel and Weisel, first in the cat and then in the monkey. Through the fortuitous discovery that the edge of the microscope slide they were using with their projector elicited more vigorous burst of firing from neurons than any of their actual stimuli, they established the existence of simple cells in cortical area V1, with receptive fields resembling Gabor functions (1959). These receptive fields were thought to be constructed from the converging inputs of simple cells. After further mapping of more complex receptive fields, they envisaged a hierarchy in which complex receptive field properties could be built by combining the outputs of the simple cells, and so on (Hubel & Wiesel, 1962; figure 1.4.1b). An extreme version of this view has become known as the 'grandmother cell' hypothesis (Barlow, 1972) in which the complexity of the cells in the hierarchy increase until there is a single cell which only fires in response to ones grandmother. However, the extent of such a proposal was questioned by a series of electrophysiological experiments recording from the prestriate cortex of macaques in the 1970s by Zeki. These demonstrated the existence of functionally specialised areas that selectively respond to specific stimulus attributes (figure 1.4.2), such as colour (Zeki, 1973; Zeki, 1978b) or motion (Zeki, 1974). This led Zeki to propose that the visual system is organized into multiple parallel, functionally specialised subsystems (Zeki, 1978a): a view still very much prevalent today.

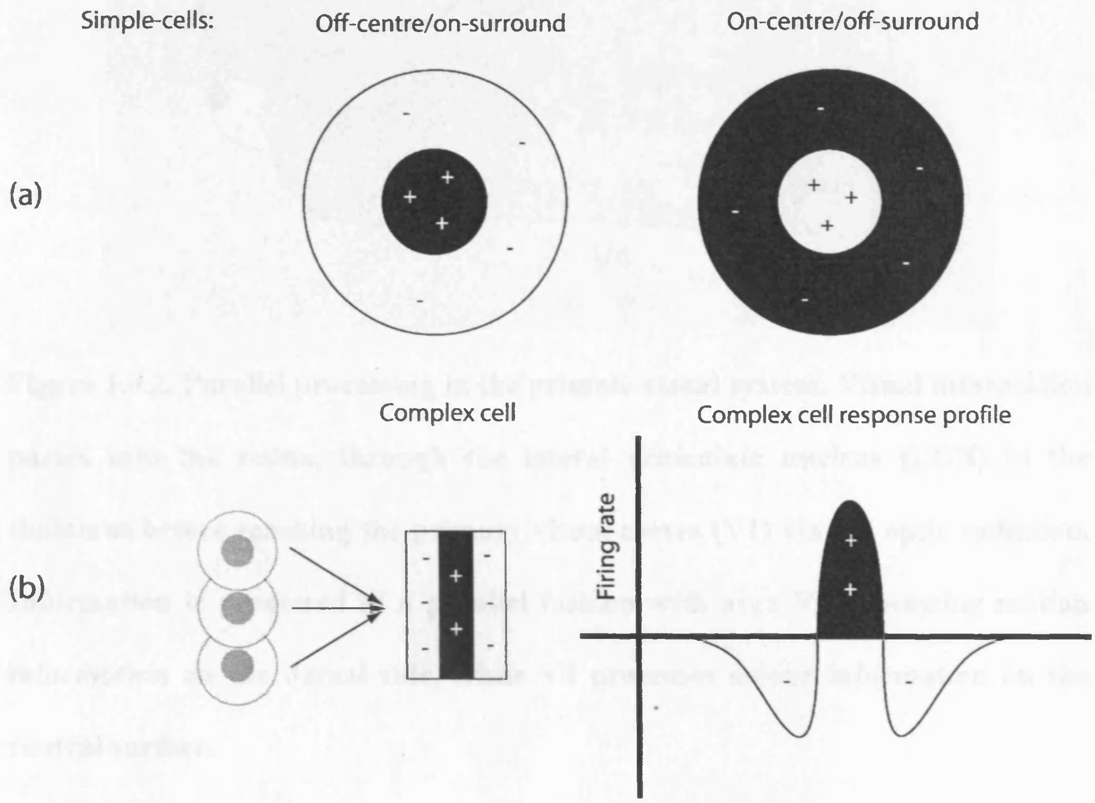


Figure 1.4.1. Schematic diagram of (a) simple cells and (b) complex cells. Positive and negative symbols represent optimal stimuli for the cells.

Further advances in anatomy, computational neuroscience and brain imaging in recent years have enhanced our understanding of the primate visual system, particularly in humans. Increasingly, the study of visual perception is becoming a cross-disciplinary science, with converging disciplines constructing a broader picture of the mechanisms of vision.

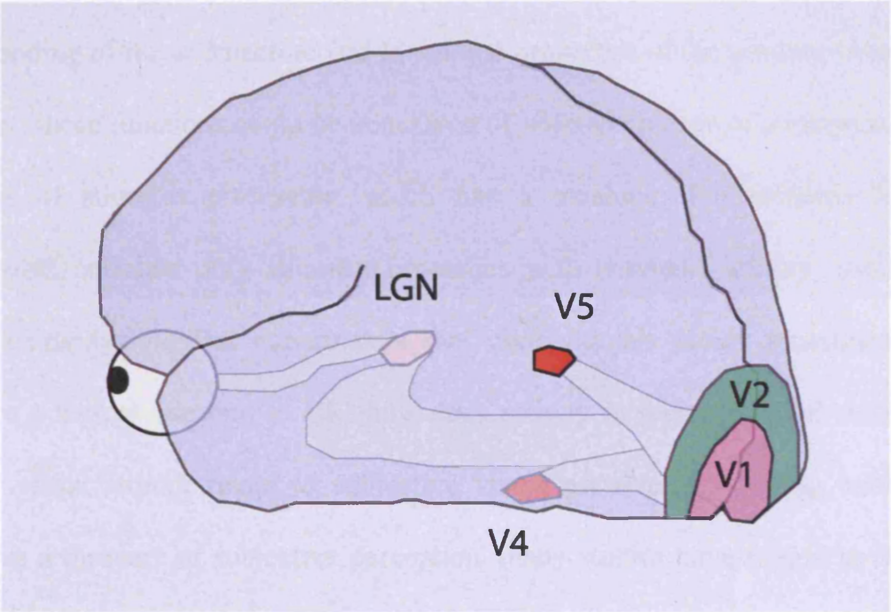


Figure 1.4.2. Parallel processing in the primate visual system. Visual information passes into the retina, through the lateral geniculate nucleus (LGN) in the thalamus before reaching the primary visual cortex (V1) via the optic radiation. Information is processed in a parallel fashion with area V5 processing motion information on the dorsal side, while V4 processes colour information on the ventral surface.

1.5 Subjective Experience as an Objective Phenomenon

The previous section discusses the historical roots that led to the present-day understanding of the architecture and functional properties of the primate visual brain. However, these functions could be conceived of without subjective awareness, purely in terms of stimulus processing, much like a machine. The majority of these experiments correlate only stimulus properties with neuronal activity, such as the early electrophysiological experiments that used animals under anaesthesia. It is therefore a logical question to ask 'how does activity in these neuronal areas which process visual stimuli relate to subjective visual awareness?' Using behavioural reports as a measure of subjective perception, many studies have sought to decouple perceptual reports from the stimulus and measure the concomitant changes in neuronal activity. In this way, experimenters have a pure measure of the correlates of visual awareness and not simply stimulus correlates. Thus, just as Helmholtz and Fechner were able to correlate stimulus properties with subjective perception, modern experimenters are able to correlate brain activity with subjective perception. In this section, we review studies that have used this experimental framework in conjunction with a variety of techniques. The most common paradigms have measured neuronal activity either with changes in subjective perception despite stimulus remaining constant (e.g. binocular rivalry), no changes in subjective perception despite stimulus changing (e.g. He et al., 1996), or have tracked changes in subjective perception that accompany cortical lesions (e.g. Zihl et al., 1983).

1.5.1. Neuropsychology

Cerebral Achromatopsia & Akinetopsia

The selective loss of the ability to see colours or motion after damage to specific areas of the prestriate cortex is referred to achromatopsia or akinetopsia respectively. These losses may be partial or complete and may accompany other deficits. For instance often achromatopsia is accompanied by prosopagnosia (failure to recognise faces), but not always (Zeki, 1990). As discussed in the last section, a selective deficit in colour perception was described by Verrey (1888), but selective visual deficits for colour or motion have only been fully accepted since the establishment of functional specialisation as an organising principle in visual system. With the demonstration in humans of a functionally specialised cortical areas for colour in V4 (Lueck et al., 1989) and motion (Zeki et al., 1991) in V5, it became apparent that these selective deficits were due to specific lesions to these functionally specialised visual areas (figure 1.4.2). This neuropsychological evidence demonstrates that the visual areas that process features are necessary to perceive them.

'Blindsight'

Blindsight is a term coined by Weiskrantz (1986) to describe a condition in patients with damage to V1 who retain the visual discriminative capacities in their blind fields despite reporting a complete lack of visual awareness. In the original paper (Poppel et al., 1973), subjects successfully localised the presence of a brief stimulus, even though they denied seeing it at all. Similar results were subsequently reported for acuity (Weiskrantz, 1986), orientation, colour (Stoerig & Cowey, 1989) and motion

(Barbur et al., 1993). It has been suggested that visual information is able to reach cortical areas such as V4 or V5 in the absence of the primary visual cortex through subcortical connections via the lateral geniculate nucleus (LGN) or the superior colliculus (Cowey & Stoerig, 1989). Indeed, an fMRI study of the patient G.Y. showed that V5 responds to visual motion presented in the 'blind' visual field (Zeki & ffytche, 1998).

However, even the existence of blindsight has been a controversial topic. While it has been questioned on the basis of the residual functioning of V1 (Campion et al., 1983; Fendrich et al., 1992), perhaps the most fatal finding is the revelation that, when pressed, these patients do report some sort of awareness for the stimuli (Barbur et al., 1993). In many of these studies the subjects reported a vague 'feeling' or a sense that 'something was there'. While in no way comparable to the rich phenomenal experience of normal vision, it is difficult not to concede that some sort of visual experience occurs. If the patient is aware of the stimuli, then discriminative capacity of the patient for stimuli in the 'blind' hemifield may simply be due to the fact that the patient is still able to base the decision on the fragments of conscious vision that remain. Therefore, according to this account discrimination in the absence of visual awareness does not occur in these patients. In recognition of this, Zeki and ffytche chose to refer to this condition as 'Riddoch Syndrome' instead, as an acknowledgement of the British army neurologist who first described it in patients suffering from gunshot wounds after the first World War (Zeki & ffytche, 1998; Riddoch, 1917).

Agnosia

In 1890 the neurologist Lissauer distinguished deficits in form recognition based on extracting basic features from those based on recognition, despite intact shape processing, naming them 'apperceptive' and 'associative' agnosia respectively. Patients with apperceptive agnosia are typically described as being unable to process basic configural properties such as size, orientation or shape and are unable to recognise or copy even simple line drawings (Efron, 1968; Milner et al., 1991). However, other abilities such as colour, motion and luminance discrimination remain intact. While patients suffering from these perceptual deficits are unable to consciously discriminate form properties, there have been instances in which some residual from information is available for motor behaviour. Patient D.F. suffered from anoxia due to carbon monoxide poisoning causing severe damage to the lateral occipital cortex (James et al., 2003), resulting in a deficit in form processing, such as recognition or line drawing and was at chance at making basic form discriminations such as orientation (Milner et al., 1991). However, even with these severe perceptual deficits, she was able to make accurate grasping actions and could correctly place a card through a narrow slot at different orientations despite being unable to make an accurate explicit judgement of slot orientation. These observations form the cornerstone to Milner and Goodale's ventral and dorsal stream hypothesis: they propose that dorsal areas code for spatial location and actions ('how'), whereas ventral areas are crucial for object recognition ('what') (Milner & Goodale, 1992). This theory, based on the 'two cortical visual systems' originally put forward by Ungerlieder and Mishkin (1982), proposes that ventral visual areas underlie conscious visual perception. As patient D.F. shows, damage to these areas affects explicit conscious perception of objects, without affecting action toward them.

In contrast, patients with associative agnosia have grossly preserved shape recognition, although experience difficulty when naming or categorising shapes. One of the earliest reported cases for this deficit was by Taylor and Warrington (1971), who described an agnosic patient who despite being unable to recognise pictures was able to correct misoriented images to their correct orientation and sort them into the appropriate semantic categories. This is thought to be due to a deficit in accessing the semantic information associated with the object or in the words of Teuber (1968), a *"normal perception stripped of its meaning."* Correspondingly, patients displaying these characteristic symptoms usually have lesions to the left occipito-temporal cortex (Ferro & Santos, 1984), a region believed to be involved in the storage of semantic information.

However, this classical distinction between apperceptive/ associative agnosia has been questioned and Farah (1990; 1994) has proposed an alternative account of these deficits. It is argued that instead there lies a distinction between discriminating the global holistic features of objects and the local elements. This proposal derives from the compound of deficits that these patients display: object agnosia is never found without other deficits, and prosopagnosia and alexia are not found without object agnosia. Therefore according to this framework face perception is impaired due to a deficit in global processing, whereas a deficit in local processes results in a deficit in word recognition. However, patients who show good object discrimination but are unable to recognise them are problematic for this alternative account and provide good evidence for the classic apperceptive/ associative distinction (Humphreys & Riddoch, 1993).

Neglect

Unilateral neglect is the deficit in ability of patients with unilateral brain damage to explore the side of space contralateral to the lesion, and to report stimuli presented in that portion of space. Most commonly, patients sustain damage to the supramarginal gyrus in the inferior parietal lobule, at the temporo-parietal junction, and deficits are most severe after damage to the right cerebral hemisphere of right-handed subjects; therefore producing left side deficits in the majority of cases (Pouget & Driver, 2000). What is particularly interesting for visual awareness is that these deficits are observed even though there is no damage to the visual cortex, suggesting that the inferior parietal lobe may play a role in awareness. This suggestion is consistent with the non-retinotopic aspects of neglect. For instance, whether stimulus in a fixed retinal position enters awareness can depend on eye and head posture as shown by performance of the line bisection task by patients with unilateral neglect (Vuilleumier et al., 1999). Correspondingly, neurons in area 7a of the posterior parietal lobe respond not only to retinotopic receptive field changes, but also to the angle of gaze (Anderson et al., 1985), and activity of the cell can be described as a function of the two. Furthermore, they are consistent with a more recent single-cell study of cells the parietal lobe of the monkey parietal cortex found that the activities of the cells in area 7a are world-referenced whereas cells in LIP are body-referenced (Snyder et al, 1998). The activity is thought to result from inputs from the neck proprioceptors for a body-referenced frames and world-referenced frames from vestibular inputs. This may explain the results of Vuilleumier and colleagues, who described the effects of eye and head rotation on the symptoms of neglect (1999).

Another interesting aspect is the fact that much visual processing remains intact, despite the patient having no awareness of the stimuli. Behavioural studies show that a considerable amount of semantic priming can occur from neglected objects (McGlinchey-Berroth et al., 1993), in contrast to the lack of priming with unseen objects in patients with unilateral occipital damage. In line with this, recent fMRI results show that selective processing of complex objects such as faces or houses still occurs despite them being in the patients' extinguished field (Rees et al., 2000). These results have been interpreted by some to be evidence for the necessity of parietal areas, in addition to visual activity, for visual awareness (Driver & Mattingley, 1998; Rees et al., 2002).

Reversible lesions (TMS)

Transcranial magnetic stimulation (TMS) can be used to transiently disrupt the function of a given cortical target, thus creating a temporary 'virtual brain lesion', making it possible to study two aspects of the contribution of a given cortical region to visual awareness. Its relatively good spatial localization and high temporal resolution allows the experimenter to ask 'what does it do?' and 'when does it do it?'. One of the earliest studies using this technique was that of Beckers and Zeki (1995), who disrupted V5 and V1 while subjects performed a motion discrimination task. They found that while TMS over V5 was effective at disrupting motion perception at between -20 to +10 ms before or after the onset of visual stimulation, magnetic stimulation of V1 abolished motion perception only at delays 60-70ms after stimulus onset. These simple observations led them to conclude that perceptually effective signals reach V5 before V1, and therefore bypass the primary sensory area.

Further studies have used TMS to investigate the role of cortical feedback in visual awareness. A recent study used TMS to elicit the perception of moving phosphenes by stimulating V5 and investigated if subthreshold stimulation of V1 could disrupt the perception of the phosphenes (Pascal-Leone & Walsh, 2001). They found that V1 pulses at around 45ms after V5 stimulation (although the brain area stimulated is actually closer to V3) were able to disrupt the perception of the moving phosphenes; most subjects reported the presence of stationary phosphenes only. The authors interpreted this to be evidence for feedback connections to V1 to be critical for the awareness of motion. Subsequent studies have used TMS to investigate the influence of back-projections from the frontal eye fields (Grosbras & Paus, 2003; Ruff et al., 2006) and the parietal cortex (Hilgetag et al., 2001; Beck et al., 2006) on visual perception, finding that such projections also have an influence on visual awareness.

1.5.2. Electrophysiology

Correlating neural activity with psychophysical performance

Some of the earliest studies to correlate single-cell firing and awake monkeys' perception (or at the very least psychophysical performance) investigated the relationship between V5 firing and performance during a motion discrimination task (Britten et al., 1992). The task required a monkey to discriminate the direction of a moving dot stimulus, which could be parametrically modulated in difficulty by varying the motion coherence of the array (figure 1.5.1a). The motion information in the random dots task is represented by direction selective neurons in area V5. When random dot motion appears in the receptive field of a V5 neuron, there is a large initial burst followed by a sustained response whose magnitude depends on the strength and direction of motion. Moreover, the animal's ability to discriminate weak motion appears to be limited by variability in the response of these neurons (Parker and Newsome, 1998). In addition, evidence from lesion and microstimulation studies demonstrates that such responses underlie the monkey's judgement in the random dots task (Newsome and Paré, 1988; Salzman et al., 1990).

However, while the responses of V5 neurons provide the evidence upon which the monkey bases its decision about direction, they do not integrate this evidence over time to form a decision. Their activity fluctuates with each passing random dot and the evidence they provide is therefore transient. While with lower coherence motion performance improves with longer viewing time, it never matches the maximal performance at high coherence, which occurs with a relatively short viewing time. Thus, information relevant to psychophysical performance accumulates over time, unlike the activity in V5. It was proposed that other neurons must 'read out' the evidence from V5. Such characteristics were found in the lateral intraparietal area (LIP) (Gold & Shadlen, 2001). Neurons in this area not only accurately predict the monkey's behavioural decision, but they also appear to accumulate evidence for the decision in response to the stimulus: LIP neurons show increasing ramp-like activity, with steeper ramps corresponding to higher coherence of stimuli (figure 1.5.1b). It is thought that when this activity crosses a threshold, a decision is made. Note that even with zero coherence stimuli, with no net motion, the activity meanders randomly, much like Brownian motion, until by chance it crosses the threshold. Such an interpretation is backed by recent microstimulation experiments on LIP (Hanks et al., 2006) where it was found that stimulation of cells increased both the probability of saccade response toward the stimulated neurons receptive field and the speed of that response.

While similar profiles have been found in other cortical areas, including the frontal eye fields (FEF) and dorsolateral prefrontal cortex, and in subcortical structures (Kim & Shadlen, 1999; Horwitz & Newsome, 2001), the relative contribution of each of these loci to either the decision process or the perceptual process is not known. This highlights a fundamental problem in many experiments investigating the neural correlates of subjective perception: that is whether the neural activity correlating with behavioural report is a reflection of subjective perception, the decision process or both (i.e. these may not be such distinct phenomenon). These issues are addressed further in section 3.3.

Figure 1.5.1. Direction discrimination task and neural responses. (a) shows the task structure. The monkey fixates for a few hundred milliseconds. Two saccade

targets appear before the motion stimulus is presented. The monkey indicates the perceived direction of motion after the stimulus disappears. In (b) and (c), the plots demonstrate how the neural activity unfolds over time after stimulus presentation. The ordinate represents the probability of pooled neural activity of directionally-selective neurons from LIP (b), and the superior colliculus (c), correctly predicting the behavioural response. Each coloured line represents a different percentage coherence of motion stimuli, as shown in the key. Adapted from Gold and Shadlen (2001).

Multistable perception

Multistable perception refers to the tendency the perception of ambiguous visual images to alternate between two or more interpretations, a classic example being the Necker cube (Necker, 1832). As discussed in section 1.4, such images played a key role in the Gestalt psychology movement at the beginning of the 20th century. Binocular rivalry is a particular class of this phenomenon whereby perception periodically alternates between the different images presented to each eye (see review Blake & Logothetis, 2002). This paradigm is an excellent tool to probe neural correlates of visual awareness as the stimulus remains constant while the subjective percept changes, thereby controlling for any confounds associated with the stimuli. Leopold and Logothetis (1996) recorded from neurons in several visual areas in the macaque, from V1 to the inferotemporal cortex, while the macaque reported its perceptual state under these conditions. The experiments found that only approximately 10% of the neurons in V1 followed the percept, whereas as much as 95% of the relevant neurons in the inferotemporal region, near the top of the visual hierarchy (Hubel & Wiesel, 1962), did so in an almost all-or-none manner. That is, when the monkey signalled that it saw the stimulus, the cell fired. When the preferred stimulus of the cell was present on the retina but the monkey reported that it did not perceive it, the cell remained silent. This suggests that neurons in the inferotemporal cortex may underlie visual awareness.

A phenomenon closely related to binocular rivalry is called 'flash suppression.' If an image is projected monocularly, with nothing presented to the other eye, the observer naturally sees this image. If a second image is then projected or 'flashed' to the contralateral eye, the observer sees only this second image and is initially blind to the first image, even though it is still coming into that eye (Wolfe, 1984). The situation can be reversed, such that in one situation, one image is perceived, but in a different situation, the other image is perceived. Like binocular rivalry, neurons in the superior temporal sulcus of the monkey respond to the subjective percept (Sheinberg & Logothetis, 1997). For example, a particular neuron may respond vigorously to an ape's face, but not to a sunburst pattern in isolation. This is consistent with previous studies, which show cells in the inferotemporal cortex with a response selectivity for faces (Gross et al., 1972; Perrett et al., 1982). If the image of the ape's face is in the right eye and the sunburst pattern is suddenly switched on in the other eye, this neuron follows the percept the monkey signals and fails to fire for the ape's face, even though its image is still present in the right eye. Thus the neuron's firing is then highly correlated with the monkey's percept. The large majority of cells in this region, part of the inferotemporal cortex, follow the percept rather than the stimulus.

The perceptual state of the animal while viewing bistable stimuli has also been correlated with activity in area LIP (Williams et al., 2003), an area of the parietal cortex previously implicated in accumulating evidence for perceptual decisions, as discussed in the previous section. While this area correlated with the perceived direction of motion of a briefly presented ambiguous motion stimulus, area V5 showed very weak correlation. Thus, this suggests that V5 is not the basis of subjective motion perception and simply correlates with stimulus properties.

Neuronal synchrony

The 'binding problem', as named by Von der Malsberg (1981), refers to the theoretical problem that the brain has in associating (or binding) different features of visual space into a unified percept, since these are processed in the different functionally specialised areas of the visual cortex. A potential neurobiological solution was presented when Gray and Singer reported that neurons in the cat visual cortex engage in oscillatory firing patterns and coordinate their responses to global stimulus properties by synchronising their responses within the gamma range of 40-60 Hz (Gray et al., 1989). Thus spatially separated cells may display strong synchronisation if different parts of the same object fall within their respective receptive fields. However, they do not synchronise if the different stimulus parts do not belong to the same object. Such a mechanism circumvents the 'one cell-one representation' problem posed by the grandmother-cell theory. This phenomenon was subsequently demonstrated to occur sub-cortical neurons in anaesthetised cats (Brecht et al., 1999), and cortical neurons in anaesthetised (Livingstone, 1996) and awake behaving monkeys (Kreiter & Singer, 1996) and seems to be ubiquitous across a wide range of species (see review, Engel & Singer, 2002). To probe its role in visual awareness, neural synchrony was investigated in the context of binocular rivalry (Fries et al., 1997). Awake strabismic cats were presented with dichoptic stimuli of patterns moving in different directions, which underwent binocular rivalry, similar to the situation described above in macaques. It was found that the synchronicity and regularity of oscillatory firing of neurons responding to the stimulus as early as V1 was increased when that stimulus dominated and was perceived. Importantly, no differences in the spiking rates of neurons were observed in these neurons representing the dominant stimulus. Such empirical observations are in line with theoretical approaches to consciousness, many of which have suggested a close link between binding and conscious perception. Thus Crick and Koch (1990) suggested that only 'bound' neuronal activity can trigger short-term memory and thus become available to consciousness.

However, the exact role that oscillatory and synchronous activity has, if any, remains controversial. The significance of the findings described above have been heavily criticised on both methodological and conceptual grounds (see Shadlen & Movshon, 1999). Moreover, there have been many reports where the perceptual state of animals performing tasks relating to binding has not correlated with synchrony. For example, Lamme and Spekreijse (1998) recorded from macaque V1, while the animal was presented with a figure-ground display composed from orientated line segments. They found no significant correlated activity between two recording sites representing the same region (figure or ground) or when representing different regions. More recently, it was found that in macaque area V5 while directional tuning correlated strongly with coherent moving plaid patterns, coherent plaids elicited significantly less synchrony than non-coherent plaids (Thiele & Stoner, 2003). One alternative function of synchrony may be its role in top-down attentional processes rather than conscious perception per se. In a recent study, Fries and colleagues (2001) recorded directly from area V4 in awake macaques while viewing two identical Gabor patches. When the animal was cued to attend to one of them, the concomitant activity in V4 increased synchronisation in the gamma range, while the firing rate remained the same. Thus the previous results may be simply due to the animal focussing attention on the relevant stimulus. However, this attentional perspective does speak to the long established view that attention is the mechanism for binding (Treisman & Gelade, 1980), and therefore has some consistency with the proposal that synchrony plays a role in binding.

Feedback to V1: late modulations

After the presentation of a visual stimulus, there is an initial cascade of neural activity transmitted through feed-forward connections. However the tuning of cells are not completely defined by this stage and later components shape the cells' response. For example, the preferred orientations of output layer neurons in macaque V1 usually change with time, and the orientation tuning may have more than one peak (Ringach et al., 1997). Simple feed-forward models cannot explain these observed properties, although they arise naturally in simulations of feedback networks (e.g. Douglas et al., 1995). In addition to the firing rate, synchronicity and oscillations of neurons, this late response has been shown to correlate with the subjective perception of the stimulus. Super and colleagues (2001) presented monkeys with a figure-ground display and found that the late response is larger when the receptive field of the recorded V1 cell is located at the inside of the figure than when the figure is distant from the receptive field, even though the stimuli at the classical receptive fields are identical in the two conditions. Moreover, this modulation occurred only when the monkey was aware of the figure. On trials in which the stimulus was presented, but the monkey did not detect it, the late modulation was absent. The onset of this differential response occurs at about 100 ms: about 60 ms later than the onset of the non-differential initial responses (figure 1.5.2). This study therefore provides evidence for the hypothesis that feedback connections are essential for phenomenal visual awareness (Lamme, 2004).

Figure 1.5.2. Population average responses for cells in macaque V1 during figure-ground detection task. (a) Response for figure present in bold line, ground in thin line. Shaded region shows difference between the figure and ground. (b) Responses on trials in which the animal sees the stimulus. The figure-ground difference remains. (c) Responses on trails in which the stimulus is presented but not reported; no late modulation of the response occurs. Taken from Super et al. (2001).

1.5.3. Human brain imaging

Brain areas correlating with awareness

Although the field of human brain imaging played a major role in opening up visual awareness as a legitimate field of study, it is equally responsible for much confusion in the matter. Activity in areas of every lobe of the brain has been correlated with subjective perception. It could be cynically noted that this is usually the part of the brain that the researcher happens to be working on. The earliest area in the visual hierarchy that has been shown to correlate with visual awareness is the LGN. Two papers recently demonstrated that activity in this subcortical nucleus correlates with the subjects' perceptual state during binocular rivalry (Haynes et al., 2005b; Wunderlich et al., 2005). Moreover, the study of Haynes and colleagues showed that regions of the LGN which have strong eye-preference, show reduced activity when the stimulus presented in their preferred eye is perceptually suppressed. This result was surprising given that an earlier macaque electrophysiological study did not find perceptual correlates in the LGN during binocular rivalry (Lehky & Maunsell, 1996). This apparent discrepancy may be due to interspecies differences or the ability of the fMRI signal to produce a population measure of neuronal activity, in contrast to single-cell firing in electrophysiology (Logothetis & Wandell, 2004).

Preceding this finding, it was demonstrated that the next stage in the visual hierarchy, the primary visual cortex (V1), could correlate with subjective perception under binocular rivalry, with different studies reporting either activations (Polonsky et al., 2000) or deactivations (Lee & Blake, 2002), according to perceptual state. Furthermore, many studies have shown that V1 correlates with perception in detection tasks, in agreement with the electrophysiological studies described in the previous section. For example, when subjects were required to detect a threshold pattern, V1 activity correlated with correct detection and false alarms (Ress & Heeger., 2003). Thus even when no stimulus was presented, but the subjects' incorrectly identified its presence, V1 responded as if it were presented. Furthermore, a combined EEG and fMRI study (ffytche & Pins, 2003) using a simple contrast detection task, showed that V1 activity correlates with subjective perception as early as 100ms, suggesting that awareness is subsumed by processes early in the visual hierarchy, without recourse to late top-down enhancement. In addition, a recent experiment has shown that perceptual completion has correlates as early as V1, indicating a possible role for this area in illusory filling in (Meng et al., 2005).

The next stages in the visual hierarchy, such as extrastriate areas or mid-level form regions, have been some of the most reliable in demonstrating the neural correlates of visual awareness. As with human V1 or electrophysiological studies, many of these experiments used binocular rivalry. For instance, Tong and colleagues exploited the well-known fact that faces and 'places' are processed in two functionally localised areas of the ventral cortex, the 'fusiform face area' (FFA) (Kanwisher et al., 1997) and the 'parahippocampal place area' (PPA) (Epstein & Kanwisher, 1998). House stimuli were presented to one eye, while face stimuli were presented to the other, resulting in perceptual rivalry. Like previous macaque studies (e.g. Logothetis et al., 1989), the subjects' subjective reports were positively correlated with neural activity, in this instance the mean activity in the FFA and PPA, when the face and house stimuli were dominant respectively. Similarly, activity in extrastriate area V5 has been shown to correlate with the subjective percept, and not simply the stimulus, in patient G.Y. when he consciously detected motion in his 'blind' hemifield (Zeki & ffytche, 1998).

Figure 1.5.3. Mean BOLD activated in the parahippocampal place area (PPA) and fusiform face area (FFA) after perceptual switches during binocular rivalry. Taken from Tong et al., 1998.

However in addition to these visual processing areas, more recent functional imaging studies have also shown non-visual areas such as the parietal cortex to correlate with visual awareness. As discussed in more detail in section 3.2, many recent studies have found a right-biased fronto-parietal network of brain areas correlating with visual awareness, in addition to areas of the visual cortex. A clear example is a recent fMRI study of the ‘attentional blink’ (AB; Marois et al., 2000), which occurs when a subject detects one target stimulus in a stream of distractors but consequently fails to detect a second target presented within around 500ms or so of the first. In the study of Marois and colleagues, they set the interval time between the first target stimulus and the second such that the second stimulus was only detected on some trials and missed on others. Comparing whole brain activity on ‘hit’ trials with ‘miss’ trials thereby showed the neural correlates of subjective perception, while the stimulus was identical. This contrast revealed multiple right-biased frontal and parietal regions, suggesting that these are critical for target detection in AB. Activations in similar areas have been reported in other fMRI studies of perceptual transitions during binocular rivalry (Lumer et al., 1997) and viewing of bistable figures (Kleinschmidt et al., 1998), change detection (Beck et al., 2001) and semantic priming (Dehaene et al., 2001). Figure 1.5.4 shows a recent meta-analysis of studies showing frontal and parietal correlates of awareness (Rees et al., 2002).

Figure 1.5.4. Meta-analysis of frontal and parietal areas that correlate with visual awareness. Each coloured circle corresponds to the most significant voxel observed in each of the studies represented in the key. Consistent activations have been observed in the superior parietal and dorsolateral prefrontal cortices, as highlighted with the large grey circles (adapted from Rees et al., 2002).

An alternative perspective from investigating which brain areas correlate with perception is to observe which areas correlate with the stimulus and *not* with visual awareness. This would imply that activity in such an area is insufficient to generate the percept. However, like areas that correlate with subjective perception, this has been shown to occur with almost every area of the cortex from V1 onwards. Using a multivariate pattern classifier Haynes and colleagues (Haynes & Rees, 2005) showed that V1 still distinguishes between different orientations of gratings even when made perceptually invisible through metacontrast masking. Mid-level object areas such as the FFA or PPA may also be selectively activated by stimuli rendered invisible by flicker fusion (Moutoussis & Zeki, 2002). Furthermore, recent results show that extremely abstract representations such as task-set that occur in the prefrontal cortex may be activated in the absence of the observers' awareness (Lau & Passingham, personal communication). Similarly, activity in the primary motor cortex can correlate with unconscious semantic stimuli that prime the subsequent motor response (Dehaene et al., 1998).

Gamma band activity correlates with awareness

Numerous animal electrophysiological studies reviewed in section 1.5.2 demonstrate a correlation between synchronous neuronal activity, especially in the gamma range, and visual awareness. Correspondingly, numerous studies have also found that synchronous activity can correlate with perception in humans using techniques with high temporal resolution, such as electroencephalogram (EEG) or magnetoencephalogram (MEG). For instance, EEG was recorded while subjects viewed an ambiguous visual stimulus ('Mooney faces') that could be perceived as either a face or as a meaningless shape (Rodriguez et al., 1999). When subjects reported seeing a face, phase synchronization at the gamma frequency occurred across widely separated brain areas encompassing anterior non-visual brain regions and posterior sensory regions likely to correspond to the visual cortex. Moreover, such a pattern of activity was absent when subjects reported seeing a meaningless shape. Similar results have also been shown in the context of binocular rivalry, during the perceptual changes in conscious awareness of one or the other of the two rivaling stimuli (Tononi et al., 1998). These transitions were accompanied by a change in the synchrony of firing of neurons representing the stimuli. In addition, widespread coherence occurred between the MEG at various non-sensory regions, in lateral and anterior brain sites, which may correspond to frontal and parietal cortices, and sensory areas responding to the stimulus that dominated perception. In contrast, there was no such coherence for the perceptually suppressed stimulus.

Awareness during the sleep-wake cycle

While sleeping and dreaming affects all of consciousness rather than specifically visual awareness, the sleep cycle offers a different viewpoint to the other studies described. The neural processes that are observed during visual dreaming seem have many things in common with those that occur during awake seeing. Sleep is conventionally divided into two phases on the basis of EEG recordings (Aserinsky & Kleitman, 1953; Hobson, 1995). During slow-wave sleep (SWS), dreaming typically does not occur and the scalp EEG is dominated by high-amplitude, low-frequency oscillations. However, during the rapid eye movement (REM) phase of sleep, when the EEG has similar patterns of activity to the waking state (characterized by low-amplitude, high-frequency signals) dreaming occurs, often resulting in rich visual experiences.

Brain activity measured with fMRI in humans during REM sleep is reduced in the primary visual cortex and other low-level visual areas (compared with non-REM phases of sleep), whereas mid-level form areas such as the fusiform gyrus are activated (Braun et al., 1995). By contrast, during SWS, early visual cortex activation is observed, whereas medial temporal areas are deactivated. Furthermore, there is a breakdown in the cortical effective connectivity, observed through wakefulness, during non-REM sleep, (Massimini et al., 2005). Suppression of activity in V1 during REM sleep is consistent with the finding that patients who have lost part or all of V1 continue to dream visually. Complete loss of dreaming is associated with unilateral damage to either frontal or parietal cortex (Solms, 1996). However, specific loss of visual dreams is associated with bilateral lesions in the medial occipitotemporal region (Solms, 1996). Overall, these experiments suggest a dissociation in brain activity during dreaming and non-dreaming, in that only areas higher than the primary sensory cortices correlate with visual experiences during dreaming.

1.5.4. Human single-unit recording

The opportunity to record directly from the human brain exists with neurosurgery procedures, including recordings of intracranial EEG, local field potentials, multiple-neuron activity, and the activity of individual neurons. Single- and multiple-neuron activity has been recorded both intra-operatively during epilepsy surgery (Ojemann et al., 1998) and surgery for movement disorders (Benazzouz et al., 2002; Davis et al., 2000; Lenz et al., 1994), and extra-operatively through chronically indwelling electrodes for treatment of epilepsy (Fried et al., 1997). Similar to those experiments in macaques described above, Kreiman et al. (2002) used flash suppression while recording from human medial temporal lobe neurons. Approximately two-thirds of visually selective neurons tested followed the perceptual alternations rather than the retinal input. For instance, a neuron that responded to a line drawing of the ex-American president Clinton was active only when the figure was perceived, but not when perception of the drawing was suppressed, even though it was still physically presented.

In other experiments, the firing of neurons in the hippocampus, amygdala, entorhinal cortex and parahippocampal gyrus were characterised both in response to the direct perception of objects and the mental imagery of them (Kreiman et al., 2000). The response to an imagined object, even though no retinal input was present, was comparable to that of the real object, both in selectivity and in firing rate. Of the neurons that fired selectively during both vision and imagery, the majority (88%) had identical selectivity. The firing rate during imagery was approximately 85% of that during actual vision. Perhaps a more striking finding is the invariance displayed by some of these neurons reported by Quiroga et al. (2005). For instance, one cell in the medial temporal lobe responded selectively to pictures of the actress Jennifer Aniston, but not to hundreds of other pictures of actresses of the same age or even to a picture of Aniston and the actor Brad Pitt. This extremely selective, sparse nature of these cells' responses borders on the so-called 'Grandmother cell' notion that the brain has a separate neuron to detect and represent every object encountered (Barlow, 1972). However, given that these neurons were found at the border between areas that represent visual information about object structure and memory-related conceptual information about object identity, it is unknown if they relate purely to visual perception or to memory.

1.5.5. Psychophysics

While the techniques described in the previous sections seek to directly correlate subjective awareness and a physiological measurement of neural activity, many studies have been able to make important inferences about the mechanisms underlying visual awareness by using psychophysics alone. This is guided by the wealth of knowledge we have gained about the visual brain and its responses to various stimuli. Perhaps the simplest of these are those that exploit visual after-effects. Adaptation has often been referred to as the psychophysicists' electrode (Frisby, 1979) as it allows one to infer the existence of neural populations through after-effects. While manipulating awareness, the experimenter may infer what neural populations were activated by the stimulus through measuring the extent of the after-effect.

This logic was applied to test the hypothesis that we are not aware of neural activity in V1 (He & MacLeod, 2001). Subjects were exposed to gratings so high in spatial frequency that they were perceptually identical to a uniform field. Consequently, the observers required more contrast to detect a test grating presented at the same orientation than one presented at the orthogonal orientation. Subjects also experienced a tilt after-effect that depended on the test pattern's tilt and its relation to the invisible orientation of the pre-exposed pattern. Given that visual system is coding for orientation of these invisible gratings, the authors conclude that subjects are unaware of neural activity in this area: most probably V1. This type of logic has also been applied to investigate awareness in the context of attention (Rees et al., 1997; Tsuchiya & Koch, 2005), midlevel vision (Moradi et al., 2005) and patient studies (Humphrey et al., 1995).

A more recent trend has been to use psychophysics as a tool to investigate the timing of visual awareness. More specifically, how perceptual times relate to neural times. One of the best examples of this is the perceptual lag of colour behind motion demonstrated by Moutoussis and Zeki (1997a, b). In these experiments, observers pair a colour stimulus with a motion stimulus that occurs 80-100ms earlier, although they perceived these at the same time. This suggests that the colour processing system encompassing the V4 complex produces conscious percept before the motion processing system – the V5 complex. Moreover, it suggests that the brain does not wait to for the other system to finish what it is processing; rather it is 'online' and binds whatever is processed. Thus these results suggest that there is no higher area that information is integrated in or re-routed to before becoming conscious. Other studies have focussed on the duration of visual stimuli, rather than the relative perceptual times. For instance, a recent study showed that adaptation to oscillatory motion or flicker alters the perceived duration of a subsequent stimulus in a retinotopic manner (Johnston et al., 2006). Consistent with the study described above, this implies, on the timescale of hundreds of milliseconds, that there is not central integrative clock mechanism in the brain. Rather, duration is coded for in a low-level distributed manner.

However, there is psychophysical evidence suggesting that what is perceived can be influenced retrospectively by subsequent events – a framework known as 'post-diction'. Visual information is integrated into a temporal buffer zone before it is perceived. While this proposal is consistent with a range of experiments including backward masking (Bachmann, 1994), the color-phi phenomenon (Kolers & von Grunau, 1976) and the disruption of the perception of phosphenes (Pascual-Leone & Walsh, 2001), it was with the flash-lag effect that this proposal was made most explicit (Eagleman & Sejnowski, 2000a). This illusion occurs when a moving object is accompanied by a spatially aligned stationary flash. Observers perceive the flash to spatially lag behind the moving object. Eagleman and Sejnowski proposed that this occurs because the perceived position of a moving stimulus is the outcome of an averaging process that occurs over 100 ms or so. However, when a salient event occurs, such as the flash, the information accumulated for the moving object is 'reset' and the visual system must accumulate positional information from scratch before it is perceived. Since this process takes 100 ms or so, the new positions for the moving object are those which occur after the flash – therefore the flash is perceived to lag the moving object. More recent evidence for such a mechanism come from the timing of perception around saccadic eye movements, such as the illusory reversal of temporal order (Morrone et al., 2005), or the illusory trans-saccadic filling-in of time ('chronostasis'; Yarrow, et al., 2001). While there is very little, if any, evidence for what the neurobiological realisation of this 'postdictive' mechanism would be, it has been speculated (Eagleman & Sejnowski, 2003) that it could be related to the extensive feedback mechanisms in the primate visual system (Shipp & Zeki, 1989).

1.6 Current theories of visual awareness

As described in the previous section, there is a wealth of experiments investigating the neurobiological foundations of visual awareness. However, rather than providing a clear framework from which to work, it has generated multiple theories, with varying degrees of compatibility, which are more often than not completely contradictory. A feature of most of these hypotheses specifies some 'magic ingredient' that distinguishes conscious from non-conscious processing of information in the visual system. This section reviews the most prominent of these and explains how they link to the empirical evidence.

1.6.1. Microconsciousness

The theory of microconsciousness is based on the parallel and modular architecture of the primate visual system (Zeki & Bartels, 1999). Combined physiological, anatomical and psychophysical evidence suggests that different specialised systems of the visual brain, which process different visual submodalities such as colour and motion, are capable of generating percepts independently of each other. For instance in humans clinical evidence (Zihl, et al., 1983; Zeki, 1990, 1991) shows that damage to the visual area that processes colour only affects colour perception and not motion perception, and vice versa; therefore the ability to consciously perceive one attribute does not depend on the ability to perceive another. Moreover, the residual visual functions of patients reviewed in section 1.5 shows that damage to the visual cortex may leave only the ability to perceive one visual attribute, in this case motion (Zeki & ffytche, 1998). These patients seemed to experience 'pure' visual motion without the other attributes such as contrast or form that also define the moving dot stimuli in this study. For instance, one patient reported 'they [the moving objects] don't appear to have any colour or shape. They look like shadows'. Consistent with this, the fMRI results showed that the only visual area active was V5 during perception of the stimulus.

It was this modular feature of the visual system that originally motivated the study of the perceptual times of visual attributes in order to answer the question of whether, in addition to being processed separately in the cortex, they are perceived separately in time (Moutoussis & Zeki, 1997a). Colour was found to be perceived some 100ms before motion when the two perceptual attributes were paired together, findings since confirmed using a colour-contingent motion after-effect (Arnold et al., 2001; for further discussion see section 2.1). Overall, these results were interpreted to mean that once the processing of a stimulus attribute within a specialised subsystem of the visual cortex is complete, it is perceived, without recourse to other brain areas; a claim backed by the anatomical fact that there is no central area to which all the specialised processing systems uniquely project (Shipp & Zeki, 1995). The major determinant in whether there is visual awareness is sufficient neural firing within the visual cortex.

1.6.2. Feedback to V1

Several of these theories posit that a certain pattern of neuronal activity may be a prerequisite for awareness, rather than simply neuronal activity per se. As discussed in the previous section, a number of electrophysiological studies have found shape detection to correlate with a late modulation in V1 activity, although the initial firing is identical whether the monkey reports seeing it or not. While these experiments have been limited to the use of figure-ground segmentation tasks, some authors have argued that this demonstrates feedback to V1 is crucial for all forms of visual awareness (Lamme & Roelfsema, 2001). Such a proposal has also found support from TMS studies in humans (Pascal-Leone & Walsh, 2001) and some earlier studies of blindsight patients. To its credit, unlike many neurobiological theories of visual awareness, this view makes the distinction between access and phenomenal awareness (Block, 1996). Lamme argues that phenomenal awareness is subserved by recurrent feedback within visual areas, whereas access to report is contingent upon attention and the associated frontal and parietal cortical areas (Lamme, 2004).

While this theory makes sense in light of macaque electrophysiological results investigating feedback to V1, it is difficult to reconcile with reported cases of patients , who have V1 missing in one hemisphere, but are still able to consciously perceive visual stimuli in their respective visual field (Barbur et al., 1993; Zeki & ffytche, 1998). However, this finding is controversial and it has been debated whether the reported experience really constitutes visual awareness at all. For instance, it has been claimed that the report of patients' perceptual experience in the blind hemifield is 'a mere awareness that something happened but with no experience of accompanying visual qualia' (Silvanto et al., 2007).

1.6.3. Neuronal synchrony

One of the most popular physiological candidates for visual awareness is neural activity synchronized in the gamma frequency range at ~35–45 Hz (Engel & Singer, 2001). This proposal originated in the theoretical suggestion that selective synchronization of neuronal firing might provide a basis for figure-ground segmentation in vision and the binding of separate features (von der Malsburg, 1981). More recently, evidence has accumulated that neurons responding to a single object synchronize their activity both within and between visual areas, and synchrony increases as a stimulus moves into the focus of attention (Engel et al., 2001), as reviewed in the previous section. We have seen that widespread synchronized activity at these frequencies characterizes MEG in the waking state and REM sleep (Llinas & Ribary, 1993), and resonance of the auditory evoked potential in the same range has been used successfully as a marker of awareness in studies of the measurement of the depth of anaesthesia (Munglani et al., 1993). Engel and Singer have proposed that synchrony may play a role in all the major processes subserving visual consciousness: arousal, sensory segmentation, selective attention and working memory; and also in the processes of 'higher-order' consciousness: motivation, action planning and symbolic processing (Engel et al., 1999).

1.6.4. Thalamo-cortical interactions

Edelman and Tononi have proposed that the key neural mechanism underlying conscious experience are rapid re-entrant interactions between posterior thalamo-cortical areas involved in sensory processing and anterior areas related to memory and executive functioning (Edelman, 1992; Tononi & Edelman, 1998). A recent formulation has three main tenets, (1) consciousness arises from 'the fast integration of a large amount of information within a dynamic core of strongly interacting elements'; (2) re-entry, via reciprocal interconnections between regions of the thalamo-cortical system, mediates this rapid integration; (3) the emergence of 'primary consciousness' (which roughly corresponds to the definition of phenomenal consciousness described earlier) depends upon the integration of current sensory processing with previously acquired memories. Tononi argues that this model of a constantly shifting 'dynamic core' of neural elements accounts for many properties of awareness: continuity and changefulness, selectivity, the focus of attention and its diffuse surround, and the wide 'access' of its contents to other psychological operations. The theory stresses the importance of the complex integration of thalamo-cortical subsystems, which are both functionally segregated and interactive. This account has similar features to the synchrony hypothesis, in particular the long-range interareal synchronisation of distant cortical sites, and studies showing increased synchronisation associated with conscious awareness support both of these theories.

1.6.5. Brainstem enabling

While many neurobiological theories of awareness are concerned with cortical dynamics, one of the most enduring suggestions for a necessary neural component is the brainstem – more specifically, the ascending reticular activating system. There are three lines of evidence that suggest a critical role in consciousness: (1) as early as the nineteen-forties, in a series of classic experiments, electrical stimulation within the reticular formation in lightly anesthetized non-human mammals, was associated with a desynchronisation of the electroencephalogram (EEG) that hallmarks awake and attentive states (Magoun, 1954); (2) Magoun (1954), and many others since, provided evidence that persistent coma resulted after bilateral lesions to the reticular activating system in the mesencephalic reticular formation of the brainstem. While this obviously addresses the issue of conscious states (wakefulness, sleeping etc.), it is more than likely that no sensory awareness exists during coma and the relation to visual awareness is clear – without being in a 'conscious state' there can be no phenomenal awareness. (3) A functional imaging study of patient G.Y. found that activity in the brainstem correlated with awareness of motion stimuli, thereby providing a more tangible link between brainstem activity and sensory awareness (Zeki & ffytche, 1998).

1.6.6. Global workspace

The 'global workspace theory' of consciousness has its roots in cognitive psychology, from the cognitive architecture forged by Newell and Simon (Newell, 1994). Newell showed the utility of a global workspace capacity in a complex system of specialized knowledge sources, which could cooperatively solve problems that no single source could solve alone. However, it was Baars who was one of the first to apply this framework to consciousness, arguing that consciousness facilitates widespread access between otherwise independent brain functions (Baars, 1983). With the proliferation of human brain imaging in the last decade or so, this theory has found a more empirical footing, and particular favour with those who argue for the necessity of frontal and parietal cortices to visual areas for awareness (e.g. Dehaene et al. 2006; Rees et al., 2002). Note however, the theoretical origins can equally be applied to other theories that advocate large-scale integration of brain states, such Edelman and Tononi's dynamic core, or the brain-stem enabling theory, which was Baars' original candidate for the neurobiological basis of the workspace.

One of the most prominent neurobiological formulations of the 'workspace' hypothesis argues that early sensory activation is necessary but not sufficient for conscious access (Dehaene et al., 2006). For instance, when neglect patients are presented with stimuli, visual areas still selectively respond to these, even though they are unseen (Vuilleumier et al., 2001). To be aware of the stimulus, there needs to be top-down amplification from parietal and frontal areas. Evidence for this proposal comes mainly from human brain imaging data, which has shown activity prefrontal and parietal areas to correlate with visual awareness (reviewed in the previous section). Once the information is conscious, it is globally available to all other subsystems of the brain, such as memory, and is eligible for motor report (Dehaene et al., 2003).

1.6.7. An emerging theme: global-integrated vs. local-modular

In the previous sections we reviewed the most prominent theories of the neurobiological underpinnings of visual awareness. While each of these suggests different mechanisms, there is one concept that defines them all: connectivity. Each of the theories described may be placed along a continuum defined by the extent and location of integration at some stage along the sensory-motor pathway (see figure 1.6.1).

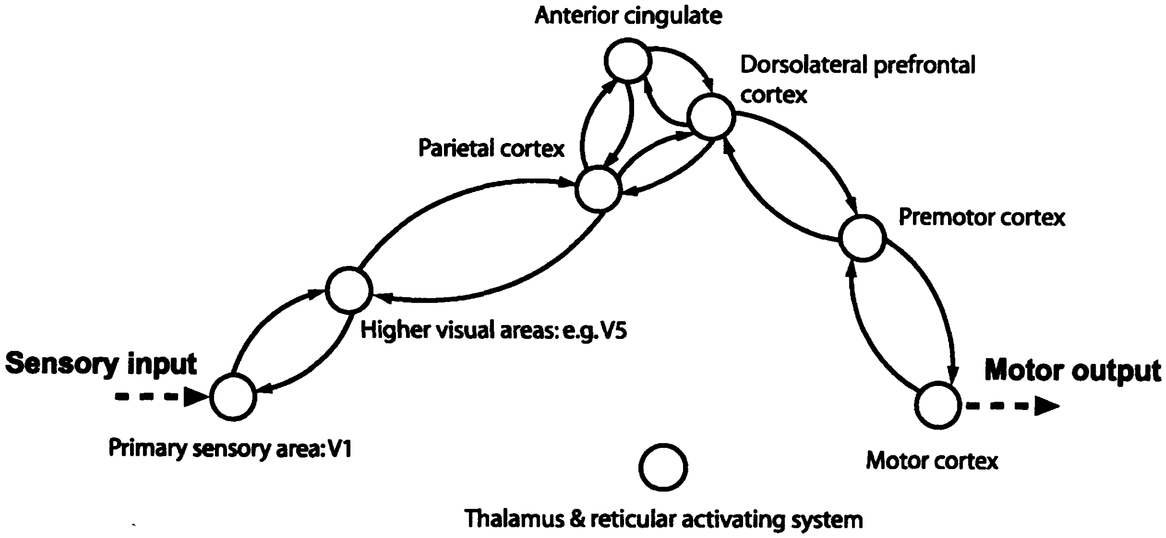


Figure 1.6.1. Schematic diagram of the sensorimotor pathway.

Thus at one end there is the microconsciousness theory which suggests that a feed-forward driving input from the retina to the visual cortex is sufficient for awareness (Bartels & Zeki, 1999). This proposes that top-down influences are not necessary for awareness and visual attributes are perceived asynchronously. Next on the continuum Lamme and colleagues suggest that recurrent interactions within the visual cortex, through feedback connections from higher visual areas to V1, are critical for visual awareness (Lamme & Roelfsema, 2001). In contrast, widespread thalamic interactions (Tononi & Edelman, 1998) or long-range connectivity from the global workspace in frontal regions (e.g. Dehaene et al., 2003) are considered to be the 'magic ingredient'. It is therefore the extent of the integration of brain states that lies at the heart of the current debate of the biological basis for sensory awareness.

1.7 Thesis aims

The aim of this thesis is to test predictions of the low-level modular theory of visual awareness against competing theories, such as the global workspace hypothesis (Dehaene et al., 2003). This modular view is summarised in the 'microconsciousness' framework (Zeki & Bartels, 1999) in which each visual processing system, such as that for colour or motion, is capable of generating a conscious correlate autonomously in parallel across space, within each of the different functionally specialised areas of the visual brain, and across time, with different attributes perceived at different times when each subsystem has finished processing the stimulus. Given the scope and wide-ranging implications of this topic, we have approached it from three diverse angles: (1) Two psychophysical experiments investigate temporal aspects of visual perception – in particular these address the issue of whether the timing of awareness is an 'online' phenomenon rather than integrated into a temporal buffer zone prior to awareness. We measure the relative perceptual times of different magnitudes of direction changes and investigate the 'flash-lag' effect (Nijhawan, 1994) and related illusions of positional localisation. (2) The first two fMRI experiments examine the necessity of frontal and parietal areas for visual awareness in the context of bistable figures, combined with dynamic causal modelling (Friston et al., 2003), and perception outside the focus of attention. (3) We look to extend the concept of modularity of awareness to that of 'access consciousness', that is the ability to give a report of a conscious experience (Block, 1996), in addition to the previous studies on phenomenal consciousness. To this end, we combine psychophysics with fMRI to investigate the interaction between report modality and visual awareness.

Psychophysics

2.1 The asynchronous perception of direction changes

2.1.1. Introduction

The timing of perceptual events of different visual submodalities has been investigated by psychophysical studies that require subjects to pair a colour with a direction of motion of alternating stimuli over short time windows. The awareness of the former precedes that of the latter by about 80-100 ms (Moutoussis & Zeki, 1997 a and b; Arnold & Clifford, 2002). Therefore over very brief time frames, the brain mis-binds the colour that is perceived at time *t* with the motion that is perceived at time *t-1*. This mis-binding introduces a serious problem which binding studies have yet to address, namely its temporal determinants. In simpler terms, the brain does not appear to wait for all the processing systems to terminate their tasks. Rather, it seems to bind what has already been perceived. This suggests that there is no central area that waits for all the processing systems to terminate their tasks before binding them together.

The perception of colour and of motion are the results of activity in two different systems, one centred around the colour centre of the cerebral cortex – the V4 complex – and the other around its motion centre – the V5 complex (Zeki 1978a; Zeki, et al., 1991). This has led perceptual asynchrony to be interpreted in terms of differences in the processing times required to reach a perceptual state (Zeki & Bartels 1999), a suggestion now supported by other psychophysical evidence. For example, Arnold and Clifford (2002) demonstrated that the size of the perceptual lag between colour and motion varies as a function of the magnitude of direction change. This result inspired us to go a step a further and ask whether activity in a single cortical system, or even area, can be fractionated in time, in such a way that one group of cells in it terminates its processing task, and hence acquires a conscious correlate, before another group. This would be so if varying the characteristics of the stimulus attributes results in a perceptual asynchrony for different characteristics of the same visual submodality. The implications of this, if found to be true, are not negligible. It would suggest that the binding of the activity of different groups of cells within the same cortical area is also not subject, over brief time windows, to a higher control and that any binding that may occur is between the results that a given group of cells have achieved at time *t* with what another group had achieved at time *t-1*. Here we test this by restricting the experiment to the single attribute of motion. This is based on the well-established fact that the response latency for directionally selective cells in V5 is greatest if stimulation in their preferred direction is preceded by stimulation in the opposite, null, direction. The time course and degree of inhibition is diminished if the preceding stimulus is at, say, 45° to the preferred direction (Priebe & Lisberger, 2002). The expectation, therefore, is that, when the two direction changes of motion are the same, the same degree of excitation and inhibition would occur in area V5 and hence the two directions of motion would be perceived simultaneously. By contrast, when the two directions of motion are, say, up and down for one side, and up and to the right for the other, the degree of inhibition for the latter direction would be much less and hence that the activity in one group of cells will reach a perceptual state before the other. The perceptual consequence of this would be that the two directions would be perceived asynchronously. The former has been tested by pairing of two orthogonal directions of motion, which were found to be perceived synchronously as we would predict (Moutoussis & Zeki, 1997a). The latter has not, and we report its results here.

Given the recent precedent to measure relative perceptual times using both a pairing task and temporal order judgements (e.g. Johnston & Nishida, 2002; Clifford et al., 2003; Bedell, et al., 2003), we use both paradigms to test whether smaller directions changes are perceived before larger ones. Our findings confirm our hypothesis that smaller changes in direction of motion are perceived before larger ones with each task. They thus demonstrate that two visual attributes processed in the same visual area and of the same temporal structure may be perceived asynchronously.

2.1.2. Materials and Methods

Pairing judgement: Four subjects (3 male and 1 female) with normal or corrected to normal vision were instructed to fixate a central cross on a computer monitor (Sony Trinitron with a refresh rate of 60 Hz) at a distance of 50 cm. whilst viewing two sets of nine randomly placed moving white squares (1.22° in length) on either side of a fixation cross on a black background subtending within a square of 20° visual angle. Both sets of squares moved in either of two directions of motion at a speed of 6.5° sec^{-1}, changing direction every 0.5 s. One set (test squares) always moved back and forth along the horizontal axis while the other set (condition squares) moved rightward along the horizontal axis, and upwards at 45°, 90° or 135° (from rightward motion) in three different conditions respectively (see figures 2.1.1 and 2.2.2). The last condition, a 180° direction change, acted as a control, with both sets of squares moving back and forth along the horizontal axis. The changes in the directions of each of these two sets of squares were defined by two square-wave oscillations of the same period of 1s, presented at 30 different phase differences with respect to each other, within the range of 0-360°. Each phase difference was presented four times in each trial in a random order. In all conditions, each trial consisted of the presentation of two sets of moving stimuli for around 6s, at the end of which subjects were required to determine the direction of motion of the condition squares when the test squares moved to the right in a 2 alternative forced choice. A key-press on the computer keyboard recorded their choice. To control for attentional bias, two additional experiments were also performed for the 90° condition. (1) Subjects had to pair the direction of the condition squares when the test squares moved left. (2) The sides on which the test and condition squares were presented were reversed.

Subjects repeated 4 trials for each condition, giving 16 choices for all 30 phase differences. For each subject, the responses for each trial were plotted as polar curves, which represent response curves (see Moutoussis & Zeki, 1997a). These plot the percentage of time that the rightward motion of the test squares was paired with the specific direction of the condition squares. For example, in the first condition this would be plotted as the percentage of time that the rightward motion of the test squares was paired with the 45° rightward motion of the condition squares. If there is no asynchrony in the perception of the change in direction of the two motion stimuli, the response curve should resemble the veridical curve, which gives a rotation angle of zero. By treating each point on the graph as a vector, a mean vector was calculated, from which a rotation angle could be derived by measuring its angle against the vertical. The difference in the relative perceptual times of the two sets of motion stimuli was then calculated, as each degree is equal to 1.43ms, since 360° = 515ms, and a two-tailed t-test performed to test its significance from zero. Since the pattern of results suggested a possible linear relationship for each subject across conditions, the correlation coefficient (Pearson's r) was calculated with a 95% confidence interval for z.

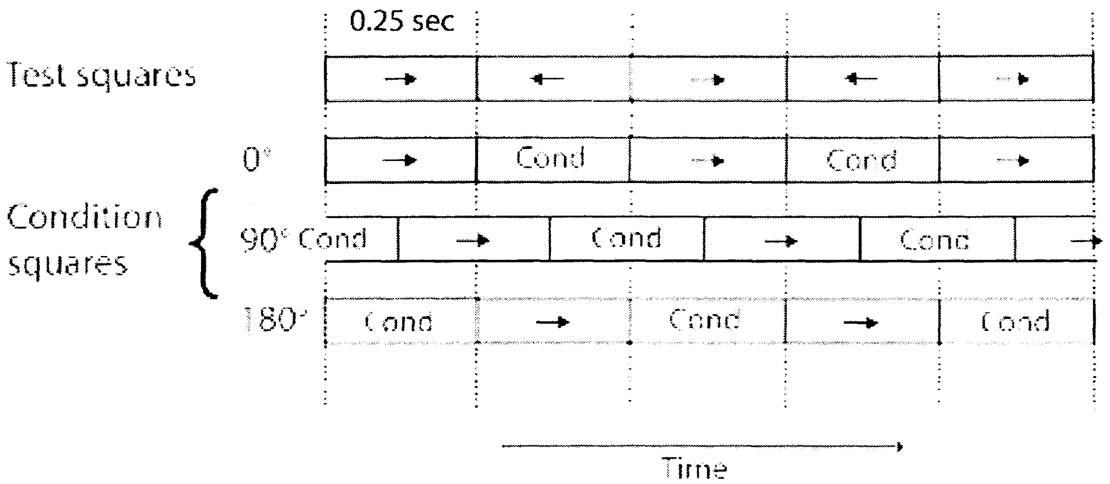


Figure 2.1.1. The direction of motion over time of the reference and test squares at three phase differences for the pairing task. 'Cond' means the condition specific direction of motion. The top row shows the direction of the reference squares, which move left and right along the horizontal axis at a constant alternation rate. The three rows below show the directions of motion of the test squares at three example phase differences, moving between rightward motion and the condition specific direction of motion. For example, at 0° phase difference (second row) both sets of stimuli move left at exactly the same time, whereas at 180° phase difference (last row) each set of stimuli move left at exactly the opposite times.

Temporal Order Judgement (TOJ): In this task, one author and 6 naïve subjects (4 male and 3 female) with normal or corrected to normal vision performed a TOJ for a 45°, 90° and 135° direction change against a 180° change, in three separate sessions consisting of 440 trials each (figure 2.1.2). Only one subject who had participated in the pairing task took part in this one. The psychometric function for the relative time that the two direction changes were perceived was derived by varying the time at which the two direction changes occurred over a period spanning 800 ms. We obtained 40 data points for each asynchrony difference. For each trial subjects fixated a central cross on a computer monitor (Sony Trinitron with a refresh rate of 85 Hz) at a distance of 50 cm, while presented with two random dot arrays subtending 20° visual angle moving downwards at a constant speed of $6.5°sec^{-1}$.The stimuli were matched to those used in the pairing judgement The side on which the 180° motion change was presented varied randomly from trial to trial. The first direction change occurred one second after stimulus presentation plus or minus random jitter time. Subjects had to indicate which dot array changed direction first after stimulus presentation.

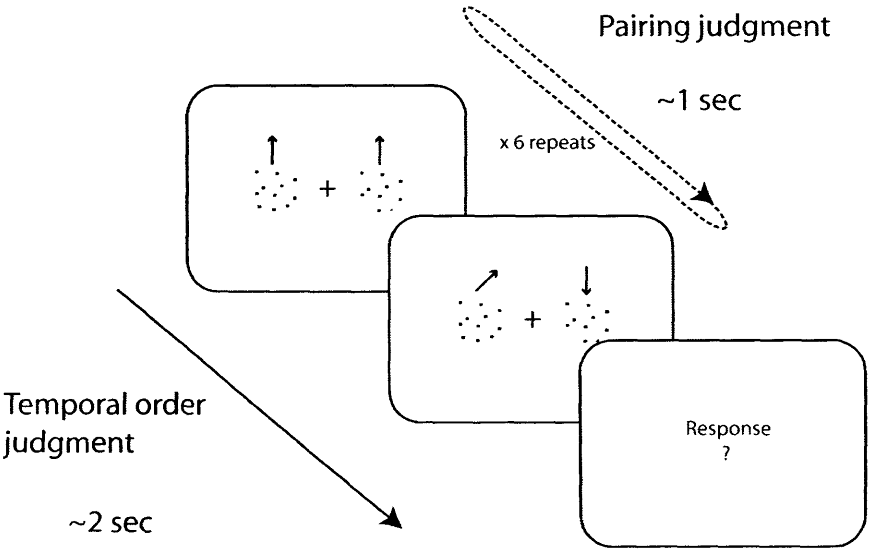


Figure 2.1.2. Stimuli for each trial of pairing judgements and temporal order judgements. Note that for pairing judgements, each dot array alternated between the two directions of motion (indicated by the arrows), whereas for the

temporal order judgement only one direction change occurred for each array. In this example, we were testing when subjects perceived a 45° direction change relative to a 180° direction change.

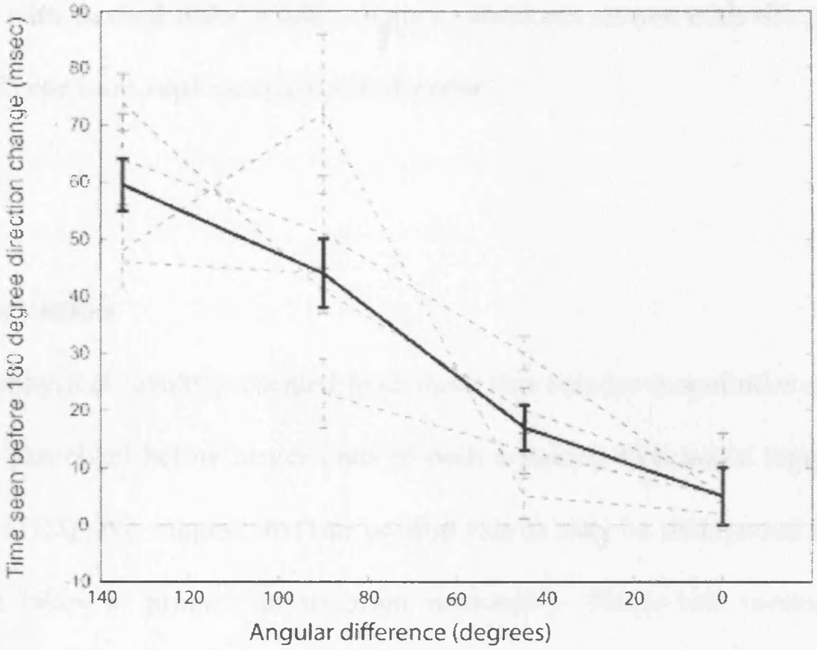
2.1.3. Results

Pairing judgment: The first three conditions (45°, 90° and 135° direction changes) produced a significant ($p < 0.001$) anticlockwise rotation of the response curve for each subject, with the exception of subjects TT in the 135° direction change condition and NC in the 45° direction change condition. The large standard deviation and subjective reports for the latter led us to conclude that, for this subject, the psychophysical task in this condition was too difficult, leading to guessing on each trial. This result was therefore discarded. The average rotation of the polar plot for all conditions across subjects was calculated and found to be highly significant ($p < 0.00001$) in the first three conditions. The last condition (pairing a 180° direction change) did not produce a significant rotation of the response curve ($p > 0.05$) in any of the subjects individually, as expected for the control condition using the same stimulus. The average rotation of the pooled response curves shows that 45°, 90° and 135° changes in the direction of motion are seen before 180° changes in direction by around 60, 44 and 17 ms respectively. The angle of direction change had a negative linear relationship to the perceptual time relative to a 180° direction change. This relationship becomes evident when the angle of direction change is plotted against the relative perceptual time differences (figure 2.2.3a), and was statistically significant for each subject ($p < 0.001$), giving correlation coefficients (Pearson's r) of -0.52, -0.49,

-0.62 and -0.59. Changing which direction of the test squares the subjects had to pair with the condition squares and the side on which each square array was presented gave the same result for the 90° condition, with an average of 50 and 47 ms respectively across subjects (t-test across subjects, $p < 0.001$, significantly different from zero; paired t-test for both controls showed no difference from main 90° condition across subjects, $p > 0.05$).

Temporal Order Judgement: We fitted each subjects' session data with a cumulative-Gaussian psychometric curve, which represented the proportion of trials on which the observer reported that the smaller change occurred before the 180° change in motion direction. From this, we derived the point of subjective simultaneity (PSS), which indicates when the observer perceived the two motion changes simultaneously. These data are summarized in figure 2.2.3b. In these plots, positive times indicate that the smaller change in direction occurs before the 180° change. Thus, positive times in these plots can be interpreted to indicate that the perception of a smaller motion change leads the perception of a larger motion change. It appears that across the 5 subjects the smaller direction change is perceived to occur on average ~125ms before the 180° change ($p < 0.0001$). Unlike the pairing task, there seems to be no negative linear relationship between the asynchrony and the magnitude of the direction change, as the PSS remains at an average of around ~125 ms for each condition. Remarkably, for two subjects the PSS could not be derived since on over 98% of trials they rated the smaller direction change to occur first, even when it was presented over 400 ms after the 180° change. One subject showed no significant shift in the psychophysical curve in all conditions ($p > 0.5$). The high inter-subject variability in the PSS, but not PSS standard deviation, of our results is consistent with previous studies of TOJs (Gibbon & Rutschmann, 1969; Cardosa-Leite et al., 2007). This variation has been attributed to differences individual response strategies applied to such judgements, and, significantly, not to delays in the processing of the stimuli. This may explain the null result in one subject, although it is also possible that a different cue other than motion, such as motion streaks, which can be used to determine motion direction (Geisler, 1999), underlies this subject's responses leading to no difference in the TOJs.

(a)



(b)

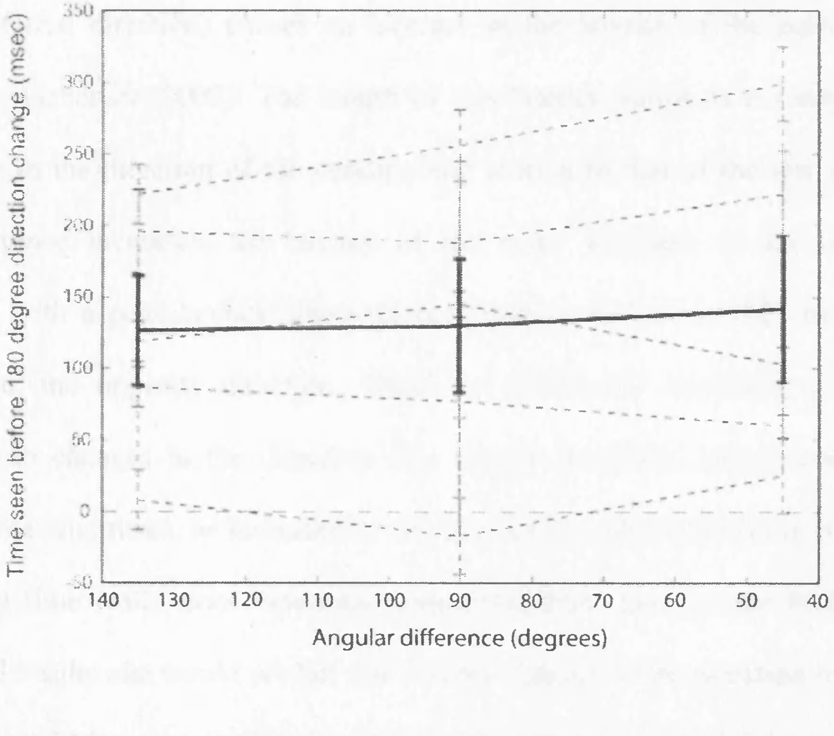


Figure 2.1.3. The time taken to perceive a change in direction of a moving stimulus before a 180° change plotted against the difference in angle between the test and condition squares. (a) perceptual asynchrony for pairing judgments, (b)

perceptual asynchrony for temporal order judgments. Data for single subjects are shown with dashed lines, while average values are shown with the continuous bold line. Error bars represent standard error.

2.1.4. Discussion

The psychophysical results presented here show that smaller magnitudes of direction change are perceived before larger ones in both a pairing task and a temporal order judgement (TOJ). We suggest that our present results may be understood in terms of the time it takes to process information neuronally. Single-cell recordings from prestriate area V5 of the macaque, which is specialized for visual motion (Zeki, 1974), show that exposure to conditioning motion stimuli prior to the test stimuli (the cells' preferred direction) causes an increase in the latency of the cells' response (Priebe & Lisberger, 2002). The length of this latency varies as a function of the difference in the direction of the conditioning motion to that of the test motion. As this difference increases, the latency of the cells' response to the test motion increases, with a peak latency when the conditioning motion is 180° from the test motion i.e. the opposite direction. These are effectively measures of the cells' responses to changes in the direction of a moving stimulus: larger changes mean longer processing times, as indicated by the increased response latencies. If the neural processing time really does determine perceptual time, then on the basis of these single-cell results one would predict that smaller changes in the direction of a moving stimulus would be perceived before larger ones if presented simultaneously. The relative perceptual times of changes in the direction of motion that we show here can therefore be explained in terms of processing time in V5.

Previous results consistent with the view that differences in neural processing times may directly translate into perceptual times have shown that the speed of processing of the same attributes may change if they differ in intensity (Roufs, 1963), share of covert attention (Carrasco & McElree, 2001) or retinal position (Carrasco et al., 2003). In addition, recent studies have demonstrated that other factors known to modulate the latency of neural processing such as attention (Paul & Schyns, 2003), salience (Adams & Mamassian, 2004) and motion transparency (Clifford et al., 2004) also affect colour-motion asynchrony. This contrasts with alternative views, that different latencies in perception are due to postdictive or comparator stages (Eagleman & Sejnowski, 2000; Moradi & Shomojo, 2005; Nishida & Johnston, 2002). The latter study interpreted the perceptual asynchrony for colour and motion to be due to differences in the temporal structure of these attributes, with colour changes being first order and motion changes being second order. There is perhaps some justice in this argument because for first order changes such as colour to be detected, only two points in time need to be sampled. By contrast, for second-order changes, such as a change in the direction of motion, a third point in time needs to be sampled. Therefore a change in colour will be detected before a change in motion, not because of differences in neuronal processing times, but because of the differing temporal properties of the changing stimuli. However, two first-order changes, colour and orientation, can be perceived asynchronously (Moutoussis & Zeki, 1997b), and here we show that two second-order changes can also be perceived asynchronously. Therefore, an explanation in terms of first and second order changes, at least in its simplest form, cannot account for perceptual asynchrony.

Our experiments resulted in a temporal asynchrony regardless of whether the judgment was one of pairing or detecting the temporal order of direction changes.

This result is consistent with the results of Viviani and Aymoz (2001), which show that colour precedes motion in TOJs. However, a recent study that used a TOJ for different magnitudes of direction change against colour changes (Bedell et al., 2003) found that the changes in colour and motion were perceived to occur at around the same time, regardless of the size of the direction change. A subsequent model by the same authors (Ogmen et al., 2004) suggests that TOJs are based on neural transients, and therefore different sizes of direction change should be perceived at the same time. However, this explanation based on transients is inconsistent. Neurophysiological data shows that transients in V5 are delayed when direction changes are larger (Priebe & Lisberger, 2002): if the perceptual asynchrony for TOJs are based on neural transients, smaller direction changes should be judged to occur before larger ones. This is precisely what happens in our experiments. Their model is therefore inconsistent with the known physiology, which shows that transients occur asynchronously (Priebe & Lisberger 2002), and with our psychophysical findings, which show that different magnitudes of directional change perceived asynchronously. Instead, the present results are consistent with the notion of different processing times, a principle that we have previously invoked to explain perceptual asynchrony (Zeki & Bartels, 1999).

The recent study of Bedell and colleagues used TOJ for different magnitudes of direction change against colour changes (Bedell et al., 2003). On the basis of the present results we would have predicted there to be a variable perceptual asynchrony for colour and motion depending on the magnitude of the change. However, it was found that the changes in colour and motion were perceived to occur at around the same time, regardless of the size of the direction change. In their study, the period prior to direction reversal was around 353 ms, whereas in the present study this was

1100ms. Therefore, in the study by Bedell and colleagues this period might have been insufficient to induce enough adaptation to affect the TOJ. Another possibility is that the perceptual asynchrony for different magnitudes of direction change in a TOJ is only apparent when the direct comparison between two changes is made. Therefore there may be some, as yet undefined, interaction between colour and motion for TOJs.

While the results for the pairing judgement show a clear negative linear relationship between the magnitude of the direction change and the perceptual asynchrony, mirroring the neurophysiology described above, the results from the TOJ do not. These suggest that, regardless of the magnitude, the smaller direction changes are all seen ~125 ms before a complete reversal. Thus although smaller changes in direction are judged before larger ones, the exact quantitative relationship is not the same for the TOJ. One possible explanation for this discrepancy is that other factors, in addition to neuronal latency, such as stimulus saliency may affect the temporal order judgement. The attentional gate model (AGM) predicts that events that occur later in time may be perceived to have occurred earlier if it has a higher attentional weighting (Shih & Sperling, 2002). For instance, after viewing a rapid serial visual presentation (RSVP) of letters, subjects ordered the items presented in the stream according to the attentional strength allocated to each item, rather than the veridical temporal order (Reeves & Sperling, 1986). The larger direction changes in the present experiments were much more salient that the smaller ones, which could cause the subject to orient their attention to the larger change. This may therefore reduce the relative perceptual asynchrony for the smaller direction changes, while having less of an effect on larger direction changes. While this speculation requires validation, there is at least a qualitative agreement between these two psychophysical methods which supports our conclusion that smaller changes in direction are perceived before larger ones.

Another issue is the difference, in both the pairing task and TOJ, is the lack of correspondence between the size of the latencies for the psychophysical results and those in the neurophysiological studies described. For instance, a 45° direction change elicits spiking approximately 20 milliseconds earlier than a 180° direction change. However, the present psychophysical experiments estimate the perceptual difference between such changes to be either 60 or 125 milliseconds for the pairing task and TOJ respectively. Therefore there are quantitative differences both between the tasks, as discussed in the previous paragraph, and between the tasks and the physiology. This may be accounted for by differences in physiology stimuli and those presented here: the adapting direction of motion was only lasted for 64 milliseconds compared to 500 milliseconds used with our stimuli. This would result in less adaptation and may therefore be responsible for the discrepancy in results. Alternatively, the latencies in neural firing may only indicate when stimulus processing begins, whereas the psychophysical tasks reflect when processing ends.

While we interpret the subjects' perception to reflect the neural latencies in V5, we assume that other brain areas outwith the visual cortex are required to make the judgment in these tasks. It is difficult to conceive of a comparison process occurring with V5 between different directionally sensitive cells. As discussed in section 1.5.2, it has been proposed that neurons in area LIP 'read out' the responses from V5 and accumulate evidence for a perceptual decision in response to the stimulus: LIP neurons show increasing ramp-like activity, with steeper ramps corresponding to higher coherence of stimuli; when this activity crosses a threshold, a decision is made (Gold & Shadlen, 2001). This may therefore be considered a candidate area making a decision regarding the pairing judgement and TOJ. In support of this, a recent fMRI study of cutaneous temporal order judgements showed that temporal discrimination, in comparison with detection, correlated with activity in the inferior parietal lobe and other brain areas proposed to be involved in temporal processing, such as the cerebellum and the basal ganglia (Pastor et al., 2004). There is a further issue of whether the accumulated activity in area LIP is responsible for the percept of motion itself; the latencies introduced in the visual pathway at V5 could translate into latencies in the parietal cortex, thereby explaining the present results. While in theory possible, we believe that such activity in posterior parietal areas are attributable to what is reported rather than what is perceived. The issue of dissociating perception and report is addressed further in section 3.3.

Our results provide strong support for the supposition that the basis of perceptual asynchrony lies in differences in processing times, and suggest that perception within a single visual submodality can be fractionated in time, depending upon the characteristics of the attributes to be tested. This fractionation goes beyond the merely functional and acquires a greater importance because of its implication. We have argued elsewhere that activity within an area can acquire a conscious correlate (Zeki & Bartels, 1999). Here we suggest that the activity of a group of cells within an area can acquire a conscious correlate independently of the conscious correlate that the activity of another group acquires. Physiologically, it has been suggested that the binding of separate visual attributes occurs through synchronous or oscillatory firing in the specialised visual areas (von der Malsburg, 1981; Engel, et al., 1999), or the selection of attributes through attentional mechanisms (Reynolds & Desimone, 1999). While in theory possible, whether such mechanisms are employed to bind attributes together in the same visual area is unclear. However, the present results provide evidence that such mechanisms could not compensate for different processing delays in the processing of stimuli prior to perception. Rather, different groups of cells within a single area can generate their own conscious correlates, which are distributed in space and in time.

2.2 Perceptual compression of space through position integration

2.2.1. Introduction

Positional localisation of a moving object presents an apparent paradox, namely that when a particular location is frozen at a given moment in time, the attribute of motion cannot exist at all (Salomon, 1970). This issue has been the subject of more recent debate, mainly due to interest in the 'flash-lag effect', which occurs when a flashed stationary object is perceived to lag behind a spatially aligned moving object (Mackay, 1958; Nijhawan, 1994). It has proved to be a fertile illusion for generating theories of visual awareness and the timing of visual perception. As discussed in the previous section, temporal aspects of perception have recently gained much interest, as it has been recognised that it is important to understand *when* awareness occurs, as well as *where* in relation to the brain.

While multiple mutually competing theories have been proposed for this phenomenon, there is no consensus on the correct account. Each has specific consequences for the brain mechanisms of visual awareness. The first proposal suggests that to account for motor delays in reacting to a moving stimulus, the visual system extrapolates the position of a moving stimulus to its future positions (Nijhawan, 1994). Therefore, such a theory is predictive. In contrast, a couple subsequent theories suggest that visual awareness is 'online'. The first of these claims that the flash-lag effect is due to differential perceptual latencies: moving objects are perceived before stationary ones thereby account for their differences in relative perceived position (Whitney & Murakami, 1998). The second online theory claims that this illusion is due to the integration or averaging of position over a period of time, leading to the moving object to appear to be ahead of the flash (Krekelberg & Lappe, 2000). In addition to positional averaging, the 'post-diction' theory claims that the brain is able to 'reset' the information it has accumulated for position in response to a salient external event, in this case a brief flash (Eagleman & Sejnowski, 2000a). The subsequent positional information gained is then 'post-dicted' to the time of the flash. This claim is of greater theoretical interest as it means that the brain is capable of time stamping when external events occur and arranging them accordingly in awareness in a temporal buffer. Finally, an attentional account proposes that the perceived lag in the flashed stimulus is due to an attentional shift across the visual field. (Baldo & Klein, 1995) With regard to the neural mechanisms of visual awareness, it is clear that while high-level theories sit more comfortably with either motion extrapolation or post-diction, only the online theories, positional averaging and differential latency, are able to accommodate the most low-level modular theories of visual awareness.

Previous studies of the flash-lag effect have mainly focussed on the relative spatial localisation of moving objects at motion onsets or during continuous motion. Similarly, in the Fröhlich effect, subjects mis-localise the initial position of a moving object in the direction of motion (Fröhlich, 1929). Here we investigate relative position localisation at both motion offsets and onsets. Using the conventional 'flash-lag' paradigm and the relative positioning of a continuously moving bar, we found that subjects mis-localise the final position of a moving object prior to its disappearance in the direction opposite to its trajectory. This is consistent with the positional averaging hypothesis (Morgan, 1975; Krekelberg & Lappe, 2000): the veridical position is averaged over a time period preceding the disappearance, thus causing it to be seen to disappear before its veridical final position. Furthermore, this offset effect is smaller than onset effects observed with either the Fröhlich effect or the flash-lag effect, suggesting that this process is weighted to the most recently sampled positions. Finally, we demonstrate that the influence of both motion onset and offset effects leads to the perceived asymmetrical compression of a moving dot array. We are thus also able to account for the compression of moving shapes when viewed through apertures, a seemingly unrelated illusion that has been unresolved since originally described by Helmholtz (1867) and Zöllner (1862). These results provide strong evidence for the proposal that the perceived position of a moving object is the result of the weighted integration of signals relating to position over a short time window.

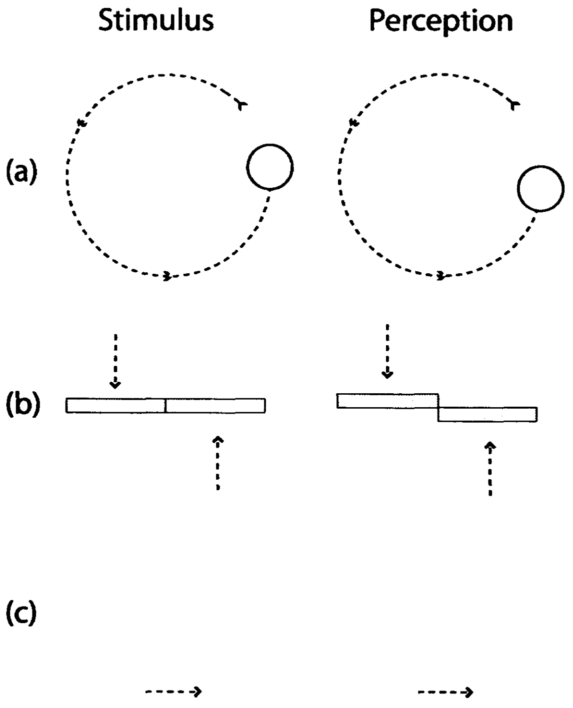


Figure 2.2.1. Schematic diagram of the three main experiments. (a) Flash-lead effect, (b) reverse-repmo, (c) compression of space. Dotted arrows represent motion trajectories.

2.2.2. Materials & Methods

All experiments were done in a darkened experimental room using a Sony high-resolution CRT monitor with a refresh rate of 100Hz and a viewing distance of 30cm. Stimuli were constructed using a PC running MatLab (Mathworks Inc.) and the Cogent Graphics package (http://www.vislab.ucl.ac.uk/Cogent/index.html). Responses were recorded via key-press on a computer keyboard. Points of subjective simultaneity were derived by using the method of constant stimuli in a 2AFC task and fitting a Weibull function (2-parameter model: shape and 50% point) to the data. Each subject had normal or corrected-to-normal vision. Informed written consent was obtained before experiments. Three naïve subjects and one of the authors (3 male) participated in all experiments. During each trial subjects fixated a central square. Unless otherwise stated, the stimuli were presented on a black background with a luminance of 5 cd/m^2.

Experiment 1: Flash-lead Effect.

We modified the flash-lag paradigm to determine the perceived position of a moving stimulus at motion offset. We refer to this as the 'flash-lead' effect. During flash-lead trials, a moving hollow circle (radius: 1.67°, filled with the black background, edges luminance of 25 cd/m^2) appeared after a random interval of under one second from the beginning of each trial and moved in a circular trajectory at a speed of 200° sec^{-1} around the fixation point. At a random position, the moving circle was briefly filled with a stationary achromatic flash of one of three luminance values (108, 34, 12.5 cd/m^2). In the following frame, both the moving circle and the flash disappeared (figure 2.2.1a). Note that this differs from previous flash-terminated cycles (e.g.

Eagleman & Sejnowski, 2000a) as the moving target actually disappears at the end of its trajectory instead of stopping. Subjects had to indicate whether the flash appeared above or below the moving circle. These trials were randomly mixed with trials measuring the conventional flash-lag effect, using the identical set-up described, except that the moving circle continued to move after the flash occurred. By varying the position of the flash relative to the moving circle, the psychometric function of the position of the flash was calculated.

Experiment 2: Reverse-repmo.

We modified the classical Fröhlich experiment, in which a bar moves in a given direction and subjects have to specify its position when it appears, in two ways: instead of having one bar, we introduced a second bar and asked subjects to determine the relative position of the two bars, at both onset and offset. We refer to the latter as the 'reverse-representational momentum' or reverse-repmo. More specifically, two bars (5.7° x 0.67°), both presented either to the left or right side of fixation (randomised trail by trial), moved towards each other vertically (speeds ranging from 4.2 to 24.7° sec^{-1}) from the bottom and the top of the screen, respectively, towards the mid-point where they were horizontally spatially aligned for one frame before disappearing. The bars did not overlap, although there was no gap between them when side-by-side (figure 2.2.1b). Subjects then indicated whether the bars passed each other or not prior to disappearance. We calculated the psychometric function of the relative positions by varying the position at which the two bars disappeared relative to each other. In a separate experiment we measured the classical Fröhlich effect by using an identical set-up. In this case the bars were presented aligned at the mid-point and moved vertically in opposite directions. Subjects had to indicate whether the bars appeared above or below relative to each other. The psychometric function was calculated by varying the position at which the two bars appeared relative to each other.

Experiment 3: Compression of space.

The above set of experiments led us to ask whether reverse-repmo and the Fröhlich effect mis-localisations may sum and account for compression of moving shapes when viewed through apertures (reviewed by Rock, 1981). In the first set of experiments, we measured the amount of compression that subjects perceived a moving diamond shaped array (test array) composed of 4 dots to undergo. Each dot was 0.95° in radius. The vertically aligned dots were 2° apart, whereas the horizontally aligned dots were 2.9° apart (see figure 2.2.1c). In the main condition, the test array briefly appeared as if moving rightwards from under an invisible occluder, was completely exposed, before moving underneath a second invisible occluder on the right, at a constant speed of 40.6° sec^{-1}. Note that the dots therefore just disappeared without being covered by a visible occluder. This set-up was reminiscent of the aperture-viewing experiments originally performed by Helmholtz (1867) and Zöllner (1862), where an object moves through a narrow slit, only exposing a small portion at a time. Observers report seeing the stimulus integrated as whole, although compressed in the direction of its motion. In our experiment the aperture was slightly wider than the moving stimulus (3.4° width), thereby briefly exposing the whole array at the same time. If the theory of positional averaging is correct, we predicted that the array should still appear compressed in size, as reverse-repmo at the leading dot should occur simultaneously with the Fröhlich effect at the trailing dot. Since the latter effect is larger, our second prediction was that the compression effect would be asymmetrical, with the trailing side of the array appearing most compressed.

The test array randomly appeared either above or below fixation on each trial. In addition to this was the reference array, which matched the exact temporal profile of the dots in the moving array, but did not move and appeared on the opposite side of fixation to it. We varied the width of the test array by adjusting the distance of the two horizontally aligned dots relative to the centre, to derive the psychometric function of the compression of it. Subjects then indicated in a force choice if the moving test array was narrower or wider than the reference array. Three additional conditions were randomly interleaved with the main one described above; differential offsets, where the whole array appeared simultaneously but had differential offsets by disappearing underneath the invisible occluder; differential onsets, where the whole array had differential onsets by appearing from underneath the invisible occluder, but disappeared simultaneously; and simultaneous onset/offsets when the whole array appeared and disappeared simultaneously. This last condition acted as a control since motion smear (Burr, 1980) could cause subjects to bias responses, overshadowing the effect of differential on-/offsets. It should be noted that in the last three conditions that when the dots appear or disappear simultaneously, they all appear or disappear on the screen in the same frame as if no invisible occluder was present. This is in contrast to the main condition where the dots appear and disappear as if from behind an invisible occluder.

The second set of experiments measured the asymmetry of the arrays, and took the same structure as those described above. There was no reference array and subjects were asked to indicate what side (left or right) appeared most compressed. To derive the psychometric curve we multiplied the X co-ordinates using:

$$X' = X \cdot (1+Ke^{X}) \qquad (1)$$

where K is a constant with thirteen values from –12 to 12. This manipulation distorted the layout of the dot array so it appeared compressed on either the left or right sides. We also quantified the asymmetry of the compression effect using a set-up similar to those traditionally used in aperture viewing experiments (see review Rock, 1981). Two achromatic rectangles (both 8.5° by 6.7°) were displayed on either side of a central fixation spot leaving a slit of 1.3°. The diamond shaped dot array moved across this slit from underneath the occluding rectangles either above or below the fixation spot at a speed of 40.6° sec^{-1}. Subjects had to indicate which side appeared most compressed as before.

Experiment 4: Flash-lead effect using bars of different widths.

A recent study of Kanai et al. (2004) found that using foveally presented stimuli in which both the moving cursor and a spatially aligned flash disappeared in the frame after the flash appeared, there to be no significant flash-lead or flash-lag effect. This is surprising given the present flash-lead effect that we report here. However, the width of the stimuli used in this previous study were much wider than those used in our first experiment. Given that the subjects' task of detecting the offset of the flash and the cursor is essentially a Vernier judgement, it seemed plausible that the negative result reported previously could be due to a lack of sensitivity with the thicker stimuli used. Previous studies (e.g. Levi et al., 2000) have shown that the width of stimuli affects the ability of subjects to detect offsets in a Vernier task. Therefore, using similar stimuli to Kanai et al., we wanted to determine whether the width of the moving and flashed bars could affect the subjects' ability to perceive the flash-lead effect.

One author and three subjects who did not participate in the experiments 1-3 took part. Two moving rectangular bars (length: 1.26°, separation of 1.3°) appeared after a random interval of under one second from the beginning of each trial and moved upwards from below fixation point at a speed of 17.9° sec^{-1}. The width of the bars on each trial was one of three values (0.042°, 0.168°, 0.265°), randomly selected. After an interval of under a second, the gap between the bars was briefly filled with a stationary achromatic flash with the same width as the moving bars. In the following frame, both the moving bars and the flash disappeared. Subjects had to indicate whether the flash appeared above or below the moving bars. By varying the position of the flash relative to the moving bars, the psychometric function of the position of the flash was calculated.

Experiment 5: Attentional bias for foveal and peripheral moving targets.

Given the substantial literature on representational momentum, we wanted to distinguish our results from this previously known effect. A series of experiments by Kerzel and colleagues have established that under steady fixation, representational momentum is due to an attentional overshoot in the direction of motion (see review, Kerzel, 2005). This is thought to only occur with apparent motion and not smooth motion, as used in our experiments. However, to ensure that an attentional overshoot or undershoot was not occurring in our experiments, we used the same reaction time paradigm introduced by Kerzel (2003) to examine the deployment of attention after implied motion stimuli. This previous study found that reaction times (RTs) to a probe stimulus presented in the direction of implied motion were faster than those to a probe presented in the direction opposite to the implied motion.

The same subjects who took part in experiment 4 participated. On each trial after a variable delay a smooth moving bar (speed: 17.9° sec^{-1}, width: 0.63°, length: 1.47°) appeared 1.98° ± fixation point and either left or right of fixation by 0.04° (central), 2.94° or 5.88° (peripheral). On trials in which the bar appeared above fixation, it moved vertically downwards and vice versa. After an interval of 350ms ± jitter of 170ms, the target disappeared. A probe stimulus (either a 'x' or a '+' symbol) was then presented 1.9° either before or after the moving stimuli's final position along its trajectory. Two of the subjects were instructed to respond using the left key as soon as they saw the 'x' stimulus and the right key as soon as they saw the '+' stimulus. The probe stayed onscreen until a response was given. This stimulus-response mapping was reversed for the other subjects.

2.2.3. Results

Experiment 1: Flash-lead effect.

Subjects perceived the moving object to lag behind the flash before both stimuli disappeared (figure 2.2.1a). This is consistent with the positional averaging hypothesis: the veridical position is averaged over a time period of 100ms or so, as previously suggested by integration times for detecting moving objects (Burr, 1981) preceding the disappearance, causing it to be seen to disappear before its veridical final position. We found that, like the conventional flash-lag effect, this effect varies with the luminance of the flash, occurring with the maximum amplitude if the luminance is high (a repeated measures ANOVA revealed a significant effect of flash luminance ($F(2.6) = 12.46$, $P<0.01$; figure 2.2.2), consistent with previous psychophysical evidence suggesting that higher luminance reduces perceptual latencies (Roufs, 1963). The earlier in time the flash is perceived relative to the moving cursor because of higher luminance, the earlier in the course of the trajectory of the moving cursor is it co-localised with. But the lead is significant even at low flash luminance. We can infer the existence of such a lead effect from previous data (Müsseler et al., 2002), although it was attributed to response bias and not interpreted to be a genuine perceptual effect. However, the effect of flash luminance makes that interpretation improbable.

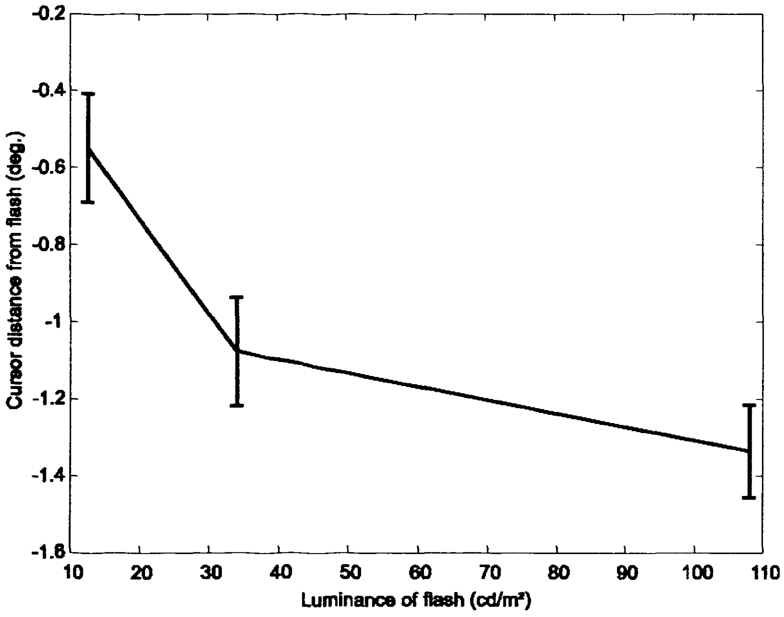


Figure 2.2.2. Group average data for the flash-lead effect at three different luminances of flash. Negative values indicate that the moving cursor is perceived to lag behind the flash. Error bars represent ± 1 SE across subjects.

Experiment 2: Reverse-repmo.

All subjects mis-localised the final relative position of the two bars in the direction opposite to their motion trajectories prior to disappearance (figure 2.2.1b, 2.2.3a), with the magnitude increasing with stimulus speed over the range used. The same effect was observed with a moving stimulus when one of the bars was stationary and aligned with the final position of the moving bar (mean: 0.31°, one sample t-test across subjects at 95% significance: $p < 0.0001$). We quantified the Fröhlich effect using this same stimulus set-up and found it to be substantially larger than reverse-repmo (figure 2.2.3b). A t-test at 95% significance revealed that both effects were significantly different from zero across all speeds ($P<0.0001$, df: 3).

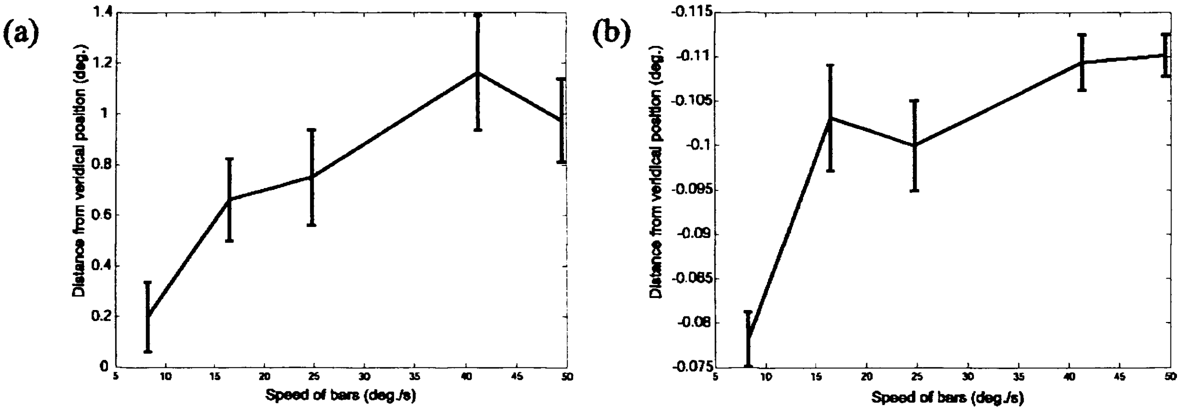


Figure 2.3.3. Group average data for the Fröhlich effect (a) and reverse-repmo (b) as a function of stimulus speed. Values on the Y-axis indicate the subjects PSS in relation to the moving bar's veridical first (a) or last (b) position in the direction of its trajectory. Error bars represent ± 1 SE across subjects.

Experiment 3: Compression of space.

The results given above show that the trajectory of a moving stimulus appears to start later and end earlier than it does veridically, causing the perceived length of its trajectory to be compressed. Can both of these effects be observed simultaneously? Our results show significant compression effects over the control condition in both the differential on-/offsets conditions and the simultaneous offsets condition (figure

2.2.4a). The simultaneous onsets condition gave a small insignificant compression effect. This is consistent with the larger mis-localisations observed at motion onsets than at motion offsets (figure 2.2.3). A repeated-measures 4 x 4 ANOVA with subjects and conditions as factors revealed significant compression effects over the control condition in both the differential on-/offsets condition and the simultaneous offset condition ($F(3,9) = 33.6$, $P < 0.0001$; using Tukey's honestly significant difference criterion for post hoc comparisons. $P < 0.01$). Note however that using subjects as a factor limits inference of the effect at the population level. Neither the simultaneous onset nor simultaneous offset conditions were large enough to be able to account for the compression effect observed in the main condition alone, although the sum of them approximates it in each subject adding to a combined compression of 1.27, which is not significantly different from the observed compression of 1.32 ($p > 0.41$ one sample t-test at 95% significance across subjects), and therefore suggests that this is due to a contribution from both onset and offset effects.

To quantify the asymmetry of compression, subjects performed a forced choice test to report which side of the array appeared to be the most compressed, i.e. on which side the middle dots appeared closest to the outer dot. Consistent with our predictions, the main condition showed a slight asymmetry in the compression to the trailing side compared to the control, which we presume is due to the larger influence of onset effects. The identical result (mean: 6.1 deg., one sample t-test at 95% significance across subjects: $p < 0.0001$, df: 3) was also observed with a stimulus set-up similar to those traditionally used in aperture viewing experiments and to our knowledge has not previously been reported. This was also apparent in the second condition when all the dots disappeared simultaneously and only differential onsets had an influence. In the third condition with only differential offsets, a significant asymmetry in the array was found, although this time the leading side was judged more compressed compared to the control condition, as expected by the small backwards mis-localisation observed at motion offsets of the leading dots. In contrast to the results of the absolute compression of the array, our results were not consistent with a quantitative prediction of the main combined onset and offset condition from the simultaneous offsets and onsets conditions. We would have predicted the asymmetry index to be smaller in the main condition than in the simultaneous onsets condition, and not the reverse, which is what we observed. All conditions were significantly different from the control as shown by a 4 x 4 ANOVA ($F(3,9) = 61.16$, $P<0.0001$) using Tukey's honestly significant difference criterion for post hoc comparisons ($P < 0.01$).

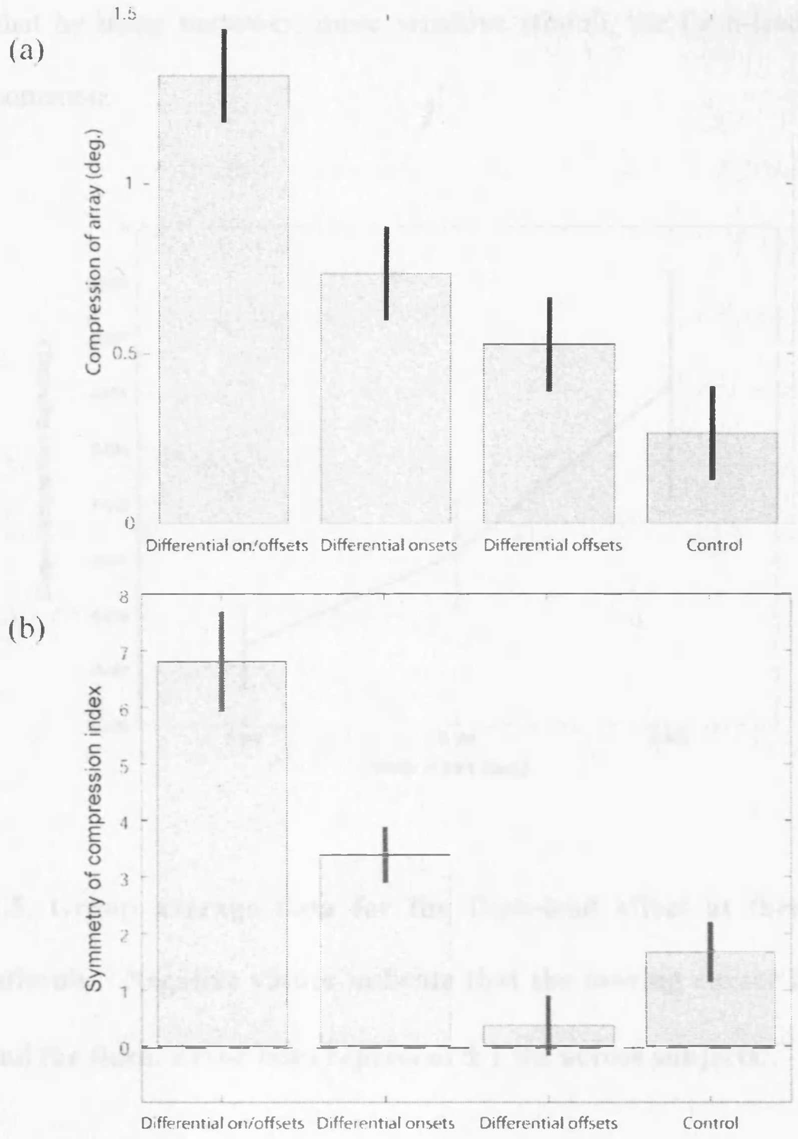


Figure 2.2.4. Group average data for the (a) size of compression, (b) the asymmetry of the moving array in the three on-/offset conditions. Values greater than the control indicate that the trailing side of the array appeared more compressed. Error bars represent ± 1 SE across subjects.

Experiment 4: Flash-lead effect using bars of different widths.

A flash-lead effect was observed for the two narrower stimuli (t-test at 95% significance, $P < 0.01$, df: 3) across subjects, but was not apparent for the widest stimulus ($P > 0.2$). We therefore replicate the previous result of Kanai et al. (2004), and show that by using narrower, more sensitive stimuli, the flash-lead effect is a robust phenomenon.

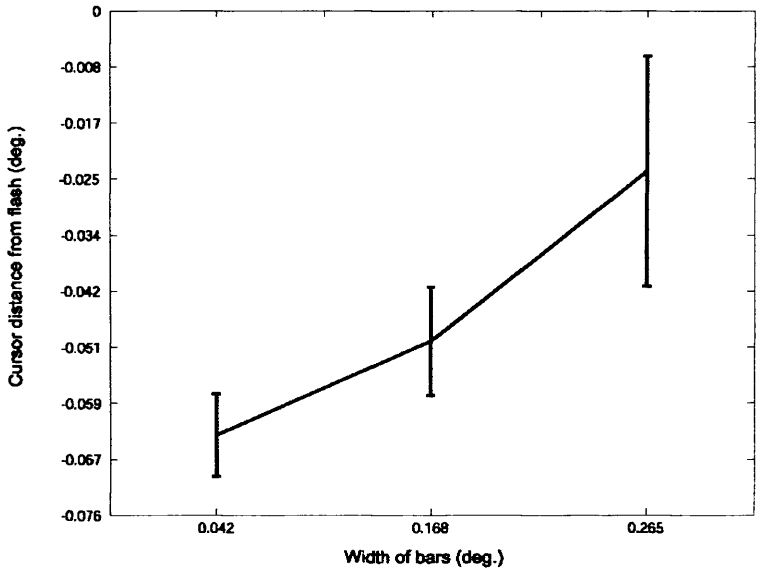


Figure 2.2.5. Group average data for the flash-lead effect at three different widths of stimuli. Negative values indicate that the moving cursor is perceived to lag behind the flash. Error bars represent ± 1 SE across subjects.

Experiment 5: Attentional bias for foveal and peripheral moving targets.

We excluded trials in which RTs were less that 100ms or more than 1000ms. Using a 2 x 3 ANOVA with eccentricity of stimulus (central, middle and peripheral) and probe location (before and after final line stimulus) as factors, we found there to be a significant effect of eccentricity (F(2,23) = 24.3, P<.001) and probe location (F(1,23) = 9.2, P<0.001). Moreover, the interaction effect of probe location and eccentricity was also significant (P < 0.001). Post hoc comparisons using Tukey's honestly significant difference criterion reveals quicker responses when the probe appeared in the direction for both peripherally presented stimuli ($P < 0.01$), but not when presented foveally ($P > 0.1$).

By using the same reaction time paradigm introduced by Kerzel (2003), we found there to be significant attentional overshoot with smooth motion in the direction of the moving cursor for the peripheral stimuli only. Therefore, we can be confident that the effects we describe in our main experiments are not subject to asymmetrical attentional shifts (either an undershoot or overshoot). A recent study of Kanai et al. (2004) found for peripheral stimuli only, the flash-lag effect occurs when the moving cursor disappeared in the same frame as the flash disappeared, which according to the averaging model should result in the flash-lead effect. Given the present result, this lead effect of moving stimuli described by Kanai et al. (2004) for the peripheral moving stimuli may be subject to the same attentional overshoot in the direction of the moving stimuli, and could therefore be considered another example of representational momentum. Our new results therefore fit with those of Kerzel (2005) in explaining why a perceived forward momentum can be obtained through attentional overshoot.

2.2.4. Discussion

The results that we report provide strong evidence in favour of the averaging hypothesis for localising the position of a moving object at a given moment in time, and are therefore consistent with a low-level modular theory of visual awareness (Bartels & Zeki, 1998). The new experiments that we have introduced have provided results which show that (a) when a moving object disappears, it is perceived to lag behind a spatially concurrent flash; (b) two moving objects aligned at their final positions with respect to each other are perceived to be mis-aligned in a direction opposite to their direction of motion; (c) a moving shape with both leading and trailing edges is perceived to be asymmetrically compressed. Together with the variants that we have given in the results, the most plausible interpretation of these experiments is that the brain averages the positions occupied during the last 100 ms or so. Note however, that the magnitude of reverse-repmo is much smaller than the Fröhlich effect. We suggest that although positional averaging is taking place, it is weighted towards the most recently sampled positions.

The position averaging theory may also explain the flash-lag effect if we assume that during a period of time after the flash, corresponding to the integration window, the average position of the moving object is calculated, resulting in the moving object being seen after the flash. This process may also take into account positions of the moving object that occurred prior to the flash, in line with data showing that the flash-initiated cycle can produce a larger flash-lag effect than during continuous motion (Ogmen et al., 2004). Similarly, the Fröhlich effect can be explained if after a certain time period from the appearance of the moving object, its average position is calculated, causing the object to be seen ahead of the veridical initial position. This enables us to account for all four of these effects within a single overall framework.

Our results cannot be accounted for by alternative explanations of the flash-lag effect, as offset effects for moving objects place tight constraints on possible explanations of positional localisation. The motion extrapolation (Nijhawan, 1994), attention (Baldo & Klein, 1995), latency difference (Purusothaman et al., 1998; Whitney & Murakami, 1998) and 'post-diction' hypotheses (Eagleman & Sejnowski, 2000a), at least in their simplest forms, would all predict that the flash should be perceived to lag, or at the very least be concurrent, with the moving cursor. The flash-lead effect described here shows that these predictions do not hold true. Furthermore, the revised version of post-diction (Eagleman & Sejnowski, 2000b) would predict that the relationship between the size of the lead effect and the luminance values of the flash should be reversed, as the more salient the flash, the more the positions of the moving cursor before it should be devalued, thereby producing a reduced or annulled flash-lead effect. A recent version of the differential latency hypothesis (Ogmen et al., 2004) is able to accommodate the flash-lead effect with a ramped response function for the position computation of moving stimuli. However, our second experiment shows that this mis-localisation is not specific to moving versus stationary objects. Their model would predict that reverse-repmo should not exist: the two bars would eventually be seen to disappear at their veridical positions and be spatially aligned, given the assumption that they both have equal perceptual latencies.

It important to distinguish the present results from related previous findings. Firstly, the backwards mislocalisation at motion offsets is surprising, given the previous 'representational momentum' literature which shows that subjects mis-locate manually the position of a moving object to a point beyond the final position of the moving object (Freyd & Fink, 1984). A series of experiments by Kerzel and colleagues (Kerzel, 2003; reviewed in Kerzel, 2005) has established that under steady fixation representational momentum is due to an anticipatory overshoot in attention in the direction of the moving target. This occurs even when the motion sequence has terminated and the stimulus disappears, which according to our model should not lead a perceived forward displacement of the final position. For example, in a previous study using smooth motion stimulus, observers judged the final position of a moving object to be after its veridical final position (Hubbard & Bharucha, 1988). However, a subsequent study using the similar stimulus parameters (Kerzel et al., 2001) found that when smooth eye movements are controlled for by making the subjects perform the task under steady fixation, the perceived forward displacement disappears. Thus, representational momentum in this case is due to an over shoot in overt attention. In the present study, we find that an attentional overshoot, or even undershoot, does not occur with smooth motion foveally. Therefore such an attentional effect is not responsible for the effects described in our main experiments.

However, we did find such an overshoot to occur with smooth moving peripheral targets. This may account for the apparent discrepancy between the present findings and recent results that show a forward mis-localisation of the moving object in a flash-terminated condition where both the moving and flashed object disappear in the frame after the flash (Kanai et al., 2004). Their effect was contingent on the moving stimulus presented peripherally, which does cause an attentional overshoot, and could therefore be due to the same attentional overshot which underlies representational momentum. The lack of lead effect for foveally presented stimuli by Kanai et al. (2004) may be explained by the lack of sensitivity in using thicker stimuli: narrower stimuli, like the moving cursor used in the present experiment, allows greater vernier sensitivity (cf. Levi et al., 2000) and therefore greater sensitivity in detecting this subtle lead effect. Our fourth experiment confirms this hypothesis. Furthermore, we believe the present flash-lead effect to be distinct from the motion extrapolation effect described by Fu, Shen and Dan (2001), who found, using a stimulus set-up similar to our reverse-repmo experiment, the final position of a moving blurred object was mis-localised in the direction of motion. Firstly, as acknowledged by the authors, it is clear that their effect depends on the blurring of targets, unlike the sharp edges used in our experiments, which they account for by the properties of biphasic temporal responses of visual neurons. Secondly, their effect peaked at low speeds; this is unlike the present effect, which increases with velocity over a comparable range of values. Finally, their sharp edged targets remained at the final location for 100ms. According to our explanation, this would result in no mislocalisation in either direction, which is what they found; the crucial difference is that the present stimuli disappeared in the frame after reaching their final position.

We further extended these observations with a novel dot array stimulus to investigate the simultaneous effects of motion onsets and offsets. Consistent with our predictions, we found that the array appears to be asymmetrically compressed. Moreover, exclusively differential motion onsets produced larger compression effects than offsets, and did so on the trailing side of the array, whereas exclusively differential motion offsets had a smaller effect and compression occurred on the leading side of the array. The larger effects of motion onsets than offsets may explain the asymmetry in the differential on- and offsets condition, and the asymmetry we observed under normal aperture viewing conditions. Therefore the weighted averaging of position is also able to account for how the sequence of parts of an object viewed through an aperture is integrated into a whole and why the image appears compressed (Rock, 1981). Each position of the component of the object is averaged over 100ms or so, thereby allowing the image to be integrated as a whole. This same integration causes the mislocalisation at motion onsets and offsets effect to sum, as demonstrated by the present experiments, which leads to the overall compression of the shape. Moreover, we are able to confirm our novel prediction, which directly leads from the weighted averaging hypothesis, that this compression effect is asymmetrical. Our explanation also accounts for the increase in compression previously observed (Morgan, Findlay & Watt, 1982) with object speed and the narrowing of aperture size. We suggest that the averaging process corresponds to the hypothetical 'post-retinal storage mechanism' proposed to account for the effects of aperture viewing (Parks, 1965), in contrast to a 'retinal painting effect' caused by eye-movements, since the compression effects observed here occurred under steady fixation.

A neurophysiological explanation for the flash-lag effect has previously been proposed by Berry and colleagues (Berry et al., 1999) based on results from retinal recordings. It was found that in response to a moving bar stimulus, the population activity precedes the stimulus arriving at that particular location. Comparable neurophysiological responses have recently been found in the temporal cortex of the macaque (Perrett et al., 2005). The simple model put forward (Berry et al., 1999) suggests that this is due to the high-contrast stimuli desensitising the responses of ganglion cells after a short time delay, which in turn causes the ganglion cells just ahead of the bar to be strongly excited as the edge begins to enter their receptive-field centre. However the response gain reduces and the firing rate declines shortly after. This feature of the model may be able to explain the weighting of position of moving objects that we have proposed here; as the response to current position is reduced, the anticipated response future one is in turn enhanced, leading to a weighted neural response with regard to the object position. Such a mechanism, combined with the relatively long integration time of human vision (Barlow 1958; Burr, 1981), may therefore account for the weighted averaging of the position of moving objects

In the context of the present thesis, this positional averaging mechanism is most consistent an 'online' view of visual awareness; that is, a stimulus is perceived as soon as it is processed. This is in line with the findings in the section 2.1 where it was suggested that neural latencies translate into perceptual latencies, and the general theory that visual awareness is due to low-level processing in the visual cortex.

Functional brain imaging

3.1 Bistable and stable figures: top-down and bottom-up interactions assessed with dynamic causal modelling.

3.1.1. Introduction

Ambiguous or bistable figures have been used throughout the last couple of centuries in perception research as they offer keen insights into how the visual system interprets the outside world and represents it in awareness. Observers perceive such stimuli to be in one of two states, which periodically 'flip' from one state to another, despite the stimulus remaining constant. Perhaps the best known of these is the Necker cube (Necker, 1832), where a wire frame picture of a cube can be perceived to be in one of two planes of depth. These fluctuations are thought to occur because the image provides ambiguous information that could be interpreted as one of two equally probable three-dimensional objects, which compete for dominance over time. However, despite the wealth of research with bistable figures over the last couple of hundred years, the mechanisms underlying this phenomenon are still under debate.

Currently the main theories of the mechanisms underlying perceptual reversals fall into two camps: 'bottom-up' and 'top-down'. Bottom-up theorists posit that relatively automatic, stimulus driven effects trigger the figure reversals: neural channels that support the dominant interpretation become passively adapted, allowing the other interpretation to then dominate. Evidence for such a mechanism includes the increasing reversal rate over viewing time (Brown, 1955), adaptation and stimulus effects on figure reversals (Nawrot & Blake, 1989; Cipywynk, 1959) and recent electrophysiological evidence showing early disambiguation of the figures

(Kornmeier & Bach, 2005). In contrast, advocates of the top-down hypothesis suggest that the reversals occur due to a 'high-level' cognitive interpretation of the stimulus. More recent formulations (e.g. Leopold & Logothetis, 1999) suggest that influences from higher cortical areas, such as the parietal or prefrontal cortex, influence lower areas of the visual cortex, such as those representing objects, through top-down modulations. Evidence for such an account comes from behavioural literature showing volitional and attentional effects on reversals (e.g. Meredith, 1962), and from fMRI studies showing a large 'fronto-parietal network' of areas active during such changes (Kleinschmidt et al., 1998). In addition to these main accounts, there are hybrid theories that incorporate both bottom-up and top-down influences on figure reversals (e.g. Long & Toppino, 2004), with the relative contribution of each effect varying according to both stimulus conditions and cognitive set. However, a causal role for either a bottom-up or top-down mechanism has yet to be demonstrated.

Bistable stimuli have recently proved popular for the study of the neural basis of visual awareness since, not only do they show the areas of the brain which correlate with the observers' subjective experience (Lansing, 1964; Logothetis & Schall, 1989; Tong et al., 1998), but also regions active during the transition from one perceptual state to another. Functional imaging studies have found that during perceptual changes a right-biased fronto-parietal network to be active; in particular the dorsolateral prefrontal and the superior parietal cortex (e.g. Lumer et al., 1998, Kleinschmidt et al., 1998), areas previously associated with working memory and shifts in spatial attention (Corbetta et al., 1993; Kastner et al., 1999). Further studies have emphasised the role of frontal and parietal areas in change detection (Beck et al., 2001; Shulman et al., 2001) and perception in general (Rees et al., 1999; Dehaene et al., 2003). These studies are consistent with the view that to be aware of a visual stimulus, or at least to be aware of a change in a visual stimulus, there must be a causal influence from the fronto-parietal network. This type of theory, often referred to as the 'global workspace theory' as reviewed in section 1.6.6, posits that the top-down modulations are key in selecting and maintaining the contents of awareness. A prediction of such a theory is that even non-ambiguous stimuli will require activation of this workspace to enter awareness. In a previous fMRI study of binocular rivalry (Lumer et al, 1998), the pattern of perception during rivalry was mimicked with stimulus induced perceptual changes between each eye, and these transitions correlated activity in frontal operculum and right inferior frontal gyrus, in addition to activity in visual areas. Thus, a contribution from higher areas such as the frontal and parietal cortices may not only be needed to perceive internally generated changes in bistable figures, but also externally induced events that occur during normal viewing, as predicted by a recent computational model (Dehaene et al., 2003).

It was these issues that motivated the present study and our aim was three-fold: we wanted to (1) measure the contribution of both 'bottom-up' and 'top-down' effects on the perceptual reversals of bistable figures; (2) quantify the different contributions that these influences have on different types of figures; (3) assess whether similar neuronal dynamics occur during externally induced perceptual transitions. To answer these questions we measured brain activity with functional magnetic resonance imaging (fMRI) in humans during perceptual transitions while viewing a Necker cube, which subjects perceive to be in one of two planes of depth (Necker, 1832), and the Rubin's vase (Rubin, 1915), which subjects perceive to be either two faces or a vase. In addition, subjects were presented with stable analogues of these figures that did not undergo rivalry and were alternated externally (stimulus-induced changes). We analysed the results using conventional analysis to examine regionally specific effects, and dynamic causal modelling (DCM; Friston et al., 2003) to examine how perception of both bistable and stable figures modulate neuronal dynamics between areas. This is therefore the first study to measure changes in effective connectivity between brain areas during perceptual rivalry. We were specifically interested in whether forward or backward connections modulate the lateral occipital cortex (LO), an area thought to represent the perceived shape of an object (Kourtzi & Kanwisher, 2001), during bistable and stable figure transitions.

3.1.2. Methods

Subjects

Nine healthy volunteers (six women and three men; mean age 23.3 ± 1.85) with normal, or corrected to normal vision, participated in the study. All subjects gave informed consent in accordance with the Declaration of Helsinki, and the Ethics Committee of the National Hospital for Neurology and Neurosurgery, London, UK, granted ethical approval for the study.

Stimuli

All stimuli were constructed using COGENT 2000 Graphics (available at www.vislab.ucl.ac.uk) running in MATLAB (Mathworks Natick, MA). The stimuli were presented centrally and projected onto the screen by means of an LCD projector. They consisted of two bistable figures, the Necker Cube and the Rubin's Vase, and two stable analogues for each of these, which do not undergo spontaneous perceptual alternations (figure 3.1.1). These consisted of two cubes in two unambiguous planes of depth, and a simple vase and two face silhouettes. Care was taken to design these stimuli to resemble the perceptual interpretations of the bistable figures as much as possible, without being bistable themselves. The bistable figures were presented in a random order for a period of 25 seconds. Subjects were required to make a right-hand button press in response to each perceptual alternation. Following presentation of the bistable figures, the exact pattern of alternations was recreated using the stable analogue using the timing reported through the key reports. Subjects were still required to report perceptual changes of these stable figures via the button press to control for motor responses. Each subject participated in two sessions, each lasting approximately 14 minutes, with 7 presentations of the 4 stimulus types (two bistable and two stable).

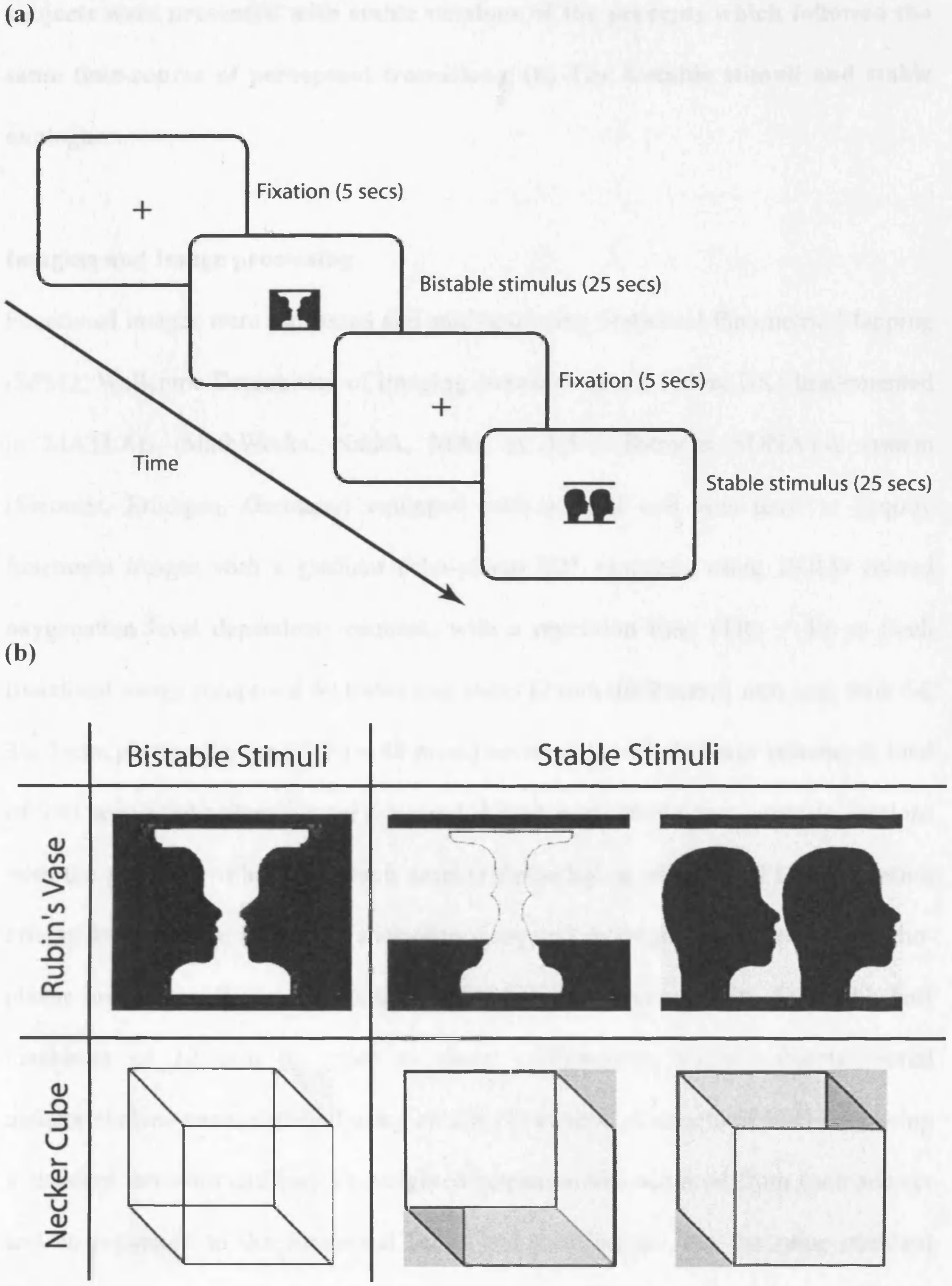


Figure 3.1.1. Trial structure and stimuli. (a) Subjects fixated a central cross on a blank screen and viewed the bistable stimulus for a period of 25s while reporting perceptual transitions via key-press. Following another short period of fixation,

subjects were presented with stable versions of the percepts which followed the same time-course of perceptual transitions. (b) The bistable stimuli and stable analogues.

Imaging and Image processing

Functional images were processed and analysed using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB (MathWorks, Natick, MA). A 1.5-T Siemens SONATA system (Siemens, Erlangen, Germany) equipped with a head coil was used to acquire functional images with a gradient echo-planar T2* sequence using BOLD (blood oxygenation level dependent) contrast, with a repetition time (TR) = 3.6 s. Each functional image comprised 40 transverse slices [2 mm thickness; 1 mm gap; 64 x 64, 3 x 3 mm pixels echo time (TE) = 40 msec] covering the whole brain volume. A total of 240 sequential volumes were acquired during each of the two separate sessions with the first four volumes of each session discarded to allow for T1 equilibration effects. Images were realigned, slice-time corrected, normalised to a standard echo-planar image template and smoothed with a Gaussian kernel with full-width half maximum of 12 mm in order to make comparisons across subjects. Serial autocorrelations were modelled using an AR (1) method. A structural MRI scan using a standard three-dimensional T1-weighted sequence was acquired from each subject and co-registered to the functional scans and transformed into the same standard space.

Data Analysis

Brain activation for each experimental condition was estimated according to the general linear model for each voxel in brain space (Friston et al., 1995). The stable and bistable stimulus transitions for both stimulus types onsets were modelled as events using the canonical haemodynamic response function to capture the BOLD onset. For the DCM analysis, the periods of presentation of the stable and bistable figures were modelled as blocks by a box-car waveform of 25s convolved with the haemodynamic response. This analysis was still in effect modelling the differences in the type of perceptual transitions, as we were comparing between blocks in which the only difference was the type of perceptual transition (internal for the bistable, external for the stable), with duration, alternation rate and task instructions identical. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and the three rotations determined from initial registration), and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 128. We performed a random effects analysis; images of parameter estimates for each contrast of interest were created for each subject (first-level analysis) and were then entered into a second-level analysis using a t-test for each contrast. This analysis considers both within- and between-subject variance and allows generalisations to be made about the population from which the subjects were taken. This contrasts with a fixed effects (first level) analysis, which uses within subject variance, providing inferences for the subjects used in the study only (Holmes & Friston, 1998).

Dynamic causal modelling (DCM)

We then analysed the data using DCM (Friston et al., 2003) to estimate the probability that one brain area exerts an influence over another, and how this is affected by experimental condition. Three distinct sets of underlying parameters are estimated. The first set represents the direct relation between brain states and any particular region, and are the primary motivation for conventional analysis of regionally specific activations in brain imaging experiments. The second set of parameters called 'intrinsic connections', refer to the influence that one brain region has on another in the absence of experimental context. The third set of parameters, called bilinear terms, is the postulated change in the 'intrinsic connections' due to experimental manipulations.

In contrast to classical analyses of neuroimaging data, these parameters allow one to make inferences about the effect of experimental manipulation on active connections between brain regions, instead of the region itself. DCM estimates the underlying neuronal activity from the haemodynamic response using a previously validated biophysical model of fMRI measurements (Friston et al., 2000; Mechelli et al., 2001). The estimated underlying neuronal activity is then used to derive the connectivity parameters (for details, see Friston et al., 2003). In brief, these two steps are iteratively repeated and correspond to the expectation (E) and maximization (M) steps of an expectation maximisation algorithm. This finds the maximum likelihood estimates of the parameters in the DCM, which are unobserved. The algorithm alternates between performing the E-step, which computes an expectation of the likelihood by including the unobserved latent variables, and the maximization M-step, which estimates the maximum likelihood estimates of the parameters by maximizing the expected likelihood from the previous E step. These parameters from the M step are then used to begin another E step, and so on (Dempster et al., 1977).

The intrinsic connections estimate the rate of change of neuronal activity in one area induced by activity in another. Contrasting with purely correlative measures of *functional* connectivity, DCM thus makes use of the temporal information contained in fMRI time series to assess *effective* connectivity, i.e., the causal relationships between activity changes in different brain regions (Friston et al., 2003; Stephan, 2004). This characterization does not depend on the units of activity, but the speed or rate of interregional coupling. It is therefore possible make inferences about feed-forward and feedback connectivity, which is particularly relevant in the present study.

Subject specific regions (6 mm-radius) were selected on the basis of the regions activations detected with statistical parametric mapping. The peak voxel activations within the regional activity were selected and defined in terms of the principal eigenvariates. These values were entered into the DCM to estimate independently for each subject the forward and backward 'intrinsic connections', the influence that one region has over another in the absence of an experimental factor, and the 'bilinear terms', the modulation of the intrinsic connections by each type of figure. For statistical analysis, we adopted a two-stage procedure that is formally identical to the summary statistic approach used in random effects analysis of neuroimaging data (Holmes & Friston, 1998). The first level consisted of the coupling parameters between regions (intrinsic connections) and the modulations of these induced by experimental manipulation (bilinear terms). The conditional expectations or modes of these parameters were taken to the second level for classical inference using t-tests. Each separate t-test of our connections entailed multiple comparisons and we therefore report our results at two levels. First descriptively at $P < 0.05$ (uncorrected), and second using corrected statistics with the Bonferroni procedure for multiple comparisons, corresponding to corrected P-values of $P < 0.0083$ for the intrinsic connections and $P < 0.0125$ for the bilinear terms.

Using regions that were significantly active in the SPM analysis, we constructed three alternative dynamic causal models within each subject. This enabled us to use Bayes factors to compare DCMs with different intrinsic connectivity patterns in order to determine the most likely intrinsic connectivity pattern of a model given our observed functional data set (Penny et al., 2004). The first alternative model was composed of a bidirectional hierarchical network (figure 3.1.3a) consisting of the primary visual cortex (V1), the lateral occipital cortex (LO), the superior parietal cortex (SPC) and the prefrontal cortex (PFC). For computational simplicity, we restricted our analysis of these areas to the right hemisphere only. The second was identical to the one described above, with the addition of a backward connection from SPC to V1. This was motivated by previous studies that have established attentional modulation occurs as early as V1 (Somers et al., 1998), through feedback connections from the parietal cortex (Buechel et al., 1998). The third alternative model was identical to our first one, with the addition of bidirectional connections from LO to the PFC. This was dictated by macaque anatomical studies showing connections between analogous areas such as TE and area 45 (Chavis & Pandya, 1976; Webster, et al., 1994).

We were then able to compare these models using a Bayesian model selection procedure to identify the most likely model for our data (Penny et al., 2004). In theory the best model should be a compromise between the fit of the model to the data and the complexity of the model, which depends on the prior covariance of the intrinsic connections. However given that the covariance is defined in a model specific fashion, models with different numbers of connections cannot easily be compared. Fortunately two methods are available that offer appropriate approximations in this case: Akaike's information criterion (AIC) and Bayesian information criterion (BIC) which have different complexity terms shown by:

$$BIC = accuracy(m) - d_{\theta}\_lnN$$
$$AIC = accuracy(m) - d_{\theta}\_ \tag{2}$$

Where d_θ is the number of model parameters and N is the number of scans. Given that almost all fMRI studies are more than 8 scans, it is obvious that BIC is reduced for larger data sets. Correspondingly, it has been shown that empirically that AIC is biased towards complex models, whereas BIC is biased towards simple models (Kass & Raftery, 1993). If the evidence using both of these models at the single-subject level is in agreement, we calculate the Bayes factor for each of model comparison of any pairs of models (m_i and m_j) given by:

$$B_{ij} \quad p(y|m_i) \quad p(y|m_j) \tag{3}$$

To determine if a model is optimal at the group level, we then take the product of the individual Bayes factors (Stephan & Penny, 2006). Therefore for each subject, we first performed pairwise comparisons between all models and then computed the group Bayes factors across subjects.

After establishing the most plausible anatomical architecture, we analysed the changes in regional connectivity. Our first analysis was performed to investigate the effects of the stable and bistable figures on interregional connectivity. We collapsed the time course of brain activity during perception of these figures together giving only bistable and stable blocks. The aim of a second analysis was to determine whether there were any differences in interregional connectivity between the two bistable figures. The stimulus function for the DCM analysis that encoded either the perception of both stable and bistable figures (first analysis) or the perception of each of the bistable figures only (second analysis), entered the dynamic causal model through V1, which allowed the resulting perturbation to propagate through the model via interconnections with LO and the other regions. The same network was used with both stimulus types. We specified bilinear terms to look at the influence of figure types (either between stable and bistable, or different bistable types) on all backward connections and the forward connections from V1 to LO. This is because we were specifically interested in testing whether backward connections from the higher areas or forward connections from V1 have a causal influence on LO under these conditions.

3.1.3. Results

Statistical parametric mapping

The data from nine subjects were submitted into a random effects analysis to identify activity in brain regions during perceptual transitions while viewing two types of bistable figures and their corresponding stable analogues. At the uncorrected level of significance, we observed increased activity around area V3 for perceptual reversals of the Necker Cube compared to those of the Rubin's Vase. However no differences were observed at the corrected level. Therefore, it appears that the neural activations observed during the transitions with both of these bistable figures are largely common to each. Next, we collapsed activity for both types of bistable transition and compared this with externally mediated changes of both stimulus types. By subtracting the activity measured during transitions between the stable figures from activity measured during the transitions between percepts while viewing the bistable figures, we were able to localise activity in areas that may responsible for selecting percepts when multiple interpretations of the retinal input are possible. For both the Necker cube and Rubin's vase figures, this contrast showed activity in the superior parietal cortex (SPC) bilaterally (peak voxel co-ordinates [34 –56 62], Montréal Neurological Institute (MNI) space), the right dorsolateral prefrontal cortex (DLPFC; [52 14 10]) and the frontal eye fields (FEF; [-32 –8 60]). In addition, lateral occipital areas, which may include the V3 complex and LO showed activity (left: [-44 -72 -12], right: [48 -78 2]). Threshold controlling false discovery rate (FDR; Genovese et al., 2002) at 5% gave peak voxel activations bilaterally in LO, SMA, superior parietal lobules, and the right DLPFC. The reverse contrast, external transitions versus bistable transitions, revealed activity mainly in the medial frontal cortex [6 10 -16], bilateral inferior parietal lobules (left: [-58 -58 20], right: [58 -64 32]) and medial temporal lobes (left: [-60 -12 –16], right: [52 -12 -12] and were significant at 5% threshold controlling FDR.

Finally, we looked for modulation of activity for both external and internal transitions above and below baseline (figure 3.1.2). For internal transitions this revealed almost identical areas to those observed when contrasted against externally mediated changes at uncorrected level and correcting for FDR. Areas that showed event-related modulations below baseline during internally mediated transitions at 5% FDR included large regions of the posterior cingulate cortex [6 –58 30], the medial frontal cortex [-6 24 –2], bilateral inferior parietal lobules (left: [-40 –68 42], right: [48 –66 38] and the superior colliculus [-10 -40 -10]. Comparing events where brain activity for externally mediated transitions occurred above the intrinsic baseline showed right biased visual areas including LO [54 -74 -4], the V3 complex [36 –96 8] and left-sided motor and somatosensory activations [-30 –22 54]. This is consistent with subjects reporting a perceptual change with a right-hand key-press. However, none of these activations were significant at 5% threshold controlling FDR. No regions showed significant modulations below baseline at 5% FDR for externally mediated stimulus transitions. However, at the uncorrected level modulations were observed in the superior parietal lobules and primary and somatosensory areas.

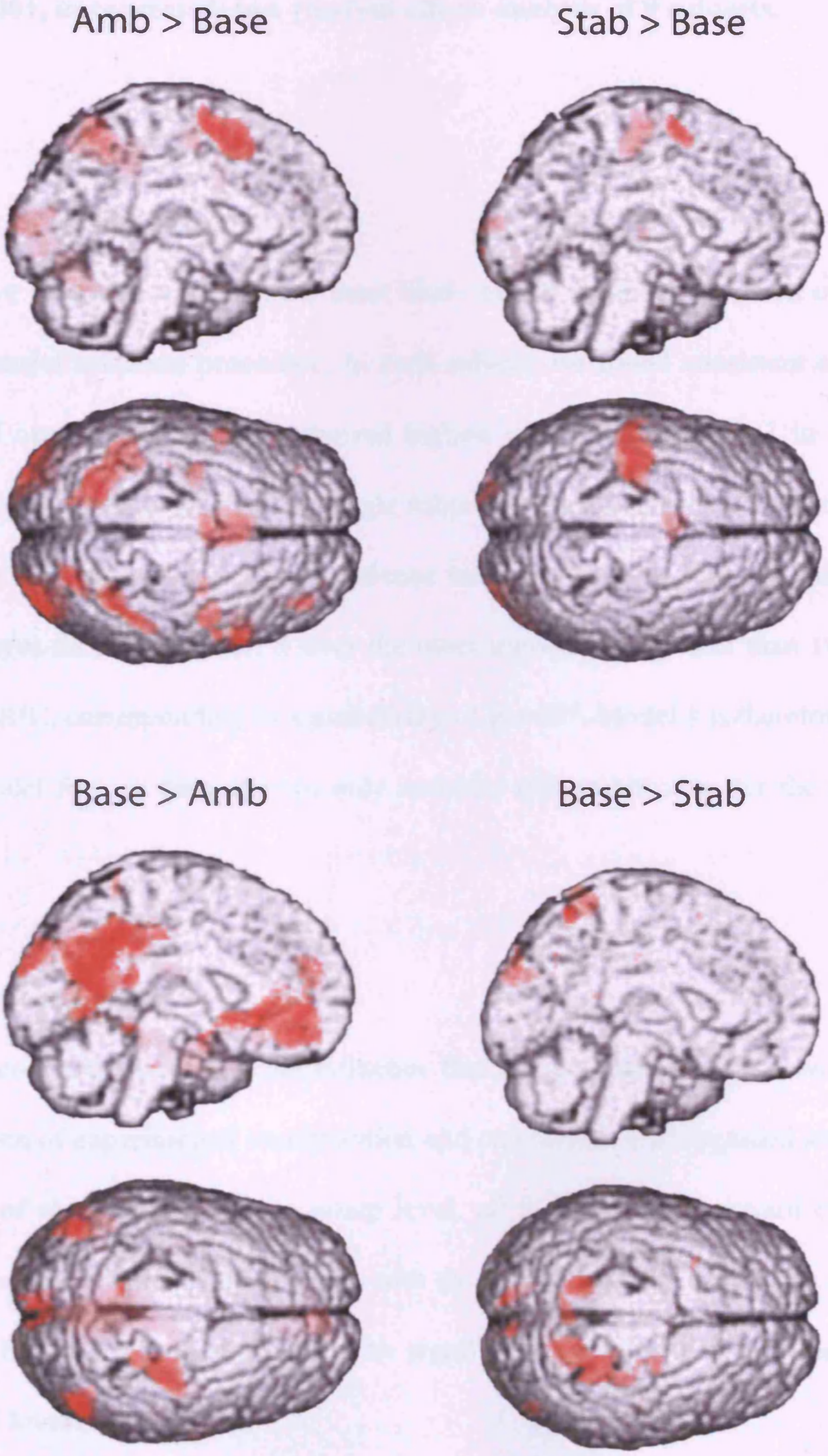


Figure 3.1.2. Event related modulations during perceptual transitions above and below baseline. Amb = bistable transitions. Stab = Stable transitions. Base =

Intrinsic baseline. Data are displayed with a statistical threshold corresponding to P < 0.001, uncorrected, in a random effects analysis of 9 subjects.

Dynamic causal modelling

Firstly, we sought to establish the most likely model architecture, given our data set using a model selection procedure. In each subject, we found consistent evidence in favour of our first model. AIC showed highest evidence for model 1 in 8 out of 9 subjects (we therefore exclude the single subject not in agreement from the rest of the analysis), and using BIC model 1 evidence was highest in all subjects (table 1). The group Bayes factor for model 1 over the other models was greater than 10^8 for both AIC and BIC, corresponding to a probability of $p < 10^{-8}$. Model 1 is therefore the most likely model for our data and we only consider this architecture for the rest of the analysis.

Intrinsic connections

Intrinsic connections refer to the influence that one cortical region has on another in the absence of experimental manipulation and can therefore be regarded as a baseline measure of connectivity. At the group level, all forward and backward connections throughout the network (figure 3.1.3), with the exception of the backwards connection between LO and V1, were found to be significantly greater than 0 at the corrected statistical level ($P < 0.0083$).

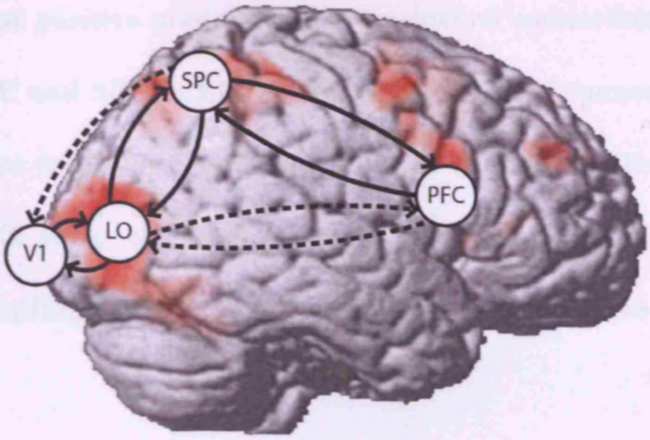
Modulations during figure presentation

Our group analysis revealed that during the presentation of the bistable figures there were significant positive modulations at the corrected level ($P < 0.0125$) from V1 to LO, from PFC to SPC and SPC to LO (figure 3.1.3). Figure 3.1.4 shows the observed and predicted BOLD response from a typical subject. During perception of externally changing stable figures, the backward connections from PFC and SPC to the SPC and LO respectively, showed significant negative modulations at the corrected level of significance. Given that we found both forward and backward connections to LO to be significantly modulated by presentation of bistable figures, we wanted to assess whether one pathway has a greater influence than the other. We therefore took both of these modulatory terms from the individual subject level for the backward and forward connections to LO and compared them at the group level using a paired t-test. The V1 to LO connection was found to be significantly larger ($P < 0.001$). Finally, we assessed the differences in interregional connectivity between the Necker cube and Rubin's vase bistable figures: no significant differences were observed, even at the uncorrected level of significance.

	Model 1		Model 2		Model 3	
	AIC	BIC	AIC	BIC	AIC	BIC
1	0.49	0.84	0.42	0.13	0.092	0.028
2	0.75	0.94	1.7e-27	1.2e-26	0.25	0.05
3	0.47	0.83	0.17	0.055	0.35	0.11
4	0.74	0.94	0.26	0.06	4.7e-05	1.1e-05
5	0.47	0.84	0.16	0.049	0.37	0.11
6	0.64	0.93	0.27	0.069	0.086	0.0039
7	0.61	0.91	0.31	0.082	0.078	0.0036
8	0.44	0.96	0.54	0.037	0.02	2.4e-05
9	0.38	0.84	0.37	0.15	0.25	0.017

Table 3.1.1. Evidence for all nine subjects for the three DCMs using Akaike's information criterion (AIC) and Bayesian information criterion (BIC).

(a)



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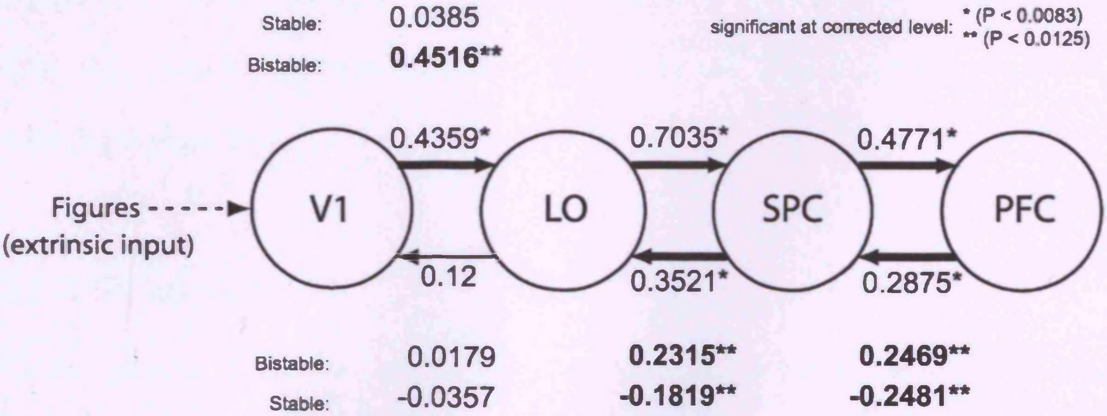


Figure 3.1.3. (a) The intrinsic connections of the dynamic causal model comprises a bidirectional hierarchy from V1 to PFC, via LO and SPC (filled

arrows). Dotted arrows represent additional connections of alternative models considered. (b) Group results for the DCM analysis. Values refer to the coupling coefficient between regions. The extrinsic input coding 'figures' comprised presentation of both stable and bistable figures and was entered into the model through via V1. All intrinsic connections, with the exception of the backward connection from LO to V1, were significant. During perception of bistable figures significant positive modulations of backward connections were observed from PFC to SPC and SPC to LO, as well as the forward connection between V1 and LO. Negative modulations of the backward connections from PFC to SPC, and SPC to LO were observed during perception of stable figures. Units represent the coupling co-efficient between different brain areas (Hz).

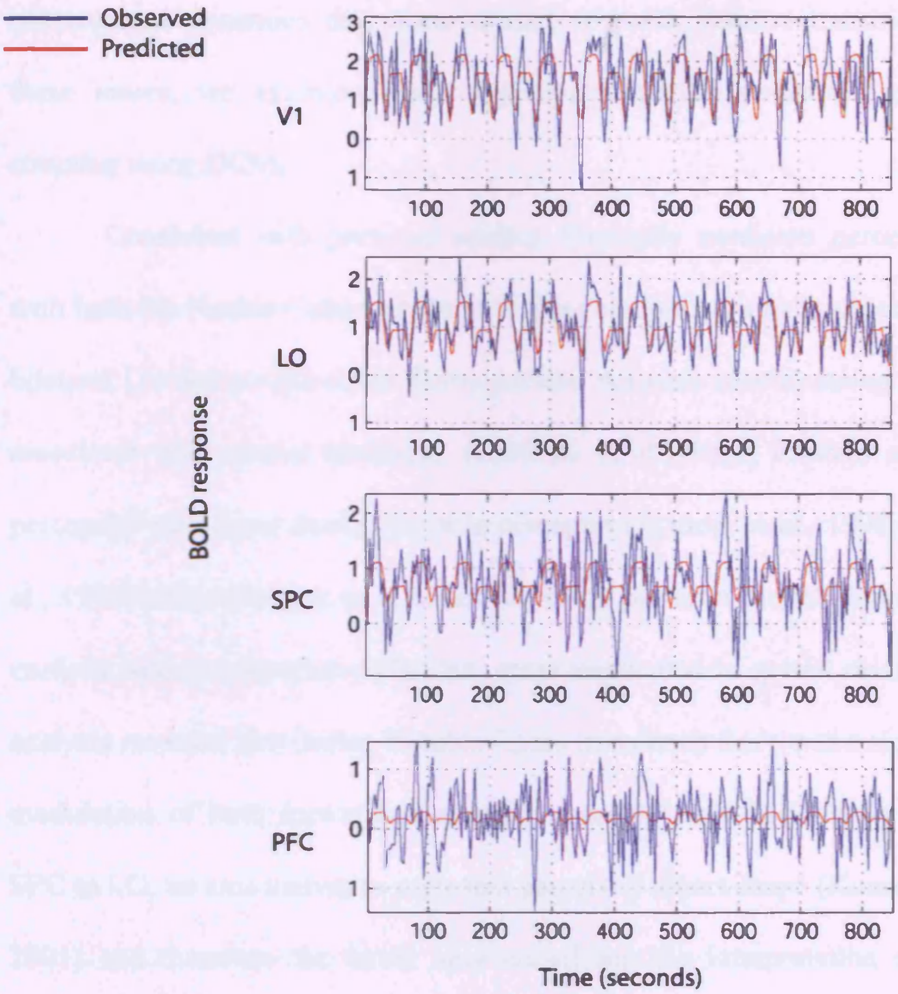


Figure 3.1.4. Fitted responses in the four regions of interest in a single subject. Blue lines represent observed BOLD response; red lines represent predicted BOLD response from DCM.

3.1.4. Discussion

In the present study we investigated the neuronal networks that underlie the perception of both bistable figures and normal stable figures. Our motivation was three-fold: to (1) asses the contribution of 'top-down' and 'bottom-up' influences on the perceptual interpretation of bistable figures, (2) quantify the differences that these influences may have on different types of figures, (3) observe the relative interregional dynamics that occur during stimulus induced transitions. To address these issues, we examined both regionally specific responses and interregional coupling using DCM.

Consistent with previous studies, internally mediated perceptual transitions with both the Necker Cube and Rubin's Vase elicited regionally specific activations in bilateral LO and a right-sided fronto-parietal network encompassing areas previously associated with spatial attention (Corbetta et al., 1993; Kastner et al., 1999) and perceptual transitions during bistable perception (Lumer et al., 1998; Kleinschmidt et al., 1998). Deactivations were observed in the posterior cingulate and medial frontal cortices, and the superior colliculus, areas implicated in spatial orienting. Our DCM analysis revealed that during bistable figure transitions there was a significant positive modulation of both forward connections from V1 and backward connections from SPC to LO, an area known to represent perceived object shape (Kourtzi & Kanwisher, 2001) and therefore the likely area underlying the interpretation of these figures. Given that we instructed the subjects to simply view the figures, we can only speculate on what initiates these top-down signals. Previous behavioural studies have provided good evidence for attention, either overtly through eye-movements (Boring, 1942; Ellis & Stark, 1978) or covertly through spatial or even feature-based attention (Meredith; 1962; Struber & Stadler 1999), to be a major factor in initiating bistable figure reversals, both of which could initiate the top-down influence to LO. In the present case we believe the latter to be the most likely, as the subjects maintained steady fixation throughout scanning. It could be argued that the V1 to LO modulations are caused by top-down modulation of V1 activity by higher areas. However, our model selection procedure demonstrated that the model with backward connections from SPC to LO, and not V1, was the most likely model for our data. It would be interesting to see whether this also holds for binocular rivalry, in which V1 is modulated according to perceptual state (Polonsky et al., 2000; Lee & Blake, 2002). Overall, our results support a hybrid theory of bistable figures that incorporates both top-down and bottom-up effects (Long & Toppino, 2004). Such a proposal suggests that these effects are not mutually exclusive, rather they simultaneously influence figure reversals across multiple processing stages. This result is therefore consistent with the seemingly disparate psychophysical literature that provides evidence for both mechanisms influencing figure reversals. Although such mechanisms have previously been hypothesised on the basis of psychophysical and conventional neuroimaging analyses, this is the first study to directly demonstrate them.

We also found no significant differences in the regionally specific effects or interregional coupling between the Rubin's Vase and Necker Cube. These observations are consistent with the notion of a common mechanism for perceptual selection underlying multistable phenomena regardless of stimulus type (Andrews & Purvee, 1997; Logothetis, 1998). In addition, our analysis shows that the forward connections from V1 to LO to be significantly more modulated than the backward connections from SPC, suggesting that bottom-up effects are more dominant, at least with the figures we used. However, we are cautious in generalising to all types of bistable figures as these may have different contributions. It is known that increasing the luminance of a figure increases the rate of reversal, suggesting that the bottom-up effect has a stronger influence with increasing stimulus strength (Cipywnyk, 1959). Moreover, the present study only addresses reversible figures and not other forms of perceptual bistability such as ambiguous (Muckli et al., 2002) or illusory motion (Sterzer et al., 2002), or binocular rivalry, which may have different mechanisms. For instance, a recent psychophysical study suggested that binocular rivalry is more stimulus-driven and less susceptible to attentional effects (Meng & Tong, 2004).

During the stimulus-induced transitions of the stable figures, we observed regionally specific activations in visual areas including the lateral occipital cortex, which may correspond to activity in retinotopic areas such as V3A and anterior lateral occipital areas known to be involved in form processing. Regions that showed event-related modulations below baseline included the SPC and medial areas of the visual cortex, with only visual areas surviving correction for multiple comparisons. Correspondingly, the DCM analysis shows a negative modulation of the connections between PFC and SPC, and SPC and LO. It should be noted however that these modulations are in relation to the collapsed effect of modulation due to both bistable and stable figures. This is therefore a measure of these connections during perception of stable compared to bistable figures, suggesting that stable figures do not evoke the same top-down modulations. Many authors have interpreted the fronto-parietal activations observed during bistable stimulus transitions as evidence for the necessity of top-down influences for visual awareness (e.g. Lumer et al., 1998; Dehaene et al., 2003). In such a framework, activity in the visual cortex alone is not sufficient for awareness of a stimulus; these higher areas, which select stimuli to be consciously perceived and enhance the sensory processing of the stimulus, must accompany it. For example, an fMRI study of semantic priming found that when words were presented unconsciously, only ventral areas were active, whereas conscious unmasked words additionally activated frontal, parietal and cingulate areas (Dehaene et al., 2001). In contrast to such a view, it has been suggested that activity in the visual area processing an attribute is sufficient to be aware of it (Bartels & Zeki, 1998; Tse et al., 2005). The present results are more consistent with the latter view. While top-down connections are positively modulated during bistable figure transitions, they are in comparison negatively modulated during stimulus mediated reversals of the stable figures, and no other regions aside from those in the visual cortex are activated during externally mediated perceptual transitions. Therefore, in the present case at least, these top-down influences do not seem to play a role in the awareness of stable stimuli.

Overall, our findings can be summarised as follows: (1) both top-down connections from PFC via SPC to LO, and bottom-up connections from V1 to LO were positively modulated while viewing bistable figures; (2) no significant differences between the Necker Cube and Rubin's Vase were found for either the regional activations or the interregional coupling; (3) top-down influences from the PFC to SPC, and SPC to LO were negatively modulated while viewing stable figures. These results support a hybrid mechanism of multistable perception that incorporates both bottom-up and top-down factors which are common to all figures types. Recent fMRI results show that during binocular rivalry neural activity as early as the lateral geniculate nucleus correlates with perception (Haynes et al., 2005b; Wunderlich et al., 2005). However, it is not established whether this is due to feedback connections from higher areas, or competitive interactions between monocular neurons within this area. Therefore, future studies should address the interactions and dissociations between top-down and bottom-up processes in the context of perceptual rivalry and visual awareness.

3.2 Neural Correlates of Conscious Perception in the Near Absence of attention

3.2.1. Introduction

As demonstrated by the literature reviewed in the introductory sections, there have recently been numerous studies investigating the neural correlates of visual awareness, which in turn have inspired various competing theories of the underlying mechanism (s). A recurring debate in this topic is whether activity in areas beyond the visual cortex, such as the frontal or parietal cortices, is required for conscious perception. It has been claimed that activity in the visual areas alone can support awareness without the need for feedback connections from these higher areas (Zeki & Bartels, 1999). In contrast, it has been argued activity in higher areas is crucial; these in turn bias activation in visual areas, to select and maintain the contents of visual awareness (e.g. Dehaene et al., 2003).

This issue is mirrored by the debate in the psychological literature, which questions the exact relationship between visual awareness and attention (and by implication, the top-down neuronal processes that underlie it). Many argue that there is a direct one-to-one mapping of visual awareness and attention, or in the words of William James '*my experience is what I agree to attend to*' (1890). For instance, 'change blindness' occurs when a subject is unable to detect even very salient changes in a visual scene (Grimes, 1996), provided there is a masking of the motion transients produced by the change (e.g. by flicker or saccades). This striking phenomenon indicates that although it seems that we have a detailed awareness of current sensory input, in actual fact this representation is very sparse. Moreover, attention seems underlie the limit on the changes we are able to detect; for instance, change blindness is reduced by exogenous cues (Scholl, 2000) and semantically relevant changes (Rensink et al., 1997), and no more than 4-5 changes can be monitored simultaneously: a limit known to occur in other attentional tasks (e.g. Pashler, 1998). Therefore, this phenomenon, in addition to others such as 'inattentional blindness' (Mack & Rock, 1998) or 'attentional blink' (Raymond et al., 1992), demonstrates how crucial attention is to perceiving visual events, and provides strong evidence for the direct correspondence between attention and awareness.

However, others have suggested that visual events can be perceived outside the focus of attention. This is perhaps best illustrated by dual-task experiments, originally performed by Braun and colleagues (Braun & Sagi, 1990; Braun & Julesz, 1998), in which the subjects' attention is distracted by a highly demanding centrally located letter discrimination task. Simultaneously, they had to either detect or discriminate simple visual features presented at a random location in the periphery. What is interesting is that performing the peripheral task did not affect performance of the attentionally demanding central task compared to when it was performed alone; likewise, subjects were able to perform the peripheral task as well with the central task as when alone. These results suggest that simple peripheral stimuli such as position, colour and orientation can be perceived without the need for top-down attention. Remarkably, a recent study using the same paradigm found that even complex natural scenes can be discriminated in the absence of attention (Li et al., 2002). How can this result be reconciled with those studies described in the previous paragraph which suggest a mandatory role for attention in awareness? One possibility is that while attention is necessary for visual awareness of certain stimuli, such as during crowding (He et al., 1996), for others, such as natural scenes in the dual-task situation, it is not.

However it must be noted that the very question of whether conscious perception can occur in the absence of attention is, in itself, a controversial one, even with the dual-task paradigms introduced by Braun (1990) withstanding. For instance, the detection of a so-called 'pre-attentive' pop-out stimulus, in which the target orientation differs from the surrounding distractors, is severely impaired while performing a central rapid serial visual presentation (RSVP) task involving letter identification (Josephs et al., 1997). While after extensive training subjects can eventually perform the task (Braun, 1998), it is argued that this is due to the freeing up of attentional resources as learning increases the efficiency with which the stimulus in the RSVP is processed and thereby reduces attentional load (Josephs et al., 1998). This in turn allows the pop-out stimulus to be detected. By this account, conscious perception cannot occur in the absence of attention, only outside the focus of attention. Given the extensive training required of subjects in the tasks used by Li and colleagues (2002) and Braun (1990) before their performance stabilises, it is possible that subjects simply learn to deploy attention to the multiple relevant target locations.

To investigate the neural basis of visual awareness, many imaging studies have used paradigms in which attention is already known to play a key role. For example, one previous study addressed the neural fate of events outside the focus of attention (Rees et al., 1999) and found no evidence for the semantic processing of words under such conditions. However, it was already known that words are not perceived outside the focus of attention; this result may therefore not extend to other stimuli, which can be perceived under these conditions, such as natural scenes. In another fMRI study of change blindness (Beck et al., 2001), successful change detection compared with unsuccessful change detection (i.e. change blindness) correlated with fronto-parietal regions usually associated with visuospatial attention (Corbetta et al., 1993; Kastner et al., 1999), and category specific areas which process the attribute detected. These results, along with others (e.g. Marois et al., 2000; Dehaene et al., 2001) support the 'global workspace' theory visual awareness (Dehaene et al., 2003). However, using these specific paradigms it is unsurprising that activity in attentional systems correlates with task performance and conscious perception, since it is already known that attention plays a crucial role. Therefore a key question is: using a paradigm, in which attention or at least the focus of attention, is not involved, does visual awareness correlate with activity in fronto-parietal regions?

The goal of the following study was to determine whether visual and fronto-parietal activity correlates with visual awareness when outside the focus of attention. To address this issue we used a dual-task paradigm similar to those described above (Braun & Sagi, 1990; Li et al., 2002): subjects were presented with letters in the central visual field and were required to discriminate either the characters (attentionally demanding) or the luminance (non-attentionally demanding). Simultaneous with this they discriminated the presence of a place stimulus presented peripherally. Thus while performing the luminance task attention would not be completely occupied centrally; its focus would be absent from the periphery while performing the character discrimination task. Those brain areas critical to visual awareness should correlate with conscious perception (i.e. hit vs. miss) for the peripheral task while performing both the attentionally demanding or non-demanding central task. Whereas global workspace theories (e.g. Dehaene et al., 2003) predict that fronto-parietal areas will correlate with perception in both conditions, modular theories (e.g. Zeki & Bartels, 1999) predict that visual areas alone will correlate with awareness of the peripheral stimuli while performing the central attentionally demanding task. During the central attentionally non-demanding condition the focus of attention will be free in the periphery. Therefore proponents of the modular theory would expect fronto-parietal areas, in addition to frontal areas, to correlate with awareness, since on trials in which the peripheral stimulus was detected, the subjects would be on average paying more attention to the target.

3.2.2. Methods

Subjects

Four healthy volunteers (one woman and three men; mean age 23.3 ± 1.75) with normal, or corrected to normal vision, participated in the study after giving written consent. They were trained to perform the psychophysical task and were scanned after their performance stabilised. All stimuli were constructed using COGENT 2000 Graphics (available at www.vislab.ucl.ac.uk) running in MATLAB (Mathworks Natick, MA).

Psychophysics

Subjects were seated in a darkened room and fixated a central cross on a computer monitor (Sony Trinitron with a refresh rate of 60 Hz) with a viewing distance of 40cm. The psychophysics consisted of three control experiments: (1) an attentionally demanding central task (letter discrimination), (2) an attentionally non-demanding central task (luminance discrimination), (3) a peripheral 'place' detection task, and two main experiments: dual-task conditions in which one of the two central tasks was performed concurrently with the peripheral task. Each condition required a significant training period. It usually took more than 14 hours (approximately 14,000 trials of all different tasks combined) in total. All tasks received the same amount of training to avoid bias for any particular one. Trials were organized in the same way and had the identical stimuli irrespective of the experimental condition (single or dual-task).

With both central task conditions each trial started with a fixation cross 200 ± 50 ms before the onset of the stimulus. At 0 ms, the central stimulus of five letters was presented. The five letters (T's and L's, either all identical characters, or one differing from the other four, and of high or medium luminance, either all identical luminance, or one differing from the other four) appeared at nine possible locations within 1.2° eccentricity (see figure 3.2.1 for task structure). Each letter was randomly rotated. After the central SOA (stimulus onset asynchrony, the time between the appearance of the central stimulus and the onset of the central mask), the letter F masked each stimulus letter. Subjects were instructed to respond by key-press to report if the five letter characters were the same or different in the attentionally demanding condition, or if the five letter luminances were the same or different in the attentionally non-demanding condition. The central SOA, starting at 500 ms, was decreased after each block of 100 trials where the performance of this task exceeded 85% correct. The procedure was terminated after the subject's performance had stabilized and the central SOA was below 250 ms. This value was chosen to limit the possibility of switching attention during stimulus presentation from the attentionally demanding central task in the dual-task condition.

In the peripheral task the stimulus (size: 3° x 4.2°) was presented 50 ms after the central stimulus onset at a 6.7° eccentricity for 33 ms and was followed by a textured mask, consisting of an achromatic textured mixture of white noise at different spatial frequencies. The peripheral stimuli were either 'places' (pictures of natural landscapes, houses, indoor scenes) or 'non-places' (textures and nonsense shapes matched for spatial frequency and luminance). Subjects were instructed to respond by key-press to report if the peripheral stimulus was a 'place' or a 'non-place'. The peripheral SOA was adjusted in the same way as for the central SOA so that performance would stabilize at less than 85% correct. Individual peripheral SOAs ranged from 50 to 84 ms.

In both dual-tasks, subjects were instructed to focus attention on the central task. On each trial, they were supposed to respond to the peripheral stimulus (with their right hand) before the central stimulus (with their left hand). The central and peripheral SOAs used for each individual subject were those that stabilised at below 85% correct for the corresponding single task conditions.

In a separate control experiment, we tested our subjects' central performance with shortened SOAs on both of the single central tasks. For each subject, the central SOA alternated in four blocks of 48 trials between two values: the subject's original SOA that was reached at the end of the training procedure, and another SOA 67 ms shorter.

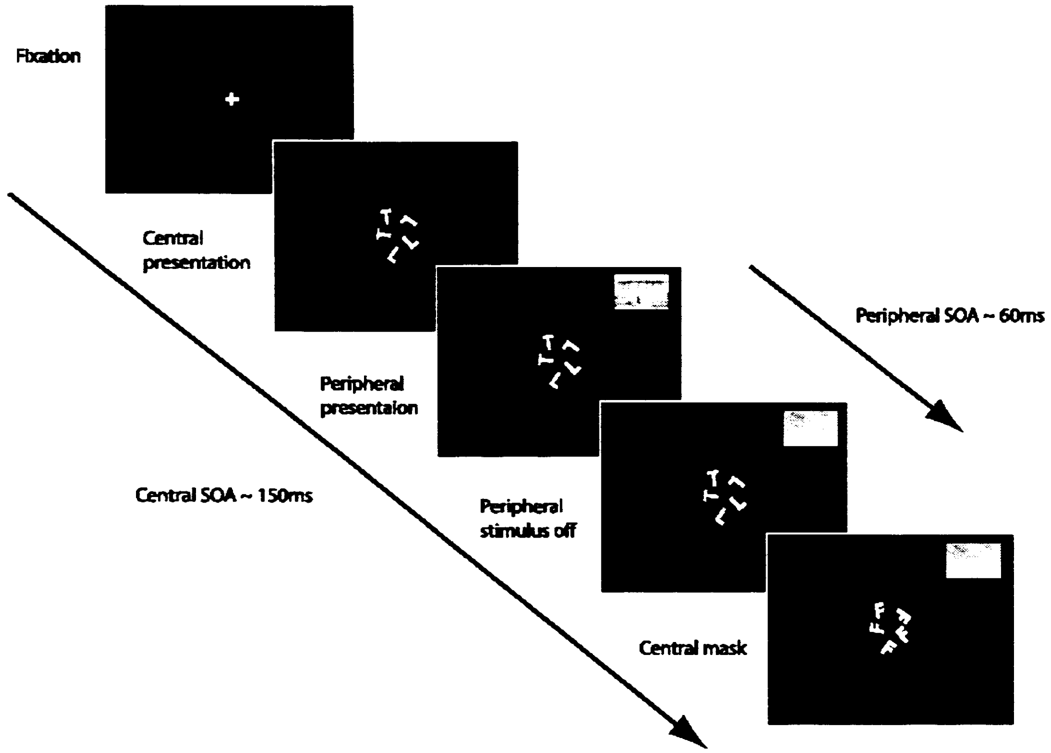


Figure 3.2.1. Schematic diagram of stimulus sequence for each trial in all conditions.

fMRI Stimuli

After the psychophysical training periods on the dual-task stabilised, subjects underwent four sessions of fMRI scanning during which they performed the dual-task conditions with the central character and luminance discrimination, using exactly the same SOAs as the final psychophysical training sessions. In each scanning session subjects performed one block each, comprising 100 trials, of the central luminance and character conditions. The order of these was randomised in each session. The stimuli were presented centrally and projected onto the screen by means of an LCD projector (60Hz refresh rate).

Imaging and Image processing

Functional images were processed and analysed using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB (MathWorks, Natick, MA). A 3-T Siemens ALLEGRA system (Siemens, Erlangen, Germany) equipped with a head coil was used to acquire functional images with a gradient echo-planar T2* sequence using BOLD (blood oxygenation level dependent) contrast, with a repetition time (TR) = 2.6 s. Each functional image comprised 40 transverse slices [2 mm thickness; 1.8 mm gap; 64 x 64, 3 x 3 mm pixels; echo time (TE) = 40 msec] covering the whole brain volume. A total of 2344 sequential volumes were acquired during 4 separate sessions with the first four volumes of each session discarded to allow for T1 equilibration effects. Images were realigned, slice-time corrected, normalised to a standard echo-planar image template and smoothed with a Gaussian kernel with full-width half maximum of 6 mm. A structural MRI scan using a standard three-dimensional T1-weighted sequence was acquired from each subject and was co-registered to the functional scans and transformed into the same standard space.

Data Analysis

Brain activation for each experimental condition was estimated according to the general linear model at each voxel in brain space (Friston et al., 1995). The presentation times for the peripheral stimuli were modelled as discrete events with the canonical haemodynamic response to capture the BOLD onset. For the two conditions (central character and luminance discrimination), performance (hit, miss, false alarm or correct rejection for place detection) for the peripheral task was modelled as 4 separate regressors on trials in which the central task was performed correctly, giving

8 regressors in total. Stimuli on trials in which the each of the central tasks were performed incorrectly were modelled as 2 separate regressors, irrespective of peripheral performance. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and the three rotations determined from initial registration), two regressors for the peripheral and central key-press responses, and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 128s. Images of parameter estimates for each contrast of interest were created for each subject and were analysed as single-subject case studies.

Retinotopic mapping

Sessions of phase-encoded retinotopy were performed at the end of the four experimental sessions. See APPENDIX 1 for methodological details.

3.2.3. Results

Psychophysics

We investigated the role of attention in place detection by using a dual-task paradigm in which a peripheral detection task, where a target was defined by the presence of a place stimulus, was performed concurrently with a central visual task that was either attentionally demanding (letter discrimination) or attentionally non-demanding (luminance discrimination). Consistent with previous behavioural studies (Braun & Sagi, 1990; Li et al., 2002), we found that for each subject in both of the dual-task conditions, central task performance showed no difference ($p > 0.05$, paired t-test) from performance under the single task condition (figure 3.2.2). Furthermore, each subject performed the peripheral place detection task under both dual-task conditions at a performance not significantly different from performance in the single task condition ($p > 0.05$). These results suggest that the place detection can still be performed outside of the focus of attention.

In the separate control experiment, all subjects performed both of the single central task conditions with an SOA shortened by 66 ms. Their average performance dropped from an average of 77% to 58% (individual *t*-test for each subject, $p < 0.01$) in the character discrimination task, but did not differ significantly for the luminance discrimination task ($p > 0.05$). This confirms that results of the dual-task with the central attentionally demanding task do not reflect a switch of attention between the two tasks; if this did occur then the central performance would have dropped significantly, as shown by the reduction in performance through a reduced SOA. It also suggests that there may be attention allocated to the peripheral task when performing the central luminance task in the dual-task situation.

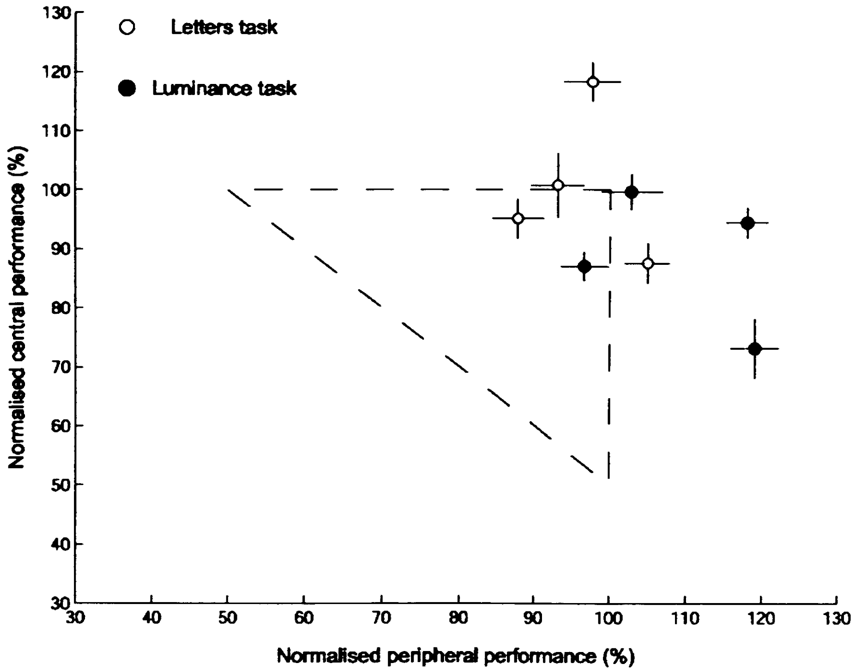


Figure 3.2.2. Individual subjects' results for dual vs. single task performance. Each dot represents a single subject's performance after stabilisation on the dual-task normalised against performance on the single task condition. Error bars represent standard error for each subject.

Retinotopic mapping

We used standard retinotopic procedures (Engel et al., 1994) to map the organisation of the occipital lobes of all four subjects and all were found to have standard angular retinotopic organisation in visual areas V1, V2d/v and V3d/v. Each subject also had an entire hemifield representation of the contralateral visual field lying beyond V3d in the posterior part of the intra-parietal sulcus, consistent with area V3A (Tootell et al., 1997). Similarly, in the ventral occipital cortex all subjects had an entire hemifield representation beyond V3v consistent with human V4 (McKeefry et al., 1997; Wade et al., 2002) and inconsistent with the definition of V4v and V8 (Hadjikhani et al., 1998). We did not isolate V3B or V7 as our maps in these areas were inconsistent across subjects. Examining the maps of stimulus eccentricity we found a large, single map encompassing V1, V2, V3 and bordering on V4 and V3A. The data from V4 suggested that it shared the same eccentricity map as these early regions, as suggested by others (Wade et al., 2002).

fMRI

To ensure that attention was successfully manipulated on each trial we only analysed trials in which the central task was performed correctly. We then partitioned the trials according to the peripheral performance, as dictated by signal detection theory (hit, miss, false alarm, correct rejection). To isolate the neural substrates of visual awareness of the peripheral stimuli in the dual-task paradigm with both the attentionally demanding and non-demanding central task, we compared brain activity during hits versus misses of the peripheral stimulus on trials in which the central task was performed correctly. Since both the task and stimuli are identical, activity revealed by this comparison must be related to the underlying subjective perception of the stimulus. As shown in figure 3.2.3, conscious detection while performing the central attentionally non-demanding task correlated with activity across the cortex in the frontal, superior parietal and occipital lobes, with the exception of subject CG, where activity was only observed in the parietal and medial sensorimotor cortices (statistical threshold at $p < 0.001$, uncorrected for multiple comparisons).

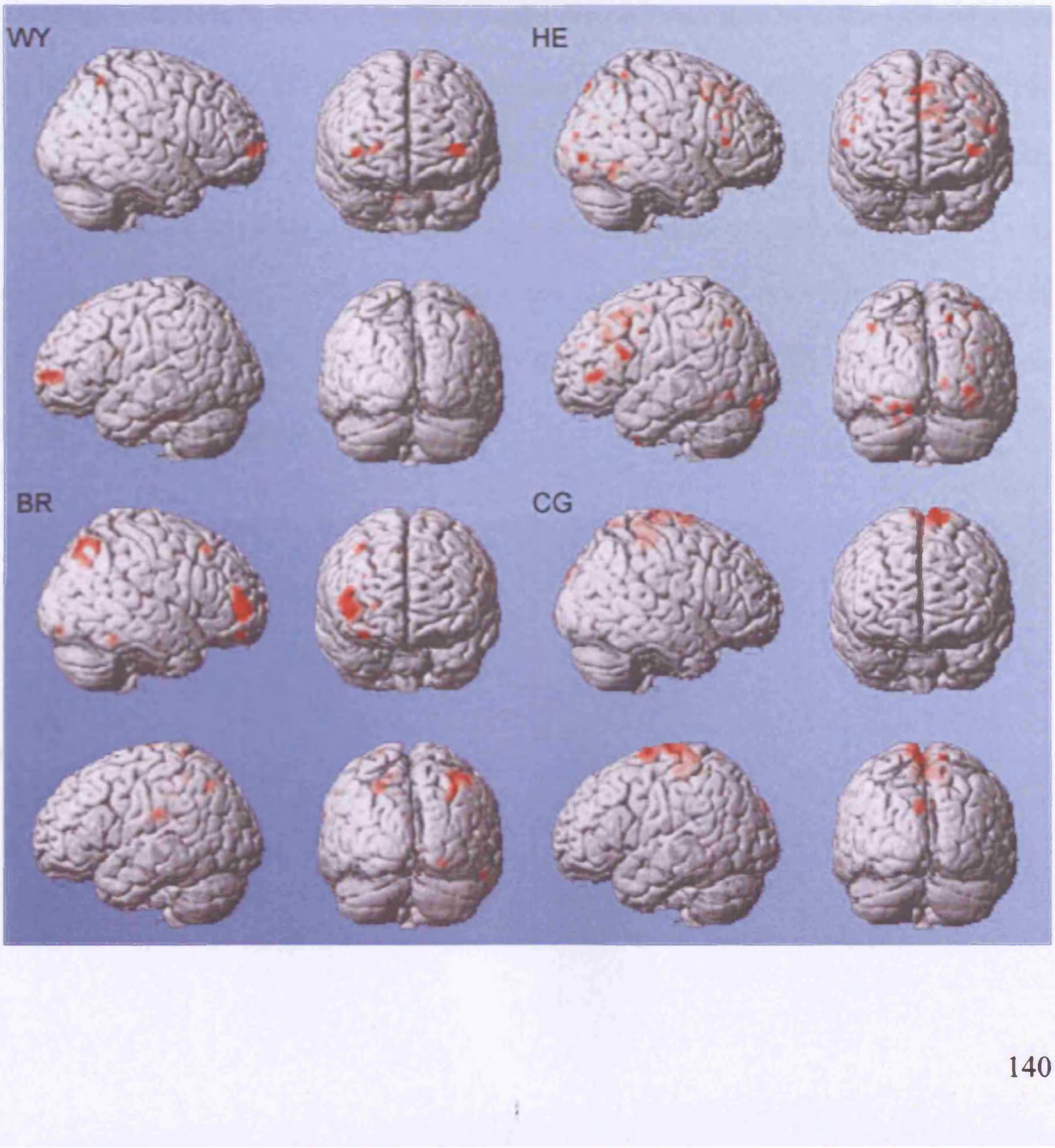


Figure 3.2.3. Main effect showing areas in which activity was higher for hits compared to misses on the peripheral task while performing the central non-attentionally demanding task (luminance discrimination). Results are displayed at a statistical threshold of p < 0.001 (uncorrected for multiple comparisons).

By contrast, successful conscious detection while performing the central attentionally demanding task yielded activity localised to the occipital lobe only (figure 3.2.4). Three subjects also showed activation around Broca's area in the left hemisphere, which may correspond to the pars triangularis or par opercularis; areas implicated in word processing (Price & Mechelli, 2005), and could be related to the letter task performed. Voxels in the parietal and frontal regions activated by conscious detection while performing the attentionally demanding task were not active even at a lowered statistical threshold ($p < 0.05$, uncorrected). For both of these contrasts in all subjects, areas of the medial fusiform gyrus near to the 'parahippocampal place area' (PPA; Epstein & Kanwisher, 1998) previously associated with conscious detection of places (Beck et al., 2001) were found to be significantly active ($p < 0.05$, family wise error, small volume correction).

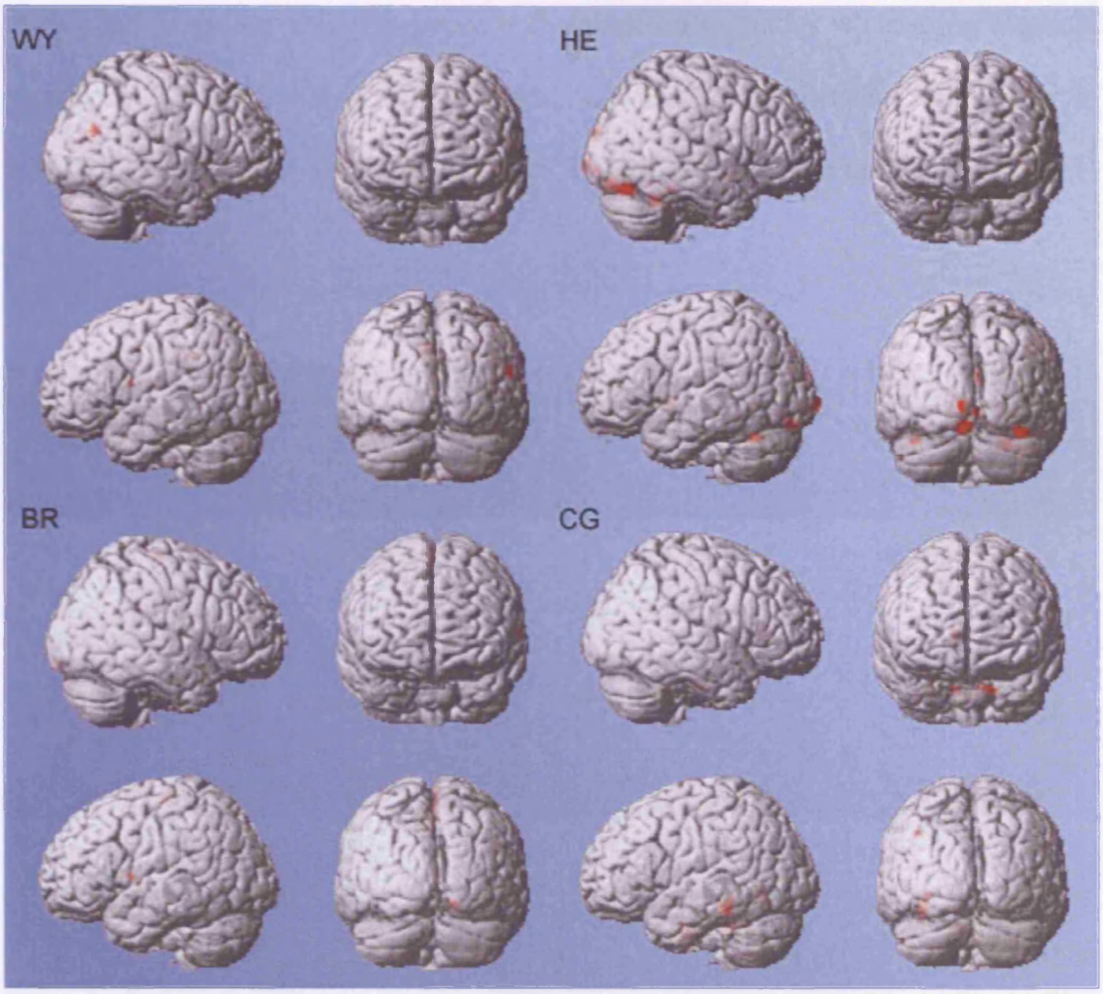


Figure 3.2.4. Main effect showing areas in which activity was higher for hits compared to misses on the peripheral task while performing the central attentionally demanding task (letter discrimination). Results are displayed at a statistical threshold of $p < 0.001$ (uncorrected for multiple comparisons).

The interaction effect (figure 3.2.5), delineating regions more responsive to conscious detection of the peripheral stimulus in the presence of attention than the absence, showed activity across frontal, parietal and occipital areas. This therefore confirms the contribution of the front-parietal cortex in detection in the presence, but not the absence of attention. However, it should be noted that there was very little consistency in the activations across subjects. This is in line with previous fMRI studies that show variability between both subjects and studies when using identical paradigms (Cabeza & Nyberg, 2000) and may be due to individual differences in functional anatomy or cognitive strategies employed during the task (Nadeau et al., 1998).

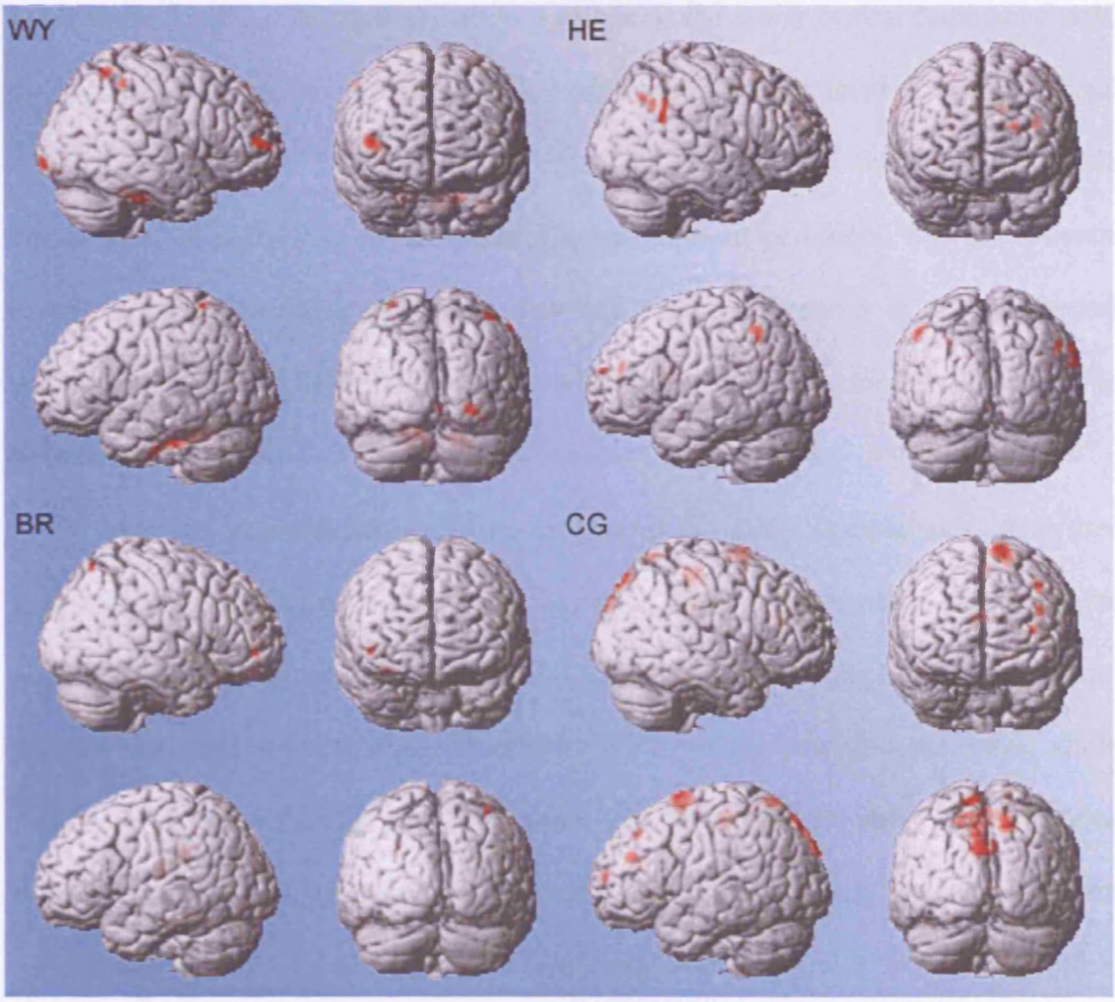


Figure 3.2.5. Interaction contrast comparing showing areas in which activity was higher for successful peripheral detection (i.e. hits compared to misses) while performing the attentionally non-demanding task, than with successful detection while performing the attentionally demanding task. Results are displayed at a statistical threshold of $p < 0.001$ (uncorrected for multiple comparisons).

Finally, we contrast the main effect of the central letters task with the central luminance task. This was to address the possibility that fronto-parietal activations for the peripheral detection task in the central letters task were not apparent because there is a baseline high level of activation in these areas due to the demands of the difficult task. Therefore any variation between the peripheral hit and miss performance are too small to be detected. In contrast, while performing the easier central luminance task, the task demands are low leading to relatively lower baseline level of fronto-parietal activity. This in turn should lead to larger differences (and therefore detectable differences) in activity in fronto-parietal areas between peripheral hits and misses. However, this contrast revealed very few and sparse activations at an uncorrected level of significance ($p < 0.001$) in each subject only, with no activations in the fronto-parietal areas.

We then overlaid the contrast images for the hit-miss comparisons described above onto flattened retinotopic maps in order observe the pattern of activations across the occipital cortex (figures 3.2.6-8). Due to technical difficulties, this was not possible for the left hemisphere of subject WY. For the conscious detection while performing the attentionally non-demanding task, this gave the strongest activations in dorsal visual areas, in particular V3 and V3A. However, there was no consistent pattern and most of these activations were only significant at a lowered statistical threshold ($p < 0.005$). Likewise the same contrast while performing the attentionally demanding central task and the interaction effects showed no real consistency across subjects. The large inter-subject variability in activations may be explained by a couple of factors. Firstly, it may be due to differences in anatomy (Cabeza & Nyberg, 2000) or cognitive strategies (Nadeau et al., 1998) as discussed above. Secondly, our results are displayed as a percentage of the global signal without any statistical threshold applied and may therefore simply reflect noise in the BOLD signal (Zarahn et al., 1997; Turner et al., 1998).However, in each subject at a very low statistical threshold ($p < 0.05$) we did observe significant voxel activations across all visual areas. Table 3.2.1 lists the p-values and z-scores for the most significant voxels. This reveals a significant activation of V1 ($P < 0.004$) in all subjects for conscious detection in the presence of attention (central luminance condition). However, a corresponding activation in the absence of attention (central letters condition) was not observed at the same threshold. Only at a much lower p-value was this apparent ($p < 0.04$) suggesting a lack of activation for this contrast.

Given that both the central and peripheral tasks were performed simultaneously, it is not clear if activity observed in these activation maps can be attributed to either alone. While the contrasts related to performance variation (hit-miss) in the peripheral task, with the central task performance constant, interaction between the tasks may have occurred. One possibility may have been to partition the activation maps according to either eccentricity (central and peripheral) or quadrant, according to where the peripheral stimulus was presented on each trials. However as noted in the previous paragraph, there was no real consistency or statistical significance in the activation maps either centrally or peripherally, apart from a few voxels at a low significance in V1. In addition, due to technical reasons, we were not able to retrieve the location of the peripherally presented stimulus on each trial.

		Luminance			Letters		
	AREA	Z-score	T	P	Z-score	T	P
CG	V1	3.38	3.38	0.0004	1.84	1.83	0.033
	V2	3.15	3.15	0.001	2.39	2.39	0.008
	V3	3.39	3.4	0.0003	3.12	3.12	0.001
	V3a	2.7	2.69	0.004	3.12	3.12	0.001
	V4	2.26	2.26	0.012	2.39	2.39	0.008
BR	V1	2.81	2.81	0.002	2.83	2.83	0.002
	V2	2.99	3.00	0.001	3.06	3.06	0.001
	V3	3.01	3.01	0.001	2.4	2.4	0.008
	V3a	2.98	2.98	0.001	2.47	2.47	0.007
	V4	2.62	2.62	0.004	4.24	4.24	0.0005
HE	V1	3.02	3.02	0.001	2.46	2.47	0.007
	V2	3.03	3.03	0.001	2.71	2.71	0.003
	V3	2.9	2.9	0.002	2.48	2.48	0.006
	V3a	3.25	3.26	0.001	2.05	2.04	0.02
	V4	2.49	2.49	0.006	2.57	2.57	0.005
WY	V1	2.77	2.77	0.003	1.89	1.88	0.03
	V2	2.35	2.35	0.009	1.76	1.75	0.04
	V3	2.22	2.22	0.013	2.63	2.63	0.004
	V3a	1.84	1.83	0.033	1.90	1.90	0.029
	V4	1.66	1.65	0.049	1.92	1.92	0.028

Table 3.2.1. Most active voxel in retinotopic regions for conscious detection in each subject while performing the central luminance and letters discrimination tasks. P stands for p-values and T for the t-values.

3.2.4. Discussion

The aim of this study was to test contrary predictions of the global workspace (Dehaene et al., 2003) and modular (Zeki & Bartels, 1999) theories of visual awareness. To this end, we investigated the neural correlates of conscious detection in the presence and absence of the focus of attention. We correlated event-related fMRI responses with detection performance of subjects in a dual-task paradigm. Our results may summarised as follows: (1) consistent with previous studies (Braun & Julesz, 1998, Li et al., 2002) we found that a peripheral target, in this case a 'place' stimulus, can be detected outside the focus of attention; (2) fronto-parietal and occipital areas only correlated with conscious detection of a visual stimulus in the presence of attention. In its absence, only occipital areas correlated with the observers' perception; (3) V1 correlated weakly with correct detection only in the presence of attention.

These findings demonstrate that frontal and parietal regions usually associated with spatial attention (Corbetta et al., 1993; Kastner et al., 1999) only correlate with visual awareness when attention is actually present; in its absence activity in only occipital areas is observed. This dissociation suggests that these fronto-parietal areas are not essential for subjective perception, consistent with the modular view of visual awareness (Zeki & Bartels, 1999). By contrast, these results are inconsistent with the 'global workspace' view (Dehaene et al., 2006; Rees et al., 2002; Baars, 2002), which would predict widespread brain activation for the conscious detection under all experimental conditions. In the search for the neural mechanisms of awareness it seems that activity in areas outside of the occipital lobe is not strictly necessary. The consistent correlate of the subjects' perception across both central task conditions were medial areas of the occipital lobe, which were near the PPA, an area known to process place stimuli (Epstein & Kanwisher, 1998; Epstein et al., 2003), and previously shown to be active during the conscious detection of places (Beck et al., 2001).

Previous imaging studies demonstrating activity in frontal and parietal areas correlating with visual awareness may have been subject to a number of attentional confounds. Firstly, by not controlling for trial-to-trial fluctuations in attentional state, observers will have performed better on trials in which they were more alert than on trials in which they were not. For instance, a recent fMRI study of metacontrast masking showed that awareness of the target stimulus correlated with activity in later visual and fronto-parietal areas (Haynes et al., 2005a). However, previous psychophysical experiments show that visibility of targets with metacontrast masking is subject to attentional modulation (Ramachandran & Cobb, 1995), with attention improving visibility. We would therefore expect that on average the trials in which the target is detected, the subjects are attending more; with the corresponding attention related brain areas in the fronto-parietal cortex showing increased activity. Another factor to consider is that attention may be diverted to the target stimulus only after it is detected. Thus in the fMRI study of change blindness by Beck and colleagues (2001), subjects may orient their attention to the target only if the change is detected. This could explain why fronto-parietal areas are more active on 'seen' trials. Finally, it is also not clear if trial-to-trial attentional fluctuations cause these fronto-parietal regions to correlate with awareness: on trials in which the subjects' attentional state (and hence activity in fronto-parietal regions) happens to be higher, the stimulus is more likely to be detected, without being absolutely necessary. While the present study cannot distinguish between these possibilities, we can be confident that the attentionally demanding central character discrimination task used presently controlled for these confounds. It was only when attention was not adequately controlled for in the central luminance task condition that fronto-parietal areas correlated with visual awareness.

Note however that these conclusions should not necessarily be taken to generalise to the neural correlates of awareness for all tasks or stimuli. For example, Dehaene et al. (2001) found neural correlates of word-priming masking outside of the occipital lobe. The complexity of such stimuli may require higher brain areas than those in the visual cortex. Moreover, awareness of multiple items across space seems to require the parietal cortex. Patients who suffer from visual extinction typically have lesions to the right parietal lobe. While awareness for single items presented in their visual field is normal (Mesulam, 1985), when an item is placed in each hemifield the patients usually fail to report the presence of the stimulus on the contralesional (i.e. left) side of space. Hence, in this situation, even though the visual cortex is intact, there is a deficit in visual awareness. However these lesions do not render the subjects blind – they are still visually aware. It is only in this specific instance of multiple items across space that a deficit is apparent. In addition, attention is typically required for binding across features (Treisman & Gelade, 1980). Simple targets such as two-tone colour discs cannot be correctly discriminated while performing the attentionally demanding central task described here (Li et al., 2002). It is therefore likely that top-down influences from the frontal and parietal cortex are also mandatory for this task.

In section 3.2.1 we discussed whether attention is really absent from the peripheral stimulus while performing the central attentionally demanding task. The aim of our study was not to address this issue; we simply sought to find the neural correlates of conscious detection while performing such a task. However, the present results provide strong imaging evidence that attention was not present in the periphery (see Henson, 2006 for discussion on inferring cognitive processes from neuroimaging data). Areas associated with visuo-spatial attention, such as the superior parietal and the prefrontal cortex (Corbetta et al., 1993; Kastner et al., 1999), are employed when attentional resources are free, although when the central load is high these areas do not correlate with performance on the peripheral detection task, suggesting an absence of attention. Therefore, the argument that extensive psychophysical training proposed by Joesphs et al (1997) frees up attentional resources does not hold for the present experiment at least.

Another intriguing aspect of the present results is the involvement of V1 during detection in the presence, but not absence, of attention. As reviewed in section 1.5, both neuroimaging and neurophysiological studies have shown that V1 can correlate with subjective perception, possibly through feedback connections from higher visual areas (Super et al., 2001) or non-visual areas associated with attention such as the parietal cortex (Buechel & Friston, 1997). These previous studies have typically used stimuli which cells in V1 are optimally tuned to, such as simple line stimuli (e.g. Super at al., 2001), unlike the complex place stimuli used presently, to which only higher visual areas in parahippocampal areas selectively respond to. Therefore, it may be surprising that V1 correlates with detection of places. However, a couple of factors may be involved. Firstly, bottom-up noise resulting in a stronger neural signal generated before V1 may improve the quality of representation of the target stimulus in higher visual areas, such as the PPA, which in turn allows correct detection of a place. According to this hypothesis, V1 would show increased activity on hit versus miss trials. Secondly, as outline above, feedback from visual higher areas may increase the activity in V1 on detected trials. The present data cannot measure feedback, although it does rule in favour feedback from higher areas, as V1 only correlated with visual awareness when the parietal cortex was active. Therefore similar criticisms of attentional confounds like those described above could be levied at previous studies which find V1 correlates with awareness, especially if the modulation is late in the neuronal response (e.g. Super et al., 2001). In other words, this could simply be a by-product of the observer orienting its attention to the target stimulus, which has previously been shown to modulate V1 (Somers et al., 1999). Consistent with this interpretation, a recent fMRI study of monoptic and dichoptic masking which controlled for attention found that only visual areas downstream of V1 correlate with the subjects' perception (Tse et al., 2005). However, the lack of V1 activity in the no-attention condition in the present experiment should be taken cautiously: our peripheral targets only covered a very small proportion of the visual field. Consequently, any subtle modulation of firing rate may only encompass a small proportion of V1 neurons, which may be missed due to limited the spatial resolution of the BOLD signal.

Overall, our findings can be summarised as follows: (1) 'place' stimuli can be detected outwith the focus of attention; (2) fronto-parietal and occipital areas only correlated with conscious detection of a visual stimulus in the presence of attention. In its absence, only medial occipital areas correlated with the observers' perception. (3) V1 correlates with correct detection only in the presence of attention. The present findings converge with others in demonstrating that it is the level of activity within the visual cortex that is the deciding factor in whether this activity contributes to awareness (Zeki & ffytche, 1998; Dehaene et al., 2000; Moutoussis & Zeki, 2002). However, the physiological processes underlying this remain poorly defined. For example, this may correspond to increased firing rate, recurrent intra-areal connections, the recruitment of addition neurons or neuronal synchrony. Therefore future studies should address these issues with high-resolution techniques such as single-cell electrophysiology or even *in vivo* fluorescent labelling (Stettler et al., 2002).

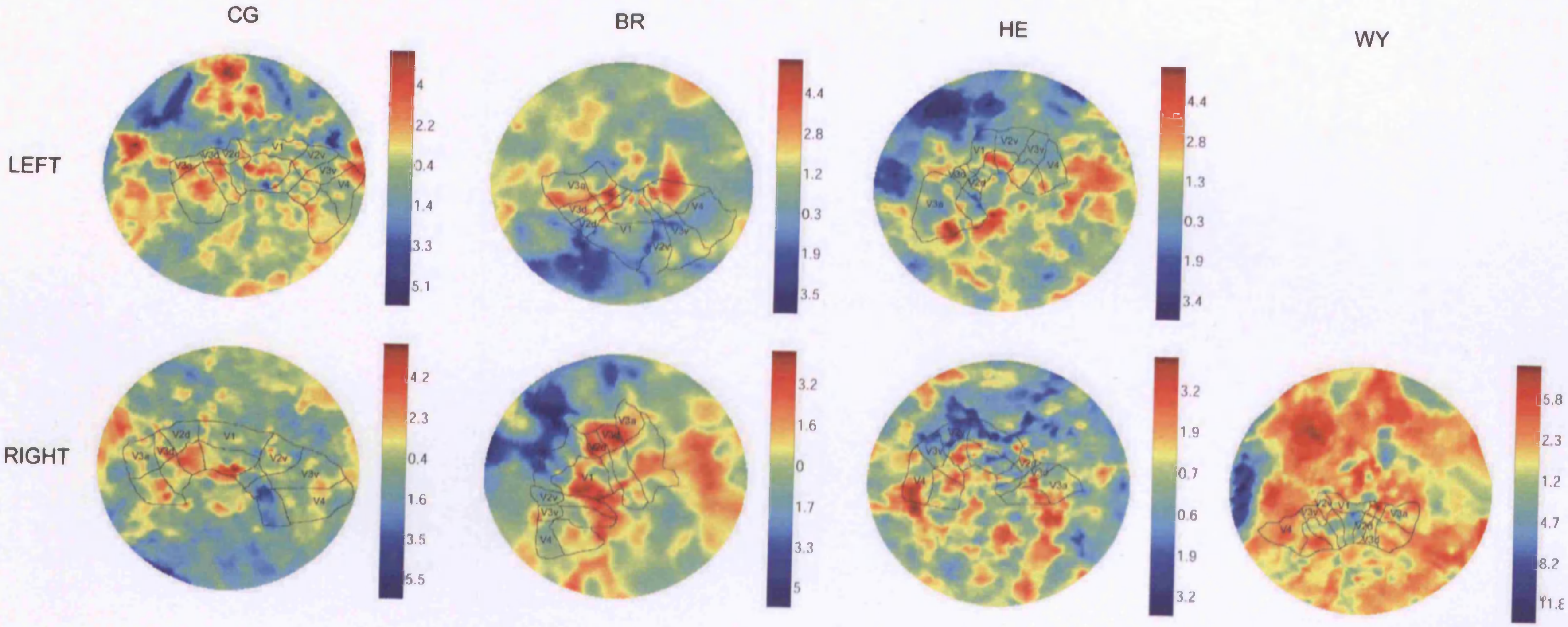


Figure 3.2.6. Flattened cortical activation maps from each subject, showing activity for the contrast of hit > miss for the peripheral stimulus while performing the attentionally non-demanding central task. The colour bars represent % global brain mean. Flattened cortical surface diameter is 75mm.

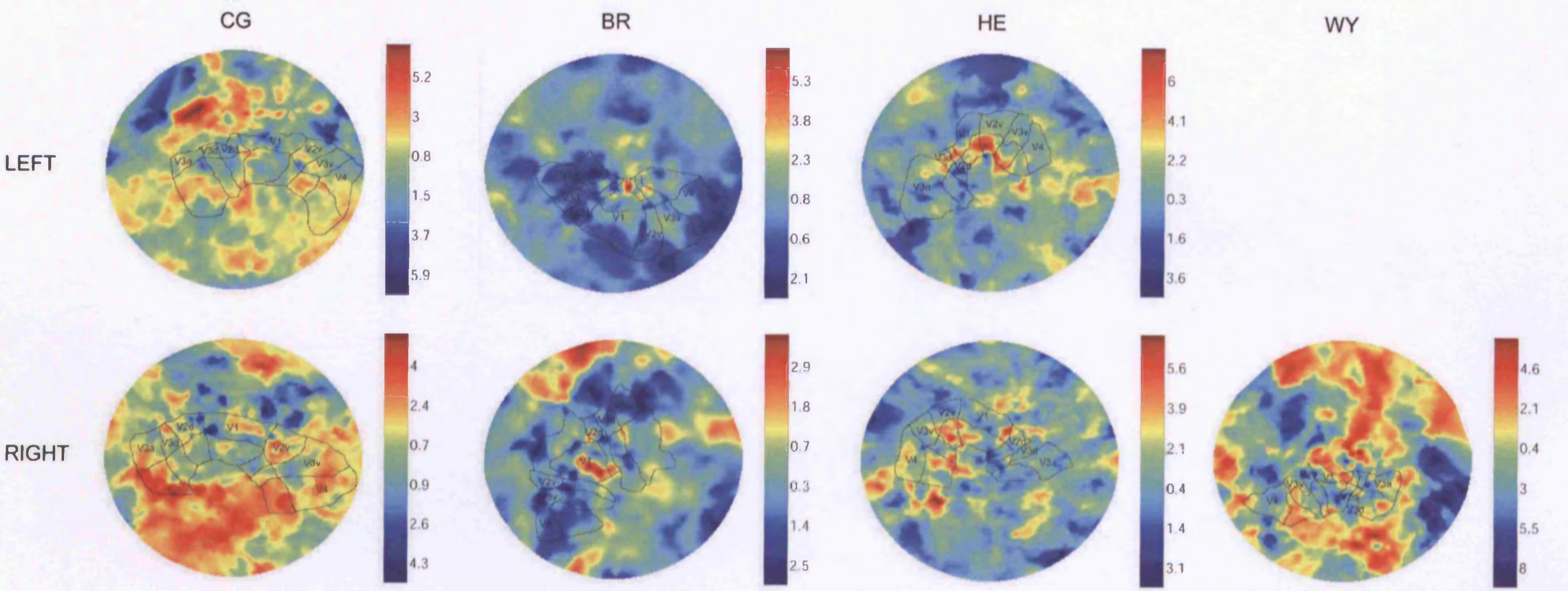


Figure 3.2.7. Flattened cortical activation maps from each subject, showing activity for the contrast of hit > miss for the peripheral stimulus while performing the attentionally demanding central task. The colour bars represent % global brain mean. Flattened cortical surface diameter is 75mm.

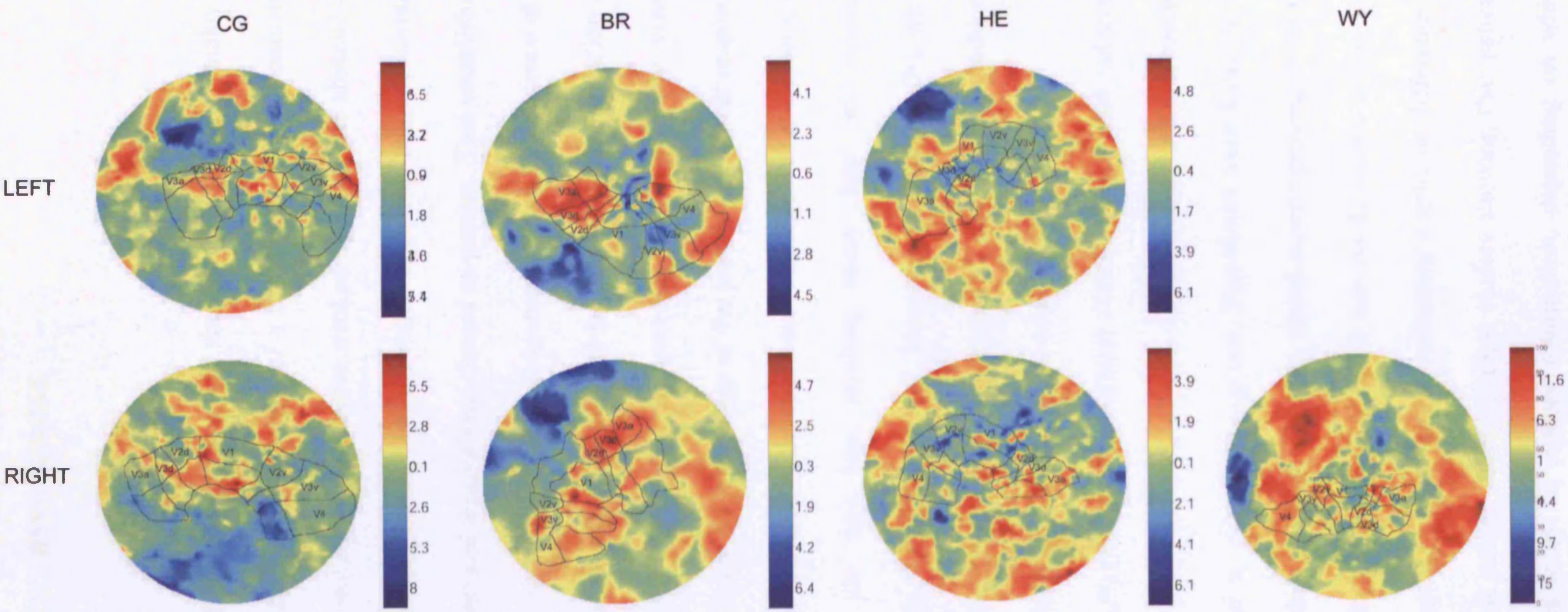


Figure 3.2.8. Flattened cortical activation maps from each subject, showing activity for the interaction effect of successful peripheral detection and attention. This contrast revealed areas more active during conscious detection in the presence of attention over detection in its absence. The colour bars represent % global brain mean. Flattened cortical surface diameter is 75mm.

3.3 Modularity of response modes and visual awareness

3.3.1 Introduction

It has been well established by signal detection theory (SDT) that to make a perceptual decision as to the presence or absence of a stimulus in the environment, observers rely on an internal sensory representation evoked by either the absence or presence of the stimulus (Green & Swets, 1966). Evoked responses below a certain criteria will be classed as absent and those above classed as present. This established view states that the sensitivity of psychophysical judgements about the presence of a stimulus, such as a luminance increment, are limited by the noise and separation of the two internal representations represented by neuronal signals in early visual cortical areas. For instance in figure 3.3.1 the noise of the present and absent response distributions clearly dictate the accuracy of the observers' response. In (a) the noise of the internal representations are very low, resulting many 'hits' and 'correct rejections', but very few 'misses' or 'false-alarms'. However, as shown in (b), when the noise of these distributions increases, the perceptual sensitivity is reduced, resulting in more incorrect responses and less correct ones.

In conflict with this prevailing view, Marcel (1993) showed that subjects' sensitivity, as measured by d-prime (d'), on a simple detection task varied according to the response modality used to give their response. Eye-blinks were found to be most sensitive, followed by finger-presses and then verbal reports proving to be the least sensitive response modality. Significantly, there was no difference in response criterion between each of these report modalities, indicating a genuine difference in sensory sensitivity. This result echoes earlier clinical studies showing that patients may have access to different levels of sensory information, depending on which response modality they use. For instance, patients with visual extinction after brain damage to the right hemisphere were found to be significantly worse at detecting a contralesional stimulus when using a key-press report than when using a verbal report (Bisiach et al., 1989). Similarly, it was found that in patients with V1 damage, eye-blinks gave a more accurate response than key-presses (Zihl & von Cramon, 1980). Related findings have recently been reported in a patient with a focal anterior cingulate cortex lesion whose performance demonstrated on Stroop and divided attention tasks depended on the response modality used (Turken & Swick, 1999). These results pose pertinent questions for the SDT view – in particular the internal representation of response distributions: why are there different d-primes when the internal representation is the same? Is that noise introduced in the visuomotor pathway after the read-out of these internal representations? Could there be a different distribution (and therefore neural populations) for each response modality? Or is one report mode more sensitive to levels of activity in early visual areas than other report modes?

Transforming a sensory stimulus into a motor act is a computationally complex process, involving multiple stages including co-ordinate transformations, response selection and a decision process. Past neurophysiological studies have demonstrated patterns of activity in neurons of the frontal and parietal cortex in monkeys consistent with both prospective and retrospective sensory and motor codes (see review Andersen & Buneo, 2002). The posterior parietal cortex in particular is thought to play a critical role in integrating sensory information with subsequent goal directed behaviour. Moreover, this area is subdivided into different subregions representing sensorimotor transformations for different response modalities, such as LIP for saccades and the parietal reach region (PRR) for reaching movements

(Andersen & Buneo, 2002). For example, Snyder and colleagues (1997) found that during a saccade task in which a monkey was required to make a delayed saccade to a target, cells in LIP responded to the target stimulus and fired during the delay period, with their activity corresponding to the location of the planned saccade. Significantly, the same response profile of neurons in this area was not observed for the task with reaching movements – these were found in the PRR. Therefore the response dissociation described by Marcel (1993) may reflect these distinct sensorimotor transformations for different response modes.

Studies of sensory awareness have typically equated subjects' report with subjective perception, as we seen have in the review section and previous experiments of this thesis. However, there is good evidence that this assumption may not be justified. Firstly, the stimulus may be consciously perceived, but is not strong enough to cross the response criterion and is therefore classed as 'not seen'. Therefore visual awareness may be graded and not binary, as the 'hit' versus 'miss' paradigms would suggest. Secondly, as the response dissociation discussed above shows rather than accurately reflecting the neural basis for visual awareness, subject reports may simply reflect the neural basis for a successful report. It is interesting to note that a fronto-parietal network of brain regions similar to those previously implicated in visual awareness (Rees et al., 2002) has been described in maintaining sensory spatial information and sensorimotor transformations (Sakai et al., 2002; Brown et al., 2004). On theoretical grounds it has been suggested that there are two types of awareness: phenomenal, that which the observer actually experiences, and access, that which the observer is able to report (Block, 1996; 2005). Conceptualised in these terms, could be argued that rather than reflecting the neural basis of phenomenal awareness, these past studies confound both phenomenal and access. Moreover, in addition to the modularity of phenomenal awareness (Zeki & Bartels, 1999) that we have explored in previous chapters, there may be modularity in access consciousness, which is reflected in both the different report mode sensitivities and the possible separate pathways for each of these. Therefore separate neural pathways may underlie the capacity to report with different response modes.

The aim of this study was to investigate the neural basis of successful detection in two response modalities. We wanted to test for a dissociation in the sensitivities of two different response modes and investigate whether the neural basis for visual awareness was distinct for each of these. Any differences would suggest a sensorimotor component to visual detection for subsequent report rather than purely sensory processes per se. To do this we scanned subjects with fMRI while they performed a simple luminance detection task in which they were required to report the percept with either a saccade or a key-press.

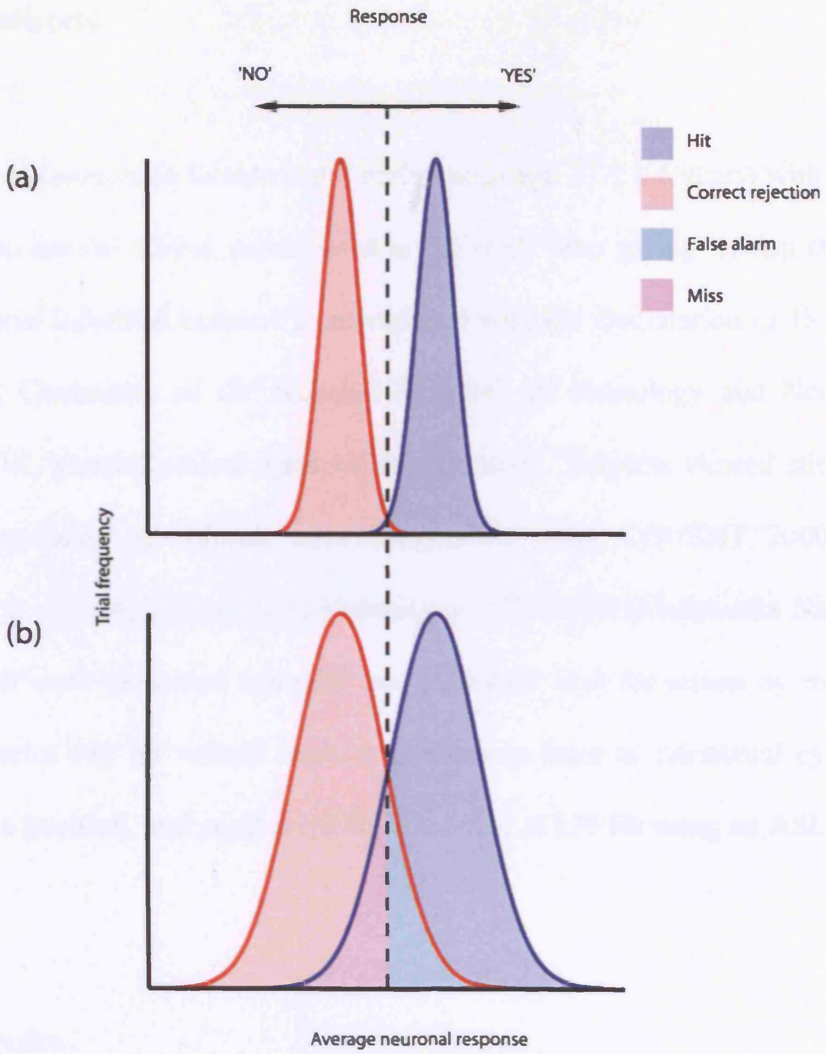


Figure 3.3.1. Internal response distributions for two stimuli with different levels of noise. The standard deviation of (a) is less than (b). The red and blue outlined response distributions represent the absence and presence of the stimulus respectively.

3.3.2. Methods

Subjects

12 healthy volunteers (4 female and 8 male; mean age 23 ± 0.6 years) with normal, or corrected to normal vision, participated in the study after giving written consent. All subjects gave informed consent in accordance with the Declaration of Helsinki, and the Ethics Committee of the National Hospital for Neurology and Neurosurgery, London, UK, granted ethical approval for the study. Subjects viewed stimulus on a grey background. All stimuli were constructed using COGENT 2000 Graphics (available at www.vislab.ucl.ac.uk) running in MATLAB (Mathworks Natick, MA). The stimuli were presented centrally and projected onto the screen by means of an LCD projector (60 Hz refresh rate). A continuous trace of horizontal eye position, vertical eye position, and pupil areas was recorded at 120 Hz using an ASL 5000 eye-tracker.

Psychophysics

Prior to scanning subjects performed a simple detection task in order to obtain their psychometric performance as a function of stimulus luminance for both the saccade and manual key-press conditions. These were performed in separate blocks of 220 trials. In both response conditions the stimulus was identical. Target present and absent trials were randomly interleaved. Throughout the entire trial two white dots (radius: 0.25^o visual angle) were present on the left and right periphery. The appearance of a central white fixation point on an achromatic background indicated the start of the trial (see figure 3.3.2 for stimulus configuration). After 800ms plus random jitter time, either a circular achromatic ring of variable luminance (radius of 6.2^o, with inner circular gap of 0.3^o) appeared for 48 ms (present trial) or did not appear at all (absent trial). The exact luminance of the stimulus was not known due to the fact that for safety reasons we were not able to use a photometer near the high magnetic strength of the scanner. Shortly after presentation (1 sec plus jitter), the fixation dot disappeared and subjects had a 1.5 second period in which to give their response (present or absent). For the key-press condition this consisted of a left or right button-press on a keypad with the index fingers of the left and right hands respectively. For the saccade condition, subjects moved their eyes to the left or right peripheral targets dots and returned to fixation. The side representing each response (present or absent) was counter-balanced across subjects. After deriving the psychometric function for both report modalities of each subject, the threshold luminance value (75% detection accuracy) of the manual key-press condition was calculated.

(a)

(b)

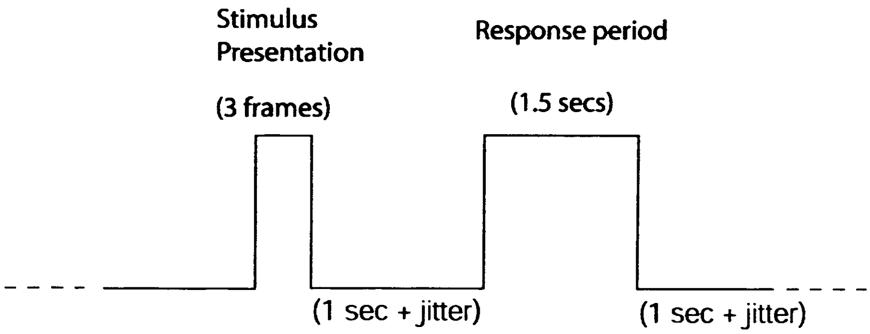


Figure 3.3.2. (a) Representation of stimulus. Subjects were required to detect the parafoveally presented luminance defined disc. (b) Trial structure.

fMRI Stimuli

After the initial psychophysical period subjects underwent two sessions of fMRI scanning during which they performed the identical detection task with each subjects threshold luminance value from the manual key-press condition used on target present trials.

Imaging and Image processing

Functional images were processed and analysed using Statistical Parametric Mapping (SPM2: Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB (MathWorks, Natick, MA). A 3-T Siemens ALLEGRA system (Siemens, Erlangen, Germany) equipped with a head coil was used to acquire functional images with a gradient echo-planar T2* sequence using BOLD (blood oxygenation level dependent) contrast, with a repetition time (TR) = 2.6 s. Each functional image comprised 40 transverse slices [2 mm thickness; 1.8 mm gap; 64 x 64, 3 x 3 mm pixels; echo time (TE) = 40 msec] covering the whole brain volume. A total of 550 sequential volumes were acquired during 2 separate sessions with the first four volumes of each session discarded to allow for T1 equilibration effects. Images were realigned, slice-time corrected, normalised to a standard echo-planar image template and smoothed with a Gaussian kernel with full-width half maximum of 8 mm. Serial autocorrelations were modelled using an AR (1) method. A structural MRI scan using a standard three-dimensional T1-weighted sequence was acquired from each subject and were co-registered to the functional scans and transformed into the same standard space.

Data Analysis

Brain activation for each experimental condition was estimated according to the general linear model at each voxel in brain space (Friston et al., 1995). The presentation period for the central disc were modelled as discrete events with the canonical haemodynamic response to capture the BOLD onset. Each trial type (hit, miss, false alarm, correct rejection) for both report modes were modelled as separate regressors, as were the motor responses, giving 10 regressors in total. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and the three rotations determined from initial registration), and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 128 s. Due to the limited number of subjects, in order to increase our statistical power we performed a fixed effects analysis, whereby all subject sessions are included in the same first-level analysis. This analysis uses within-subject variance allowing inference for the subjects used in this study only, in contrast to a random or mixed effects analysis which considers both within- and between-subject variance (Holmes & Friston, 1998).

3.3.3. Results

Psychophysics

The results from 3 subjects were discarded, as the eye-position data was not of sufficient quality to reliably estimate their responses on each trial. In the pre-scanning behavioural sessions we obtained the psychophysical thresholds for the detection task using both response modes and found them to be nearly identical in each subject. Figure 3.3.3 shows data from 4 representative subjects. Comparing across saccade and key-press response modes of the behavioural data from the scanning sessions, we found no significant differences in d' (paired t-test, $p = 0.5421$) or response criterion ($p = 0.5154$) across subjects. However, some subjects showed large differences in d' according to response mode. While this is not consistent across the subjects, it does cast doubt on whether d' is a reliable measure of perception and suggests the involvement of other factors, such as sensorimotor noise. Table 3.3.1 shows the hit and false alarm rates, d' and the response criterion (c) for all 9 subjects.

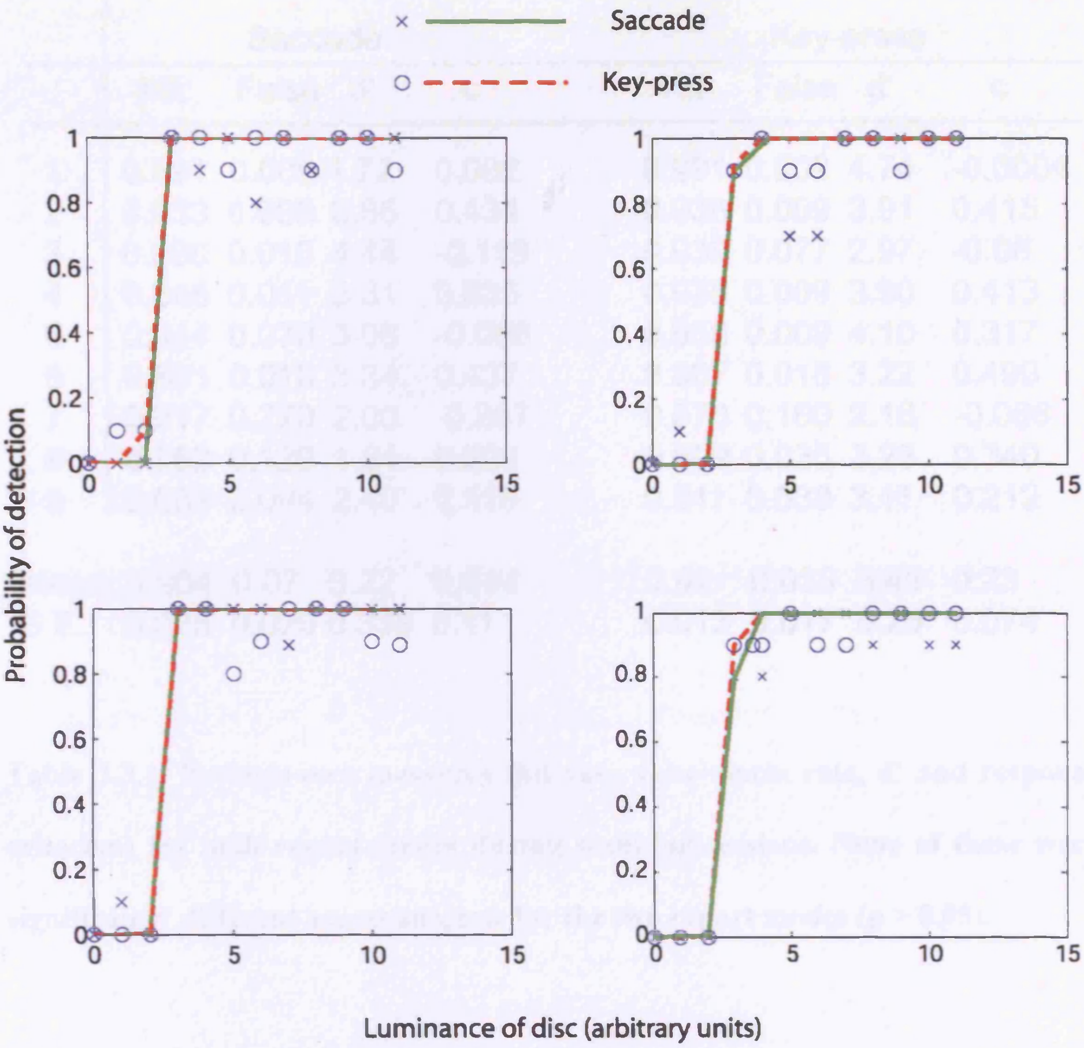


Figure 3.3.3. Psychometric functions of the detection task from 4 representative subjects. The curves for the saccade and key-press conditions were identical in both slope and 50% point. Crosses and circles represent real data from the saccade and key-press conditions respectively. Solid lines represent the fitted cumulative Weibull function.

	Saccade				Key-press			
	Hit	False	d'	c	Hit	False	d'	c
1	0.991	0.009	4.72	0.002	0.991	0.009	4.74	-0.0004
2	0.933	0.009	3.86	0.434	0.938	0.009	3.91	0.415
3	0.990	0.018	4.44	-0.119	0.939	0.077	2.97	-0.06
4	0.846	0.011	3.31	0.635	0.938	0.009	3.90	0.413
5	0.944	0.070	3.06	-0.058	0.958	0.009	4.10	0.317
6	0.891	0.018	3.34	0.437	0.867	0.018	3.22	0.499
7	0.917	0.270	2.00	-0.387	0.878	0.160	2.16	-0.086
8	0.762	0.129	1.84	0.209	0.899	0.025	3.23	0.340
9	0.861	0.094	2.40	0.116	0.911	0.039	3.11	0.212
Mean:	0.904	0.07	3.22	0.014	0.92	0.039	3.48	0.23
S.E. :	0.025	0.029	0.339	0.11	0.013	0.017	0.25	0.074

Table 3.3.1. Performance measures (hit rate, false-alarm rate, d' and response criterion) for both report modes during scanning sessions. None of these were significantly different across subjects for the two report modes ($p > 0.05$).

fMRI

The fMRI data from 9 subjects were submitted into a fixed-effects group analysis. To localise brain areas responsive to the presence of the target stimulus, we compared brain activity on trials in which the stimulus was presented with those in which it was absent, collapsing across task performance and response modality. As shown in figure 3.3.4, threshold controlling false discovery rate (FDR; Genovese et al., 2002) at 5% revealed activity localised to the occipital lobe, encompassing early visual areas, which may include V1/V2 (peak voxel co-ordinates [4 –78 –6], Montréal Neurological Institute (MNI) space), the right V3 complex [28 –88 28] and lateral occipital areas (left: [-50 -74 2], right: [52 -68 -8]).

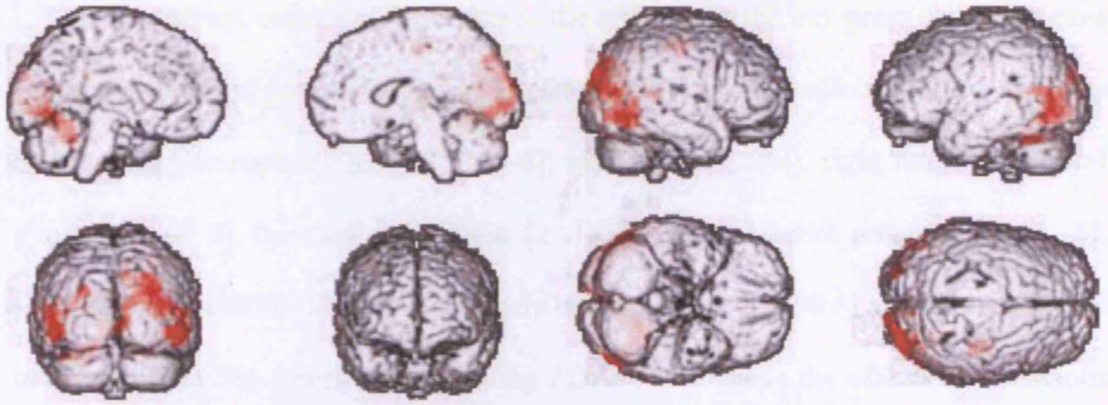


Figure 3.3.4. Main effect of stimulus presence. Results are displayed with a statistical threshold on $p < 0.001$ (uncorrected for multiple comparisons).

By comparing trials on which the stimulus was successfully detected, with those in which it presented but missed, we were able to delineate the brain areas underlying the subjective perception of the stimulus, since in both cases the stimulus is identical, but only the subjective perception differs (figure 3.3.5). Moreover, by looking at the effect of report mode, we are able to investigate the interaction of report and visual awareness. In the saccade report condition at a corrected statistical significance (5% threshold controlling FDR), this reveals the bilateral inferior parietal cortex (left: [-50 –60 46, right: [52 –56 52]), the right dorsolateral prefrontal cortex [42 56 10] and the middle frontal gyrus bilaterally (left: [42 12 56], right: [-50 –60 46]). To then ensure that these activations were not simply due to a main effect of subsequent saccade direction, we performed the same comparison but used an exclusive mask ($p = 0.05$, uncorrected) with the contrast that compared all trials in which the subjects looked left ('present') with all trials in which the subjects looked right ('absent'). Therefore those activations that remain after masking should be specifically related to the conscious detection of the stimulus. This showed activity in the same areas at a corrected level of significance (5% threshold controlling FDR).

In contrast, conscious detection of the stimulus in the key-press condition gave activity in the right precentral gyrus [34 –20 54], the left cerebellum [-24 -54 -26], the bilateral hippocampus (left: [-32 -30 –6], right: [26 -4 -20]), right middle temporal gyrus [38 –64 2], the medial thalamus [2 -14 2], right posterior putamen [34 -6 -8], right caudate nucleus [14 12 20] and early occipital areas [8 –90 6] at a corrected level of significance 5% threshold controlling FDR. To visualise the effects of conscious detection rather the motor intention or planning for the left key-press, we used an exclusive mask (p = 0.05, uncorrected) on this comparison with the contrast of all 'present' trials with all 'absent' trials in the key-press condition. This gave significant activations in the left posterior hippocampus, right primary motor cortex, the right middle temporal gyrus. the medial thalamus, right posterior putamen and the right caudate nucleus, at a corrected level of significance 5% threshold controlling FDR.

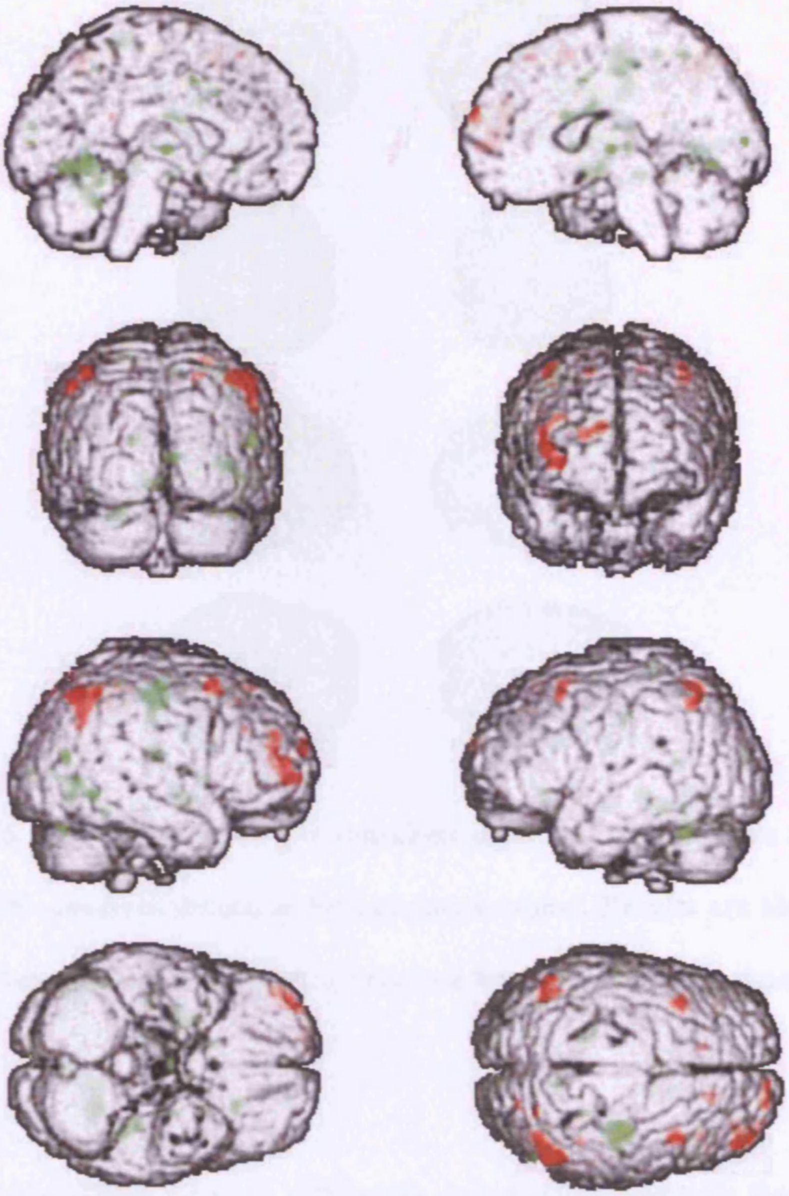


Figure 3.3.5. Brain activations revealed by the contrast of 'hit' versus 'miss', for the saccade and key-press conditions shown in red and green respectively. Results are shown with a statistical threshold of $p < 0.001$ (uncorrected for multiple comparisons).

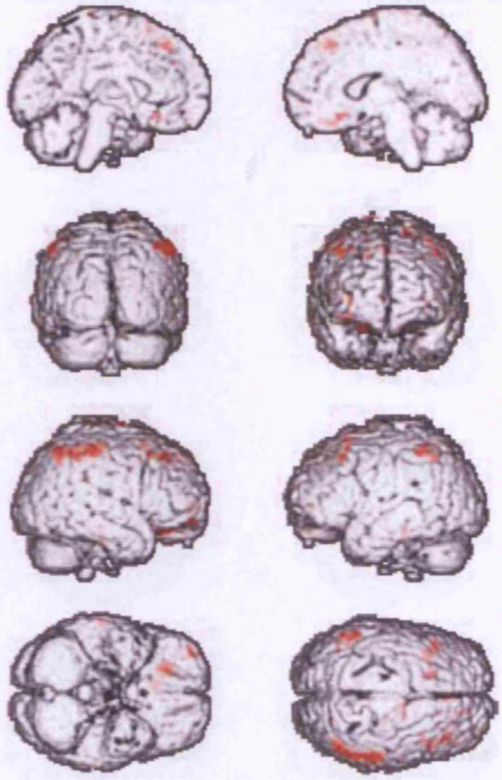


Figure 3.3.6. Interaction effect for conscious detection with saccade report over activity with conscious detection for key-press report. Results are shown with a statistical threshold of p < 0.001 (uncorrected for multiple comparisons).

The interaction effects revealed differences in activations between these contrasts. Correspondingly the contrast showing areas more activated by conscious detection in the saccade condition than the key-press condition revealed the bilateral inferior parietal cortex, bilateral inferior frontal gyrus, the right middle and superior orbital frontal gyrus and the left superior middle gyrus (5% threshold controlling FDR; figure 3.3.6). The opposite contrast identified activations, at an uncorrected level of significance only ($p < 0.001$), in early occipital areas, the medial thalamus, left cerebellum, right posterior putamen, the right middle cingulate cortex, the right primary motor cortex, the right middle temporal cortex and the right posterior thalamus (figure 3.3.7).

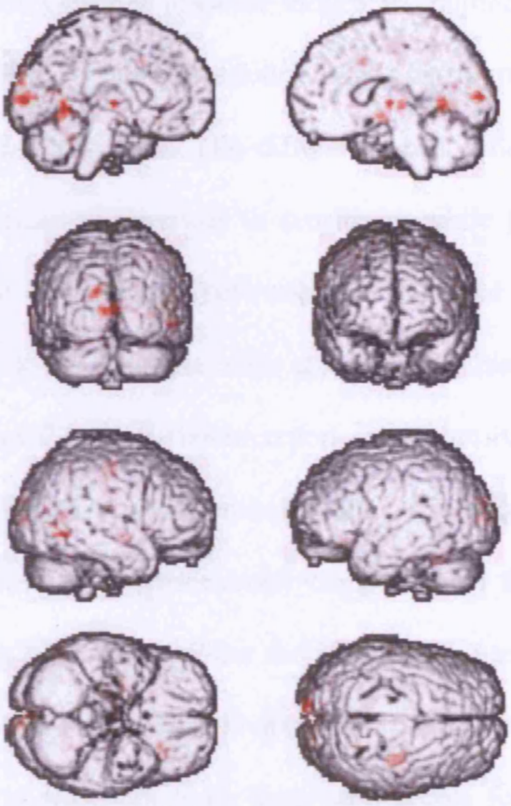


Figure 3.3.7. Interaction effect for conscious detection with key-press report over activity with conscious detection for saccade report. Results are shown with a statistical threshold of $p < 0.001$ (uncorrected for multiple comparisons).

In addition, we performed a conjunction analysis (Nichols et al. 2005, Friston et al., 2005) of the SPMs of the minimum T-statistic over the two orthogonal contrasts 'hit versus miss' for the saccade and key-press conditions. This should reveal brain areas underlying awareness, independently of response modality. However, no voxels were found to be significant, even at a low statistical threshold ($p < 0.05$, uncorrected for multiple comparisons).

3.3.4. Discussion

The aim of this study was to investigate the interaction between visual awareness and response modality. We used a simple detection task in which subjects were required to report their perception with two response modes, in conjunction with event-related fMRI. Our results can be summarised as follows: (1) contrary to previous behavioural studies (Marcel, 1993), we find that two different report modes, saccades and key-presses, have no significant differences in sensitivity while performing a detection task, (2) two completely distinct brain networks were revealed for conscious detection of the stimulus specific to the response mode consequently used. Overall, our findings suggest that despite equality in different report mode sensitivities, separate neural networks determine whether a visual stimulus can be subsequently reported. These results therefore demonstrate a sensorimotor component to the neural correlates of visual awareness specific to the response modality being used that is distinct from purely perceptual processes. Unlike previous studies, by using different response modes we were able to tease out brain areas responsible for successful conscious report.

As discussed in section 3.3.1, according to SDT to make a perceptual decision, the sensory evidence is matched to a response criterion (Green & Swets, 1966). Neurobiologically, the process of making a motor act in response to a sensory stimulus involves a complex interplay between cortical and subcortical regions, matching the appropriate motor response to sensory input. The visual system provides sensory evidence for the decision, which is then integrated in sensorimotor regions such as LIP in the posterior parietal cortex in preparation for making a saccade, or in PRR for making a reaching movement (Andersen & Buneo, 2002). Lying at the apex of the sensory and motor pathways are the so-called 'executive' mechanisms of the prefrontal cortex, providing a flexible rule-based behavioural and cognitive organisation (Shallice, 1998). Anatomically, these are organised into cortico-thalamo-basal ganglionic loops and are thought to select the behaviourally relevant response appropriate for the context (Goldberg, 1985; Passingham, 1993). Our results, taken as a whole across both of the response modes, show that successful detection and report of the stimulus, as shown by the hit versus miss comparison, correlates with brain activity in all of these regions. However, the surprising aspect to these results is that this contrast for each of the response modalities have no areas in common, indicating that the critical stages for detecting a reporting the presence of a stimulus lie at distinct phases of the sensorimotor pathway. In terms of SDT (Green & Swets, 1966), these areas may be considered the stages at which noise arises along the pathway.

The conscious detection in the saccade condition revealed a network of areas including the frontal eye fields, the right inferior parietal lobe and bilateral middle frontal gyrus (figure 3.3.5). Both electrophysiological studies in monkeys (Andersen & Buneo, 2002) and human imaging studies (Prado et al., 2005) have implicated the posterior parietal cortex in sensorimotor roles and the maintenance of spatial coordinates for action. Moreover, similar fronto-parietal areas are believed to have a role in response selection (Rowe at al., 2000). Thus these areas can be regarded as selecting a subsequent response after conscious detection. Our results indicate that these areas are critical for sensory information to translate into appropriate saccadic response. In contrast, successful detection and subsequent key-press response revealed activity in the posterior thalamus, left cerebellum, right posterior putamen, the right middle cingulate cortex, the right primary motor cortex, left posterior hippocampus and the right middle temporal cortex (figure 3.3.5). With the exception of the latter two regions, it is interesting that these areas are the same as those associated with response preparation and execution in previous fMRI studies (Kim et al., 1993; Allison et al., 2000). Therefore it may be the case that the critical stages in reporting the presence of a stimulus for the key-press response are downstream in the perception-action cycle of those areas involved in the saccade response. A role for medial areas of the temporal cortex, especially the hippocampus, in action and visuomotor processes has been suggested by previous fMRI studies using delayed performance task. Activity in these areas was found to be time-locked to the response cue during 'Go' and negatively during 'no-Go' trials, ruling out any associative roles (Theonissen et al., 2002) and is thus consistent with the proposed role of the hippocampus in voluntary movement (Halgren, 1991). Therefore, the increased activity in the posterior hippocampus and temporal cortex in the present results for detection and report with key-press is consistent with a role for selecting the correct response for the stimulus.

Surprisingly, the main effect of conscious detection of the stimulus did not correlate with early visual activations in the saccade condition, unlike the key-press condition which shows a band of activity along the calcarine sulcus, most likely corresponding to the primary visual cortex. As reviewed in section 1.5, many studies have shown early visual activity to correlate with awareness in tasks similar to the one used here. For instance, in a simple grating detection task, hit trials were found to correlate more with activity in early visual areas than miss trials (Pins & ffytche, 2003). However, this and other studies have invariably used key-press reports to probe subjective perception, and are therefore consistent with our results. The intriguing aspect is the lack of correlation in the saccades condition. This suggests that the role played by V1 in visual awareness (Tong, 2003) may be contingent upon the subsequent response mode, at least in humans. Previous macaque studies have demonstrated a correlation between visual awareness and V1 activity with detection (Super et al., 2001) and visual search tasks (Roelfsema et al., 2003), while using saccades as a response mode. However, as far as we are aware, the present study is the first human neuroimaging experiment to use saccades to probe the correlates of subjective perception. This lack of correlation shown presently may represent a genuine species difference for the role that early visual areas in detecting stimuli and reporting with saccades. Alternatively, methodological differences may also account for this, such as the difference between fMRI and single-cell physiology (Logothetis & Wandell, 2004).

However, one possible confounding factor for the lack of activity in early visual areas for the saccade condition in our results is the effect of saccadic suppression. Psychophysical, electrophysiological and neuroimaging studies show that neural responses to visual stimuli, particularly in low-spatial frequencies (Burr et al., 1994), can be suppressed during or even prior to saccades. In humans, this was recently shown to occur as early as V1 and the LGN (Sylvester et al., 2005). Due to the low temporal resolution of the BOLD signal, it was not possible to disambiguate the influence of these oculomotor effects from purely stimulus related activity. Therefore, the lack of correlation of V1 with subjective perception in the saccades condition may be due to the fact that extra-saccadic signals reduce early visual responses. While we cannot completely discount this possibility, a couple of lines of evidence make it unlikely. Firstly, a recent combined fMRI and psychophysical study demonstrated that the reduction in BOLD signal in area V1 due to saccadic suppression only occurs when the saccade and stimulus are less than 80 ms apart (Vallines & Greenlee, 2006). Therefore a reduction in activity related to suppression of stimulus processing can be discounted given that the separation in our experiment was over 1 second. Secondly, since we were primarily interested in the interaction between the response modes and specifically in the differences in activity between the hit versus miss contrast between the two response modes, we believe that any saccadic effects would be controlled for. Assuming the effects of the saccades are the same for both responses, these should drop out in the hit versus miss contrasts, leaving only the correlates of visual awareness elicited by the stimuli. Importantly, the gap between the stimulus and the response, rules out any non-linear interactions between saccadic and stimulus signals, which are known to occur on a smaller time-scale (Huettel & McCarthy, 2000) that could confound this contrast.

In contrast to the previous work of Marcel (1993), we failed to show a consistent difference between the d-prime of the response modalities across subjects. Two explanations for this apparent discrepancy may be considered. Firstly, methodological differences between the two studies make direct comparisons difficult. The previous study of Marcel did not use saccades as a response mode, only eye-blinks, verbal reports and key-presses. In addition, the stimuli subtended only 2° of the visual field and were presented for 200ms in the previous study, in contrast to the larger 5.5° diameter stimuli on-screen for 50ms used presently. Future behavioural studies are needed to determine whether this discrepancy is due to response modes, stimuli or an interaction between these factors. Secondly, our psychophysical measurements may not have been sensitive enough to detect a difference in performance between the two report modes. It could be considered a ceiling effect, as during the detection task the hit rates were high for both modalities, thereby masking differences in sensitivity. While the identical psychometric functions obtained prior to scanning for these modalities underlines the equality in psychophysical performance, we are still cautious in completely discounting the existence of such as dissociation in the sensitivities of the report modes. Our psychometric functions shown in figure 3.3.3 were extremely steep. This may conceal more subtle differences in thresholds. Due to the limited time available for the initial psychophysical testing for each subject in the scanner, it was not possible to explore a thorough range of luminance values for the detection task that may have revealed significant differences in the psychometric functions.

While these behavioural results are inconsistent with previous studies in normal subjects, our fMRI results do find some consistency with previous studies showing a response dissociation in patients with neglect (Bisiach et al., 1989). While the symptoms of neglect have traditionally been categorised as sensory or motor, recent proposals have emphasised the sensorimotor transformations involved in these deficits (e.g. Pouget & Driver, 2000). Damage to the inferior parietal cortex, in addition to perceptual deficits, impairs initiating movements towards targets on the contralesional side (Mattingly et al., 1998). Moreover, many of the brain regions implicated in neglect include the posterior parietal cortex, the dorsolateral prefrontal cortex and sub-cortical regions such as the basal ganglia (Karnath et al., 2002). The heterogeneity in the deficits may be explained by distinct damage to multiple stages along this sensorimotor process. Physiologically, it has been demonstrated that distinct areas of the parietal cortex, such as LIP and PRR, underlie sensorimotor transformations for saccades and reaching respectively (Andersen & Buneo, 2002). Moreover, the present results implicate exclusive sensorimotor regions in the successful report of the stimulus specific to the response mode used. Significant differences in the detectability of targets between report modalities in neglect patients, such as those described by Bisiach and colleagues (1989), may therefore be due to selective damage to these different areas underlying the different response modes.

How do these results stand with current theories of visual awareness? Firstly, they identify components to the neural correlates of awareness that are related to the motor report and not to the percept. Such findings have resonance with the theoretical suggestion that awareness can be broken down into two components: 'phenomenal consciousness' in which corresponds to the subjective percept or qualia; and 'access consciousness' which is related to the ability to make voluntary report about what is perceived (Block, 1996; 2005). While many theories of awareness do not make a distinction between these or specific predictions for their neural underpinnings, two contradictory proposals have been made. On the one hand, the global workspace view (Dehaene et al., 2003) suggests that once a percept is phenomenally conscious it is then available for report – there is not distinction between phenomenal and access. By contrast, it had been hypothesised that activity in the visual cortex is sufficient for phenomenal perception whereas the fronto-parietal areas are required for access (Lamme, 2004; Block, 2005). This is consistent with the results presented here. Moreover, we are able to identify sub-components specific to each response mode.

In summary, we find networks of brain areas correlating with visual awareness that are contingent upon the response modality used to subsequently give a behavioural report. One striking aspect to our results is that conscious detection with each report modality did not have any brain areas activated in common. Given the reliance of studies of visual awareness on behavioural reports, in light of the current findings, the significance of many of these results may have to be reassessed to accommodate this sensorimotor component. By using different report modes, for the first time we have been able to fractionate the neural correlates of consciousness into those areas responsible for successful conscious report. We suggest that the present findings have gone some way to demonstrating the neurobiological basis of conscious 'access' for different response modes.

Conclusions

The aim of this thesis was to test the hypothesis that low-level neural mechanisms underlie visual awareness. To do this, we use a two-pronged strategy with: (1) psychophysical studies to measure the timing of visual perception, (2) fMRI to measure brain activity whilst tracking subjective reports of perception. The two psychophysical experiments investigated temporal aspects of visual perception – in particular these addressed the issue of whether the timing of awareness is 'online' rather than integrated into a temporal buffer zone prior to perception. We measured the relative perceptual times of different magnitudes of direction change and investigated the 'flash-lag' effect (Nijhawan, 1994) and related illusions of positional localisation. The first two fMRI experiments examined the necessity of frontal and parietal areas for visual awareness in the context of bistable figures, combined with dynamic causal modelling (Friston et al., 2003), and perception outside the focus of attention. Finally, we looked to extend the concept of modularity of awareness to that of 'access consciousness', that is the ability to give a report of a conscious experience (Block, 1996), in addition to the previous studies that have investigated the neural correlates of phenomenal consciousness. To this end, we combined psychophysics with fMRI to investigate the interaction between report modality and visual awareness.

In one sense the experiments were successful, with our findings largely compatible with our initial low-level theory of visual awareness. We found the results consistent with an online view of the timing of awareness, good evidence that visual awareness does not require the frontal and parietal cortices, and finally, we demonstrated that the modularity of awareness may be extended to access consciousness. However, in another sense the entire undertaking was naïve, as the mechanisms underlying conscious visual perception are unlikely to be delineated in a single thesis. Despite the vast number of experiments on this topic, the theories for the neurobiological candidates of visual awareness seem to be just as numerous and we were unable to explore them all. For instance, we have not investigated the putative role for neuronal synchrony (Engel & Singer, 2001) or the brainstem (Magoun, 1954). Each of these issues in themselves would require more than a lifetime's work. However, in the context of the present thesis, we believe that the low-level view of visual awareness embodied in the microconsciousness framework (Zeki & Bartels, 1999) stands up to direct tests of its predictions. Moreover, our results directly contradict predictions of integrated global theories of consciousness (Dehaene et al., 1998; Rees et al., 2002) and suggest that awareness may be disintegrated across both space and time. Therefore, in our small way, we hope to have contributed to the answer of one of the most fundamental scientific questions asked, and helped solve the 'easy' problem of consciousness (Searle, 1993).

Appendices

Appendix 1: Object Localisers

The aim of this experiment was to determine the location of regions involved in the processing of the local visual environment ('places') and faces to act as a localiser of for experiment 3.2. Previous studies have characterised functionally specialised regions that respond selectively to these stimuli: the 'parahippocampal place' (Epstein & Kanwisher, 1998; Epstein et al., 2003) and the 'fusiform face' (Kanwisher et al., 1997) areas respectively.

Stimuli & Task

We used a simple block based design in which the four subjects from fMRI experiment 3.2 viewed 5° by 7.5° monochrome pictures of faces or places. The face stimuli were overlaid onto a rectangular textured background to match the place stimuli for spatial frequency and size. Each block lasted 22.5 seconds, with each image presented for 1 second, with a 0.5 seconds gap in-between with a random jitter of 0.2 seconds. Blocks with places alternated with blocks of faces for a total of 20 blocks in total. Subjects were instructed to fixate a dot in the centre of the screen and perform a one-back memory task with the stimuli within each block and to press a button with their index finger to indicate an identical match between two subsequent stimuli.

Imaging & Image processing

Functional images were processed and analysed using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB (MathWorks, Natick, MA). A 3-T Siemens ALLEGRA system (Siemens, Erlangen, Germany) equipped with a head coil was used to acquire functional images with a gradient echo-planar T2* sequence using BOLD (blood oxygenation level dependent) contrast, with a repetition time (TR) = 2.6 s. Each functional image comprised 40 transverse slices [2 mm thickness; 1.8 mm gap; 64 x 64, 3 x 3 mm pixels; echo time (TE) = 40 msec] covering the whole brain volume. A total of 161 sequential volumes were acquired during each session with the first four volumes of each session discarded to allow for T1 equilibration effects. Images were realigned, normalised to a standard echo-planar image template and smoothed with a Gaussian kernel with full-width half maximum of 6 mm.

Data analysis

Brain activation for each experimental condition was estimated according to the general linear model at each voxel in brain space (Friston et al., 1995). The face and place stimuli were modelled separately as blocks by a box-car waveform of 22.5s convolved with the canonical haemodynamic response to capture the BOLD onset. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and the three rotations determined from initial registration), and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 128 s. Images of parameter estimates for each contrast of interest were created for each subject (first-level analysis).

Results

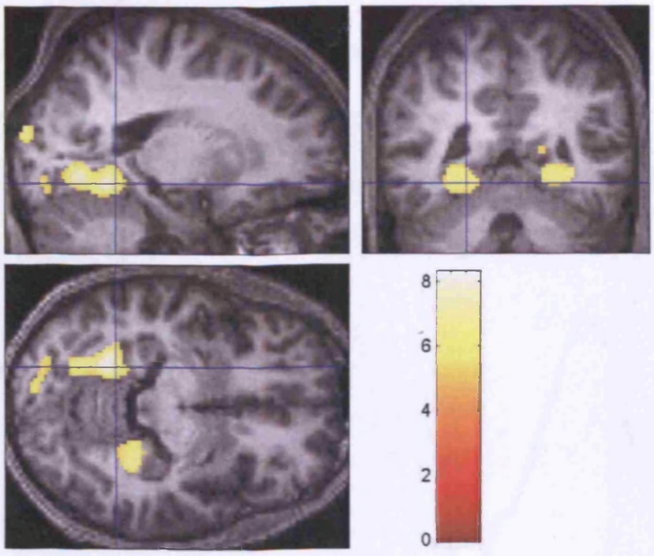
To functionally localise areas involved in the processing of face stimuli we compared activity from the face blocks with the place blocks. This revealed FFA activity unilaterally in 3 of the 4 subjects; the occipital face area (OFA) unilaterally in 2 subjects and face selective regions in the superior temporal sulcus (STS) bilaterally in 3 subjects, and unilaterally in 1. The opposite contrast was performed to localise areas associated with place stimuli. All 4 subjects showed activity in the bilateral parahippocampal cortex with the [place > face] contrast.

Subject	FFA	OFA	STS	PPA
CG	R: [40 -46 -30] L: -	R: [42 -82 -10] L: -	R: [54 -54 6] L: -	R: [-28 -40 -10] L: [-24 -56 -12]
WY	R: [40 -56 -20] L: -	R: - L: -	R: [52 -62 0] L: [-50 -50 8]	R: [28 -36 -22] L: [-20 -46 -10]
HE	R: - L: -	R: [48 -68 -10] L: -	R: [58 -54 14] L: [-42 -54 8]	R: [24 -34 -22] L: [-20 -42 -14]
BR	R: - L: [-46 -54 -24]	R: - L: -	R: [62 -42 10] L: [-46 -36 8]	R: [30 -46 -10] L: [-24 -46 -12]

Table A.1.1. MNI co-ordinates of the FFA, OFA, STS and PPA of each subject.

Figure A.1.1 shows the localised face selective areas and PPA of subject one in axial saggital and coronal slices, superimposed onto the normalised structural brain image. Figure A.1.2 shows the time course of the BOLD signal of the peak voxels from the PPA and FFA of subject 1 during the first 150 seconds of the localiser scan. Overall, the results confirm the functional selectivity of areas processing these mid-level object categories.

(a)



(b)

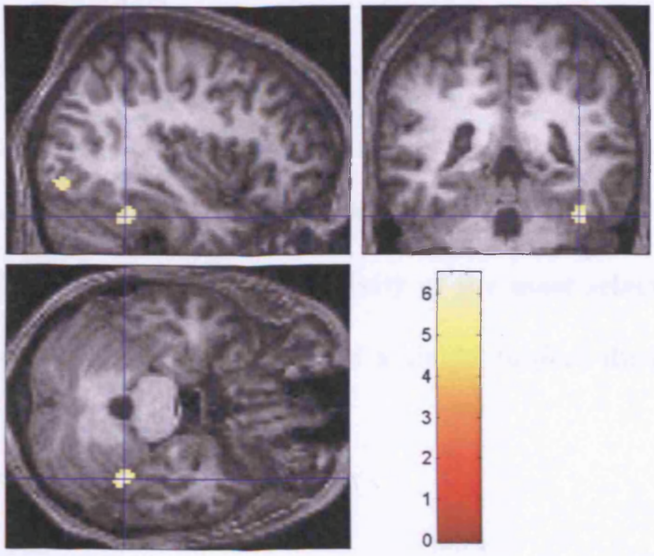


Figure A.1.1. Axial, saggital and coronal slices of contrasts (a) [places>faces] (b) [faces>places] for subject CG superimposed onto a normalised T1 weighted structural image. (a) shows bilateral PPA activity, while (b) shows FFA and OFA

activity unilaterally only. Functional image corrected for multiple comparisons with family-wise error (FWE) $p < 0.05$. Colour bars represent t-values.

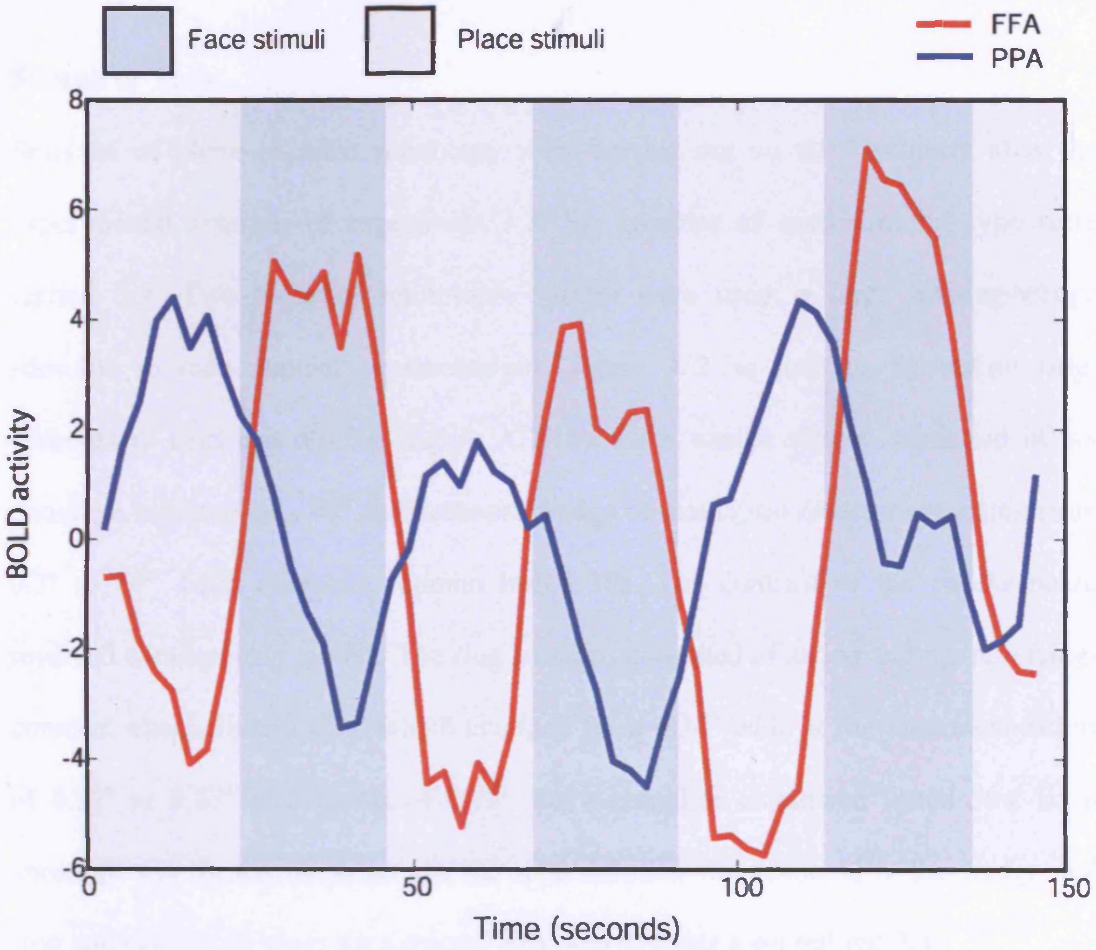


Figure A.1.2. Time-course for BOLD activity of the most selective voxel of the left PPA for places and FFA for faces of a single subject during the localiser session.

Appendix 2: Retinotopic mapping

Stimuli & Task

Sessions of phase-encoded retinotopy were carried out on all 4 subjects after the experimental sessions of experiment 3.2. Six sessions of each stimulus type were carried out. Two types of retinotopic stimuli were used: a large rotating-wedge stimulus to map angular representation (figure A.2.1a) and an expanding ring-stimulus to map eccentricity (figure A.2.1b). Each wedge session consisted of six complete rotations of a 45° checkerboard wedge of maximum contrast extending from 0.7° to 10°. Each complete rotation lasted 30s. The contrast of the checkerboard reversed continuously at 4Hz. The ring stimulus consisted of an expanding, reversing-contrast, checkerboard ring, which changed from 0.36° wide at the innermost radius of 0.67° to 2.47° at a radius of 8.78°. Each complete expansion lasted 30s. Each stimulus was shown six times and the total duration was identical in the wedge and ring sessions. In all cases the subjects' task was to fixate a central red dot.

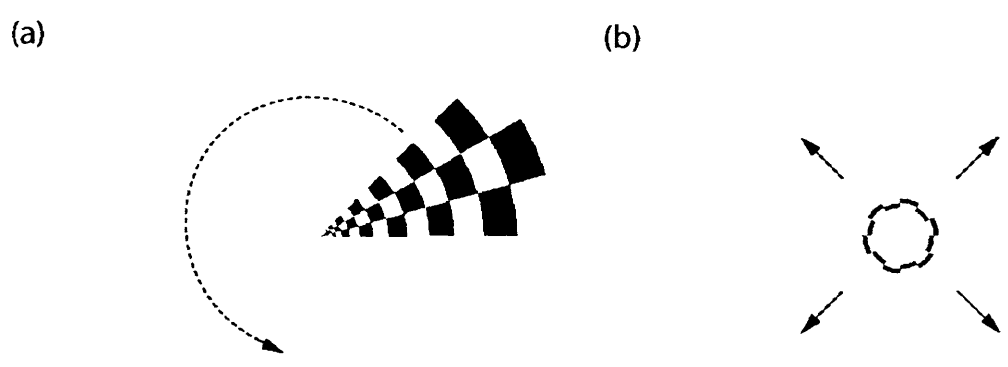


Figure A.2.1. Screen shots of stimuli used for phase-encoded retinotopic mapping. Dotted arrows represent trajectory of stimulus, (a) rotating wedge, (b) expanding ring.

Imaging & Image processing

Functional magnetic resonance data were acquired on a Siemens 3T Allegra scanner (Siemens, Erlangen, Germany) fitted with a head-coil. Subjects viewed a screen via an angled mirror onto which stimuli were projected using an LCD projector. This display extended 15° horizontally and 10° vertically from the fixation cross. BOLD contrast weighted echoplanar images (EPIs) were acquired for all functional scans. Each complete volume was acquired as a series of 30 axial slices of 2mm thickness with 1mm gaps in between, tilted so that they were parallel to the calcarine sulcus. The in-plane resolution was 3x3mm. Each slice was acquired in 65ms (TE = 30ms) meaning that the entire volume was acquired in 1.95s. There were no gaps between volume acquisitions. The first 8 volumes were discarded to allow for T1 equilibration effects. A T1 weighted anatomical image was acquired from each subject after the second functional session. Each anatomical image was segmented into gray and white matter using mrGray software (Teo et al., 1997). The occipital lobes and neighbouring cortical structures of each subject were flattened for further visualisation (Wandell et al., 2000).

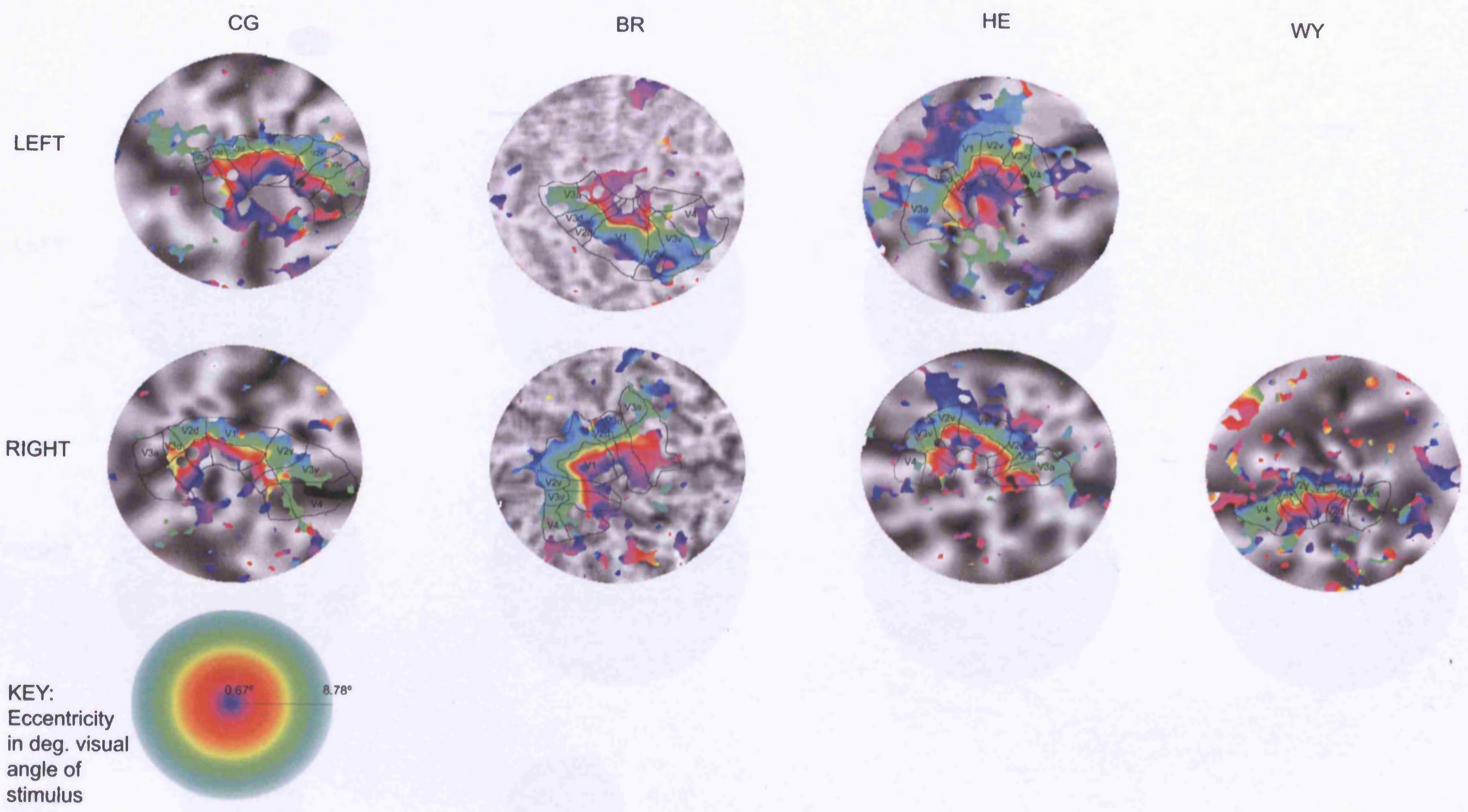
Data analysis

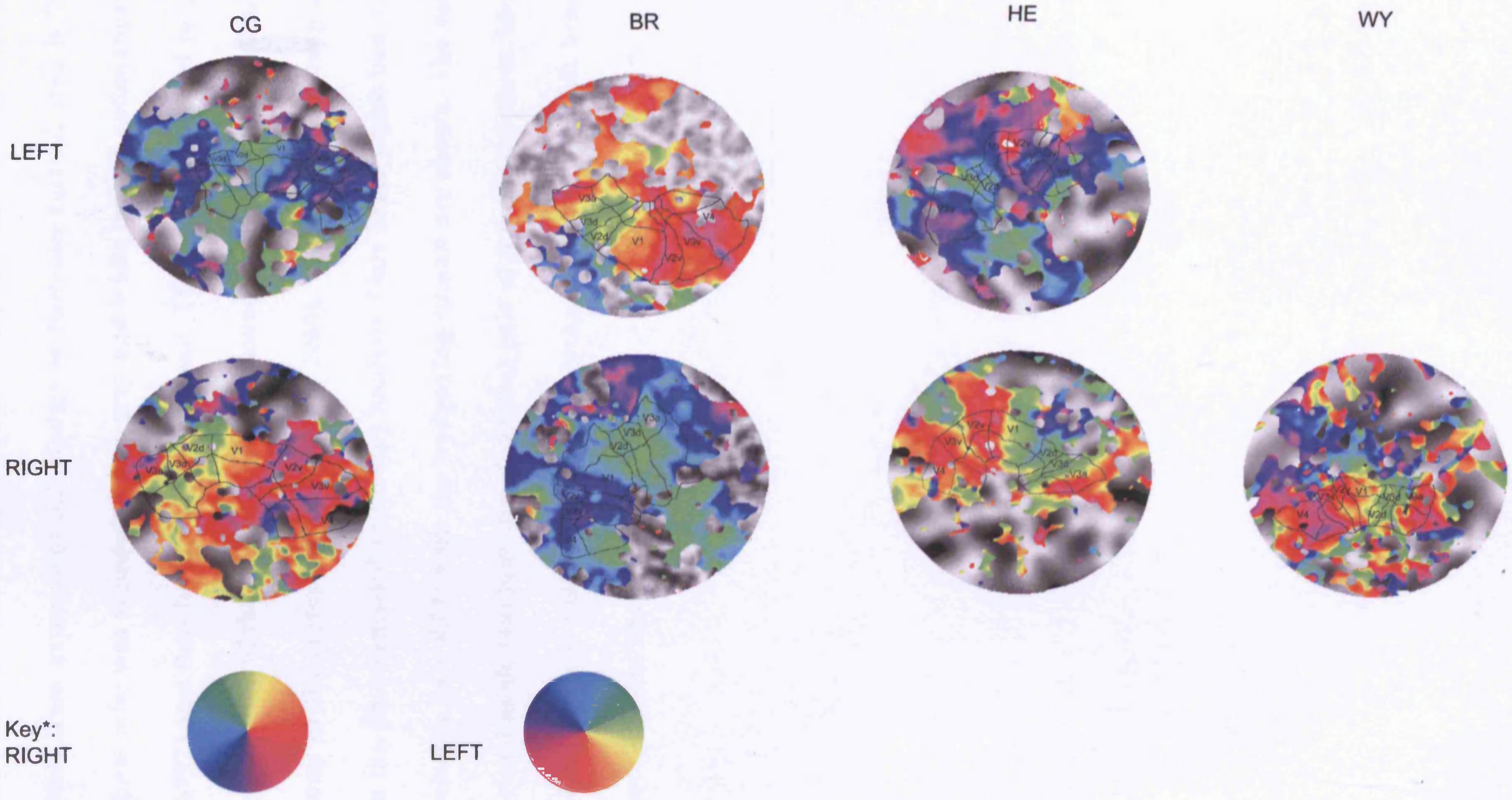
All images were pre-processed using SPM2 (available from the Wellcome Department of Imaging Neuroscience at [illegible]). Images acquired for retinotopy were realigned to the first volume of the first session of experiment 3.2

using sinc interpolation. These images were then resliced to produce a final voxel resolution of 3x3x3 mm. All images were temporally filtered with a high-pass filter with a cut-off of 128 s. Serial autocorrelations were modelled using an AR (1) method. The anatomical image was coregistered to the mean, realigned functional image for each subject.

Definition of Regions of Interest (ROIs)

Retinotopic data was analysed in a standard fashion (Engel et al., 1994) using SPM2. Only voxels that had significant correlations with the wedge/ring stimuli are reported ($P < 0.01$, uncorrected for multiple comparisons). ROIs were drawn by eye on a flatmap of the angular representation. The fovea and eccentricity lines were overlaid on these flatmaps to guide the drawing (figure A.2.2). Using this technique we could reliably delineate the fovea, V1, V2d/v, V3d/v, V3A and V4 (figure A.2.3). Any voxel that was assigned to two different ROIs was removed from both of them. Individual subject variation in the topography and size of visual areas were consistent with results from previous studies (e.g. Andrews et al., 1997; Dougherty et al., 2003), where it has been show that the surface area of visual areas may vary between individuals by up to a factor of two.


CG
BR
HE
WY
LEFT
RIGHT
V1
V2d
V2v
V3d
V3v
V3a
V4
KEY:
Eccentricity
in deg. visual
angle of
stimulus
0.67°
8.78°



*Left and right keys are reversed for subject BR

Figure A.2.2. Flattened representation of phase and eccentricity maps for 4 subjects from experiment 3.2. Radius of flattened cortical area is 75mm. The occipital lobe was segmented into grey and white matter automatically (Teo et al., 1997) and then further edited by hand. These data were used to construct a representation of the grey-white matter boundary and this was used to produce a flatmap of the cortex (Wandell et al., 2000). Overlaid on this map are results from the phase-encoded retinotopy analysis. Only areas which had a significant correlation ($p < 0.01$) with the wedge/ring stimuli are shown. The colour codes the visual angle that best stimulates that part of the cortical sheet. Identification of visual areas is shown here. Due to technical reasons the left hemisphere of subject WY was unavailable.

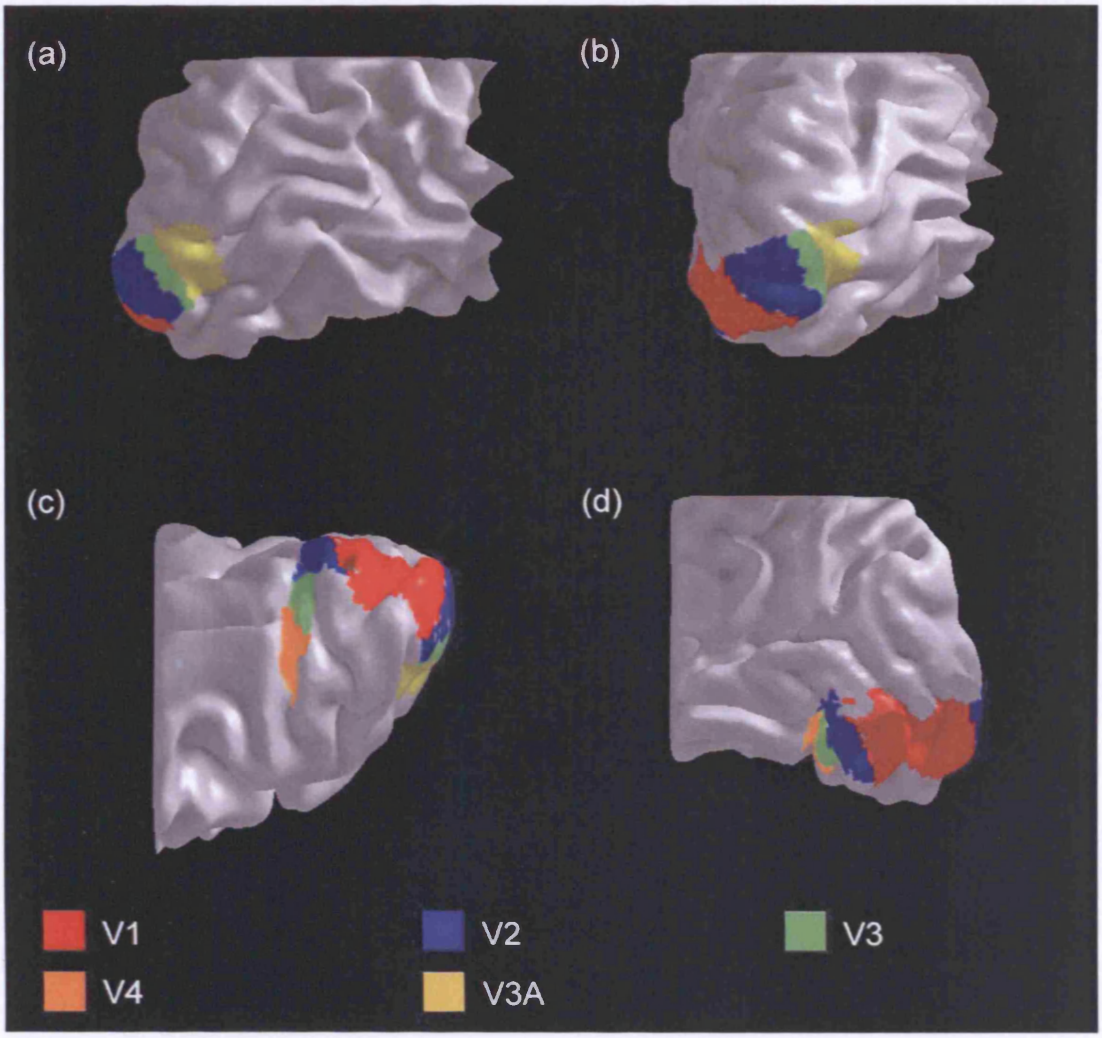


Figure A.2.3. Visual areas shown on the right occipital lobe. Four views, (a) lateral , (b) dorsal, (c) ventral, (d) medial, of 3D reconstructions of the cortical surface of subject HE. Overlaid on these are the visual areas identified using this subject's retinotopic maps.

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