Bangor University

DOCTOR OF PHILOSOPHY

Motion processing in the upper and lower visual fields

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Award date:
2002

Awarding institution:
University of Wales, Bangor

Link to publication

Motion Processing in the Upper and Lower Visual Fields

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Thesis submitted for examination for the degree of PhD in
Psychology.

University of Wales, Bangor, June, 2002

Acknowledgements

No doubt I have caused endless frustration to several people while working toward this thesis. Two in particular deserve honourable mention; my partner, Heather, who has never doubted my ability to achieve my goals, and my supervisor, Prof. Jane Raymond, who might now see her extraordinary patience rewarded. I'm pleased also that my parents were able to see me take advantage of opportunities not available to them.

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General Abstract

Physiological evidence suggests there are numerous regions within visual cortex that have a pronounced retinotopic bias toward one vertical hemifield, or code exclusively for a single vertical hemifield. The strongest evidence of this kind is for a processing bias toward the lower visual field within the dorsal pathway. Given the evidence that global motion perception in humans is critically dependent on dorsal mechanisms, it was predicted that the lower visual field would prove to be functionally specialised for processing global motion. This hypothesis was tested in a series of five experiments. In Experiments 1-3, observers discriminated motion direction in partially coherent random dot kinematograms, under several stimulus conditions: in isolation, with dynamic noise or a static texture distractors simultaneously present at fixation, in bidirectional 'transparent' motion stimuli, and in multisegmented kinematograms containing contrasting directions of motion. The lower visual field was found to be more sensitive to global motion in all conditions, except when a static dot texture was present in the visual field, when no hemifield effect was observed. In Experiment 4, observers viewed a texture 'patch' composed of numerous line elements in which they discriminated global orientation. No vertical hemifield effect was found, both with and without similar distractor stimuli at fixation, suggesting that the lower field advantage previously found was not due simply to enhanced global processing, regardless of the class of stimulus. Experiment 5 had observers covertly track a single, rapidly moving object that abruptly vanished, then spatially localise the vanishing point. Accuracy was found to be significantly higher in the upper visual field. The results suggest that the upper and lower visual fields may be functionally specialised for processing local and global motion, respectively. Finally, a case study is presented in which the performance of an adult albino (JK) is compared with age-matched normals. JK demonstrated a reversed asymmetry for global motion, suggesting that the quality of visual input in infancy might determine vertical hemifield effects for motion perception.

Chapter 1: A Brief History of Functional Asymmetry in the Brain

At the gross anatomical level, there appears to be a high level of bilateral symmetry in the human brain. Indeed, the cerebral hemispheres appear to be mirror images of each other. Accordingly, for many years each hemisphere was considered to contribute equally to the biological bases for behaviour (Finger, 1994). This view has now changed considerably. It is well over a century since Broca (1861) published the first paper, based on a case study, suggesting that the left hemisphere is functionally specialised for the production of spoken language[1]. Over the next century, neuropsychological studies provided considerable further evidence of functional asymmetry between the hemispheres in both the auditory and visual domains (see Ivry & Robertson, 1998 for a review).

The first evidence of functional differences in the hemispheres of healthy adults came to light when Kimura (1961) showed that the left hemisphere exhibits an advantage for processing auditory linguistic information. Similar findings of subtle differences in the processing of visual stimuli soon followed and are now commonly reported. The emerging pattern suggests that the left hemisphere preferentially processes high spatial frequencies, while the right hemisphere preferentially processes low spatial frequencies (see Ivry & Robertson, 1998 for a comprehensive review of these studies). There is now also evidence of anatomical differences between the cerebral hemispheres. For example, Geschwind and Levitsky (1968) found that the planum temporale, a region specialised for speech comprehension, is normally larger in the left hemisphere.

Thus, there is converging evidence that the processing of some aspects of both visual and auditory stimuli differ according to cerebral hemisphere. Less well known, however, are findings of both physiological and functional differences in the vertical dimension of the visual system.

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[1] The first report was actually made much earlier by Marc Dax, who presented a paper to a medical society meeting in Montpellier, France in 1836. However, he died the next year and his findings remained unpublished.

Nevertheless, evidence of functional differences between the upper and lower visual fields (henceforth: UVF and LVF)[2] actually predates Broca's (1861) work.

Aubert and Forster (1857) published the intial finding. They reported that stimuli presented at increasing eccentricities in the vertical hemifields are better resolved at greater eccentricities in the LVF than in the UVF. In the following eighty years, several papers reiterated this LVF acuity advantage (e.g., Landolt & Hummelsheim, 1904; Low, 1943; Wertheim, 1894). Reports of finer temporal resolution in the LVF also appeared (Hylkema, 1942; Phillips, 1933).

In a highly influential early study of the human retina, Østerberg (1935) found higher cell densities in the upper hemiretinae (which mediates LVF vision) than in the lower hemiretinae (mediating UVF vision). In consequence, most subsequent reports demonstrating a LVF advantage on a range of psychophysical tasks relied heavily on this finding for their primary explanatory variable. Noticeably absent was a consideration of the possibility of functional asymmetries emanating within brain regions. There are probably two reasons why this was the case. Firstly, experiments involving complex visual processing, subserved by cortical mechanisms, had yet to be undertaken. Secondly, there are no obvious brain structures akin to the cerebral hemispheres that might have accounted for the processing differences observed in the vertical dimension of the visual system.

In the mid 1970's, however, Breitmeyer and colleagues (Breitmeyer, Julesz, & Kropfl, 1975; Julesz, Breitmeyer, & Kropfl, 1976) observed processing differences between the vertical hemifields for stimuli defined by their stereo disparity, i.e., the degree to which the images differ when represented in each retina. Because the ability to perceive stereopsis is dependent on cortical mechanisms, processing differences between the

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[2] The LVF is defined as that region of space lying below the horizontal meridian, as determined by the point of gaze, or fixation. The UVF is that region of space lying above the horizontal meridian. Both hemifields extend vertically and laterally to the point where peripheral vision is no longer possible.

vertical hemifields could no longer be assumed to be due to asymmetries in sensory-level mechanisms. Furthermore, subsequent studies investigating high-level visual processing have shown that the magnitude of functional differences between the vertical hemifields is often significantly larger than between the horizontal hemifields (e.g., Christman & Niebauer, 1997; Fecteau, Enns, & Kingstone, 2000).

Anatomical differences that might account for Breitmeyer et al.'s (1976) finding came a decade later. Single cell recordings from monkeys ascertained that two functionally distinct regions of visual cortex, V3 and VP, represent only the LVF and UVF, respectively (Burkhalter, Fellemen, Newsome, & Van Essen, 1986; Burkhalter & Van Essen, 1986). Functional imaging data has confirmed that this is also the case in humans (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998), and evidence is now growing that cell populations within a number of other brain regions have pronounced receptive field biases toward the LVF [3].

An important observation, discussed in detail later, is that all of the cortical regions demonstrating a retinotopic bias toward the LVF are located within the brain's dorsal visual pathway, comprised of numerous subregions, most of which contain large populations of cells able to compute visual motion. Discriminations made in response to moving stimuli should, therefore, provide a highly suitable method by which to explore cortically mediated functional differences between the vertical hemifields. This view provided the theoretical background for this thesis.

The following chapters review the literature that have stimulated and guided my interest in the vertical hemifields, sourced from the fields of neurophysiology, experimental psychology, and neuropsychology. These begin with a brief overview of the primate visual system.

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[3] A cell's receptive field coincides with an area of the retina which, when stimulated by light, influences the firing of the cell. Receptive field biases within a brain region may result from greater numbers of cells coding for particular areas of the retina, or by the presence of cells coding for some regions but not others.

Chapter 2: A Brief Overview of the Primate Visual System

2.1 Two Visual Pathways

A great deal of evidence indicates that the primate visual system is characterised by a high degree of parallel processing. This is performed primarily by two anatomically and, arguably, functionally distinct pathways. Parallel processing can be observed as early as the retina, but is especially evident within the dorsal and ventral pathways in visual cortex. The function of the two neural pathways has been argued to equate with the two primary goals of the visual system. These are (i) to subserve object identification (ventral pathway), and (ii) to compute the spatiotemporal attributes of an image, necessary for both perception and the visual control of action (dorsal pathway; e.g., Milner & Goodale, 1992). In the past twenty years, this dichotomous approach has heavily influenced visual system theory, including, in the past decade or so, discussion of vertical hemifield effects.

In the retina, ensembles of photoreceptors respond to changes in light intensity. Fluctuations in light intensity across space and time are then transformed into patterns of neural activity. This neural activity is transported from the retina to the brain via the ganglion cells, which together make up the optic tract.

There are two principal types of ganglion cells. Parvo-cells, which comprise approximately 80% of the optic tract, are most densely packed in and around the fovea. These cells are physically smaller than magno-cells but, because they are present in larger numbers, have a greater sampling ability. Their optimal responses are to low and moderate temporal frequencies (approximately 1-20 Hz) over a wide range of spatial frequencies (Derrington & Lennie, 1984). Parvo-cells also exhibit narrowly tuned spectral sensitivity mediated by opponent colour mechanisms, in which the centre and surround of the cell's receptive field show peak sensitivity at differing wavelengths. The output of the cell (excitation or inhibition) is therefore a function of the two wavelengths and the differences in light intensity between neighbouring regions of the visual field.

Magno-cells are most densely packed in the peripheral retina. They comprise approximately 10% of the optic tract, and are distinguished anatomically by their relatively thicker axons, which allow neural impulses to be conducted at higher temporal frequencies (5-40 Hz). However, their optimal sensitivity to low spatial frequencies, coupled with relatively large receptive fields, produce much poorer spatial resolution in comparison with parvo-cells. Spectral stimulation is broadband, with peak sensitivities of the centre and surround of the receptive field being identical. This suggests that magno-cells have little or no role in the computation of colour (Derrington & Lennie, 1984).

Approximately 10% of ganglion cells project directly to the superior colliculus. However, the majority project to the dorsal sections of the lateral geniculate nuclei (LGN) in the thalamus. Before reaching the LGN, the optic nerves partially cross, or decussate, at the optic chiasm. As a result, the axons of ganglion cells originating in the left halves of each retina run to the left LGN, while the right LGN receives inputs from the right half of each retina. The receptive field topography of LGN cells is highly similar to that of the retina and, for this reason, the LGN has previously been viewed as simply a relay station between the retina and primary visual cortex, or V1. However, it is now known that there are large numbers of projections running backward from V1 to the LGN which, when inactivated, reduces the overall output of the LGN (Felleman & Van Essen, 1991). Thus, similar to the cross talk found between regions of visual cortex, a feature-linked feedback-feedforward loop appears to exist between the LGN and cortex. This reciprocal connectivity is hypothesised to produce signal gain (Sillitoe, Jones, Gerstein, & West, 1994).

The bulk of LGN axons terminate in layer IVc of area V1, or the primary visual cortex. Here, the division between magno- and parvo-cells is maintained, with sublayers IVcα and IVcβ receiving magno and parvo inputs, respectively. V1 cells essentially behave as multidimensional filters, responding to to a range of stimulus features including orientation, direction, binocular disparity, colour, length, spatial frequency, and luminance (Van Essen, Anderson, & Felleman, 1992).

Beyond V1 neurons become generally more refined in their response profiles, displaying selectivity for fewer stimulus dimensions. In addition, receptive field sizes tend to be progressively larger as the synaptic distance from V1 increases. There is also considerable evidence that beyond V1, within 'extrastriate' cortex, the visual system maintains the segregation into two anatomically and, arguably, functionally distinct pathways (e.g., Felleman & Van Essen, 1991; Goodale & Milner, 1992; Ungerleider & Mishkin, 1982).

The ventral pathway projects to occipitotemporal and inferotemporal regions. Neurons within these regions appear to preferentially process 'within-object' attributes, and highly distinct patterns of activation can be observed during the memorising and recognising of specific visual patterns (Tanaka, 1993; 1996). Thus the ventral pathway appears to be specialised for object identification, without apparent need for encoding information regarding spatial location. The ventral pathway has been conceptualised by various authors as the 'what' (Ungerleider & Mishkin, 1982) 'colour-form' (Van Essen & Maunsell, 1983), or 'perceptual' pathway (Goodale & Milner, 1992).

The 'dorsal' pathway projects to areas V3, V3a, the motion-specific middle temporal area (MT/V5)[4] and onward to posterior parietal regions, which are increasingly being identified as providing somatosensory inputs for the purposes of motor control (Milner & Goodale, 1995). Neurons within dorsal regions appear to play a crucial role in spatially localising stimuli. Hence, the dorsal pathway has been variously conceptualised as the 'where' (Ungerleider & Mishkin, 1982), 'motion' (Van Essen & Maunsell, 1983) and 'action' pathway

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[4] The middle temporal area is associated with motion processing only in New World monkeys (Snowden, 1994). In both Old World monkeys and in humans, a homologue is more usually located within the lateral and ventral aspects of the inferior temporal sulcus (Beckers & Zeki, 1995). In this thesis, I maintain the convention of using the term 'MT' when referring to the monkey brain, regardless of species. However, when referring specifically to the human homologue, the term V5 is used.

(Goodale & Goodale, 1992). Figure 1 illustrates the routes taken by the dorsal and ventral pathways through visual cortex.

Because of the importance of cortical visual mechanisms to the experiments reported in this thesis, the following chapters review the anatomical and functional characteristics of several ventral and dorsal subregions in greater detail, with particular attention paid to evidence for physiological and functional biases toward the vertical hemifields.

Although Livingstone and Hubel (1988) postulate that magno and parvo cells map directly onto the dorsal and ventral pathways, respectively, there is growing evidence that such direct mapping does not occur. For example, inactivation of either magno and parvo cells in the LGN is equally effective at blocking activity in ventral region V4 (Ferrara, Nealey, & Maunsell, 1992). Furthermore, layer 4B of V1, from where the bulk of projections to the dorsal pathway emanate, is now known to accommodate converging inputs from both magno and parvo sources (Sawatari & Calloway, 1996). However, while it appears that inputs to the ventral pathway might comprise equal contribution from parvo and magno cells, the parvo contribution to the dorsal pathway does appear to be negligible. Inactivation of magno cell layers within the LGN causes a significantly greater reduction in MT activity than does inactivation of the parvo layers (Maunsell, Nealey, & DePriest, 1990). Figure 1 illustrates the approximate mapping of dorsal pathway regions in the primate brain.

2.2. Previc's Synopsis

In a highly influential review article, Previc (1990) postulated that the ventral and dorsal pathways in many primate species, including humans, are functionally linked to processing in the UVF and LVF, respectively. Since this initial paper (1990; and expanded upon in Previc, 1998) findings of vertical hemifield effects have invariably been discussed in relation to Previc's synopsis. A brief description of his ideas is therefore warranted here.

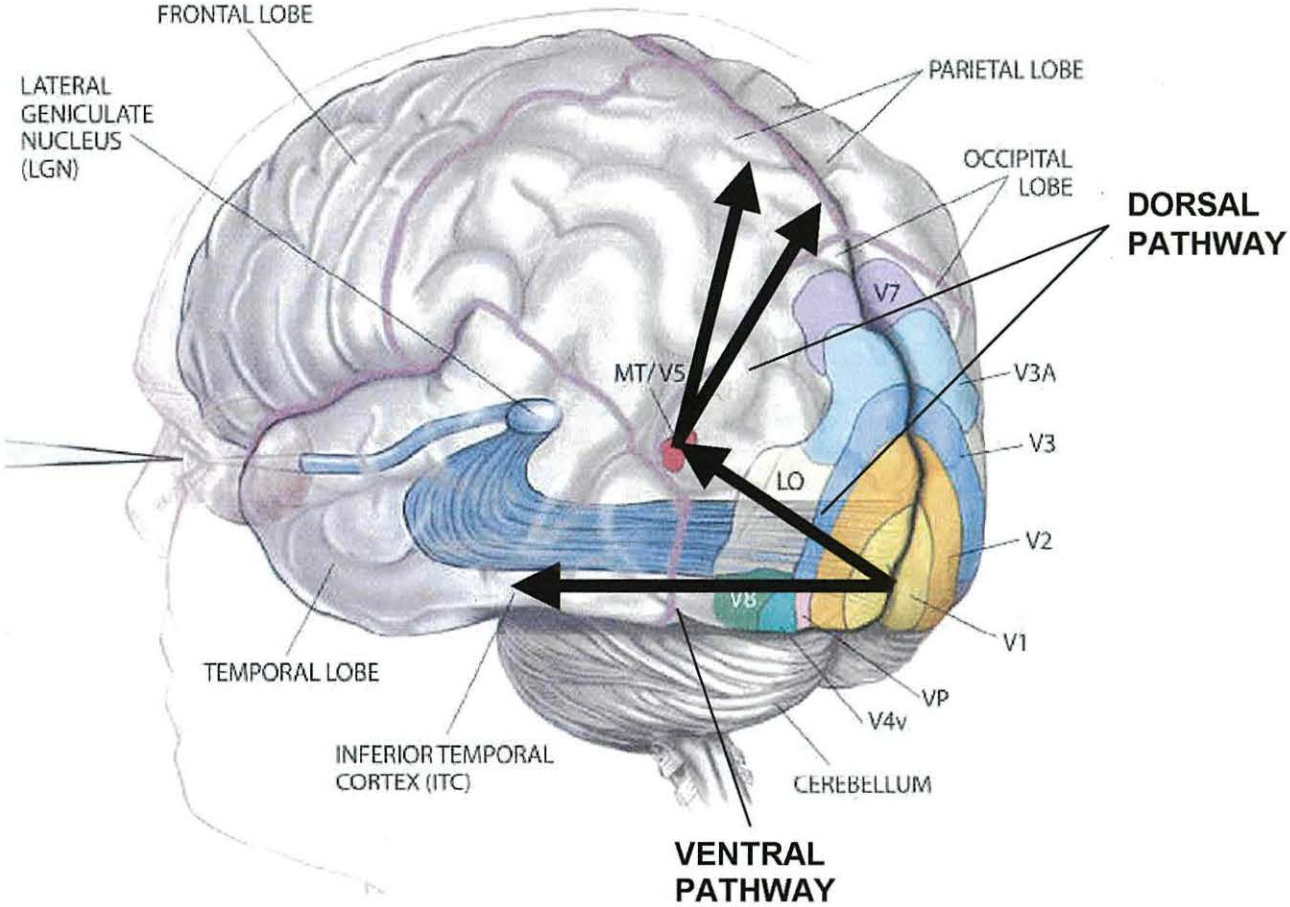

Figure 1. Routes taken by the dorsal and ventral pathways through visual cortex within the left hemisphere. The arrangement within the right hemisphere is a mirror image. After passing through MT/V5, the dorsal pathway proceeds independently to a number of regions within the parietal lobe. In contrast, the ventral pathway is considered to be unitary from V1 to inferior temporal cortex. Adapted from Scientific American, November 1999, p.72.

He notes that the transition from a largely arboreal to a terrestrial habitat, and a mainly bipedal posture, has resulted in the arms and hands being used primarily for manipulation, rather than postural support (e.g., Napier, 1980; Temerin & Cant, 1993). Thus, when standing on a horizontal surface and fixating on a target object, the head is dorsal to the lower limbs. As a result, reaching and grasping movements are more likely to take place below fixation, i.e., in the LVF, and within the region of space immediately forward and lateral to the body (peripersonal space). Because the dorsal pathway provides the bulk of visual inputs to parietal regions with reciprocal connections to premotor cortex (e.g., Milner & Goodale, 1992), Previc postulates that dorsal visual mechanisms will similarly be biased toward the LVF.

However, he also identifies perceptual costs associated with the evolutionary advances. Fixating on a target object while making prehensile movements towards it produces a diplopic image of the upper limbs (Previc, 1990). Similarly, fixating distally during forward locomotion produces the highest optical flow rates in the LVF, effectively blurring the ground plane image (Lee, 1980; Young & Oman, 1974). Under both conditions, it becomes difficult to resolve the finer featural attributes of LVF stimuli. In order to counteract these optical degradations, Previc argues that visual mechanisms operating in the LVF preferentially process the global features of both static and moving stimuli. Relevant to the present thesis, Previc makes the specific prediction that the LVF will prove to be more sensitive to global motion than the UVF.

Conversely, he notes that for bipedal primates, objects occurring in the UVF tend, due to the slant of the ground plane toward the horizon, to be at greater distance from the observer (within ‘extrapersonal’ space) than objects found in the LVF (Gibson, 1961; Cutting & Vishton, 1995). Furthermore, objects above fixation more often present, compared to the LVF, against a less cluttered background (Gibson, 1961; Lee, 1980). Thus, the UVF is suggested to provide the more suitable conditions in which to rapidly and accurately identify objects, before they are permitted to enter peripersonal space. Hence, Previc predicts that visual mechanisms within the ventral pathway will prove to be biased toward the UVF.

Chapter 3: Physiological Evidence for Functional Differences Based on Vertical Hemifield

3.1 Retina

Within the human eye, the density of both cones and rods is normally higher in the upper hemiretinae than the lower hemiretinae. This arrangement is especially evident in photoreceptors receiving their inputs from regions of the visual field beyond 6^{O} eccentricity (Østerberg, 1935; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Curcio, Sloan, Kalina, & Hendrickson, 1990). Ganglion cells are also more densely packed within the upper than the lower hemiretinae. This is the case regardless of eccentricity (Curcio & Allen, 1990; Stone & Johnson, 1981). Electroretinographic data mirror these findings. Mean response amplitudes to contrast reversal stimuli are reported to be approximately 20% higher in the upper hemiretinae (Marx & Zrenner, 1989).

3.2 Thalamus

A tentative finding of a retinotopic bias toward the LVF in the dorsal region of the LGN was reported almost twenty years ago by Connelly and Van Essen (1984), following a re-analysis of earlier data derived from the macaque by Malpeli and Baker (1975). Their suggestion has recently been confirmed. High-resolution (4 tesla) fMRI scans of human thalamus demonstrate that a larger proportion of the LGN represents the LVF than the UVF. Although data were collected from only five individuals whose activation size and shape varied, the same vertical hemifield pattern was nevertheless observed bilaterally in all cases (Chen, Zhu, Thulborn, & Ugurbil, 1999).

None of these studies was able to ascertain whether magno and parvo cell densities differ according to vertical hemifield representation. Similarly, it has yet to be determined whether magno cells project asymmetrically to dorsal V1, which represents the LVF, nor whether the massive feedback connections from V1 to the LGN (Felleman & Van Essen, 1991) also demonstrate a LVF bias. Thus, functional specialisation within each hemifield's representation within the LGN cannot yet be confirmed.

Although the sensory stages of the visual system appear to be physiologically equipped to preferentially process stimuli within the LVF, this does not necessarily imply that an initial locus for functional specialisation in the vertical hemifields has been identified. However, Williams (1990) has argued that evidence of functional specialisation within both the retina and LGN is essential if Previc's (1990; 1998) general theory is to survive. In its absence, he claims, such a major functional cortical division remains computationally, though not biologically feasible.

3.3 Superior Colliculus

The tendency to explore distal and upper space with saccadic eye movements is a conspicuous feature of the primate visual system, though it is used far more by humans than by other primates (Dursteler & von der Heydt, 1992). In contrast, the vast majority of nonprimate species need to move their head in order to fixate (Rizzolatti, Gentilucci, & Matelli, 1985). Thus, the critical role of the primate superior colliculus in scanning and saccadic search operations, without the need for head movements (Bender & Butter, 1987), suggests that a processing bias toward the UVF might be the case.

In many nonprimate mammals greater numbers of collicular cells are found to have receptive fields with a representational bias toward the UVF (Drager & Hubel, 1976; Sprague, Berlucchi, & Rizzolatti, 1973) and collicular lesions in rodents result in obvious neglect of upper space (Foreman, 1983; Marshall, 1978; Sprague & Meikle, 1965; Sprague et al., 1973). However, there appears to be no corresponding vertical bias in the primate colliculus, although data have only been obtained from anaesthetised monkeys. The primate colliculus does receive abundant direct inputs from the lateral intraparietal area (Andersen, Brotchie, & Mazzoni, 1992), which, as is discussed later, is involved in the preparation of saccades and has a strong receptive field bias toward the UVF.

3.4 Area V1

In the classical anatomical view of primate V1, the base of the calcerine sulcus is considered to correspond directly with the horizontal meridian. While the LVF is wholly represented in the upper bank of the fissure the UVF is deemed to be wholly, and equally, represented in the lower bank (e.g., Stensaas, Eddington, & Dobell, 1974). In the macaque, the surface area of the upper bank tends to be slightly larger than that of the lower bank, suggesting a greater number of cells coding for lower visual space (Tootell, Switkes, Silverman, & Hamilton, 1988; Van Essen, Newsome, & Maunsell, 1984). Humans show generally show greater diversity than macaques in the size and shape of the occipital lobe, and a similar anatomical asymmetry has yet to be reliably established (Rademacher, Caviness, Steinmetz, & Galaburda, 1993).

Nevertheless, several studies indicate the possibility of functional asymmetry between the upper and lower banks of the calcerine fissure. For example, two studies, one employing fMRI scans (Sereno, Dale, Reppas, Kwong, Belliveau, Brady, Rosen, & Tootell, 1995) and the other MRI scans in conjunction with magnetoencelography (MEG; Aine, Supek, George, Ranken, Lewine, Sanders, Best, Tiee, Flynn, & Wood, 1996), have documented instances in which stimuli presented to the LVF produced activation within the lower bank of the calcerine fissure.

Furthermore, MEG amplitudes produced in response to checkerboard stimuli presented at eccentricities as small as 0-6^{O} in either the UVF or LVF, are reported to be twice as strong in the upper than the lower bank of the calcerine sulcus. When the same stimuli were presented simultaneously to both vertical hemifields, higher amplitudes from the upper bank were found in only six of the ten subjects (Portin, Vanni, Virsu, & Hari, 1999). However, response amplitudes from these six individuals were similar in magnitude to those elicited by a single stimulus. This finding suggests there may be considerable functional, as well as anatomical diversity, within this region of visual cortex in humans.

As is the case with the LGN, it has yet to be established whether any anatomical or functional biases toward the LVF within V1 are associated with a preponderance of magnocellular inputs. Current evidence demonstrates that in monkey all V1 afferents, with the exception of those terminating in V2, project to the LVF-biased dorsal extrastriate regions V3 and MT. Because these projections appear to originate exclusively within layer 4B (Maunsell & Newsome, 1987), Previc (1990) has suggested that this cortical layer may be the point of functional divergence for the vertical hemifields.

3.5 Area V3

Although the majority of dorsal extrastriate areas show some degree of retinotopic bias toward the LVF (Maunsell & Newsome, 1987), V3 is unique in being the sole cortical region known to represent the LVF only. This region is located in the fundus of the lunate sulcus immediately anterior to V2 (Van Essen, Newsome, Maunsell, & Bixby, 1986). Initially, V3 was considered to be the dorsal section of a single functionally distinct region, representing the entire visual field. However, evidence is now clear that V3 and VP (ventral posterior) are functionally distinct regions representing the LVF and UVF respectively (Burkhalter et al., 1986; Felleman & Van Essen, 1987). There is an increasing recognition of the importance of V3 for visual motion processing (Braddick et al., 2001; Smith et al., 1998). For this reason, V3 will be discussed here in some detail.

There are considerable anatomical differences between macaque and human V3. Whereas this region is highly compressed in the horizontal dimension on the macaque cortical surface, human V3 is far larger, occupying as much cortex as the ventral or dorsal banks of V1 and V2 (Tootell, Mendola, Hadjikhani, Ledden, Liu, Reppas, Sereno, & Dale, 1997).

In the macaque, V3 has strongly myelinated reciprocal connections with the dorsal banks of both V1 and V2 and, in common with V2 V3 is completely silenced by inactivation of V1 (Girard, Salier, & Bullier, 1991a). There is a strong forward projection from V3 to MT (Maunsell & Newsome, 1987) and projections are also evident to posterior parietal areas V6 and V6a. These projections are limited to the extreme periphery of the LVF (Shipp, Blanton, & Zeki, 1998). In addition, there is an exclusively forward projection to V4 (Felleman & Van Essen, 1984).

Strong selectivity for multiple stimulus attributes suggests that, in the macaque, V3 neurons are not simply feature detectors. Distinct tuning profiles have been established for disparity, orientation, temporal frequency, directionality, spatial frequency and colour. However, no systematic relationship has been found between any of these stimulus features, and so processing of distinct stimulus attributes such as, for example, directionality and colour, do not appear to be segregated (Gegenfurtner, Kiper, & Levitt, 1997).

Spatial tuning within macaque V3 is strongly biased toward lower frequencies. 80% of cells show peak response at frequencies less than 1c/deg, with a median of 0.4c/deg. Recordings have yet to be made from any cells that respond to frequencies greater than 4c/deg. Temporal tuning, on the other hand, is unusually broad, spanning 4.4 octaves, with a median peak of 6 Hz (Gegenfurtner et al., 1997).

The percentage of cells exhibiting directional selectivity appears to vary acording to whether the monkeys under study are active or anaesthetised. Initial reports using active monkeys found only 12-15% of cells to be directionally selective (Baizer, 1982; Van Essen & Zeki, 1978). However, two more recent estimates using monkeys who were both anaesthetised and paralysed (Felleman & Van Essen, 1987; Gegenfurtner et al., 1997) estimated directional selectivity to be a feature of either 61% or 57% of neurons, respectively. A striking finding is that none of these cells are found in layer 4, which receives the bulk of inputs from V1. It has therefore been suggested (Felleman & Van Essen, 1987) that directionality may not be inherited from V1, despite signals originating in V1's motion-rich layer 4B.

Large numbers of directionally tuned cells in macaque V3 show their peak response to patterned rather than component motion (Gegenfurtner et al, 1997). This suggests that they have facilitatory receptive fields, in which the surround response reinforces the centre response in a nonlinear fashion, when both centre and surround receive broadly similar inputs. This receptive field mechanism is hypothesised to underlie global motion processing (Born, 2000; Born & Tootell, 1992).

Strong correlations between patterned motion and cell responses are found in 40% of V3 cells, a similar figure to that of MT (Gegenfurtner et al., 1997).

Human fMRI data confirm V3's preference for global motion. Coherent RDKs activate human V3 to the same extent as the motion-specific cortical area V5 (Braddick et al., 2001; Smith et al., 1998). However, the movement of a single element appears to be largely ignored by V3 neurons, producing little activation (Smith et al., 1998).

Thus, in a conventional hierarchical view of visual cortex, V3 appears to be the earliest site at which global directions of motion are computed in humans, suggesting that V3 plays an important part in determining psychophysical performance. Indeed, in Zihl, Von Cramon and Mai's (1983) seminal case study of akinetopsia following bilateral lesions to the posterior temporal cortex (including area V5), there remained some phenomenal sensitivity to low velocity motion. PET images from the same patient a decade later ascertained that V3 was indeed the most likely source of this residual motion processing (Shipp, DeJong, Zihl, Frackowiak, & Zeki, 1994).

As might be expected of a dorsal pathway region, early investigations revealed no evidence for colour selectivity within V3 (Baizer, 1982; Van Essen & Zeki, 1978; Zeki, 1983). However, this property has now been well established, though the numbers of cells displaying chromatic sensitivity appears to rely heavily on luminance contrast. At high contrasts sensitivity to colour was poor with only 21-26% demonstrating selectivity (Felleman & Van Essen, 1987; Gegenfurtner et al, 1997), while at low luminance contrast 54% of cells demonstrate colour selectivity (Gegenfurtner et al., 1997). This finding is in line with V3's generally strong sensitivity for stimuli defined by low luminance contrasts (Gegenfurtner et al, 1997). The origin of the colour signals is unclear. Only feedforward connectivity with V4 has been established (Felleman & Van Essen, 1984), so they most likely originate in the small numbers of parvo cells found in layer 4B of V1 (Sawatari & Calloway, 1996).

3.6 Area VP

VP is located ventrally to V3 within the lunate sulcus, and represents the UVF only (Burkhalter & Van Essen, 1986; Burkhalter et al., 1986). As is the case with V3, human VP covers a considerably larger area on the cortical sheet than its counterpart in the macaque (Tootell et al., 1997). According to one report, VP and V3 are not contiguous in all cases, and may be separated by as much as 10mm in humans (Shipp, Watson, Frackowiak, & Zeki, 1995). Furthermore, direct connectivity between the two regions has yet to be established (Felleman & Van Essen, 1987), adding to the view that V3 and VP do not comprise a single, functionally homologous region representing the entire visual field, as was first thought.

There are considerable functional differences between human and macaque VP that cast doubt on their homology. Consequently, in both monkey and human, VP has yet to be consistently allocated a place within either the dorsal or ventral pathways. In humans, fMRI data show VP to be highly motion sensitive, perhaps more so than V3, according to one report (Tootell, Reppas, Dale, Look, Sereno, Malach, Brady, & Rosen, 1995). Like V3, VP also demonstrates much stronger activation to global than to single element motion (Smith et al, 1998). Thus, neuroimaging work strongly suggests that human VP might be a dorsal pathway region.

The picture derived from macaques is quite different. Here, single cell data show VP to have only a small minority of directionally selective cells, along with generally low-levels of myelination (Burkhalter & Van Essen, 1986; Van Essen et al., 1986). Unlike other dorsal extrastriate areas demonstrating a high degree of motion selectivity, VP receives no direct inputs from V1, with the ventral bank of V2 providing all known inputs (Burkhalter et al., 1986; Girard et al., 1991a; Van Essen et al., 1986). Furthermore, a similar percentage of cells display colour selectivity as are found in V4, and their density does not decrease with eccentricity (Burkhalter & Van Essen, 1986). Thus, in contrast with what has been gleaned from humans, these findings strongly suggest that, in the macaque, VP is a component region of the ventral pathway. This view is supported by data showing the bulk of VP's projections to terminate in V4 (Burkhalter & Van Essen, 1983).

3.7 Area V4

Primate area V4 (occasionally referred to as the V4 complex) occupies an intermediary stage in the ventral pathway, located mainly in the dorsocaudal region of the prelunate sulcus, and extending onto the adjoining banks of the lunate and superior temporal sulci. In monkey, direct inputs appear to originate within V2, V3 and VP, and posterior inferotemporal cortex is its main projection zone (Tanaka, 1993; 1996). Small projections are also made to dorsal regions, MT and MST (Ferrera, Rudolph, & Maunsell, 1994). Inputs from V2 appear to originate in both the magno and parvo layers of the LGN, as blocking activity in either type of cell layer is equally effective in reducing activity within V4 (Ferrera et al., 1992).

V4 cells are highly selective for both high spatial frequencies and stimulus orientation (Tanaka, 1993; 1996) and, although they do not simply respond to any particular spectral wavelength, they are responsive to relative changes in wavelength within neighbouring regions of space (Zeki, 1983). It is uncertain to what degree inputs from V3 and VP comprise signals from colour selective cells (Burkhalter & Van Essen, 1983; Felleman & Van Essen, 1984; 1987). Nevertheless, known cell characteristics almost certainly suggest that V4 plays a prominent role in both colour and object perception (Tanaka, 1993; 1996).

The extent to which V4 represents the vertical extent of the visual field remains unclear. In macaque, single cell recordings from anaesthetised and immobilised animals have identified receptive fields that encompass each vertical hemifield (Hikosaka, 1998). However, the putative human homologue of V4, identified by neuroimaging, appears to represent the contralateral UVF only and was initially labelled as V4v (ventral). A corresponding superiorly located region, V4d (dorsal), is widely assumed to exist but has yet to be adequately identified (Sereno et al., 1995; Tootell, Dale, Sereno, & Malach, 1996; Tootell et al., 1997; though see McKeefry & Zeki, 1997, for possible LVF representations in the vicinity of V4v).

3.8 Inferotemporal Cortex

The posterior inferotemporal cortex occupies a large region between the anterior tip of the posterior middle temporal sulcus and the ascending limb of the inferior occipital sulcus, and dorso-ventrally between the lip of the fundus of the superior temporal sulcus and the lip of the fundus of the occipitotemporal sulcus (Van Essen, Felleman, De Yoe, Olivarria, & Kneirim, 1990; Hikosaka, 1998). Neurons within this region are strongly associated with pattern discrimination, and will often discharge only to elaborate geometrical shapes (Tanaka, 1993; 1996), including primate faces (Perrett, Smith, Potter, Mistlin, Head, Milner, & Jeeves, 1985). Single-unit recordings suggest that the principal projection area, the anterior inferotemporal cortex, is crucial to the memorisation of visual patterns (Tanaka, 1993; 1996) considered due, in part, to their sustained discharges, which can last up to several hundred milliseconds (Gross, Bender, & Gernstein, 1979). fMRI scans have shown that the entire occipito-inferotemporal region of cortex activates in a unitary fashion when visual memory is accessed (Goldenberg, Podreka, Steiner, Willmes, Suess & Deecke, 1989) suggesting that the ventral pathway comprises a functionally unitary system subserving object recognition.

Although central vision is most strongly represented in macaque posterior inferotemporal cortex, Hikosaka (1998) has ascertained that the distribution of cells coding for the upper and lower regions of space differs according to both subregion and hemisphere. In the ventral bank of the superior temporal sulcus, receptive fields centred within the UVF and LVF are intermingled, resulting in the lack of a discernible horizontal meridian. However, in the right hemisphere only, there is a receptive field bias toward the LVF. In the lateral convexity of the gyrus within the right hemisphere, cells with receptive fields centred in the LVF lie between two adjacent areas representing the UVF and, again a horizontal meridian cannot be ascertained. In contrast, in the left hemisphere, where a horizontal meridian can be identified, there is a marked bias in receptive fields toward the UVF.

The reasons for these vertical anisotropies remain unclear as receptive field sizes are similar within each subregion and the neural discharges of cells representing each vertical hemifield do not seem to differ. However, conservative consideration appears warranted, as data was collected from only three monkeys.

In anterior inferotemporal cortex, receptive field sizes are especially large, commonly more than 100^0 in diameter. They encompass the UVF and LVF without apparent bias (Hikosaka, 1998).

3.9 MT/V5

In both macaques and humans, MT/V5 is sited in the occipital lobe, posterior to the junction of the inferior temporal and lateral occipital sulci (Watson, Myers, Frackowiak, Hajnal, Woods, Mazziotta, Shipp, & Zeki, 1993). In both macaque and rhesus monkeys a much larger number of MT cells have receptive fields that encompass the LVF than the UVF (Gattas & Gross, 1981; Maunsell & Van Essen, 1987).

In the macaque, incoming signals from other dorsal regions are received, and reciprocated, from layer 4B of V1, V2 and V3 (Maunsell & Newsome, 1987). Projections are also received, and reciprocated, from V4 (Ferrera et al., 1994). Reciprocal connectivity is also the case with areas dorsal areas 7a, 7b, V6, V6a and MST (Maunsell & Newsome, 1987). Inputs from V1, V3 and V4 appear to be largely dispensible as ablation or reversible inactivation of V1 (which completely silences V3, Girard et al., 1991a; and V4, Girard, Salin, & Bullier, 1991b) silences only 20% of MT cells (Bullier & Girard, 1988; Rodman, Gross, & Albright, 1989). In contrast, ablation of both V1 and superior colliculus totally silences MT (Rodman, Gross, & Albright, 1990).

Over 90% of MT neurons are direction selective (Maunsell & Van Essen, 1983a) with psychometric and single-cell neurometric functions being statistically indistinguishable (Britten, Shadlen, Newsome, & Movshon, 1992). There is a growing collection of human neuroimaging studies suggesting that V5 is the only brain region to process all forms of visual motion. Indeed, stimuli as diverse as apparent motion (e.g., Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998), incoherent (e.g., McKeefry, Watson, Frackowiak, Fong, & Zeki, 1997) and coherent global motion (e.g., Braddick et al., 2001), hallucinatory (e.g., ffytche, Howard, Brammer, David, Woodruff, & Williams, 1998), illusory (e.g., Zeki, Watson,

& Frackowiak, 1993) and imaginary motion (e.g., Goebel et al., 1998), linear and rotational transformation (e.g., Barnes, Howard, Senior, Brammer, Bullmore, Simmons, Woodruff, & David, 2000), mental rotation (e.g., Alivisatos & Petros, 1997) as well as motion after-effects (e.g. Tootell et al., 1995) have all been observed to activate this region.

Although the majority of MT cells show selectivity for centrifugal motion (Maunsell & Van Essen, 1983a), this preference manifests strongly only beyond 12^0 eccentricity. Closer to the fovea, a centripetal bias becomes evident (Albright, 1984). Moreover, recent fMRI and evoked potential data from both normals and patients with callosal damage indicates that the V5 regions in each hemisphere communicate with each other differently according to whether centripetal or centrifugal motion signals are being transmitted. Centripetal motion signals appear to be transported via a direct callosal pathway, while centrifugal signals are transported via a yet to be determined, but most likely subcortical, route. Thus, despite the relative paucity of centripetally tuned cells within MT, motion toward the central region of the visual field is computed more rapidly than centrifugal motion signals (ffytche, Howseman, Edwards, Sandeman, & Zeki, 2000).

3.10 MST

A neighbouring (sometimes referred to as a 'satellite') region of MT, MST (medial superior temporal) has a receptive field topography that is also strongly biased toward the LVF (Maunsell & Newsome, 1987). Although a human homologue has yet to be adequately established for this area, De Jong, Shipp, Skidmore, Frackowiak, and Zeki (1994) have made a tentative identification.

MST appears to be highly selective for processing optic flow (centrifugal motion) during forward locomotion. In the dorsal subsection of MST, cells are narrowly tuned for single features of optic flow, such as expansion and rotation (Lagae, Maes, Raiguel, Xiao, & Orban, 1994), with twice as many cells selective for centrifugal than centripetal motion (Geesaman & Andersen, 1996). In addition, many cells show a preference for the speed gradients that are characteristic of optic flow motion patterns (Duffy & Wurtz, 1997).

3.11 Area 7a

Along with MT, 7a is one of the most widely studied areas of the dorsal system. Visual inputs are thought to originate primarily within MT and MST. 7a shares their strong representational bias toward the LVF (Maunsell & Van Essen, 1987). Neurons in this area are predominantly, though not exclusively visual, being sensitive to a variety of other inputs including somatosensory, vestibular and proprioceptive signals (Steinmetz, Motter, Duffy, & Mountcastle, 1987).

The majority of the visually responsive cells are direction-selective, displaying both a retinotopic distribution and directional tuning bandwidths similar to those found in MT. Approximately half of cells are tuned to centripetal motion, with only 14% showing a centrifugal preference (Steinmetz et al., 1987).

Prominent recipient regions of 7a are area 7b, the posterior cingulate gyrus (area 23), which is involved in sensorimotor hand control, and superior region 8 of the frontal eye field. Projections, representing the LVF periphery only, are also sent to V6a (Shipp et al., 1998).

3.12 Area 7b

Area 7b, located on the intraparietal gyrus, contains two distinct cell populations. One group of cells fire in response to stationary objects less than 10 cm from the body, and the other group to moving targets within one metre of the body that are looming toward the centre of the receptive field. Both these populations show a retinotopic bias toward the LVF (Leinonen & Nyman, 1979; Leinonen, Hyvarinen, Nyman, & Linnankoski, 1979). Accordingly, lesions in this area lead to neglect of peripersonal space in monkeys (Rizzolatti et al., 1985). However, activation in response to visual stimuli beyond peripersonal space is observed when a stick is used to manipulate objects (Iriki, Tanaka, & Iwamura, 1996). This ability to modify body schema suggests that some 7b neurons are not restricted to coding space in corpracentric (body-centred) coordinates, but are able to transfer to motor-space coordinates during tool use (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997).

Area 7b projects unidirectionally to area 6 of the inferior premotor cortex (Graziano, Yap, & Gross, 1994). Here, subregions F4 and F5 process proximal arm movements (Fogassi, Gallese, Fadiga, Gentilucci, Luppino, Matelli, & Rizzolatti, 1996) and grasping movements (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), respectively. Lesions to both areas show a bimodal (tactile and visual) neglect of space immediately adjacent to the body, along with impaired contralateral reaching movements (Rizzolatti, Matelli, & Pavesi, 1983), while electrostimulation produces smooth eye movements with a pronounced LVF bias (Wagman, 1964).

3.13 Lateral Intraparietal Area

In monkey, the principal area computing the retinotopically-based coordinates used for shifting both spatial attention and intended eye position is the lateral intraparietal area (LIP; Snyder, Batista, & Andersen, 1997). In terms of visual field representation, LIP is an anomalous dorsal pathway region. Despite having reciprocal connections with both V3 and MT (Blatt, Andersen, & Stoner, 1990) single cell recordings have demonstrated a strong representational bias toward the UVF (Li & Andersen, 1994; Thier & Andersen, 1996). Reversible inactivation of LIP, via muscimol injection, produces hypometric upward-directed saccades, with little effect on downward saccades (Li, Mazzoni, & Andersen, 1999). A role in visual memory has also been ascertained (Andersen et al., 1992; Li et al., 1999).

3.14 Area V6

Macaque V6 is located on the anterior bank of the medial parieto-occipital sulcus. The parieto-ocipital sulcus (area POS) in humans is suggested to be a somewhat smaller homologue (Vanni, Tanskanen, Seppä, Uutela, & Hari, 2001). All V6 cells are visually responsive and demonstrate similar preferences to V3 cells in terms of directionality, speed, and orientation tuning (Galletti, Fattori, Battaglini, Shipp, & Zeki, 1996).

Although the entire visual field is represented within macaque V6, a number of factors result in a much more detailed representation of the peripheral LVF. Firstly, the central 20^{o} of the visual field is not magnified relative to the periphery. Secondly, the direct projections received from V2 originate solely from the dorsal bank (i.e., LVF), and are confined to eccentricities greater than 30^{o} (Galletti, Fattori, Gamberini, & Kutz, 1999a). Evidence that such direct connectivity might also exist in humans comes from a study of MEG-derived responses from the postulated human homologue of V6. Response latencies here were simultaneous with those recorded in V1 (Vanni et al., 2001). Thirdly, inputs from V3 lack the upper 10^{o} of the LVF (Galletti et al., 1999a). However, human MEG responses from the central 20^{o} of the visual field do not display a LVF bias (Portin et al., 1999).

Macaque V6 has reciprocal connectivity with peripheral represenions in MT (Galletti et al., 1996), MST (Shipp et al., 1998) and with area 7a (Galletti et al., 1996). Connections are also made with superior region 8 of the frontal eye field (Shipp et al., 1998), which, as mentioned earlier, shows a retinotopic bias toward the LVF (Bender, 1980). Other recipient regions include area 6 of premotor cortex (Matelli & Luppino, 1992), especially area F7, which is involved in the computation of arm movements within a shoulder-centred coordinate system (Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991).

3.15 Area V6a

The vast majority of the inputs to V6a originate in V6. Other inputs originate in V3, MT, MST and 7a, though none are thought to be pervasive. In contrast to V6, direct projections from V2 are absent. Only 61% of V6a cells are visually responsive. A significantly larger number of cells have receptive fields that include the LVF, and these tend to have smaller receptive fields than those representing the UVF (Galletti, Fattori, Kutz, & Gamberini, 1999b).

Tuning preferences are similar to those of V3 and V6 and there is a preference for global directions of motion. The percentage of cells selective for orientation and direction does not differ according to vertical hemifield or eccentricity, although there is a preference for much slower speeds within the central 20^{O} of the visual field, suggestive of a role in the visual support of prehensile movements. Nonvisually responsive cells appear to receive the bulk of their inputs from area F7 of the premotor cortex (Battaglia-Mayer, Ferraina, Genovesio, Marconi, Squatrito, Molinari, Lacquaniti, & Caminiti, 2001).

In terms of cell distributions, V6a is peculiar in two respects. Firstly, there is no apparent pattern to the distribution of visual and nonvisual cells. Both types of cell can be observed to occur either within groups or in isolation, without obvious rule. This lack of arrangement is unique in primate cortex. Secondly, there is no discernible visual topography. 'Receptive-field jumping' is so disorderly that neighbouring cells not only exhibit vastly differing sizes of receptive field, but also code for central, peripheral, ipsi-, or contralateral regions, including mixed UVF and LVF representations (Galletti et al., 1999b).

Because large areas of visual field have multiple representations in V6a, it has been suggested that subregions may act as functionally separate local networks able to compute the 'real-position' coordinates of target objects. In addition, approximately 10% of visual neurons have receptive fields that are not organised in retinotopic coordinates ('real-position' cells) but are anchored to a single spatial location regardless of eye position, i.e. displaying corpracentric coordinates.

As with areas 7b and V6, V6a's recipient cells are mainly found in premotor cortex area 6 (Matelli, Luppino, D'Amelio, Fattori, & Galletti, 1995; Shipp & Zeki, 1995), whose role in reaching movements would rely on such 'real-position' inputs. Thus, processing within V6a appears to be crucial for combining visual and arm movement signals.

3.16 Area KO/V3b

Using PET and fMRI neuroimaging techniques, Orban and colleagues (Dupont, De Bruyn, Vandenberghe, Rosier, Michiels, Marchal, Mortelmans, & Orban, 1997; Orban, Dupont, De Bruyn, Vogels, Vandenberghe, & Mortelmans, 1995; Van Oostende, Sunaert, Van Hecke, Marchal, & Orban, 1997) identified a motion processing area midway in the horizontal portion of the lateral occipital sulcus, approximately 15-20 mm medial and posterior to V5. Although this region responded only weakly to random dot patterns containing 50% coherent motion, there was strong activation to the kinetic boundary produced by opponent directions of the same type of motion stimuli. This pattern of activation was not found in neighbouring area V3. Strong selectivity for kinetic (motion-defined) boundaries was subsequently observed across a wide range of stimulus conditions. The area was named 'kinetic occipital' (KO; Orban et al, 1995).

Shortly afterward, Smith et al. (1998), also using fMRI techniques, observed the same cortical region to exhibit strong activation for global motion, with no special preference for kinetic boundaries. Accordingly, they suggested use of the term 'V3b'.

The functional discrepancy has yet to be resolved. However, although none of the original studies (i.e., Dupont et al., 1997; Orban et al., 1995; Van Oostende et al., 1997) ascertained the retinal topography of KO, Smith et al. (1998) found 'V3b', like V3, to represent the contralateral LVF only. Orban agrees that KO might prove to have a similar retinotopy to V3 (G.A. Orban - personal communication). Neither research team has yet to establish connectivity with other cortical regions.

3.17 Cerebellum

The cerebellum plays an important role in sensorimotor integration related to pursuit eye movements. In feline species, this region receives the bulk of its visually derived inputs, via the pontine nucleus, from dorsal extrastriate regions that are biased toward the LVF (Bjaalie, 1985). Although an equivalent connectivity has yet to be demonstrated in humans, the receptive fields of the vast majority of neurons in the flocculonodular region (Miles, Fuller, Braitman, & Dow, 1980), and the paraflocculus and fastigial nuclei (Fuchs, Robinson, & Straube, 1994) of monkey cerebellum are biased toward the LVF. Accordingly, ablation or inactivation of the primate flocculus causes pursuit eye movements characterised by involuntary upward drifts (Zee, Yamazaki, Butler, & Gucer, 1981).

3.18 Electrophysiology

The second component of the event related potential waveform, the P100, has an onset latency of 60-80 ms and peaks around 100-130 ms. This component appears to be generated within extrastriate visual areas (Mangun, 1995). It has long been recognised that the P100 appears approximately 10-20 ms earlier, in response to both checkerboard and grating stimuli, when presented to the LVF than the UVF (e.g., Eason, White, & Oden, 1967; Lehmann, Meles, & Mir, 1977; Lehmann & Skrandies, 1979; Miniussi, Girelli, & Marzi, 1998; Sano & Adachi-Usami, 1990; Skrandies, 1984). A similar finding has been reported from the use of dynamic random dot stereograms containing crossed disparities (Fenelon, Neill, & White, 1986). In addition, amplitude strength to both the P100 and N100 (150-220 ms, thought to include subcomponents derived from the frontal cortex; Mangun, 1995) components are found to be stronger for LVF vs. UVF presentations (Katsumi, Tetsuka, Mehta, Tetsuka, & Hirose, 1993; Miniussi et al., 1998; Mitchell, Wolter, & Neville, 1999; Orban & Muller, 1991; Yu & Brown, 1997).

The robust nature of these results led Skrandies (1987) to propose that stimulation of the vertical hemifields taps functionally independent neural generating mechanisms. Further evidence for this notion comes from an analysis of visual evoked potentials from 56 subjects aged 10-69 years, screened for refractive errors and retinal health, viewing checkerboard stimuli of varying spatial frequencies. No vertical hemifield differences were observed in the normal age-related decreases in response amplitude. However, while P100 latencies were unaffected by age in response to LVF stimulation, a correlation was found between response latencies and increasing age for UVF stimulation. This was especially the case for stimuli composed of high spatial frequencies (Sano & Adachi-Usami, 1990).

3.19 Single-Cell Response Latencies

A strictly hierarchical view of the visual system would suggest that, ‘higher’ visual areas will respond with longer latencies than ‘lower’ visual areas, due to the number of synapses encountered by the incoming signal

(Felleman & Van Essen, 1991). Although multisynaptic transmission is the norm within the ventral pathway, single synapse projection from V1 to extrastriate dorsal regions is common. It might be expected then, that single cells within these regions might also exhibit uniform response latencies.

This appears to be the case. In anaesthetised macaques, flashed stimuli are observed to produce coinicident single-cell activation within areas V3, MT and MST. Responses are rapid, occurring on average only 6-9 ms later than the average V1 response (Schmolesky, Wang, Hanes, Thompson, Leutgeb, Schall, & Leventhal, 1998). In contrast, a distinct temporal hierarchy was observed within ventral regions.

The lack of a distinct processing hierarchy in the dorsal pathway supports the view that dorsal regions play a pivotal role in 'on-line' visuomotor processing (Milner & Goodale, 1992; Goodale & Milner, 1995). As a large proportion of visual inputs from the peripheral LVF emanate from the observers own body, transmission delays affecting visuomotor coordination would be costly.

3.20 Conclusion

The evidence for vertical physiological asymmetries in the visual system of primates is summarised in Figure 2. This illustration shows clearly that there is considerable evidence for a physiological bias for the LVF in the dorsal pathway. This evidence, added to the preponderance of directionally selective cells within dorsal regions therefore supports the guiding hypothesis of this thesis; that the LVF will demonstrate a functional superiority for global motion processing.

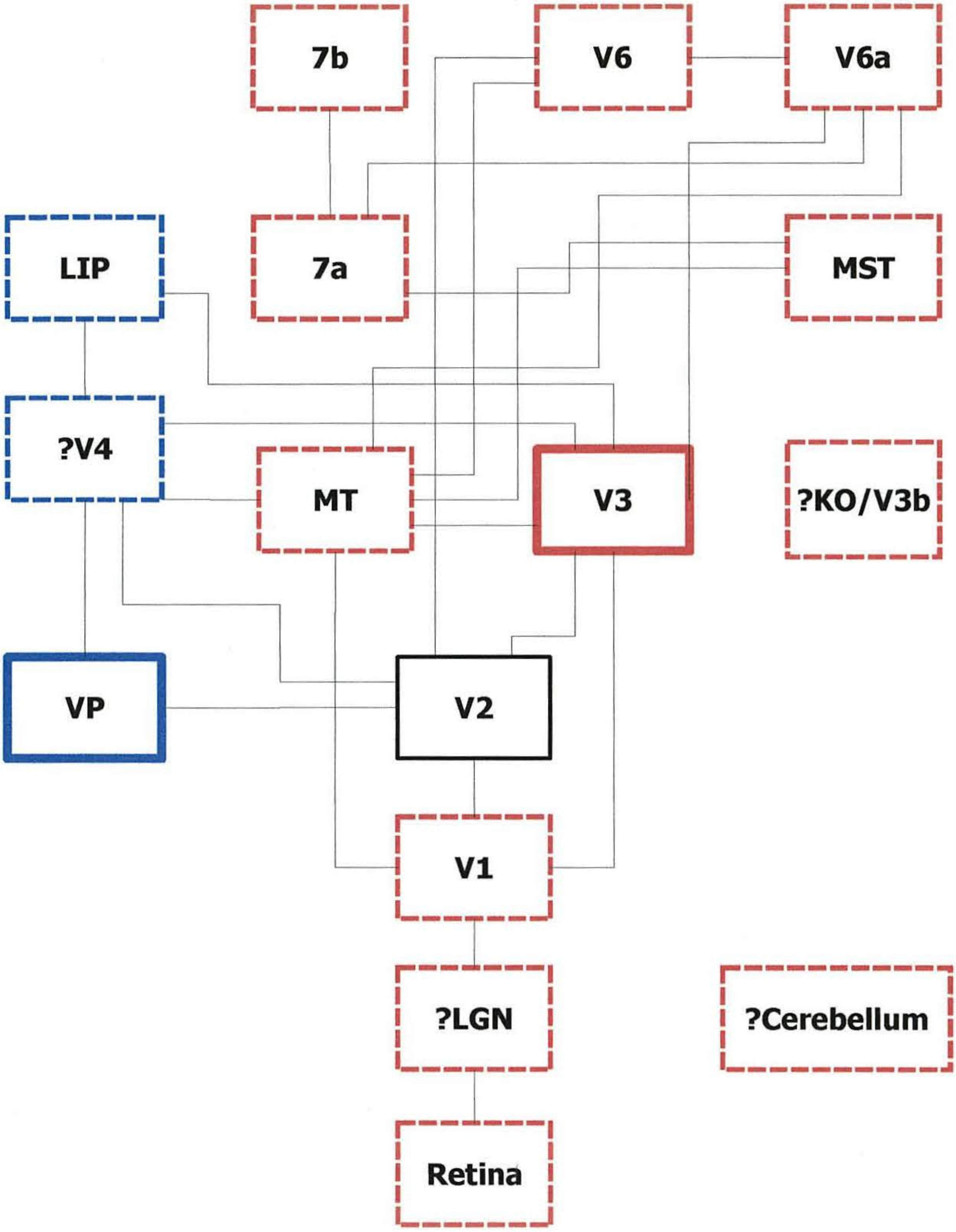

Figure 2. Subcortical and cortical regions in the macaque brain which demonstrate a representational bias toward a vertical hemifield along with currently known connectivity. Solid red borders indicate regions representing the LVF only, solid blue borders indicate regions representing the UVF only. Dotted red and blue borders indicateevidence that the region demonstrates a representational bias. Questions marks are used where data are limited or discrepant.

Chapter 4: Behavioural Evidence for Functional Differences Based on Vertical Hemifield

4.1 Visual Acuity

Visual acuity was the subject of the earliest published work that identified functional differences between the vertical hemifields. Employing a two-point discrimination task with two subjects, Aubert and Forster (1857) found that resolution was maintained at larger eccentricities in the LVF than in the UVF. Landolt and Hummelsheim (1904) later replicated these findings. Although Wertheim (1894) was also able to replicate the general effect using grating stimuli, he reported that the LVF advantage manifested only at eccentricities greater than 20^{O}.

Low (1943) measured acuity throughout the visual field in 100 adults using Landolt rings [5]. Again, performance in the LVF was generally found to be superior to the UVF, although he noted the presence of considerable inter-subject diversity. Millodot and Lamont (1974) employed the same stimuli to map visual acuity along the vertical meridian, from the fovea to 40^{O} in the periphery, at 5^{O} intervals. They also found a performance advantage in the LVF, in all three subjects tested.

The foregoing studies used stimuli characterised by relatively high spatial frequencies and levels of contrast. In order to ascertain whether the LVF acuity advantage manifested only within a narrow range of spatial frequencies, Skrandies (1985a) recorded contrast sensitivity thresholds from twenty subjects at an eccentricity of 5^{O} in both vertical hemifields and at seven different spatial frequencies from 0.45–13.74 c/deg. Although mean maximal contrast sensitivities were higher in the LVF (3.85 c/deg) than the UVF (2.63 c/deg), contrast sensitivity functions (contrast threshold x spatial frequency) revealed superior visual acuity in the LVF at all frequencies tested. A LVF sensitivity advantage within the low to moderate spatial frequency range has

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[5] The Landolt ring stimulus is a circle with a break in the circumference. The task is to determine at which angle of rotation the break occurs.

been reported by several other authors (Lundh, Lennerstrand, & Derefeldt, 1983; Murray, MacCana, & Kulikowski, 1983; Rijsdijk, Kroon, & van der Wildt, 1980). However, in contrast to the findings of Skrandies (1985a) and earlier reports, a substantial reduction, or absence, of the LVF advantage was found when high spatial frequencies were tested (Lundh et al., 1983; Rijsdijk et al., 1980). Thus, a consistent relationship between the LVF acuity advantage and the spatial frequency of the stimuli employed has yet to be found.

Nevertheless, a number of authors have attempted comparisons between the visual acuity data and the peripheral morphology of the retina. All concluded that differences in visual acuity in the vertical hemifields could be explained, in large part, to differences in photoreceptor densities (ten Doesschate, 1946; Drasdo, 1977; Dawson & Maida, 1984).

However a recent finding suggests that the LVF advantage in visual acuity can be reversed by attentional factors [6]. Employing a Landolt-square task, Yeshurun and Carrasco (1999) determined that, if observers were given a cue as to the upcoming location of the stimulus, they were more accurate at detecting a line-gap in the visual periphery than when no cue was made available. Moreover, the increase in spatial resolution was significantly greater from 1.5^{O}-6^{O} in the UVF than the LVF.

4.2 Size and Length Discrimination

Chukova (1995) presented squares (reference stimuli) and rectangles (test stimuli), differing in width by 8-60 minarc, simultaneously in mirror locations in each vertical hemifield. The task was to judge whether the test stimulus was larger than the reference stimulus. The smallest size discrimination thresholds were observed when the reference stimulus was placed in the UVF and the test stimulus in the LVF. In contrast, Fukisima and

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[6] Attention refers to those neural processes that promote the processing of relevant or salient stimuli; this is thought to be achieved via a combination of increased baseline activity within cells coding for a specific location, enhancement of response to particular stimulus attributes, and the suppression, or filtering of irrelevant information (e.g., Kastner & Ungerleider, 2000).

Faubert (2001) asked subjects to make relative estimations of line length and found a greater magnitude of errors in the LVF when the reference line segments (1.43-7.13^{O} in length) were placed in the UVF, than vice-versa. Discriminations made in the LVF where characterised by consistent underestimations.

The latter observation is surprising given the results of a study conducted by Breitmeyer, Battaglia and Bridge (1977). They presented a textured surface viewed through an 8.9 deg^2 aperture at a distance of 66 cm. The surface was then tilted backward and forwards until subjects indicated that the objective vertical had been reached and the angular tilt was then recorded. Under monocular viewing conditions the mean deviation from the objective vertical was nonsignificant. However, with binocular viewing there was a significant vertical hemifield effect. The portion of the stimulus located above fixation was more likely to be judged as tilted away from the observer, to be at a greater distance from the observer, and so smaller than its objective size. Conversely, that portion of the stimulus located below fixation was more likely to be judged as closer to the observer, and therefore to be larger in size.

4.3 Luminance Sensitivity

Scotopic sensitivity in the vertical hemifields appears to depend on both nutritional status as well as retinal morphology. Sloan (1947) ascertained that normal subjects (but not Vitamin A deficient subjects with otherwise normal retinas) are able to discriminate low-luminance targets at greater eccentricities in the LVF than the UVF. Riopelle and Bevan (1953) replicated the findings for healthy adults. A later study of 153 adults showed that the expected decrease in luminance sensitivity with increasing age proceeds more rapidly in the UVF than the LVF (Haas, Flammer, & Schneider, 1986).

4.4 Colour Perception

There is some evidence that opponent-wavelength processes are present at eccentricities up to 30^{O} in the UVF, yet absent beyond 12^{O} in the

LVF (Metha, Vingrys, & Badcock, 1994). This would suggest that a UVF advantage might be observed on colour discrimination tasks. However, a number of studies have shown a colour discrimination advantage for the LVF. One study reported the highest sensitivity to red, green, blue and yellow lights to be in the lower nasal retina (Carlow, Flynn, & Shipley, 1976). Similarly, Leinonen and Elenius (1994) report that chromatic targets, especially those of longer wavelengths, are detectable at higher eccentricities in the LVF, while Pennal (1977) found superior performance on a colour- matching task in the lower-left visual quadrant.

It is possible that these findings are at least partly due to the superior luminance sensitivity and temporal resolution in the LVF (e.g., Hylkema, 1942; Low, 1943; Phillips, 1933; Riopelle & Bevan, 1953; Skrandies, 1985a; Sloan, 1947) as it is necessary to first detect a stimulus before any assessment of hue can be made. For example, Pennal (1977) presented coloured stimuli for as little as 30 msecs, which may well have been an insufficient duration to activate colour-opponent mechanisms.

When relative discriminations of colour are made to successively presented stimuli, LVF performance declines more rapidly than UVF performance as the temporal interval between the two stimuli is increased (0-900 msecs; Heider & Groner, 1997). This finding not only indicates that colour persistence is stronger in the UVF, but there may be higher densities of parvo cells coding for the UVF. In contrast, there is evidence that the LVF is more sensitive to the colour of a moving stimulus. When Bilodeau and Faubert (1997) presented drifting isoluminant red-green sine-wave gratings at eccentricities up to 80^{O}, colour sensitivity was found to be higher in the LVF vs. UVF at all eccentricities between 20^{O}-80^{O}.

4.5 Temporal Resolution

Temporal sensitivity is normally ascertained using the critical flicker fusion task, in which the rate at which a single stimulus is flashed is increased until a constant presentation of the stimulus is perceived. This yields a critical flicker threshold, defined as flashes per second (Hz). Note that performance on flicker sensitivity tasks cannot be attributed solely to sensory mechanisms, as temporal resolution is often maintained in cases of pathology involving retinal degradation (Lachenmayr & Gleissner, 1992).

A LVF advantage is usually, but not always, reported in studies incorporating performance comparisons between the vertical hemifields. Phillips (1933) attempted the first investigation of temporal sensitivity throughout the visual field. He presented the critical flicker stimulus to patients with cortical lesions as well as three control observers, at eccentricities of 10-40^{O}, in 10^{O} steps, in each of the visual quadrants. Controls showed superior flicker resolution in both LVF quadrants. When Hylkema (1942) presented the same stimulus at similar eccentricities along the vertical meridian, thirteen of twenty subjects also showed greater flicker sensitivity in the LVF, five showed no vertical hemifield difference and two produced a UVF sensitivity advantage. In contrast, however, Kleberger (1954) reported considerable variability in performance between the vertical hemifields of 30 subjects, with no consistent pattern observed.

More recently, Skrandies (1985b) tested flicker fusion sensitivity in 15 subjects at both 5^{O} and 10^{O} in the vertical hemifields. At 5^{O} mean thresholds were found to be 20.45 Hz in the LVF and 18.63 Hz in the UVF. Thresholds at 10^{O} eccentricity were 19.50 Hz and 18.03 Hz, respectively. Both between-hemifield comparisons were statistically significant. Skrandies (1985b) then had the same subjects complete a second, more difficult double flicker discrimination task. In this variation, double flashes were presented and the subject's task was to adjust the interflash interval until a single flash was perceived. Again, a LVF sensitivity advantage was found. At 5^{O} eccentricity, a mean interflash interval of 82.75 ms was required to perceive two flashes in the UVF, with 92.80 ms required in the UVF. At 10^{O}, the figures were 91.69 and 100.91 ms, respectively. Again, both hemifield comparisons were significant. In a third experiment, eight separate luminance levels were presented in the single flicker condition. As expected, reductions in luminance levels resulted decrements in flicker sensitivity. However, the UVF was found to require a luminance level 1.75x that of the LVF in order to achieve the same temporal resolution.

In contrast to these findings, however, Yasuma and colleagues (Yasuma, Miyakawa, & Yamazaki, 1986) reported no sensitivity difference between the vertical hemifields on the single flicker task. Yasuma et al's (1986) stimulus was, with a diameter of 34 minarc, by far the smallest employed by any of the previously cited studies. This might account for their results.

4.6 Reaction Times

There is a high level of agreement for findings of shorter manual reaction times in the LVF, in response to nonmeaningful stimuli. The first such report was made by by Hall and Von Kries (1879). Stimuli were presented along the vertical meridian at eccentricities of 30^O and 60^O and mean reaction times were found to be 34 ms shorter in the LVF at 30^O, rising to 46 ms at 60^O. Payne (1967) reported the same effect with dim photopic stimuli at an eccentricity of 15^O, on both the vertical meridian (10 msecs LVF advantage), and in the nasal retina (20 ms LVF advantage). Osaka (1976), Gawrysyszewski and colleagues (Gawryszewski, Riggio, Rizzolatti, & Umilta, 1987), and Sheliga and co-workers (Sheliga, Craighero, Riggio, & Rizzolatti, 1997) have all reported similar results.

In contrast, Magrotti, Cosi, and Borutti (1980) were unable to observe a LVF advantage at 5^O, although significantly shorter LVF response times were found at 20^O, while Cocito, Favale, and Tartaglione (1977) found the effect to depend on the spatial frequency of the stimulus; at 1 c/deg a significant LVF advantage was found but a nonsignificant difference was found with 3 c/deg stimuli.

Skrandies (1987) postulates that the LVF response time advantage reflects the sensory advantage provided by higher photoreceptor densities in the upper hemiretinae. Indeed, when Lichtenstein and White (1961) compared

Østerberg's (1935) retinal morphology data with their own motor reaction time data, they concluded that reaction times were inversely related to retinal photoreceptor densities. On the other hand, Previc (1990) suggests that the effect is more likely to be the product of cortical sensorimotor integration mechanisms that are biased toward the LVF. He cites evidence that saccadic eye movement latencies to nonmeaningful stimuli show the opposite effect; a latency advantage of approximately 20 ms in favour of the UVF (e.g., Heywood & Churcher, 1980).

An alternative explanation, however, is that attentional resources are preferentially allocated to the LVF when the location of a stimulus onset is uncertain (Gunter, Wijers, Jackson, & Mulder, 1994; Rezec et al., 1999). For example, when two stimuli are presented simultaneously in the vertical hemifields and subjects are required to covertly attend to a designated stimulus, reaction times are significantly lower for stimuli in the attended UVF vs. unattended LVF location (Gunter et al., 1994).

Lamble, Laakso and Summala (1999) have provided a real-world replication of the reaction time data by means of an attentionally demanding in-car task. Subjects drove a test car at 50 km/hour, and were instructed to maintain a distance of 40 metres behind a lead car. The test car contained nine LED displays at varous locations on the steering wheel, dashboard, and mirrors. Every 333 msecs a randomly assigned LED would display a random chosen digit from 1-9. Subjects were required to verbally report the identity of this digit, which required foveation, thus placing the lead car within the visual periphery. On some trials, the lead car decelerated rapidly while the subject completed the digit task. The dependent variable was the subject's response latency to press the brake pedal. This measure was then analysed alongside the distance between, and relative velocity of the two cars, in order to determine a time-to-collision value.

No direct UVF vs. LVF comparisons were made. However, safer time-to- collision values were found when subjects attended to the LED display placed on the rear vision mirror (left hand drive), placing the car in front at an eccentricity of 42^{O} in the lower-left visual quadrant, than with an LED located on the dashboard immediately forward of the driver, placing the front vehicle at an eccentricity of 4^{O} in the UVF.

4.7 Sensorimotor Coordination

Two recent studies have explicitly tested the postulated link between LVF-biased dorsal regions and motor coordination. Danckert and Goodale (2001) had subjects make rapid pointing movements to five square targets varying in size between 1.9 and 30mm in width, presented at an eccentricity of 5^{O} in the UVF or LVF. In the LVF a linear relationship was observed between the peak velocity attained during the reaching movement and target width. This was not observed in the UVF, where peak velocities were also significantly slower. Furthermore, no speed-accuracy tradeoff was observed in the LVF as, with the exception of the smallest target, reaching within the LVF also demonstrated greater end-point accuracy.

Earlier Danckert and Goodale (2000) had presented data from an interesting variation on this experiment. They timed subjects as they imagined making exactly the same pointing movements as in the study described above. A linear relationship between target width and reaching duration was again observed when the imagined movements were made in the LVF. No such relationship was found for imagined UVF stimuli. Supporting Previc's (1990; 1998) views, Danckert and Goodale (2001) concluded from the two studies that the dorsal visual mechanisms neural circuitry used for processing stimuli in the LVF are functionally specialised for controlling visually guided movements of the upper limbs.

The second study investigated the influence of of age-related visual deterioration on postural stability. Employing 156 persons aged 63-90 years, Lord and Menz (2000) found a significant correlation between the degree of loss of peripheral vision in the LVF and the amount of corrective sway required to maintain a stable posture on a compliant floor surface.

4.8 Stereopsis

Stereopsis refers to the perception of depth mediated by cortical cells able to combine the disparate inputs projected onto the retina of both eyes. This ability provided the first clear evidence that processing differences between the vertical hemifields were due to cortical, rather than sensory mechanisms. Breitmeyer et al. (1975) presented dynamic random dot stereograms, devoid of monocular depth clues, to both vertical hemifields and found that stimuli defined by crossed disparities were more accurately perceived in the LVF than the UVF. In contrast, stimuli defined by uncrossed disparities showed a UVF advantage. Fox (1982), and Previc and co-workers (Previc, Weinstein, & Breitmeyer, 1992; Previc, Breitmeyer, & Weinstein, 1995) have since replicated the initial finding.

There is evidence to suggest that there might be a general processing preference within the LVF for those parts of objects perceived as protruding into the foreground. When viewing static, horizontally oriented figure-ground displays made up of two equivalently sized, symmetrical regions, the lower region is perceived as figure at well above chance levels. This occurs regardless of colour, temporal constraints, and despite prior labelling of the upper region of the stimulus as ‘figure’ (Vecera, Gilds, & Lonsdale, 1999).

4.9 Discrimination of Words, Letterstrings, and Digits

In their seminal study of visual field differences in word and letter recognition, Mishkin and Forgays (1952) reported that the recognition of single words was significantly more accurate in the LVF than the UVF. However, the authors acknowledged that their data might have been confounded by differences in illumination between the vertical hemifields. Subsequent studies are characterised by inconsistent results.

In the case of single-letter recognition, one study reported no performance difference between the vertical hemifields (Worral & Coles, 1976), while another found a performance advantage in the UVF (Klein, Berry, Briand, D’entremont, & Farmer, 1990). In contrast, Skrandies (1987) reported that 14 of 15 subjects were better able to identify single numerals at 5^{O} eccentricity in the LVF. The single anomalous subject exhibited such a high level of performance in both vertical hemifields that a ceiling effect was observed.

Vertical hemifield performance asymmetries are reported to be absent for the discrimination of both random letter-strings (Webb, Fisher-Ingram, & Hope, 1983) and legitimate three letter syllables (Hellige, Cowin, Eng, & Sergent, 1991). However, complicating the picture, when Lambert, Beard, and Thompson (1988) required subjects to categorise the target words, approximately equal numbers of observers demonstrated UVF and LVF performance advantages.

Most recently, Goldstein and Babkoff (2001) conducted a series of four lexical decision experiments in an attempt to ascertain under which conditions vertical hemifield asymmetries might manifest. In the first experiment, a UVF advantage, especially strong in the upper-right quadrant, was found for both latency and accuracy when legitimate words were presented for 150 ms. However, no vertical hemifield asymmetry was observed for orthographically and phonologically legal nonwords that differed from the legitimate words by only one letter. This pattern of results was observed at eccentricities ranging from 3^{O} to 8^{O} and regardless of whether the data being examined were from observers' first or fourth experimental session.

4.10 Visual Memory

There is evidence to suggest that when visual patterns are encoded into long term memory they are subject to a systematic bias that results in a wider-angle view than was originally presented. This observation was made first by Intraub and Richardson (1989). They had subjects view photographs for 15 seconds then draw the scene from memory. They found a robust tendency to assume a wider-angle view than was actually the case. Featured objects were reduced in size, and horizontal, but especially vertical boundaries, were expanded. This occurred despite the drawing surface having the same horizontal to vertical ratio of the original stimulus. The same result was later found when viewing times as short as one second were used (Intraub, Gottesman, Willey, & Zuk, 1996).

Previc and Intraub (1997) subsequently reanalysed Intraub and Richardson's (1989) data by selecting specific points in the original stimuli and comparing these with the locations of their redrawn counterparts. They found that the redrawn images exhibited a pronounced downward shift. This shift was significantly larger for those points located in the upper half of the original scene, suggesting that visual memory for objects creates a systematic expansion of upper space.

A further study appears to demonstrate that the relative spatial location of stimuli is memorised more accurately when presented to the LVF (Genzano, Di Nocera, & Ferlazzo, 2001). In this experiment, patterns comprising eight identical square blocks, straddling the UVF and LVF in equal numbers, were presented on a computer monitor, for either 10 or 20 s before disappearing. Subjects were required to reconstruct the spatial pattern from memory, using the original component blocks, via 'drag and drop' mouse movements. A LVF advantage was found for reconstructing the original shape.

Importantly, although the LVF advantage was diminished by the presence of perceptual distractors (continually changing geometric shapes on the background of the display during the response phase), it was absent when observers performed a concurrent motor coordination task with the nonresponding arm. If the LVF advantage had remained in the motor distractor condition, it could be argued that the vertical hemifield effect involved purely perceptual mechanisms. The motor distractor effect arguably demonstrates a functional link between perceptual processing of LVF stimuli and dorsal visuomotor mechanisms.

4.11 Global Judgements

Genzano et al's (2001) main conclusion was that the memorising of mutiple spatial coordinates was more accurate for LVF stimuli. Nevertheless, another explanation for the findings is feasible. This study effectively tested the ability to memorise and reconstruct the global configuration of stimuli composed of multiple components. Because the blocks (the local components) were identical, it was unimportant whether or not they were relocated in their original location. Therefore, superior memory for the outline, or global shape, of the stimulus produced by the component blocks might better explain the LVF advantage.

Support for this view comes from Christman (1993). In two experiments, he found both shorter response latencies and greater accuracy for identifying the global level of Navon letter stimuli [7] in the LVF. In the UVF, a similar processing advantage was reported for the local stimulus features. In a further study of global perception a horizontal rectangle formed by illusory contours was presented to each vertical hemifield (Rubin, Nakayama, & Shapley, 1996). Observers reported a greater awareness of the subjective percept in the LVF than in the UVF, where the illusory contours faded, leaving only the objective portions of the stimulus.

Later, Atchley and Atchley (1998) questioned whether Rubin et al.'s (1996) findings might be due to free eye movements being permitted. To test this hypothesis, they presented four circles in each corner of an invisible square, 2.5^{O} - 4.5^{O} from fixation in the vertical hemifields. Without warning, the inner quadrant of each circle within one hemifield abruptly disappeared, creating four 'pacman' type objects creating the perception of an illusory square. With central fixation, no valid spatial precue [8], and a stimulus duration of 150ms, no LVF advantage was found for perceiving the subjective stimulus.

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[7] Navon stimuli are hierarchically structured stimuli, usually alphanumeric characters, in which the whole stimulus (global level) is discerned by the spatial configuration of numerous identical smaller elements (local level), which may, or may not, differ from the global identity.

[8] Spatial precues are indicators purporting to signify the upcoming location of the target stimulus. They can be neutral (convey no information), valid (convey true information), or invalid (convey false information).

4.12 Eye Movements

When scanning a visual scene, there is a robust tendency for approximately two-thirds of initial saccades to be aimed upward. This is the case whether searching for targets that are actually present (Chedru, LeBlanc, & Lhermitte, 1973; Hall, 1985; Previc, 1996) or are memorised (White, Sparks, & Stanford, 1994). Furthermore, saccades made to targets in the UVF show a highly reliable latency advantage of approximately 20-30 ms, and their end-points are more accurate than those made to LVF targets (Chedru et al., 1973; Enright, 1984; 1989; Hackman, 1940; Hall, 1985; Heywood & Churcher, 1980; Honda & Findlay, 1992; Levy-Schoen, 1969; Miles, 1936; Previc, 1996; Zelinsky, 1996; though see Miller, 1969 for a nonsignificant LVF latency advantage of 12 ms).

It has also been observed that downward saccades have a tendency to include a small converging component, estimated to be 1^{O} radially per 8^{O} vertically (Enright, 1989). This occurs even when a change in depth is not signalled by the stimulus. To focus accurately, this convergence movement is necessarily followed by a slower, corrective divergence of the eyes (Enright, 1984; 1989; Collewijn, Erkelens, & Steinman, 1988). However, Honda and Findlay (1992) have ascertained that the latency of convergence and divergence movements made during saccades to near and far targets does not differ between the UVF and LVF. Thus, latency differences for saccades made toward the vertical hemifields appear to result from the inherent upward bias in saccadic-attention-scanning mechanisms, rather than processing biases within the vergence system.

4.13 Visual Search

The most consistent behavioural evidence for a processing advantage in the UVF vs. LVF is found in the visual search literature. When surrounded by similar distractors, target stimuli are identified with greater accuracy and shorter latencies when located within the UVF, and especially within the upper-right quadrant. This effect has been observed in both pre-school and school-age children (Hall, 1985) as well as in adults (Beer et al., 1996; Chaikin Corbin, & Volkmann, 1962; Chedru et al., 1973; Christman & Niebauer, 1997; Fecteau et al., 2000; Hall, 1985; Previc, 1996; Previc & Blume, 1993; Previc et al., 1992; Previc & Naegele, 2001; Yund, 1997; Zelinsky, 1996).

There are a number of reasons to suggest that the UVF search advantage results from an inherent vertical asymmetry in attentional mechanisms, rather than superior oculomotor or object recognition mechanisms, as some authors have suggested (e.g., Heywood & Churcher, 1980; Findlay, Newell, & Scott, 1992; Godoy, Luders, Dinner, Morris, & Wyllie, 1990).

Firstly, as previously discussed, a LVF advantage is normally found for the detection of a single stimulus presented without distractors and/or spatial precues (e.g., Aubert & Forster, 1857; Carlow et al., 1976; Hylkema, 1942; Low, 1943; Sloan, 1947; Phillips, 1933; Riopelle & Bevan, 1953; Skrandies, 1985a). Secondly, increasing attentional load by either increasing the number of distractor items (e.g., Previc, 1996; Previc & Blume, 1993) or by the introduction of a secondary task at fixation (Beer et al., 1996), produces and/or strengthens the UVF (especially upper-right quadrant) advantage. These effects can be observed whether the target stimulus differs from distractors in a number of stimulus attributes (i.e., feature search), or in a single stimulus attribute (i.e., conjunction search). Thirdly, although spatially valid leftward and rightward precues presented at fixation produce processing benefits, valid upper and lower precues have a negligible influence (Previc et al., 1992). Fourth, a UVF advantage has been observed even when eye movements are not permitted (Previc et al., 1996, Experiment 2) or when the visual display disappears before eye movements are made (Chaikin et al., 1962). Fifth, when eye movements are permitted during a trial, scanning generally commences in the upper-left quadrant (Chedru et al., 1973; Hall, 1985; Yund, 1997) yet search performance is consistently found to be superior in the upper-right quadrant (e.g., Previc, 1996). Sixth, although counterintuitive, subjects appear significantly less likely to make a saccade when a target appears in the upper-right quadrant, especially during conjunction search (Previc, 1996). The last three points in particular suggest that a covert attentional shift toward the UVF can effectively substitute for an upward saccade.

Two studies have investigated whether interactions exist between visual search mechanisms operating in the vertical and depth planes, i.e., visual search in 3D space (Previc et al., 1992; Previc et al., 1995). Both required subjects to identify squares or diamonds embedded within random dot stereograms. In agreement with previous studies (Breitmeyer et al., 1975; Fox, 1982), performance advantages were found for crossed disparity targets in the LVF and uncrossed disparity targets in the UVF. This effect was strengthened when observers were uncertain as to the vertical location in which the stereogram would appear (Previc et al., 1992). The lower-left visual quadrant demonstrated particular difficulty in discriminating uncrossed disparity stereograms. However, contrary to findings from visual search tasks performed at a single depth gradient, the strongest performance for uncrossed disparity targets was found in the upper-left, rather than the upper-right quadrant (Previc et al., 1995).

There are two dissenting studies in the visual search literature. In the first, von Grünau and Dubé (1994) reported that search for an upward tilted 3D cube presented amidst downward tilted distractors was located more quickly in the LVF than the UVF. The authors concluded that the UVF search advantage must depend on the presence of specific target features. Hence, the UVF bias is modulated by the use of ecologically valid targets (downward tilted cubes not being normally encountered in the LVF) presented in the relevant view-angle.

To address the possibility that the UVF advantage is confined to certain types of stimuli, Previc and Naegele (2001) repeated von Grünau and Dubé's (1994) experiment with two variations. Firstly, they permitted subjects to make eye movements during the search phase and, secondly, they replaced von Grünau and Dubé's (1994) original response mode (target absent/present) with a four alternative spatial forced choice as to the location of the target (four visual quadrants). Under these conditions a UVF advantage was found for both latency and accuracy, regardless of the tilt (upward or downward) of the target cube. Further variations, in lighting direction (above/below) and using cubes rotating about the vertical axis, failed to reinstate the LVF latency advantage found by von Grünau and Dubé (1994). Previc and Naegele (2001) therefore concluded that the UVF bias is more likely to be dependent on the type of search task rather than particular target features, as von Grünau and Dubé (1994) had proposed.

The second dissenting study employed line segments in which the target and distractors had different oblique, orientations (Ellison & Walsh, 2000). Contrary to other findings, when the visual array covered the whole screen (i.e., both UVF and LVF) no significant difference in reaction times was found between the vertical hemifields. However, when the array was confined to one vertical hemifield at a time, search latencies were found to be significantly faster in the LVF.

Chapter 5: Neuropsychological Evidence for Functional Differences Based on Vertical Hemifield

5.1 Neglect of Lower Space

Damage to right parietal cortex, especially the posterior regions, often produces difficulties in orienting and responding to stimuli located in space contralateral to the damaged hemisphere, a condition referred to as 'unilateral neglect'. Clinically, symptoms may manifest in mundane fashion, such as a patient ignoring food placed on the left side of a plate or drawing pictures devoid of those features occurring left of the midline. Because these symptoms occur in the absence of hemianopia and optic ataxia, and are often multimodal, a deficit in the ability to effectively orient attention in the horizontal dimension is widely considered to be the case (e.g. Robertson & Marshall, 1993).

There is a rapidly growing number of studies in which patients with unilateral neglect are observed to display concurrent neglect of lower space, especially within the lower-left quadrant (e.g., Bender & Furlowe, 1945; Bender & Teuber, 1948; Butter, Evans, Kirsch, & Kewman, 1989; Halligan & Marshall, 1989; Kagayama, Imagase, Okubo, & Takayama, 1994; Làdavas, Carletti, & Gori, 1994; Morris, Mickel, Brooks, Swavely, & Heilman, 1986; Nathan, 1946; Nichelli, Venneri, Pentore, & Cubelli, 1993; Pitzalis, Di Russo, Spinelli, & Zoccolloti, 2001; Pitzalis, Spinelli, & Zoccolotti, 1997; Rapscak, Cimino, & Heilman, 1988; Rubens, 1985). Generally, detection of a single stimulus presented in either vertical hemifield is normal, but 'extinction' of the LVF stimulus results when stimuli are simultaneously presented to both vertical hemifields (e.g., Butter et al., 1989; Rapcsak et al., 1988). Neglect of lower space can also be multimodal, and has been observed to in the tactile (e.g., Rapscak et al., 1988) and auditory domains (e.g., Butter et al., 1989).

Symbol cancellation tests, in which patients search for and cross out target symbols intermingled with distractor symbols, reveal higher rates of omission in the lower region of the display, especially within the lower-left quadrant (e.g., Halligan & Marshall, 1989; Nichelli et al., 1993; Pitzalis et al., 1997). Left neglect patients also demonstrate particularly long latencies in visual evoked potentials when gratings are presented to their lower-left quadrant, compared with other quadrants (Pitzalis et al., 1997).

Pitzalis et al. (2001) report a further important finding. They tested 14 left-neglect patients on horizontal line-bisection tasks performed on the frontoparallel plane, at an eccentricity of 20^{O} in each vertical hemifield. They found, as hypothesised, that neglect patients produced significantly larger rightward misbisections in the LVF than the UVF, compared to a control group. This task was performed with the stimulus presented 40 cm from the body. However, when the same task was performed with the stimulus placed 160 cm from the body, with stimulus eccentricity maintained, the vertical hemifield asymmetry was largely eliminated. This pattern of data suggests that neglect of lower space is somehow critically linked to peripersonal space.

The neuropsychological tests used to determine neglect of lower space are normally performed within peripersonal space and on a flat surface, rather than the frontoparallel plane. Furthermore, free movement of the eyes is generally permitted. Thus, upper and lower space tends to be defined in relation to the stimulus, rather than in objective upper-lower coordinates. Pitzalis et al's (2001) findings therefore suggest that, in many cases, neglect of lower space might have become confounded with neglect of peripersonal space.

Finally, a recently reported case questions the previously observed link between parietal insult and neglect of lower space. Ergun-Marterer and colleagues (Ergun-Marterer, Ergun, Mentes & Oder, 2001) report a 27-year old female who suffered highly localised bioccipital lesions resulting from an embolic infarction. Her most prominent behavioural symptom was a marked neglect of lower space.

5.2 Neglect of Upper Space

Observations of neglect within upper space have long been associated with damage to the temporal lobe, though these patients present in much smaller numbers than those exhibiting left-lower neglect. For many years upper neglect was considered to largely result from concomitant damage to the underlying optic radiations (Meyer's Loop). Van Buren and Baldwin (1958) were the first to report a patient with UVF neglect who had damage limited to the temporal lobe. A later study of 74 epileptic patients who had undergone either a partial or complete temporal lobectomy (Jensen & Seedorf, 1976) largely confirmed Van Buren and Baldwin's (1958) findings. Further evidence for a functional link between the temporal lobe and the UVF comes from patients with pattern sensitive temporal lobe epilepsy. Their seizures are more easily elicited by UVF stimulation (Soso, Lettich & Belgum, 1980).

Damage to the optic radiations alone invariably results in patients being fully aware of having a visual field loss. In contrast, focal damage to the temporal lobe more often results in patients being unaware of any deficits (Jensen & Seedorf, 1976; Van Buren & Baldwin, 1958). This has led to the suggestion that neglect of upper space, as with neglect of lower space, is due to an attentional deficit.

In the past decade or so, further cases of frank UVF neglect have appeared. A typical case (Shelton, Bowers, & Heilman, 1990) concerned a 66 year-old male patient suffering bilateral inferior temporooccipital infarctions who displayed symptoms opposite to those of the more commonly reported LVF neglect patients. Thus, he bisected lines below the objective midpoint and neglected the upper portion in both self-drawn pictures and during cancellation tasks. Interestingly, although he extinguished stimuli within the UVF when both vertical hemifields were stimulated, he could often detect the UVF stimulus when it was placed 30 cm closer than the LVF stimulus. This suggests there may be a functional link between neglect of upper space and extrapersonal space. Adair and colleagues (Adair, Williamson, Jacobs, Na, & Heilman, 1995) later described a female patient with a similar pattern of brain damage and behavioural deficits.

Chapter 6: Evidence for Functional Differences Based on Vertical Hemifield from Motion Perception Studies

6.1 Velocity Discrimination

McColgin (1960) conducted the first study comparing performance in the vertical hemifields on a motion perception task. He presented stimuli resembling clock hands at various positions within the visual field and measured the absolute velocity threshold for clockwise, counterclockwise, vertical and horizontal movement. No vertical hemifield performance asymmetry was observed, though he did report a trend toward lower thresholds for vertical motion in the LVF and for horizontal motion in the UVF.

Later, Smith and Hammond (1986) measured relative velocity discrimination in response to two square-wave gratings, extending from 0.5-5.5^{O} in each vertical hemifield, and drifting rightward and leftward at speeds ranging from 2-8 deg/sec. Again, no overall vertical hemifield effect was observed, though two subjects showed a consistent, yet opposite, vertical hemifield performance asymmetry.

6.2 Motion Sensitivity Assessed Using Grating Stimuli

Ohtani and Ejima (1997) presented horizontally oriented sinusoidal gratings subtending 1.5^{O} to each vertical hemifield at an eccentricity centred on 3.5^{O}. Movement was produced by a change in phase angle varying from 90-270^{O}, across 2 x 250 msec video frames. Subjects indicated the direction in which they had perceived the grating to move. Otherwise similar vertically oriented stimuli are perceived as moving rightward or leftward with equal probability. In the case of horizontally oriented stimuli, however, although observers reported seeing upward and downward movement with equal probability in the UVF, they consistently reported downward movement in the LVF.

6.3 Motion Sensitivity Assessed Using Random Dot Kinematograms

Random dot kinematograms (henceforth: RDK) consist of a series of images composed of randomly positioned stationary dots. When these images are viewed in rapid succession, within the same region of space, the component dots are perceived to be moving, a phenomenon labelled 'apparent motion'. The value of this technique as an effective tool for measuring sensitivity to visual motion lies in the ability of the experimenter to manipulate the signal to noise ratio within the stimulus (Williams & Sekuler, 1984). This is achieved by having a percentage of the component dots move in a coherent, or uniform direction ('signal') while the remaining dots move in a random fashion ('noise'). The minimum number of signal dots required for an accurate discrimination of the signal direction therefore quantifies each observer's sensitivity to the global direction of motion [9].

Correct responses are necessarily based on the perceived global direction of motion because the trajectory of any individual dot, or of small numbers of dots within any local region of the stimulus, cannot be relied upon to represent the signal motion. Instead, observers must average or 'integrate' the diverse dot trajectories over the entire region of space occupied by the RDK (e.g., Braddick & Qian, 2001; refer Figure 3). Most importantly, in humans, this computation appears to be performed solely within cortex (Braddick, O'Brien, Wattam-Bell, Atkinson, Hartley, & Turner, 2001; Smith et al, 1998).

Four studies employing RDKs have particular relevance to the present investigations. However, only one set out to explicitly test whether the vertical hemifields show motion sensitivity differences (Rezec et al., 2000).

Edwards and Badcock (1993; Experiment 3) had observers view semi-annular RDKs, 8^{O} in diameter, anchored on the horizontal meridian and presented in either the UVF or LVF. Duration was 8-frames (400 msecs). Both

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[9] The term 'global motion' refers to the uniform or coherent direction of motion ascertained by a 'pooling' or 'averaging' algorithm applied to diverse motion signals within a specific region of the visual field.

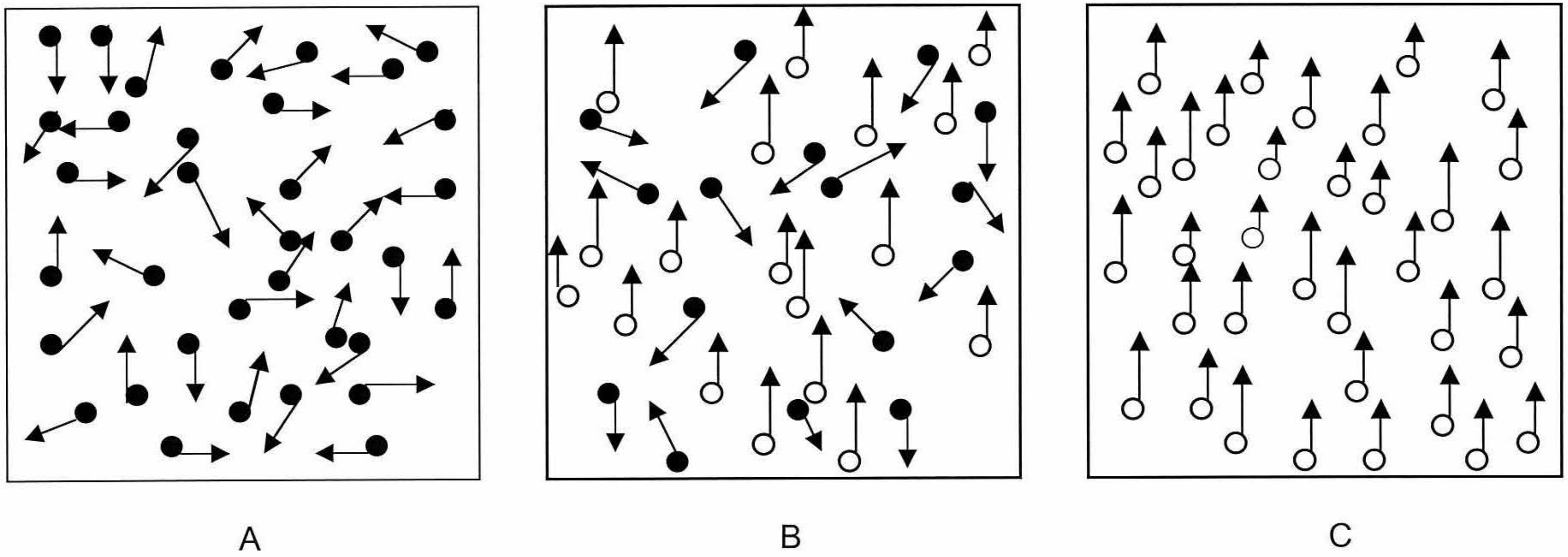

Figure 3. A schematic of the RDK paradigm. In block A, the trajectories of the component dots are wholly random (i.e., the stimulus has a coherence level of 0%). In Block B, half of the component dots display random trajectories (noise dots) while the remaining dots display coherent upward motion (signal dots). In this case the coherence level is 50%. In block C, all dots are moving upward, displaying 100% coherent motion. The minimum number of signal dots required to make an accurate discrimination of the coherent direction of motion provides a threshold measure in which motion sensitivity can be quantified.

centripetal and centrifugal motion was presented and, in an attempt to simulate an optic flow field, small speed gradients of 6-8 deg/sec were employed. Although only two subjects were tested, both produced lower motion coherence thresholds in the LVF. However, while one subject was found to be more sensitive to centripetal motion, the other demonstrated a centrifugal directional bias.

Next, Raymond (1994; Experiment 2) had six subjects view upward and downward motion in 2.5^{O} square RDKs, centred at 5^{O} eccentricity on the vertical meridian. Stimulus duration was 4-frames (105 msecs). The purpose of this study was to ascertain whether the vertical hemifields demonstrate directional anisotropies and so the question of whether the vertical hemifields differ in motion sensitivity *per se* was not formally addressed. However, she reported significantly lower upward vs. downward motion thresholds in the LVF, while in the UVF, sensitivity to motion along the vertical axis was found to be isotropic, with thresholds similar to the downward thresholds recorded from the LVF. Thus, the LVF appears to have produced a smaller mean motion coherence threshold than the UVF.

In order to study losses in motion sensitivity in glaucoma patients, Joffe, Raymond and Chrichton (1997) measured motion sensitivity, using thresholds averaged across the four cardinal directions, in 14 controls at eccentricities of 9, 15, and 21^{O} in each vertical hemifield. Their RDKs were circular, with a 3^{O} diameter, and contained dots moving at 2.63^{O}/sec for 5-frames (400 msecs). Performance in the vertical hemifields was found not to differ.

Finally, Rezec et al., (2000; Experiment 1) similarly reported the absence of a sensitivity difference between the vertical hemifields for 14 subjects viewing circular RDKs with an 8^{0} diameter. These stimuli contained horizontal axis motion only, and were presented for 200 msecs at an eccentricity of 15^{0}, in each of the visual quadrants.

Stimulus parameters from these four studies are summarised in Table 1.

Study	**n**	**RDK Size**	**Location/Eccentricity**	**Duration**	**Velocity**	**Dot Diameter**	**Density**	**Directions Tested**	**Effect/Trend**
Edward & Badcock (1986; Experiment 3)	2	Semi-circular: 12^{O} diameter	Up to 8^{O} on vertical meridian	8 x 50 msec frames	0-6^{O}/sec	12'	0.21 dots/deg^2	Centripetal Centrifugal (toward fixation)	LVF advantage
Raymond (1994; Experiment 2)	6	Square: 2.5^{O} width	On vertical meridian: centred at 5^{O}	4 x 26 msec frames	5^{O}/sec	1.31'	21.4 dots/deg^2	Upward Downward	LVF advantage
Joffe et al., (1997; control data)	14	Circular: 3^{O} diameter	9, 15 and 21^{O} on vertical meridian	5 x 80 msec frames	2.63^{O}/sec	4.3'	10.6 dots/deg^2	Upward Downward Leftward Rightward	No hemifield effect
Rezec et al., (2000; Experiment 1)	14	Circular 8^{O} diameter	In quadrants: centred at 15^{O} oblique	200 msecs	7^{O}/sec	7.2'	2.4 dots/deg^2	Rightward Leftward	No hemifield effect

Table 1. A summary of the RDK stimulus parameters employed in four studies in which motion sensitivity was measured in the vertical hemifields.

Chapter 7: A Brief Outline of the Experiments Conducted

7.1 A Rationale for the Experiments

The evidence from the foregoing review of the relevant behavioural literature generally supports the view that the vertical hemifields are functionally specialised to process different aspects of incoming visual information. Such functional specialisation can be characterised by a UVF advantage for processing the local or featural attributes of stimuli, and a LVF advantage for processing global attributes (e.g., Previc, 1990; 1998; Skrandies, 1987). Furthermore, performance differentials appear not to be limited to sensory levels of visual processing, but to involve higher level cognitive functioning, including attentional effects. However, with the possible exception of the visual search paradigm, for which there is now substantial evidence for a UVF processing advantage, the evidence from other sources remains somewhat less than comprehensive.

In particular, there is a distinct paucity of work investigating motion processing in the vertical hemifields, and what has been attempted is characterised by mixed results (Edwards & Badcock, 1993; Joffe et al., 1997; Raymond, 1994; Rezec et al., 2000). This is especially surprising in view of the neurophysiological evidence, which indicates that regions of the dorsal visual pathway mediating motion processing, such as V3, MT and MST, preferentially process visual information emanating from below fixation (e.g., Burkhalter et al., 1986; Felleman & Van Essen, 1987; Gattas & Gross, 1981; Maunsell & Van Essen, 1987; Smith et al., 1998).

Thus, performance on visual motion tasks provided a suitable behavioural means by which to further investigate the hypothesis that the vertical hemifields in humans are functionally specialised for processing different aspects of visual information. Indeed, the pattern of data emerging from non-motion behavioural paradigms, along with Previc's (1990; 1998; discussed in Chapter 1) theoretical synopsis suggesting that the LVF is functionally specialised for global level perceptions, predicts that the LVF should be observed to demonstrate a particular sensitivity advantage, or functional specialisation, for the perception of global motion.

The thesis consists of five experiments and a case study. The stimuli employed in Experiments 1-3, and in the case study, were variants on the RDK paradigm, and so directly tested global motion perception. The RDK paradigm was chosen for the following reasons; (i) the computations underlying the percepts generated by this class of stimulus are reasonably well-understood (e.g., Braddick & Qian, 2001), (ii) as a consequence, RDKs are currently the principal method employed for assessing sensitivity to global motion signals in monkeys as well as in both normal and clinical human samples, (iii) furthermore, as discussed in the previous chapter, all previous investigations measuring sensitivity to global motion in the vertical hemifields (Edwards & Badcock, 1993; Joffe et al., 1997; Raymond, 1994; Rezec et al., 2000) have employed this class of stimulus, thus allowing the data from the present studies to be meaningfully compared with previous work.

Nevertheless, finding a vertical hemifield effect (hypothesised here to constitute a LVF advantage) for global motion on RDK tasks would not, in itself, be evidence of functional specialisation. It may, for example, merely be indicative of a general LVF processing advantage for the global level of any stimulus, whether static or moving. To test this possibility, a novel experiment was designed, in which observers were required to spatially integrate diversely oriented static lines in order to extract a global orientation of the whole stimulus. If a similar vertical hemifield effect were found for both this task and the RDK tasks, the notion of a single vertical hemifield being specialised for processing global motion would be unsustainable. However, should the global orientation task produce a performance advantage in the opposite hemifield to that of global motion tasks, or should no vertical hemifield effect be observed, the fundamental hypothesis would be supported.

Nevertheless, even if the hypothesised functional specialisation for global motion were supported by findings from the global orientation task, the possibility would remain that the RDK tasks simply tapped a vertical hemifield effect that might be observed for all classes of motion stimuli. Investigating vertical hemifield sensitivity in response to all forms of motion would be beyond the scope of a single thesis. However, a particularly obvious distinction can be made between global motion, as presented in RDKs, and local (i.e., single-element) motion. Indeed, the neural machinery that appears to underly the percepts of global and local motion appear to remain separate throughout visual cortex (Born, 2000; Born & Berezovski, 2000; Born & Tootell, 1992). It would have been premature therefore, to presume that the same vertical hemifield effect would manifest for both global and local motion stimuli.

Thus, in order to further ascertain whether the vertical hemifields differ in sensitivity to global and local motion signals, a final experiment was conducted in which observers were required to covertly track the trajectory of a single moving element in each vertical hemifield. Again, if the local motion task produced a similar vertical hemifield effect to that found in the RDK tasks the hypothesis that a single vertical hemifield is functionally specialised for processing global motion would be invalidated. However, should differing patterns of sensitivity be observed for global and local motion in the vertical hemifields, or should a vertical hemifield effect be observed for global, but not local motion, the guiding experimental hypothesis would be supported.

7.2 The Experiments in Brief

Experiment 1 explored sensitivity to unidirectional motion and had two principal goals. Firstly, to better ascertain which stimulus parameters might be most important for eliciting vertical hemifield effects in global motion processing. Secondly, to expand on the previous work by presenting partially coherent RDKs to each vertical hemifield in two further novel conditions. In an initial condition, foveal viewing was unencumbered. In a second condition, an RDK containing wholly random (noise) dot motion was presented at fixation, and in a third condition, a static dot pattern was similarly presented.

Distractor stimuli might be expected to tax the visual system by 'pulling' attentional resources away from the test stimulus and toward the distractor. However, there is also evidence to suggest that concurrent stimulation within the visual field can positively influence discriminations made in the vertical hemifields. For example, a secondary task at fixation has been found to benefit object identification in the UVF (Beer, Galloway, & Previc, 1996), while Rezec, Bosworth, and Dobkins (2000) observed a LVF motion sensitivity advantage only when random motion distractors were also present within the visual field.

Experiment 2 tested vertical hemifield performance on a motion 'transparency' task. Observers judged both directions of motion in an RDK containing two superimposed 'sheets' of dots that moved perpendicularly relative to each other. Single-cell data from monkeys has shown that performance on this task is also crucially dependent on cortical mechanisms (Qian & Andersen, 1994a; Snowden, Treue, Erickson, & Andersen, 1991) that are known to have a physiological bias toward the LVF. Moreover, there is evidence to suggest that the perception of two moving surfaces within a transparent RDK cannot be performed in parallel, but must occur serially (Cobo, Pinilla, & Valdes-Sosa, 1999; Pinilla, Cobo, Torres & Valdes-Sosa, 2001; Valdes-Sosa, Cobo, & Pinilla, 1998; 2000). This suggests that perception of bidirectionality might depend on the allocation, disengagement, and reallocation of attention from one direction of motion to the other. Again, this ability may differ according to vertical hemifield.

The goal of Experiment 3 was to determine whether the vertical hemifields might differ in susceptibility to the effects of 'motion capture'. The stimuli used here were RDKs composed of three regions. A central test region differed from two flanking regions in both its motion coherence level and its signal direction. When segmented RDKs contain a greater percentage of coherent motion within some regions, there is a tendency for the stronger motion signals to produce perceptual 'capture' of the weaker motion signals (Møller & Hurlburt, 1996; Nawrot & Sekuler, 1990). This creates the percept of a nonsegmented RDK, which contains one uniform direction of motion. The ability to maintain the perception of contrasting motions therefore demonstrates resilience to motion capture effects.

Experiment 4 sought to determine whether vertical hemifield effects for processing global motion might also exist on a non-motion task that is computationally analogous in many respects to the RDK paradigm. The stimulus consists of a number of line elements, some of which share a common orientation (signal), while others are randomly oriented (noise). Similar to RDK stimuli, the line segments must be spatially integrated across the entire stimulus in order for a global percept of orientation to be achieved. As with Experiment 1, performance on this task was measured both with and without a foveal distractor, which contained line segments with wholly random orientations.

Vertical hemifield effects in the perception of a single moving object were investigated in Experiment 5. The aim here was to test the possibility that the mechanisms underlying global and single element motion might operate to different effect in the vertical hemifields. The stimulus was a round object, which appeared suddenly at an unpredictable location in either the UVF or LVF, travelled rapidly along a horizontal path, then abruptly vanished at an unpredictable point in its trajectory. The task was to determine the location of the vanishing point. In addition to comparing spatial localisation abilities within the vertical hemifields, the magnitude of the ‘representational momentum’ effect was also investigated. This effect is characterised by judged forward displacements of the actual vanishing point of a moving stimulus (e.g., Hubbard, 1994).

Finally, a case study is presented in which the performance of an albino observer is compared with the data obtained from Experiments 1. Albinism was chosen because of its detrimental effect on retinal development. The higher density of ganglion cells found in the upper hemiretinae of adults is not present at birth, but develops during infancy (Schwartz, Dobson, Sandstrom, & van Hof-van Duin, 1987). However, the albino retina suffers arrested development within the first year of life (Wilson, Mets, Nagy, &

Kressel, 1988b). Because the quality of early sensory input has been shown to impact on cortical development (Garey & DeCourten, 1983; Kingsbury & Finlay, 2001), the possibility of differing sensitivity to global motion in the vertical hemifields of albinos and normals offers an opportunity to comment on the aetiology of functional differences in the vertical hemifields. Previc (1990) has argued that vertical hemifield effects in high-level vision must be 'hard-wired' and so be relatively impervious to experience. However, some commentators (e.g., Breitmeyer, 1990; Bryden & Underwood, 1990) counter that the environment encountered during infancy is sufficient to produce functional vertical asymmetry without a need for 'hard-wiring'.

Experiment 1: Sensitivity to Global Motion in the Vertical Hemifields with and without Foveal Distractors

Abstract

There is growing physiological evidence to suggest that the vertical hemifields differ in sensitivity to global motion. However, few behavioural studies have addressed this possibility. Presenting unidirectional RDK stimuli to 33 observers, this investigation tested motion sensitivity, using a psychophysical staircase procedure, at three different locations in each vertical hemifield (on the vertical meridian and in each visual quadrant), to four directions of motion (rightward, leftward, upward, downward), at two stimulus durations (5-frames and 10-frames) and in three further conditions; with the stimulus presented in isolation; with randomly moving dots at fixation; and with static dots at fixation. Results indicate that the LVF is more sensitive than the UVF to global motion when an RDK stimulus is presented in isolation, and when a random motion distractor is present at fixation. No hemifield effect was found in the static dot condition. The UVF proved to be especially sensitive to downward motion, while a smaller upward motion bias was found in the LVF. Motion sensitivity in the vertical hemifields was independent of performance in the horizontal hemifields.

Chapter 8:

Experiment 1: Sensitivity to Global Motion in the Vertical Hemifields with and without Foveal Distractors

8.1 Introduction

There is a scarcity of studies measuring global motion sensitivity in the vertical hemifields of normal observers. In all but one case, hemifield differences in motion sensitivity *per se* were not the primary goal of the investigation. Two studies investigated directional asymmetries in various regions of the visual field (Edwards & Badcock, 1993, Experiment 3; Raymond, 1994, Experiment 2). Both demonstrated a trend toward greater sensitivity in the LVF. A third study was concerned with decrements in directional sensitivity throughout the visual field in glaucoma patients, with normal observers acting as controls (Joffe et al., 1997). No vertical hemifield difference was found. Only an unpublished study by Rezec et al., (2000; Experiment 1) was concerned primarily with vertical hemifield effects in motion sensitivity. Again, they report no general vertical hemifield effect. Refer Table 1 for a summary of the methods used in these studies.

Although all four studies employed RDK stimuli, their stimulus parameters and methodologies varied widely, and it is feasible that this may account for the discrepant findings. Thus, the aim of this study was to firstly determine whether the vertical hemifields differ in sensitivity to global motion, and secondly, to ascertain whether vertical hemifield-specific directional anisotropies exist. To achieve this goal I first attempted to identify from previous studies those stimulus parameters that appear to be necessary for eliciting motion sensitivity differences in the vertical hemifields. I then attempted to expand upon the previous studies by testing motion sensitivity under a wider range of experimental conditions.

Because Edward and Badcock (1993) tested only two observers it would be unwise to make inferences from their findings. However, a comparison of the methods employed by Joffe et al., (1997), Raymond (1994), and Rezec et al., (2000) indicate three particular stimulus parameters that might impact on the likelihood of elicting vertical hemifield effects in motion perception.

Firstly, there are considerable differences in dot density. Both Joffe et al's (1997) and Rezec et al.'s (2000) dot density was much lower than that employed by Raymond (1994). Furthermore, their dot sizes were relatively large compared to those used by Raymond (1994). Low density RDKs are thought not to activate motion integration mechanisms as effectively as higher density stimuli (Braddick et al., 2001). With this in mind, the present study employed dots similar in size to those employed by Raymond (1994), but presented at a density nearly 20x that employed by Rezec et al (2000).

Secondly, there are differences in the motion directions tested. Although Joffe et al. (1997) reported a mean threshold derived from all four cardinal directions, Raymond (1994) measured sensitivity for both directions along the vertical axis, while Rezec et al., (2000) tested horizontal axis motion only. At fixation, sensitivity to motion along the horizontal axis is isotropic (Raymond, 1994) and there is no *a-priori* reason to expect that this would differ in either vertical hemifield. However, Raymond (1994) did report greater sensitivity for upward vs. downward motion in the LVF. Thus, to better determine whether directional anisotropies exist in the vertical hemifields, the present study measured thresholds for all four cardinal directions of motion.

Third, Joffe et al's (1997) dot speed was the lowest of the three studies and this factor, combined with the relatively long lifetime of each frame and the availability of cues as to the forthcoming location of the stimulus, may have rendered the task too easy to have elicited vertical hemifield effects in healthy observers [10]. Indeed, the dot speeds employed in all four studies were below the optimal response of V5 cells (10^{O}/sec; Chawla, Phillips, Buechel, Edwards, & Friston, 1998). A velocity close to this level, and within the tuning

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[10] This underlies the need for research that explicitly addresses vertical hemifield effects in normals. Joffe et al.'s interest lay in the performance of a clinical population and the stimulus parameters were selected with the visual abilities of these observers in mind.

bandwidth of 80% of V3 cells (Felleman & Van Essen, 1987) was therefore employed here.

All previous studies presented stimuli at a single duration only. However, the relationship between response accuracy and the number of component frames within an RDK is nonlinear. This is evidenced by an initial dramatic improvement in thresholds with increased frames that asymptotes at about 10 frames (McKee & Welch, 1985; Raymond & Isaak, 1998; Snowden & Braddick, 1989; Williams & Sekuler, 1984). This 'temporal recruitment' effect is thought to reflect cooperativity among cells with similar directional tuning (Snowden & Braddick, 1989; Williams, Phillips, & Sekuler, 1986). To ascertain whether temporal recruitment effects differ between the vertical hemifields, RDKs composed of two different frame numbers were presented here; a shorter 5-frame stimulus, to measure sensitivity differences, and a longer 10-frame stimulus, to establish whether additional motion information is utilised more effectively by either vertical hemifield.

When tested on the horizontal meridian normal subjects do not exhibit lateralisation effects for global motion (Bosworth & Dobkins, 1999; Raymond, 1994). Nevertheless, interaction effects between the horizontal and vertical hemifields have been reported in both visual search studies and with Navon-type stimuli (see e.g., Christman & Niebauer, 1997; Fecteau et al., 2000; Niebauer & Christman, 1998). To determine whether this is also the case with motion perception, I presented RDKs at three separate locations within each vertical hemifield, a central region located on the vertical meridian, and in each of the visual quadrants.

A final additional manipulation involved presenting both moving and static RDKs at fixation simultaneously with the peripheral test stimulus. This was done to determine the robustness of any vertical hemifield effect found. Distractor stimuli might be expected to tax the visual system by 'pulling' attentional resources away from the test stimulus and toward the distractor. Thus, the degree to which the distractor adversely affects motion thresholds might reflect the ability of motion mechanisms in each vertical hemifield to inhibit processing of the distractor stimulus. However, there is also evidence to suggest that concurrent stimulation within the visual field can positively influence discriminations made in the vertical hemifields. For example, a secondary task at fixation has been found to improve object recognition in the UVF (Beer et al, 1996), while Rezec et al., (2000; Experiment 2) observed a LVF motion sensitivity advantage only when a test stimulus was presented to one visual quadrant, while the remaining three quadrants contained RDKs displaying noncoherent motion.

The motion-distractor was purposely chosen so as not to convey any information that may have 'primed' directional judgements, a manipulation shown to have particularly deleterious effects on direction perception (Raymond, O'Donnell, & Tipper, 1998). This stimulus contained wholly noncoherent, directionally wide-band noise which, compared to the no-distractor condition, effectively decreased the signal-to-noise ratio for the direction of motion in the test RDK. Thus, this distractor was intended to tax the noise reduction mechanisms hypothesised to extract the signal direction from the noise distribution in partially coherent RDKs. If the LVF is functionally specialised for global motion processing it seemed reasonable to expect that additional motion noise would have less effect on performance in the LVF than in the UVF.

The possible effects of the static distractor were less clear. Studies have shown that RDKs containing intermingled moving and static dots have a detrimental effect on motion sensitivity in both humans (e.g., Baker, Hesse, & Zihl, 1990; Vaina, LeMay, Bienfang, Choi, & Nakayama, 1991) and in monkeys (Snowden et al., 1991). Presumably, this is an indication that global motion mechanisms have difficulty inhibiting static dots. On the other hand, because the static and moving dots were spatially offset, it was also possible that the textured dot pattern might provide a perceptual referent by which the global direction in the test RDK could be compared. In this case, lower thresholds might result.

8.2 Method

8.2.1 Participants

Thirty-three undergraduate observers participated in this study for partial course credit. All were either emmetropic or used prescribed optical corrections and were inexperienced psychophysical observers naïve to the purpose of the study. None reported having undergone surgery to correct visual problems, nor any prior or present neurological condition. None had received a diagnosis of dyslexia [11].

Observers were randomly allocated in equal numbers to one of the three distractor groups [12]. The 'no-distractor' group consisted of 8 females and 3 males with a mean age of 19.7 years (s.d. = 1.1 years); the 'motion-distractor' group were 10 females and 1 male with a mean age of 21.2 years (s.d. = 3.0 years); the 'static-distractor' group comprised 7 females and 4 males with a mean age of 21.4 years (s.d. = 3.0 years).

8.2.2 Apparatus

All stimuli were generated by a Power Macintosh 8500/120 computer and were displayed on a 17" AppleVision 1710 monitor with a vertical refresh rate of 60 Hz. A height-adjustable chair and ophthalmologic viewing brace were provided to maintain a steady and comfortable viewing posture.

8.2.3 Stimuli

The fixation spot was a 0.1^0 white square, presented for 333 msecs either 5^0 below (for UVF locations) or 5^0 above (for LVF locations) the centre of the monitor.

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[11] Dyslexics were excluded from participation in all experiments as evidence suggests that some demonstrate deficits in motion perception (e.g., Everatt, Bradshaw, & Hibbard, 1999; Hill & Raymond, 2002).

[12] A mixed design was chosen because concern has been raised that performance in the vertical hemifields might be unusually susceptible to the order of task presentation in within-subject designs, despite efforts to counterbalance (see Nieubauer & Christman, 1998).

Both the test and distractor RDKs and the static dot patterns contained an average of 213 white dots, each with a diameter of 1.31 minarc and contained within a borderless square area subtending 2.18^0 x 2.18^0. Mean dot density was 45 dots/deg^2. The space-averaged (dot and background) luminance of both the test and distractor stimuli was 0.97 cd/m^2, presented against a luminance of 0.01 cd/m^2 provided by the monitor background, thus providing a luminance contrast of 98% between the RDK and the surrounding regions of the monitor.

The lifetime of a single test RDK frame was equivalent to one screen refresh (i.e., 16.6 ms) and successive frames were presented without an interstimulus interval. With each new frame, both signal and noise dots were displaced by 10.48 minarc, corresponding to a velocity of 10.5 deg/sec. Noise dots were randomly repositioned without regard to their prior locations and dots moving out of the stimulus area were ‘wrapped-around’, reappearing in the mirror location on the opposite side.

Test RDKs were presented for durations of 5-frames (83 msecs) and 10-frames (166 msecs) at three separate locations in each vertical hemifield. In the upper-centre and lower-centre locations the RDK was presented in the centre of the monitor. In the upper-left and lower-left quadrants, each RDK was presented leftward of this position at a centre-to-centre distance of 5^O. The upper-right and lower-right RDKs were located at a similar distance rightward of the monitor centre. Hence, the diagonal distance from both the upper and lower fixation points to the centre of each quadrant RDK was 7.07^O. Figure 4a illustrates the relative locations.

Both the motion- and static-distractors were centred on the prior location of the fixation spot. They appeared and disappeared simultaneously with the test RDKs. Their dot size, density and mean luminance was identical to those of the test RDKs. The motion-distractor contained only noncoherent motion (i.e., there were no signal dots) and the component dots moved in an identical fashion to the noise dots in the test RDK. The ‘static-distractor’ consisted of a single, stationary RDK frame whose dot pattern was randomly

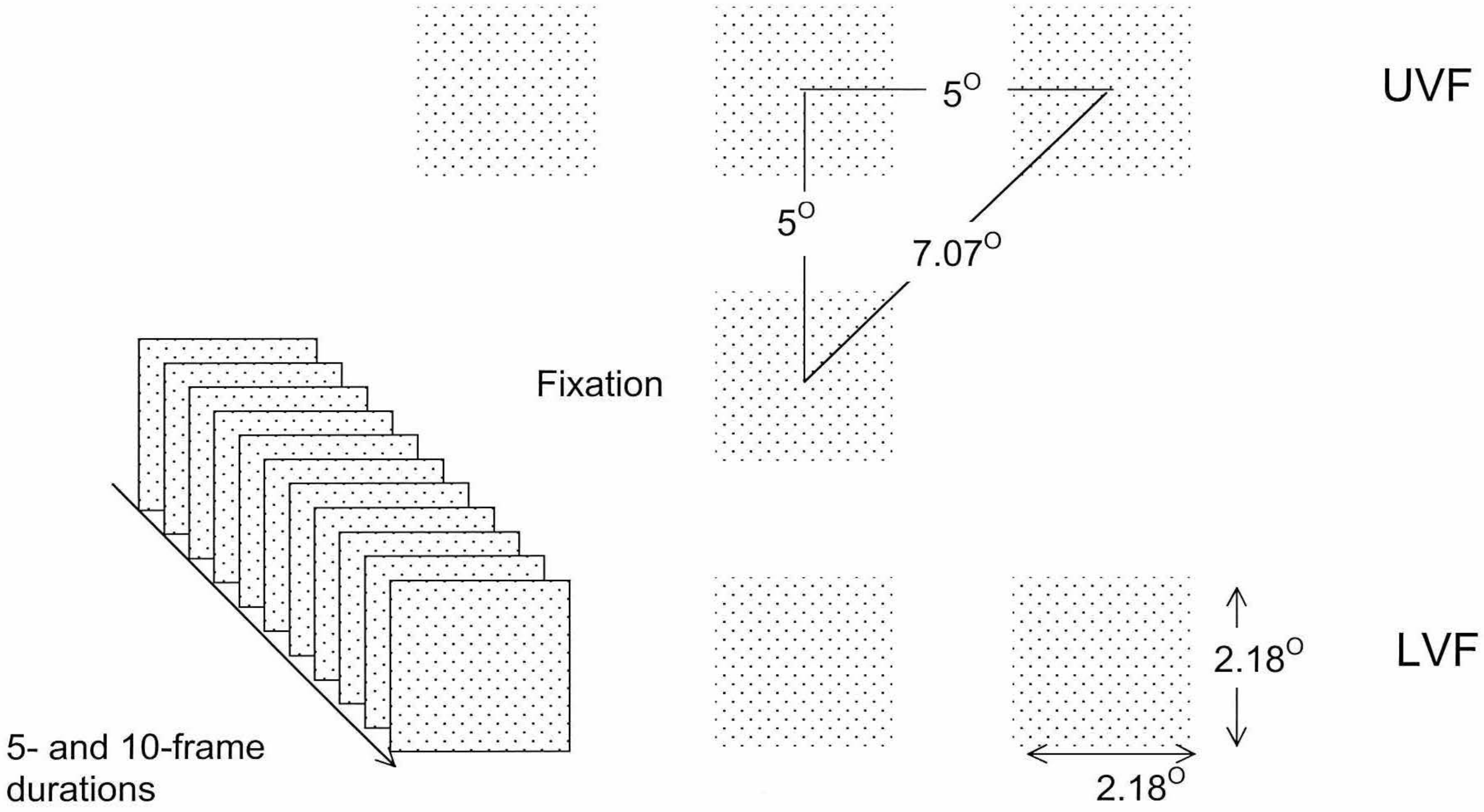

Figure 4a. Schematic of the locations of the RDKs employed in Experiment 1. In the ‘no-distractor’ condition, the central distractor RDK was absent.

produced and so differed on each trial. This pattern was then re-presented for the relevant number of frames.

8.2.4 Procedure

All observers viewed the displays binocularly at a distance of 92 cm in a dimly lit room. Trials were initiated by the experimenter, and presented at a pace found to be comfortable for individual participants. The fixation spot, signifying the onset of each trial, was followed, without interstimulus interval, by either a test RDK alone ('no-distractor' group) or by the simultaneous presentation of a test RDK and a distractor ('motion-distractor' and 'static-distractor' groups). Figure 4b illustrates the timeline of a typical trial.

On each trial, the percentage of signal dots in the test RDKs were determined by four randomly interleaved 2-down, 1-up psychophysical staircases, testing rightward, leftward, upward, and downward motion. The first trial in any single direction was always presented at 100% coherence. A correct response on two successive trials with the same signal direction resulted in the percentage of signal dots being halved for the next trial in the same direction. Conversely, an incorrect response resulted in the percentage of signal dots being increased by half the current value for the next trial in that direction. The staircase was terminated after six such response reversals for each direction, and a coherence threshold was calculated from the mean percent coherence used in the last six reversals. This value represents the coherence value needed for correct identification on 71% of trials. One staircase was presented at each location, at both durations.

Observers verbally reported the perceived global direction within the test RDK. Responses were entered into the computer by the experimenter, who was blind to the stimuli. No feedback was given. Each session began with practice trials and data collection commenced only when participants indicated that they understood the procedure. The order of presentation of each location x duration block was randomised for each observer.

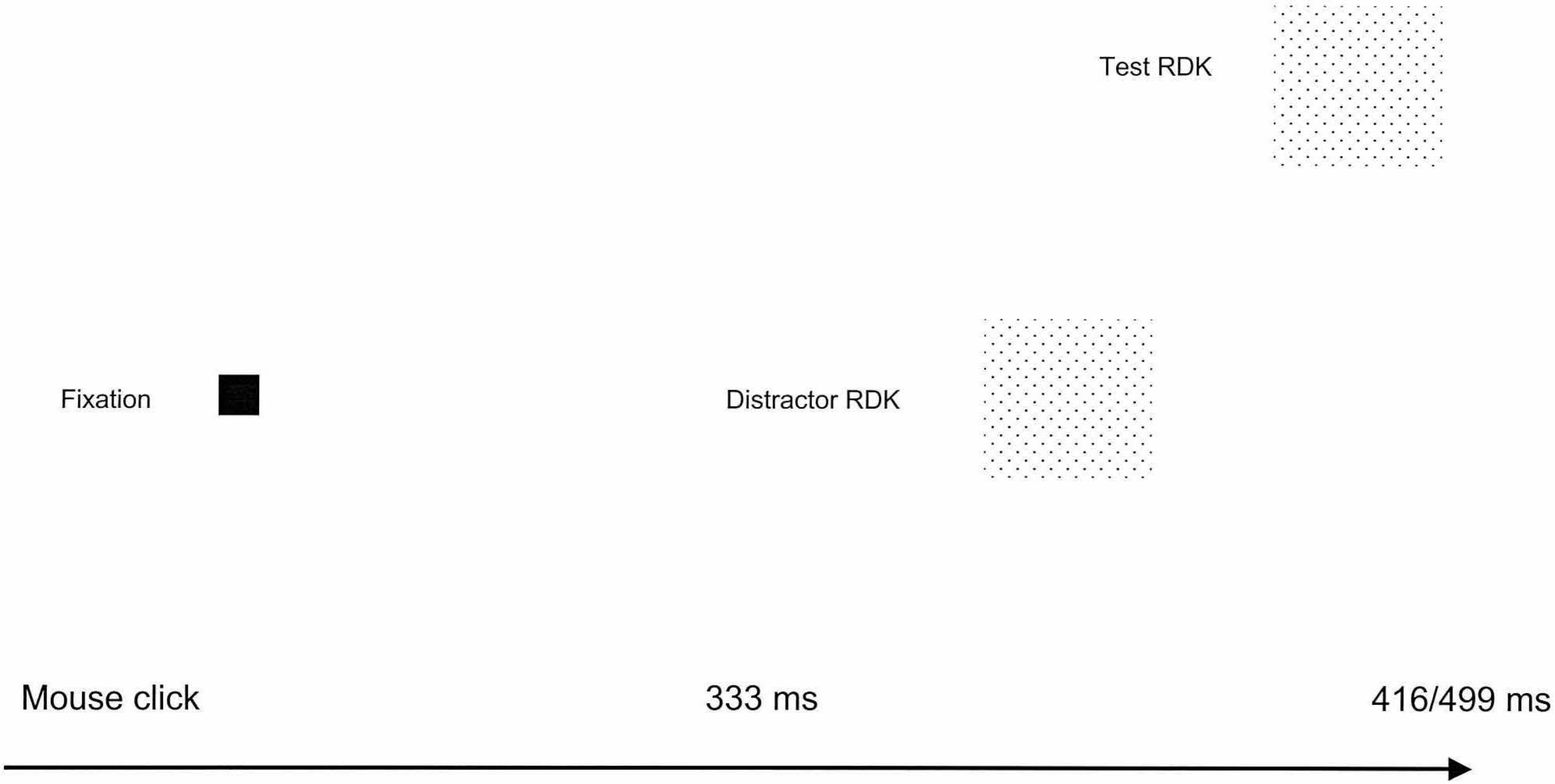

Figure 4b. Time line of a typical trial. A mouse click resulted in a presentation of the fixation marker. After 333 ms the fixation marker disappeared and was replaced, without any interstimulus interval, by a simultaneous presentation of the test (judged) and distractor RDKs. The distractor RDKs (motion and static) were centred on the prior location of the fixation marker. In the example shown, the test RDK is presented in the upper-right quadrant. In the no-distractor condition, the offset of the fixation marker resulted in no further stimulus present at fixation.

8.3 Results

This experiment had two aims. Firstly, to ascertain whether the vertical hemifields differ in motion sensitivity and under which experimental conditions hemifield effects are observed. Secondly, to ascertain whether directional anisotropies exist in the vertical hemifields. To address the first question, the directional thresholds obtained from each test RDK location were collapsed into single motion coherence thresholds. These thresholds were then subjected to a mixed ANOVA with distractor group (no-distractor, motion-distractor, and static-distractor), as a between-subjects factor, and vertical hemifield (UVF, LVF), horizontal location (left, centre, and right) and duration (5-frames and 10-frames) as within-factors.

A main effect of vertical hemifield was found, F (1, 30) = 38.51, p < .01, reflecting generally higher global motion sensitivity within the LVF vs. UVF. There was a main effect of duration also, F (1, 30) = 90.15, p < .01, with lower overall thresholds obtained at the 10-frame vs. 5-frame duration. In agreement with previous work (Bosworth & Dobkins, 1999; Raymond, 1994) no effect of horizontal location was found, and this factor is disregarded in further analyses. There was similarly no main effect of distractor group. However, a significant vertical hemifield x group interaction was found, F (2, 30) = 4.09, p < .05. A vertical hemifield x duration interaction was absent, suggesting there is no difference in temporal recruitment abilities in the vertical hemifields. No three-way interactions were observed (these data are illustrated in Figures 5a and 5b).

Figures 5a and 5b suggest that the source of the distractor group x vertical hemifield interaction lies in the static-distractor group. To confirm this, the data from each distractor group were subject to separate within-subject ANOVAs (duration x vertical hemifield).

These analyses revealed a LVF sensitivity advantage in both the no-distractor, F (1, 10) = 17.11, p < .01, and motion -distractor groups, F (1, 10) =

23.09, p < .01, with the absence of any interactions in both cases. However, the vertical hemifield effect was absent in the static-distractor group.

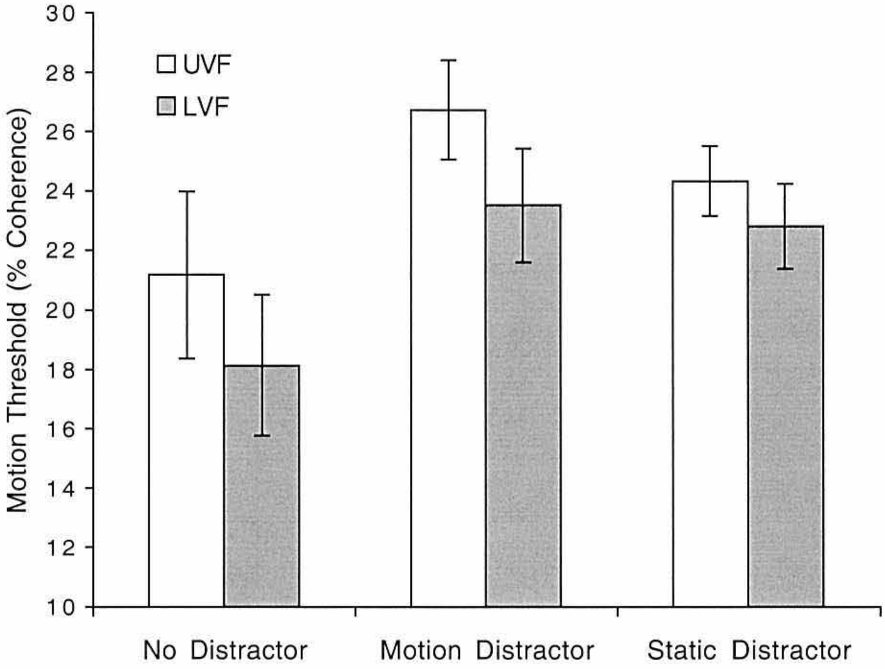

Figure 5a. Motion coherence thresholds obtained in the UVF and LVF at the 5-frame duration as a function of distractor group. Vertical bars represent +/- 1 standard error of the group mean.

To assess the prediction that hemifield-specific directional anisotropies would be found for motion along the vertical axis, direction thresholds from each of the test RDK locations were averaged across locations and groups as a function of vertical hemifield and included in two three-way within-subjects ANOVAs employing vertical hemifield and direction as factors. At the 5-frame duration, a main effect of direction was observed, F (3, 30) = 4.00, p < .05, as well as a significant vertical hemifield x direction interaction, F (3, 30) = 17.76, p < .01. This pattern was repeated at the 10-frame duration; a main effect of direction, F (3, 30) = 6.68, p < .01, and a significant vertical hemifield x direction interaction, F (3, 30) = 19.92, p < .01. One-way, within-hemifield ANOVAs performed at the 5- and 10-frame durations revealed significant effects of direction in all cases, p < .01 at both durations in the UVF and p < .01 and p < .05 in the LVF, for the 5- and 10-frame durations, respectively. Direction thresholds are plotted in Figures 6a and 6b as a function of vertical hemifield and duration.

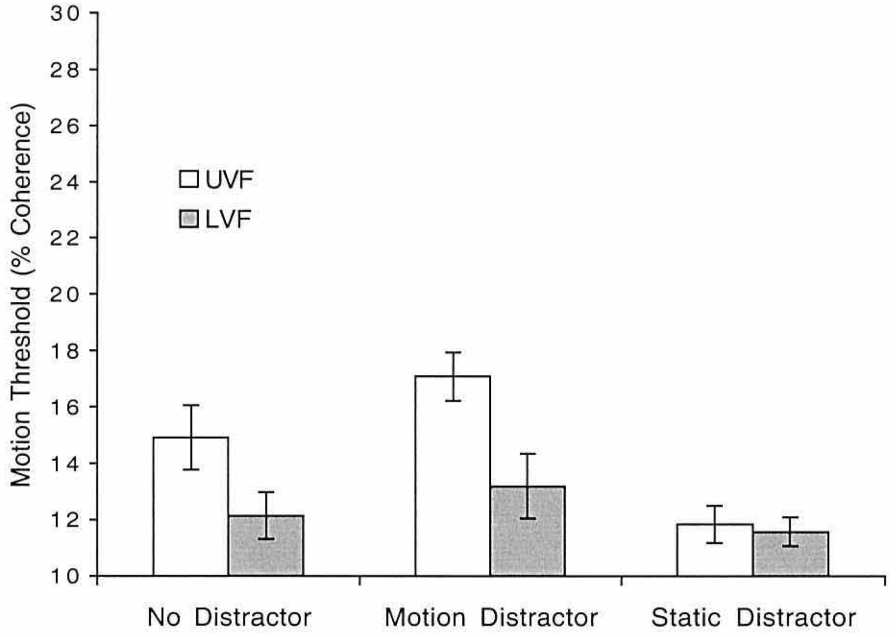

Figure 5b. Motion coherence thresholds obtained in the UVF and LVF at the 10-frame duration as a function of distractor group. Vertical bars represent +/- 1 standard error of the group mean.

As Figures 6a and 6b illustrate, thresholds obtained from vertical axis motion show the opposite pattern of sensitivity in the vertical hemifields, regardless of duration. As hypothesised, and in agreement with Raymond's (1994) finding, planned means comparisons revealed a sensitivity advantage for upward vs. downward motion in the LVF, for both 5- and 10-frame durations (both p < .05). Conversely, in the UVF, a downward sensitivity advantage was evident for the 5- and 10-frame durations (both p < .01).

Sensitivity differences were also obtained for motion along the horizontal axis, though the pattern was less clear. In the UVF, the right-left comparison was nonsignificant at the 5-frame duration, but a significant difference was found, in favour of rightward motion (p < .05) at the 10-frame duration. In contrast, a leftward sensitivity advantage ($p < .05$) was found in the LVF at 5-frames, with a nonsignificant result at 10-frames. This suggests there may be subtle, direction specific differences in temporal recruitment abilities in the vertical hemifields.

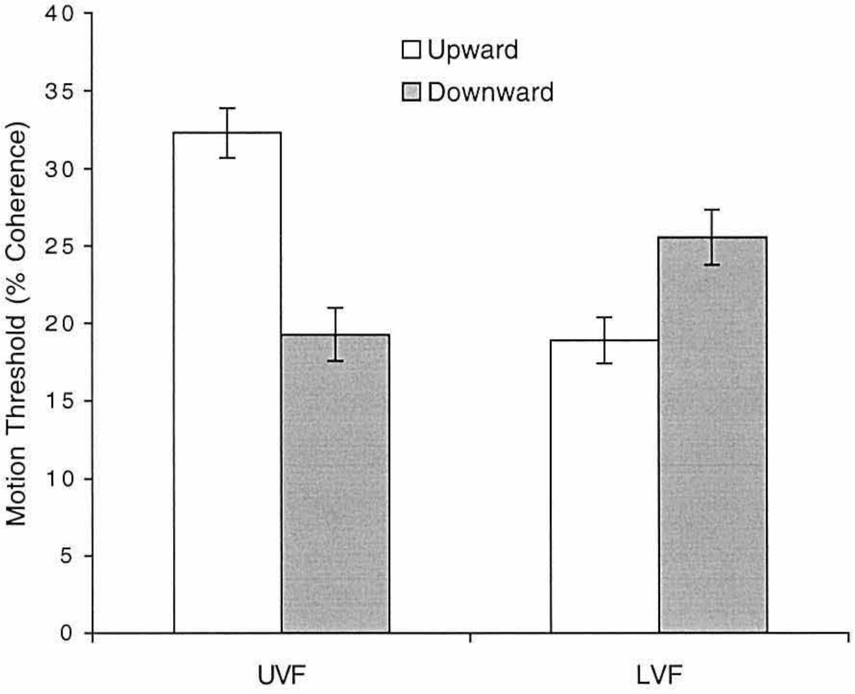

Figure 6a. Coherence thresholds for vertical axis motion obtained in the UVF and LVF at the 5-frame duration. Data are collapsed across the distractor groups. Vertical bars represent +/- 1 standard error of the mean.

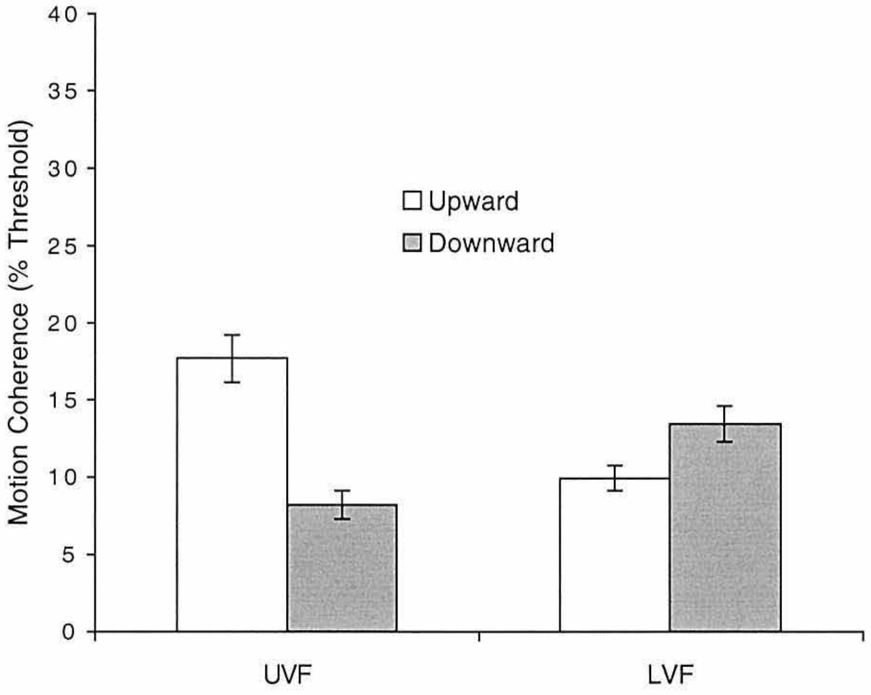

Figure 6b. Coherence thresholds for vertical axis motion obtained in the UVF and LVF at the 10-frame duration. Data are collapsed across the distractor groups. Vertical bars represent +/- 1 standard error of the mean.

8.4 Discussion

The purpose of this experiment was to determine whether the vertical hemifields differ in sensitivity to global motion, and to better identify the stimulus parameters that might elicit a performance difference. A second aim was to ascertain whether the vertical hemifields exhibit differing patterns of anisotropy for motion direction.

Two findings are particularly salient. A sensitivity advantage for global motion was observed in the LVF when either no distractor was present, or when a motion-distractor was simultaneously presented at fixation. However, no hemifield effect was found in the static-distractor condition. Robust hemifield-specific anisotropies were observed for motion along the vertical axis. This was evidenced by heightened sensitivity to upward motion in the LVF and to downward motion in the UVF. Other findings of note include a lack of any interaction between the horizontal and vertical hemifields, and a similar degree of temporal recruitment ability in both vertical hemifields.

One question must be addressed. Because eye movements were not monitored, it could be argued that sensitivity differences between the hemifields resulted from the habitual shifts in gaze from the fixation spot to the test RDKs. This doubt is compounded by the use of blocked locations, in which the fixation point acted as a valid spatial precue. Nevertheless, there are a number of reasons to suggest that (i) observers did not habitually refixate, (ii) if they had, performance in the UVF would most likely benefit, and (iii) randomly located stimuli might have produced a larger LVF advantage. Some of these points were discussed in the literature review, but they are worth reiterating and expanding on here because they are applicable to all of the experiments reported in this thesis.

Firstly, it is highly unlikely that the stimulus duration was sufficient to have permitted refixation. Even with a predictive target location and practice, express saccades normally require a minimum of 100 ms to program, with additional time needed for transit (Fischer & Rampsberger, 1984; 1986). This programming time alone is longer than the stimulus duration employed in the 5-frame condition. Although at least one study has explicitly tested the efficacy of the 'instruction-only' fixation method (Jordan, Patching, & Milner, 1998), the mean distance of the eye movements they observed was consistently less than 0.5°.

Secondly, upward saccades are faster and more accurate than downward saccades (Chedru et al., 1973; Enright, 1984; 1989; Hackman, 1940; Hall, 1985; Heywood & Churcher, 1980; Honda & Findlay, 1992; Levy-Schoen, 1969; Miles, 1936; Previc, 1996; Zelinsky, 1996). Furthermore, the simultaneous presentation of two stimuli of the same size and luminance, such as in the motion- and static- distractor conditions, would produce hypometric saccades (Findlay, 1982; Ottes, van Gisbergen, & Eggermont, 1984) while saccades directed toward the visual quadrants tend to be slower than those aimed along the vertical meridian (Bahill & Stark, 1975). Both points suggest that habitual refixation would favour central vs. quadrant locations. However, no effect of horizontal location was found.

Thirdly, the ability to predict the location of a forthcoming stimulus does not appear to improve performance in the LVF. Rezec et al. (2000) found that valid spatial precues presented in the visual periphery actually produced higher motion thresholds in the LVF compared to trials in which no precue was presented. Similarly, in a visual search task, Previc et al. (1992) observed a UVF advantage for both response latency and accuracy with both neutral and valid precues

The main finding of a LVF motion sensitivity advantage in two of the three distractor-groups supports and extends previous data (Edwards & Badcock, 1993; Raymond, 1994). The finding also lends some support to Previc's (1990; 1998) view that the LVF is functionally specialised for processing global motion. Leaving the result from the static-distractor group aside for the moment, there are two reasons to suggest why a LVF advantage was found here but not by Joffe et al. (1997) and Rezec et al. (2000; Experiment 1).

One possibility concerns the much higher dot density presented here. Low dot densities afford less opportunity for summation mechanisms to take effect within receptive fields (Braddick et al., 2001). Thus, whether or not a LVF motion processing advantage is observed might depend on some minimum dot density being present within an RDK. A comparison of RDK dot densities employed in studies that have elicited superior performance in the LVF (i.e., the present study and Raymond, 1994) with those showing no vertical hemifield effect (i.e., Joffe et al., 1997; Rezec et al., 2000; Experiment 1) suggests that this minimum density might lie somewhere between 10 and 20 dots/deg^2.

Further, motion-processing mechanisms in the LVF may be activated more efficiently at higher velocities. Imaging work indicates the optimal tuning response of V5 cells to be 10^{O}/sec (Chawla et al., 1998). This equates with the speed used in the present study and is considerably faster than the velocity used by, for example, Joffe et al. (1997). The optimal response of macaque V3 cells is higher still, with 50% displaying a peak-firing rate at 16°/sec (Felleman & Van Essen, 1987). Thus, slower moving stimuli might be relatively ineffective at producing a LVF performance advantage on motion tasks.

It is feasible that motion processing in the LVF benefits from a combination of high dot density and fast velocities. This notion would seem to fit with ecological theories of vision, which place strong emphasis on both the highly textured appearance of the ground plane image (Gibson, 1961) and the high rates of optic flow in the LVF experienced during forward locomotion (Lee, 1980; Young & Oman, 1974).

What might explain the LVF sensitivity advantage being found in the no-distractor and motion-distractor groups, but not in the static-distractor group? It seems highly unlikely that the observers in this group differed in any systematic way from obervers in the other groups. Identical criteria were required for all participants, who were then randomly allocated to each group.

The motion-distractor operated as predicted as it produced increased motion thresholds, in both vertical hemifields, relative to the no-distractor condition. The additional motion noise could have had two effects. The mere presence of a distractor might have resulted in limited attentional resources being allocated to both the distractor and the test stimulus, resulting in less effective processing of the signal direction in the test RDK. However, if the presence of a distractor alone had resulted in limited attentional resources being allocated to the test stimulus, a similar increase in thresholds would be expected in the static-distractor group., The second possibility is that the additional motion noise was included in the summation process, making the signal direction of motion more difficult to extract from the noise distribution. This would explain why the motion distractor caused a greater increase in thresholds at the 5-frame duration, than did the static-distractor.

At the 5-frame duration, the presence of the static dot pattern initially raised motion thresholds, relative to the no-distractor condition, in both vertical hemifields. Thus, at this duration, the static dot pattern acted in the same manner as the motion distractor. However, at the 10-frame duration, performance in both the UVF and LVF was similar to that of the LVF in the no-distractor group. Thus, equal performance in the vertical hemifields in the static-distractor group was not due to any adverse effect on motion processing in the LVF, but to the static dots somehow aiding motion perception in the UVF.

The only difference between the two distractors lay in the presence or absence of motion. This indicates that the distractor stimuli would have engaged fundamentally different visual mechanisms. If the LVF is functionally specialised for processing global motion, it is reasonable to assume that attention will be more effectively allocated to the LVF during motion tasks. Also, as the requirement for processing resources is increased, such as in the motion-distractor condition, the attentional resources available for global motion perception should be more effectively garnered in the LVF. Conversely, if the UVF is specialised for pattern and object recognition, as the visual search literature might suggest, then the need for increased resources due to the presence of a textured dot pattern, may have facilitated the allocation of attention toward the UVF.

This view suggests a top-down, late-selection, attentional mechanism able to be directed toward certain regions of the visual field, while suppressing responses to other locations, according to current processing demands. Single cell recordings obtained from monkey cortex support this view. Seidermann and Newsome (1999) presented monkeys with two partially coherent RDKs, one of which required a discrimination of direction while the other was ignored. Attentional modulation occurred late on all trials, suggesting modulation within MT cells only after some decision process had occurred. At the 5-frame duration in the static-distractor condition, there may have been insufficient time for attentional modulation of UVF motion mechanisms to take effect. However, with an additional five frames, attentional modulation of motion mechanisms may have been achieved, with processing benefits for the UVF.

A perceptual explanation is also possible. The presence of a static dot pattern with a high luminance contrast, located close to the test RDK, might have provided a stationary referent by which the coherent motion signals could be compared. The stimuli were viewed in dim lighting and so the motion-defined border of the monitor surround would be unlikely to have offered the opportunity to provide a similar referent, due to its low contrast. Furthermore, although increases in spatial resolution do not aid perception of global direction in RDKs (Morgan, 1992; Smith, Snowden, & Milne, 1994) attending to the textured dot pattern might have increased resolution of the border between the static dots and the background, allowing the texture border to be compared with the signal direction in the test RDK. Perhaps this ability to make motion-static signal comparisons does not differ according to vertical hemifield. If so, moving the static dots closer to the test RDK should not only produce lower thresholds in both vertical hemifields, but also maintain the equal hemifield performance. This possibility is addressed in Experiment 1A.

Whether perceptual or attentional in origin, the reason for the lack of a vertical hemifield effect in the static-distractor group adds further weight to evidence of a cortical, rather than a sensory locus for many vertical hemifield effects. Because the motion- and static-distractors were identical in spatial frequency and luminance, a sensory basis for the findings could only be reasonably argued if the LVF advantage had been found in all three distractor groups.

The upward vs. downward sensitivity bias found in the LVF concurs with Raymond's (1994) finding, and with evidence that MT cells representing the central 12^{O} of the visual field exhibit a centripetal directional bias (Albright, 1984). Raymond (1994) suggested that the bias might supplement optic flow computations, facilitating figure/ground segmentation against the centrifugally moving background normally encountered during forward locomotion. This is certainly feasible, however, it is equally likely that the anisotropy plays a role in the visual control of the forward sweep of the arm toward a target object.

The downward motion bias found in the UVF contrasts with the findings of Raymond (1994) and Edwards and Badcock (1993), both of whom found directional sensitivity to be isotropic within this hemifield. There is a single report, however, in which the same anisotropy was observed, although the methododology was dissimilar (Naito, Kaneoke, Osaka, & Kakigi, 2000). In this study, two red bars measuring 1.8^{O} x 0.1^{O}, spatially separated by 5^{O}, were presented alternately for 2-3 secs with a temporal gap of 16 msecs. Apparent motion, in either an upward or downward direction was produced. MEG amplitudes, which correlate with the degree of motion perception (Kawakami, Kaneoke, & Kakigi, 2000), were recorded. In contrast to findings from RDK studies (Raymond, 1994; the present study) Naito et al. (2000) found no anisotropy for vertical directions in the LVF. However, in the UVF response amplitudes to downward motion were significantly larger than to upward motion. Furthermore, the origin of the MEG response was determined to be located in dorsal extrastriate cortex.

The authors proposed that this anisotropy results from ecological demands made on the visual system. Due to the effects of gravity, objects in free-fall are encountered more often than upward moving objects. In addition, because the horizontal plane is slanted downward from the horizon to the observer, objects approaching from far space also tend to move progressively lower in the visual field. Thus, the visual system may simply have acquired a heightened sensitivity to those aspects of the visual array encountered most often. The fact that the anisotropy has been observed with both single element and global motion, which would be expected to activate different motion mechanisms, lends support to this notion.

The discrepancy between the findings of Raymond (1994) and Edwards and Badcock (1993), and those of Naito et al., (2000) and the present study, might also be explained with reference to stimulus velocity. Raymond's (1994) dots moved at 5^{0}/sec, while Edwards and Badcock (1993) employed a speed gradient ranging from 6-8^{0}/sec. In contrast, dot motion in the present study was 10.5^{0}/sec, while Naito et al.'s (2000) extrapolated velocity was considerably higher, at over 300^0/sec. If the downward movement of an object within the UVF often signifies movement toward the body, it is reasonable to expect that cells coding for this combination of direction and visual field might be optimally tuned for higher velocities simply because fast, downward moving objects would be potentially more of a threat than slow moving objects. The available data suggest that the velocity at which the UVF anisotropy for downward manifests might be somewhere between the 5^0/sec employed by Raymond et al. (1994) and the 10.5^0/sec employed in the present study.

To conclude, the LVF does appear to have a sensitivity advantage for global motion, although this might manifest only within certain stimulus parameters. In addition, the hemifield effect appears able to be modified according to the quality of other stimuli simultaneously present within the visual field. Random motion at fixation maintains and increases the LVF advantage, while a static textured pattern tends to improve performance in the UVF. This modification of motion sensitivity might be the result of attentional factors, coming into play as a result of task demands. There are robust directional anisotropies in each vertical hemifield, evidenced by a heightened sensitivity to downward motion in the UVF and upward motion in the LVF. Both anisotropies can be argued to have ecological value.

Chapter 9:
Experiment 1A: Adjacent vs. Foveally Located Static Distractors

9.1 Introduction

The purpose of this experiment was to investigate why the 'static-distractor' condition of Experiment 1 produced no vertical hemifield effect. If the static dots had provided a perceptual referent with which motion signals could be compared, locating the static dots alongside the moving dots should strengthen this percept, producing further increments in performance. However, when static and moving dots are intermingled motion perception in humans is adversely affected (Baker et al., 1990; Vaina et al., 1991) and neural response in monkey cortex is reduced (Snowden et al., 1991). Thus, it is possible that contiguous static and moving patches could also produce performance decrements, a result that would allow the perceptual referent explanation to be ruled out.

Two modifications were made to the original stimulus configuration. Firstly, the static-distractor and test RDK were repositioned immediately adjacent to each other. Secondly, a further identical static-distractor was presented on the opposite side of the test RDK. Thus, the test RDK was flanked on two sides by static-distractors, effectively increasing the ratio of static to moving dots from 1:1 to 2:1.

9.2 Method

9.2.1 Participants

Participants were seven females and three males with a mean age of 23.1 years (s.d. = 4.00 years). All had normal or corrected to normal acuity. None had participated in Experiment 1.

9.2.2 Apparatus

The experiment was performed with the same apparatus used in Experiment 1.

9.2.3 Stimuli & Procedure

The fixation spot was identical in composition and location to that employed in Experiment 1, though the duration was extended to 1000 ms.

The complete stimulus was rectangular, subtending 6.54^0 x 2.18^0 of visual field. It was divided into three equally sized (2.18 deg^2) regions with no intervening gap. The two outer segments (the adjacent distractors) contained static dots, identical in size, density and luminance to those displayed in the 'static-distractor' condition in Experiment 1. The inner segment (the test region) contained a test RDK that was identical to those employed in Experiment 1 in all respects. The global direction of motion displayed by the test region on each trial was determined by the same staircase procedure employed in Experiment 1. Stimulus duration was 5-frames (83 ms).

The test region within each stimulus was located in the same quadrant locations employed in Experiment 1 (refer Figure 3). Stimuli were not presented to the upper- and lower-centre locations. Thus, the distance from the fixation point to the centre of each test stimulus was 7.07^O. All participants completed two staircases at each quadrant location. In one condition, the adjoining static-distractors were located immediately above and below the test RDK (vertical orientation; the lower border of the stimulus being 1.73^O and the upper border 8.27^O from the horizontal meridian), while the second block had distractors positioned on the immediate left and right of the RDK (horizontal orientation; the left border was 1.73^O and the rightward border 8.27^O from the vertical meridian). These separate orientations were presented to offset the possible effects on direction discrimination of having the test dots moving either toward and away from the static dots, or toward empty space.

Immediately upon offset of the fixation spot, the stimulus was presented. Combinations of quadrant and distractor orientations were presented in randomised blocks. In all other respects the procedure was identical to that employed in Experiment 1.

9.3 Results and Discussion

In order to ascertain whether hemifield effects accrued as a result of locating the static dots adjacent to the test RDK, comparable data from the 'static-distractor' group in Experiment 1 (i.e., thresholds obtained from the four quadrant locations at the 5-frame duration) were compared to the data obtained here. Figure 7 illustrates the effect of locating the static-distractor adjacent to the test RDK rather than at fixation.

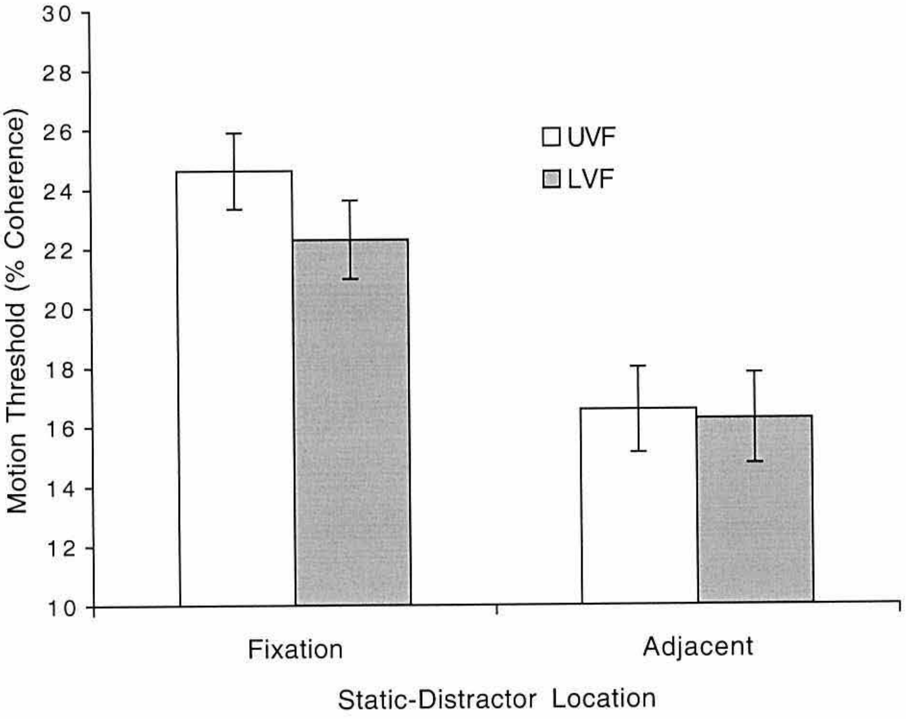

Figure 7. Motion coherence thresholds obtained from the UVF and LVF as a function of static-distractor location. Fixation data are from the static-distractor group in Experiment 1 and were measured at the 5-frame duration in the left and right visual quadrants only. Adjacent data were collected in this experiment. Vertical bars represent +/- 1 standard error of the mean.

A three-way mixed ANOVA was performed with static-distractor location (fixation, adjacent) as the between factor and hemifield (UVF, LVF) and motion direction (rightward, leftward, upward and downward) as within factors. This revealed a main effect of static-distractor location F (1, 20) = 15.59, p < .01, reflecting generally lower mean coherence thresholds when the static-distractor was located adjacent to the test RDK. A main effect of motion direction was also obtained, F (3, 60) = 5.09, p < .01. There was no effect of vertical hemifield. In addition to the expected vertical hemifield x motion direction interaction, F (3, 60) = 8.84, p < .01, there were two-way; static-distractor location x motion direction, F (3, 60) = 9.13, p < .01, and three-way; static-distractor location x vertical hemifield x motion direction, F (3, 60) = 4.40, p < .01, interactions.

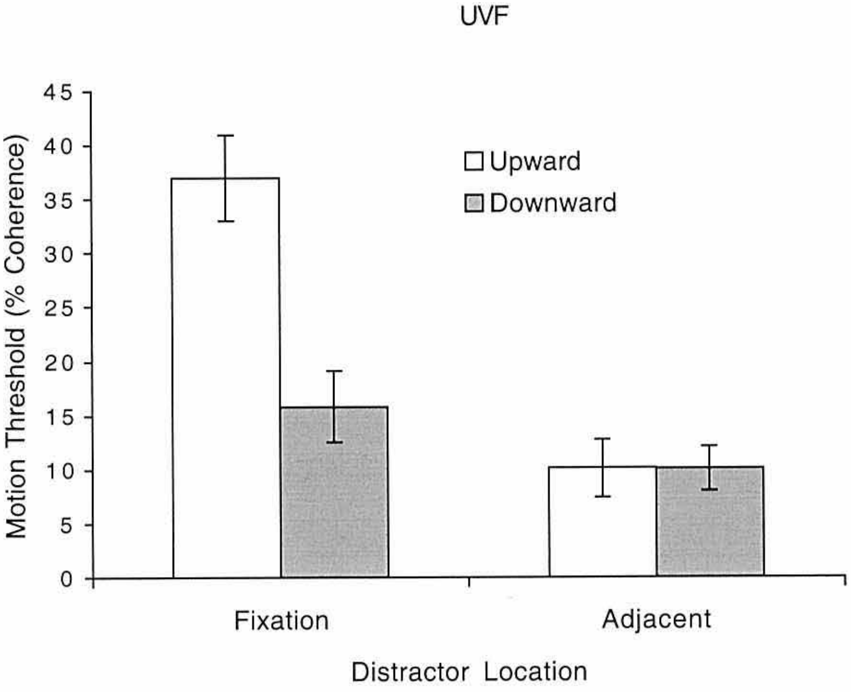

Figure 8a. Motion coherence thresholds for vertical axis motion obtained in the UVF as a function of static-distractor location. Fixation data are from the static-distractor group in Experiment 1 and were measured at the 5-frame duration in the left and right visual quadrants only. Adjacent data were collected in this experiment. Vertical bars represent +/- 1 standard error of the mean.

An interesting aspect of the data was the differing effect of the adjacent distractor on horizontal vs. vertical axis motion. While rightward motion thresholds showed modest improvements as a result of the adjacent distractor location (UVF, 26.54% vs. 22.98; LVF, 26.41% vs, 23.01%), leftward thresholds increased in both the UVF (19.14% vs. 23.01%) and LVF (17.80% vs. 21.73%).

In contrast, both vertical hemifields demonstrated improved thresholds for both upward and downward motion. In the UVF, upward thresholds were reduced from 36.99% to 10.14%, while downward thresholds dropped from 15.82% to 10.10%. In the LVF, upward thresholds were 17.94% with a static-distractor at fixation and 7.45% with adjacent distractors. Downward thresholds were 27.07% and 12.88%, respectively. Within-hemifield means comparisons performed on vertical axis motion in the adjacent distractor group revealed isotropy in the UVF for directions of motion along both the horizontal and vertical axes. However, although in the LVF, motion along the horizontal axis was isotropic, the sensitivity advantage for upward vs. downward motion found in Experiment 1 was maintained ($p < .05$). Figures 8a and 8b plot these data for each hemifield.

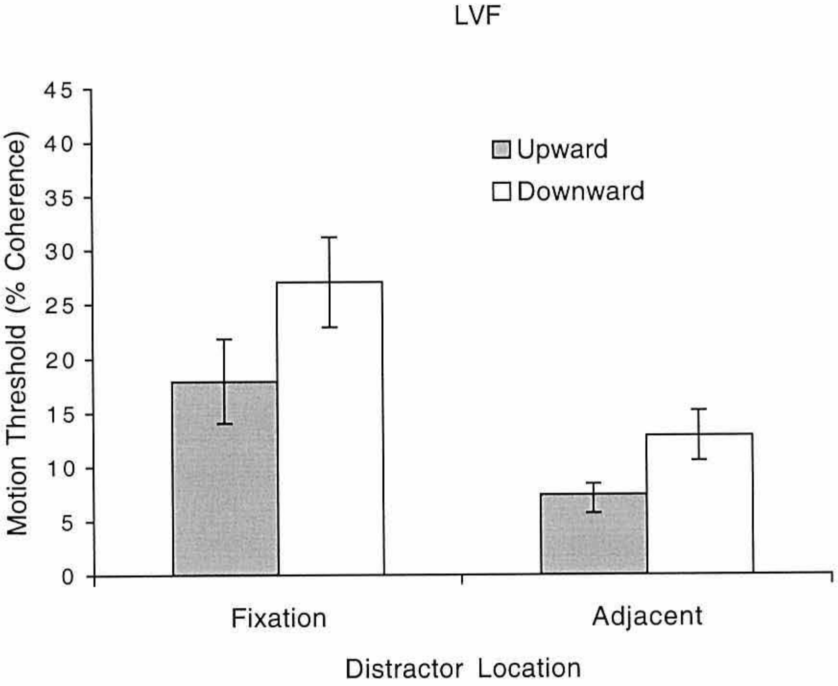

Figure 8b. Motion coherence thresholds for vertical axis motion obtained in the LVF as a function of static-distractor location. Fixation data are from the static-distractor group in Experiment 1 and were measured at the 5-frame duration in the left and right visual quadrants only. Adjacent data were collected in this experiment. Vertical bars represent +/- 1 standard error of the mean.

Because the adjacent-distractor produced only modest gains in rightward motion thresholds, and no gain for leftward thresholds, it would appear that sensitivity to horizontal axis motion had reached a peak in the 5-frame static-distractor condition in Experiment 1. On the other hand, enhancement in motion sensitivity within the UVF in the adjacent-distractor group can be largely explained by the strong improvement in upward motion thresholds. At first sight, it might be argued that the unusually high threshold obtained from the static-distractor group in Experiment 1

(36.99%) may have been due to some experimental artefact. However, this appears to be highly unlikely, given that a similarly high direction threshold (34.59%) was obtained in the upper visual quadrants, at the 5-frame duration, in the 'motion-distractor' group. Thus, the adjacent-distractor does appear to have further enhanced motion sensitivity in the UVF, but only where it had previously proven to be particularly poor. In the LVF, large gains are apparent for both upward and downward motion. However, the fact that the vertical anisotropy found in Experiment 1 was also observed here suggests there is some functional value in maintaining sensitivity to upward motion in the LVF, across a range of stimulus conditions.

This study has provided mixed results and cannot, therefore, provide a definitive answer as to why the UVF performs comparably with the LVF when a static texture is simultaneously present in the visual field. If performance increments had been observed for all directions of motion in both hemifields, the perceptual referent explanation might have been supported. However, the adjacent static distractor had differing effects according to motion direction. Thus, this experiment further demonstrates that hemifield effects in motion sensitivity cannot be considered without taking into account the directions of motion under observation.

At this stage of investigation, further studies could take one of two alternative directions. One approach would be to base further research directly on the results obtained in Experiments 1 and 1A. In this case, the LVF processing advantage would be further assessed under conditions in which RDK dot speed and density were manipulated. This would provide a more comprehensive picture of the specific experimental conditions necessary to elicit a LVF processing advantage on unidirectional RDK tasks. In contrast, vertical hemifield performance could be compared on a number of other motion paradigms, employing both RDK and non-RDK stimuli. This approach would provide a broader picture, indicating the particular motion tasks that might be performed more efficiently in the LVF.

In order to provide a wider basis for future research, I chose the second of these alternative approaches. Thus, Experiment 2 departs from the unidirectional motion paradigm employed in Experiments 1 and 1A and investigates vertical hemifield performance on a bidirectional motion task.

Experiment 2: Perception of Transparent Motion

Abstract

In this study, the ability to accurately perceive both directions of motion in an RDK comprised of two sheets of coherently moving dots was assessed in the visual quadrants of 10 observers. All observers completed the experiment at an 8-frame (133 ms) duration, while seven completed further trials at a 12-frame (200 ms) duration. Performance was significantly better when stimuli were presented to the LVF vs. UVF, but only at the 8-frame duration. Again, there was no effect of horizontal hemifield. Although accuracy in the vertical hemifields did not differ significantly for directions of motion along the horizontal axis, the determining factor in the LVF advantage appears to be heightened sensitivity to motion along the vertical axis. Because the computation of bidirectionality is hypothesised to require a serial, rather than a parallel computation, it is suggested that motion mechanisms in the UVF might be less able to reallocate attention from the first to the second sheet of moving dots, as effectively as motion mechanisms in the LVF.

Chapter 10:
Experiment 2: Perception of Transparent Motion

10.1 Introduction

Transparent motion refers to the perception of two (or more) global directions of motion perceived to be superimposed within a single region of the visual field. This is not merely a laboratory-induced phenomenon, but is often encountered by the visual system under natural conditions of partial occlusion or semi-transparency. Examples include a shadow moving across a surface that is itself moving in a different direction, or a shoal of fish swimming upstream against running water.

This hypothesised mechanism for transparent motion perception appears to be predominantly one of central vision, as the percept is markedly poorer when transparent stimuli are viewed in the visual periphery. However, only one previous study (De Bruyn, 1997) has systematically measured peripheral viewing of bidirectional RDKs and stimuli were presented to the right visual field only (B. De Bruyn - personal communication). The reported rapid deterioration in performance suggested to me that bidirectional RDKs might provide a further suitable paradigm in which to compare motion processing abilities in the vertical hemifields.

The ability to discriminate bidirectionality has proved difficult to reconcile with the majority of models of motion perception. Detection of motion energy within limited spatiotemporal bandwidths, such as occurs in V1, is certainly able to represent two motion distributions. However, the 'aperture problem' remains. That is, cells that simply detect motion energy can be sensitive only to velocities perpendicular to their receptive field orientation and thus are unable to effectively compute the velocity of any patterned stimulus (Marr & Ullman, 1981). Theoretically, the separate distributions of local motion signals could be used to group bidirectional motion vectors. However, at the detection stage, some additional non-motion basis for the grouping, such as colour or disparity, would be necessary. Under natural conditions these cues are often available but, because superimposed motion vectors can also be perceived in transparent RDKs, whose component dots differ only in motion cues (Qian, Andersen, & Adelson, 1994), a biologically feasible model of motion transparency must be able to operate on the basis of motion inputs alone.

For unidirectional global motion, these limitations can be overcome by pooling local motion vectors across space. This second stage requires that some noise reduction algorithm be utilised in order to suppress extraneous signals that do not conform to the global pattern of motion (Britten & Heuer, 1999). However, when encountering dual distributions of motion, the majority of the proposed algorithms either result in the mutual inhibition of both directions of motion or, alternatively, average the two vectors into a single motion estimate (Braddick & Qian, 2001; Qian et al., 1994). Both outcomes prevent the perception of superimposed bidirectional motions, thus emphasising the inherent conflict between noise reduction and the perception of transparency that has yet to be effectively addressed in many models of motion perception.

A key finding is that neither spatiotemporal factors nor the class of stimulus employed is necessarily the determining factor as to whether or not motion transparency is perceived (Qian et al., 1994). When component dots representing the two directions of motion within a transparent RDK are paired, i.e., are positioned equidistant from each other such that dot density is homogenous across space, transparency is not perceived (Qian et al., 1994; Qian & Andersen, 1994a; 1994b). However, when the component dots are positioned independently of each other, perception of motion transparency becomes possible. Thus, the presence of local fluctuations in dot density is hypothesised to impede the suppression or averaging of the signals representing both directions of motion. If sufficiently strong, the resulting motion signal residues representing each direction are hypothesised to enable perception of the two directions (Braddick & Qian, 2001; Qian et al., 1994).

At the fovea, the angular difference required to segment two transparent directions of motion can be as small as 13^0 (Wishart & Braddick, 1997). However, when De Bruyn (1997) displayed linear expanding or contracting dot motion superimposed on rotational motion, he found that at 10^0 eccentricity, the necessary angular separation increased to 90^0, while at 20^0 eccentricity, the same bidirectional RDKs were indistinguishable from unidirectional RDKs displaying an averaged trajectory of the two orthogonal directions.

This deterioration in performance cannot be attributed to a lack of sensitivity to motion signals *per se*, or to peripheral scaling factors, as thresholds for unidirectional global motion do not deteriorate so rapidly with increasing ecccentricity (e.g., Joffe et al, 1997). Furthermore, defocusing, increasing dot density, or decreasing dot speed has little effect on the loss of ability to segregate the two directions of motion (De Bruyn, 1997).

From an ecological standpoint it can be predicted that segmentation of superimposed global motions would be better achieved in the LVF. Due to the highly textured nature of the LVF (Gibson, 1961; Lee, 1980) it is more likely that both semi-transparent and occluding surfaces would be encountered here. Current understanding of the physiological basis for perception of transparent motion further suggests that a LVF advantage would be found in this task. V1 cells respond more strongly to paired than to unpaired dot motion and almost equally well to unidirectional and transparent stimuli. This pattern of response suggests there is only weak suppression between opposing directions of motion within V1 (Qian & Andersen, 1994; Snowden et al., 1991), indicating that activity here would correlate poorly with the perception of motion transparency. In contrast, the firing rates of MT cells are reduced by approximately 40% in response to a transparent motion stimulus, compared to responses made to unidirectional stimuli (Snowden et al., 1991). Thus, activity within MT/V5 is identified as the locus for suppression between the two directions. This region, and possibly MST (Qian & Andersen, 1994), appears to be able to extract the residual signals needed to perceive transparency. The prominent LVF bias found within MT and MST in the higher primates (Gattas & Gross, 1981; Maunsell & Van Essen, 1987) and in other regions in which motion signals are spatially integrated (e.g. V3; Felleman & Van Essen, 1987; Burkhalter et al., 1986) would therefore suggest that a LVF bias would be found on a motion transparency task.

Behavioural studies further suggest that perception of bidirectionality does not involve a parallel process. Rather, observers appear to compute first one, then the second direction, in a serial fashion (Cobo et al., 1999; Pinilla et al., 2001; Valdes-Sosa et al., 1998; 2000). The order in which the two motion directions are processed should be indicated by differing rates of response accuracy, with greater accuracy for the first direction computed. It might also prove interesting, therefore, to determine whether accuracy for particular directions of motion differs according to vertical hemifield.

10.2 Method

10.2.1 Participants

Ten healthy, right-handed undergraduate participants, seven females and three males, with a mean age of 24.2 years (s.d. = 5.2 years) acted as observers. All had normal or corrected visual acuity, and were inexperienced psychophysical observers naïve to the study's purpose. Partial course credits were given in return for participation.

10.2.2. Apparatus and Stimuli

The apparatus was identical to that employed in Experiment 1. The fixation spot was a 0.1^0 white square presented for 1000 msecs. Each RDK comprised a borderless area of 2.18 deg^2 consisting of two fully coherent sheets of dots moving in perpendicular directions. On any one trial, 50% of the dots were displaced in a single horizontal direction while the remaining 50% were displaced in a single vertical direction. Thus, four bidirectional stimuli were presented: upward-leftward, upward-rightward, downward-leftward and downward-rightward.

Each RDK contained 256 dots, each of which measured 1.31 minarc in diameter, giving a mean density of 54 dots/deg^2, or 27 dots/deg^2 for each direction of motion. Space averaged luminance of the RDK was 1.24 cd/m^2 presented against a surrounding monitor luminance of 0.01 cd/m^2, providing a contrast of 98%. With each successive frame both signal and noise dots were displaced by 10.48 minarc, corresponding to a velocity of 10.5 deg/sec. The component frames were redrawn every 16.6 msecs. All ten participants viewed the stimuli at an 8-frame (133 msecs) duration.

Seven participants also performed the same experiment at a further 12-frame (200 msecs) duration.

10.2.3 Procedure

All trials were viewed binocularly at a distance of 92 cm in a dimly lit room. Each trial was initiated by the experimenter, and successive trials were presented at a pace found to be comfortable for individual participants. Simultaneous with the offset of the fixation spot, an RDK was presented, in separate blocks, to each of the four visual quadrants whose locations were identical to those employed in Experiment 1 (refer Figure 4a).

Each block consisted of 32 trials, i.e., eight trials for each of the four combinations of direction. These were randomised within each block. Observers completed two such blocks at each of the four quadrant locations and, where applicable, at both durations. The task was to report the two directions of motion in any preferred order. The order of report was not recorded as pilot work indicated that observers tend to habitually report the horizontal direction first. This would not necessarily represent the order in which the visual system computes the two directions. Participants were aware, however, that each trial always contained one movement direction along the vertical axis and one along the horizontal axis.

Verbal responses were keyed into the computer by the experimenter, who was blind to all stimulus presentations. No feedback was given. Practice trials were made available before data collection, and the experiment commenced only when participants indicated that they understood the procedure.

10.3 Results

The proportion of trials in which both directions of motion were correctly identified was calculated for each observer in each of the quadrants tested. Data from all ten observers obtained at the 8-frame duration are graphed in Figure 9. This demonstrates greater accuracy in both LVF vs. UVF quadrants. A two-way ANOVA performed on the data from the 8-frame duration (vertical hemifield x quadrant location) confirmed a main effect of vertical hemifield, F (1, 9) = 15.07, p < .01. As predicted, observers were able to correctly identify both directions of motion on a greater proportion of trials when the stimulus was presented to the LVF (0.616) than to the UVF (0.527). There was no effect of quadrant location, though a trend toward superior performance in the left visual field was evident (p = .07). However, no interaction effect was obtained. Thus, as in Experiment 1, the motion mechanism underlying the LVF advantage on this task is not influenced by horizontal location or hemifield. In contrast to the above results, a similar ANOVA performed on the data from seven observers using a 12-frame duration, produced no main effects, nor any interaction effects. In this case, the proportion correct scores for both directions of motion were 0.79 in the UVF and 0.83 in the LVF. All subsequent analyses are performed on data from the 8-frame duration only.

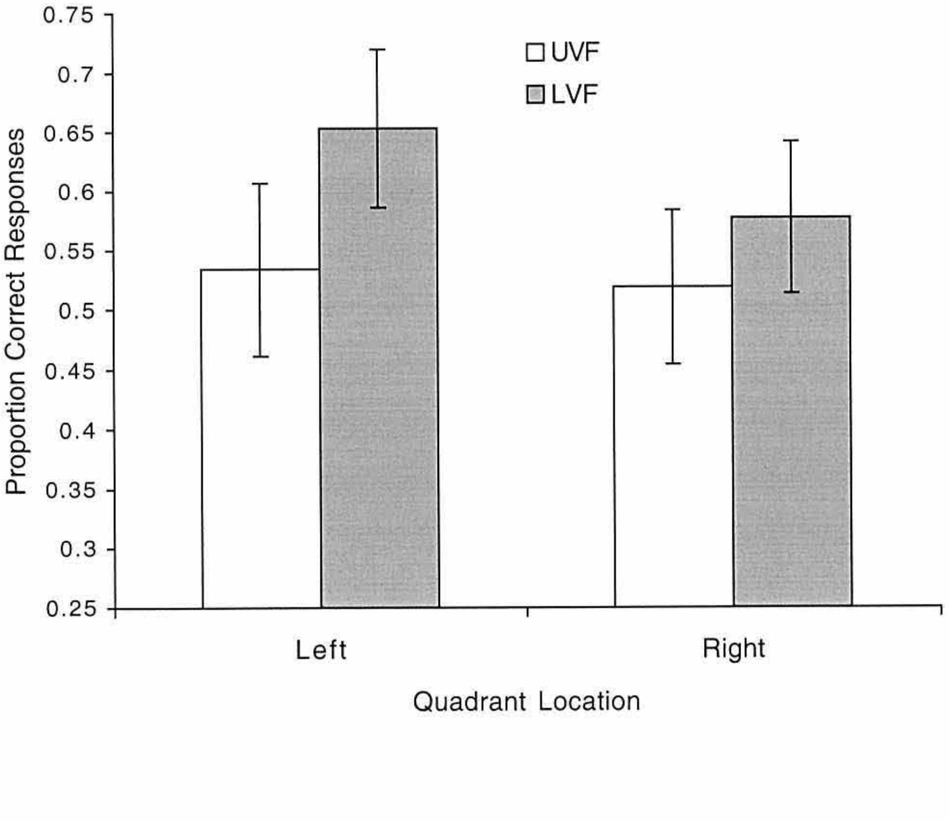

Figure 9. Mean proportion correct responses to both directions of motion obtained in the UVF and LVF as a function of visual quadrant. Vertical bars represent +/- 1 standard error of the group mean.

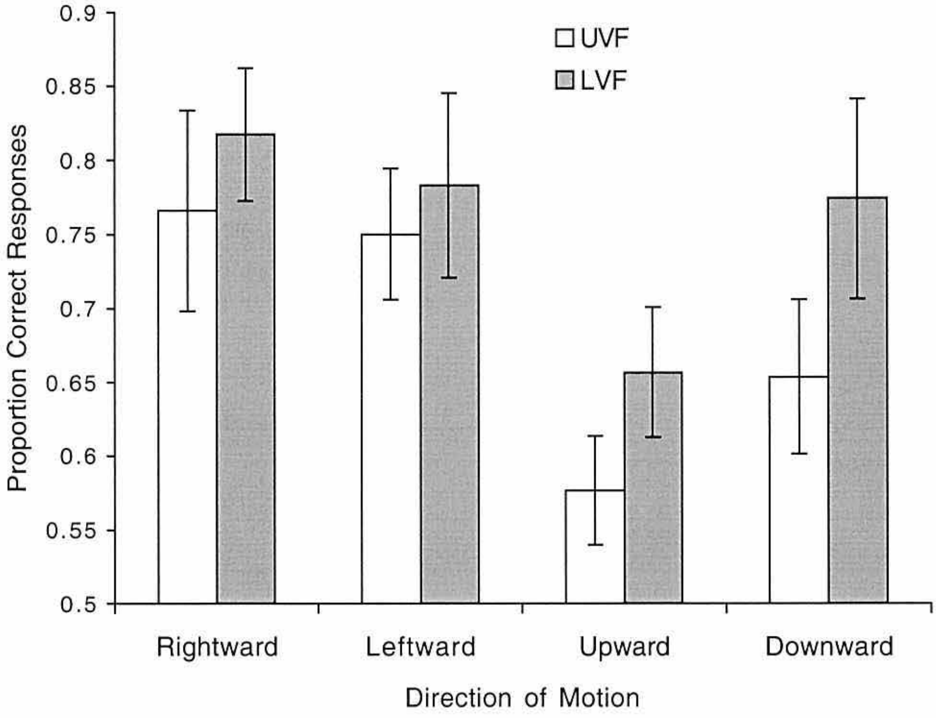

Figure 10. Mean proportion correct responses for each direction of motion, irrespective of the accuracy of response for the orthogonal direction, obtained in the UVF and LVF. Vertical bars represent +/- 1 standard error of the mean.

In order to ascertain whether anistropies for motion direction occur in motion transparency perception in the vertical hemifields, the proportion of correct responses made for each individual direction of motion was calculated, irrespective of the accuracy of responses made to the orthogonal direction. These data are displayed in Figure 10. Two observations are particularly noteworthy. Firstly, in contrast to the findings in Experiment 1, there are no vertical hemifield-specific anisotropies. Secondly, the directional anisotropy observed in the LVF is the opposite than that found in Experiment 1.

A two-way ANOVA performed on these data (vertical hemifield x motion direction) revealed a main effect of motion direction, F (3, 27) = 7.24, p < .01, but no interaction effect. Means comparisons revealed that while horizontal axis motion did not differ between the vertical hemifields, the LVF proved to be significantly more sensitive than the UVF to both upward and downward motion (both $p < .05$).

10.4 Discussion

The results of this experiment indicate that observers were better able to perceptually segment two rapidly presented, superimposed, orthogonal global directions of motion in the LVF than in the UVF. As is the case with unidirectional motion, the LVF sensitivity advantage was independent of performance in the horizontal hemifields. The data further suggest that the determining factor for the LVF advantage was heightened sensitivity to motion along the vertical axis.

There is no evidence to suggest that observers were simply unable to perceptually segment the two directions of motion in the UVF. If they were, they would be expected to have spatially integrated the two moving sheets of dots, resulting in the perception of a single dot surface moving in an oblique direction. Had this been the case, the two orthogonal directions could be deduced from the oblique direction (Treue, Hol, & Rauber, 2000). This strategy would be expected to have resulted in isotropic sensitivity to the four individual motion directions, rather than the sensitivity advantage found for horizontal directions of motion, in both vertical hemifields.

The perception of motion transparency may be considered to involve a serial, rather than parallel process, characterised by the successive allocation of attention to each sheet of dots to enable accurate report. Both behavioural and electrophysiological evidence shows that when attention is purposely directed to one moving surface within a transparent RDK, perception of the unattended surface is perturbed (Cobo et al., 1999; Valdes-Sosa et al., 1998; 2000). Motion after-effects to an unattended sheet are similarly perturbed (Lankheet & Verstraten, 1995; Raymond et al., 1998). These findings are consistent with the notion that surfaces, and not necessarily regions of space, provide the fundamental entities on which attentional selection operates (He & Nakayama, 1995).

It is reasonable to assume that the direction of motion reported most accurately represents the motion-defined surface receiving the initial allocation of attention. Two patterns within the data therefore suggest that observers gave priority to the horizontal motion component with the secondary allocation to the vertical component. Firstly, sensitivity was generally greater to horizontal vs. vertical motion in both hemifields. Secondly, the vertical hemifields did not differ in sensitivity to either rightward or leftward motion, yet the LVF was more sensitive than the UVF to both upward and downward motion.

Because observers were free to choose which axis of motion to report first, they were not constrained to attempt to first process the direction of motion on any particular axis. Thus, allocation of attention to the horizontal axis would appear to have occurred by default, possibly reflecting some intrinsic directional priority when faced with superimposed horizontal and vertical motion. The top-down nature of this processing priority is further underlined by the fact that the two sheets of dots contained no featural cues, other than direction, which might have biased the allocation of attention. Put simply, the allocation of attention to the horizontal component would appear to be determined by motion processing mechanisms, rather than by task instruction or some featural aspect of the stimulus.

Two possibilities come to mind as to why observers were less able to process the second direction of motion in the UVF. If the horizontal component were processed faster in the LVF, this would have allowed more time for discrimination of the vertical motion component. This view is supported by the null finding in those observers who completed further trials at the 12-frame duration. With the four additional frames (66 ms), motion mechanisms in the UVF might have been able to compute both directions to the same ability as the LVF. However, this explanation alone cannot account for the relatively poor sensitivity to upward motion found in both vertical hemifields. It appears more likely that after first processing the direction of motion along the horizontal axis, attention was redeployed more effectively when the vertical component comprised downward, rather than upward motion.

Alternatively, the horizontal motion component might have been processed with equal speed in both the UVF and LVF, but the disengagement and/or redeployment of attention from the horizontal to the vertical component was undertaken more efficiently in the LVF. Similarly, Valdes-Sosa et al (2000) have suggested that when attending to one component direction, the other component is not simply unattended, but is actively suppressed. Thus, the time required to reallocate attention, the attentional ‘dwell-time’ (Duncan, Ward & Shapiro, 1994; Ward, Duncan & Shapiro, 1996) (redefined as the ‘surface dwell time’ when applied to transparent motion; Pinilla et al., 2001) may be shorter in the LVF than in the UVF.

Experiment 3: Susceptibility and Resilience to Motion Capture

Abstract

Motion capture refers to motion signals within one region of the visual field influencing the perception of motion within a nearby region. To determine whether the vertical hemifields differ in susceptibility to motion capture effects, RDKs composed of three segments were presented. Two flanking (inducer) regions contained 50% coherent motion in identical directions along the horizontal axis. The central test region contained the opposite direction of signal motion, the coherence level being determined by a psychophysical staircase procedure. Susceptibity to motion capture is quantified as the minimum coherence value needed to produce perception of the motion direction in the central region. The results obtained suggest that the LVF is less susceptible to motion capture effects. However, in contrast to the previous experiments, a significant interaction was found between the vertical and horizontal hemifields, due to an especially strong susceptibility to motion capture effects in the upper-left visual quadrant.

Chapter 11:
Experiment 3: Susceptibility and Resilience to Motion Capture

11.1 Introduction

In order to to segment the visual array into separate regions, and ultimately objects, the motion integration mechanisms studied in Experiments 1 need to be supplemented by further mechanisms that are able to detect motion discontinuities. Motion discontinuities signify the presence of motion-defined (kinetic) boundaries, used by the visual system to perceptually segregate neighbouring regions of the visual field displaying velocity differences. Psychophysical evidence indicates that two distinct processes are employed for this task. Edge detection algorithms initially detect local differences in motion attributes. This provides the basis for motion integration processes to propagate from a motion-defined boundary into neighbouring regions of space (e.g., Braddick, 1993). Conversely, region-based segmentation has its onset within regions displaying a high degree of homogeneity of motion signals, and accretes outward from this point until local differences in motion attributes are encountered (e.g., Møller & Hurlbert, 1996).

The detection of discontinuity between areas of moving textures with contrasting directions is observed to fail under certain stimulus conditions. When this occurs, the global direction of motion perceived within one spatial region can be erroneously perceived to be similar to that of a neighbouring region. This has been demonstrated using multisegmented RDKs comprising alternating bands containing partially coherent dot motion and random dot motion. When the bands are narrow, partially coherent motion induces a similar direction of illusory motion within the random motion band (Nawrot & Sekuler, 1990), a phenomenon known as motion assimilation (Mackay, 1982) or motion capture (Ramachandran, 1987). However, with wider bands, the contrasting motions can be readily perceived (Nawrot & Sekuler, 1990). Susceptibility to motion capture effects therefore indicates a lack of effectiveness of motion segmentation mechanisms, while resilience to motion capture effects suggests effective motion segmentation mechanisms.

As with motion transparency, the ability to perceive contrasting motion in the peripheral visual field has yet to be systematically studied. However, Murakami and Shimojo (1993) have shown that viewing contrasting motion at eccentricities greater than 5^{O} tends to promote the perception of motion capture. This was demonstrated with circular RDKs composed of a central disk containing stationary dots, and moving dots in the outer annulus. With increasing eccentricity (2.8-10^{O}), perception of the direction of movement of the dots in the outer annulus tended to transfer to the stationary dots.

The authors concluded that the normal deterioration in sampling resolution with increasing eccentricity acts to blur motion-defined boundaries, favouring the accretion of a global direction of motion across the whole stimulus. It might be predicted, then, that greater sensitivity to global directions of motion in the LVF might act to diminish the perception of motion-defined boundaries, resulting in stronger motion capture effects in the LVF vs. the UVF.

The physiological evidence is unclear as to whether vertical hemifield effects will be found on a motion contrast task. Focal lesioning of macaque MT produces only mild impairment in the ability to discriminate motion-defined boundaries (Lauwyers, Saunders, DeBruyn, Vogels, Vandenbussche, & Orban, 1995). Furthermore, single-cell recordings from monkey (Marcar, Xiao, Raiguel, & Maes, 1995), in addition to imaging work with humans (Dupont et al., 1997; Orban et al., 1995; Reppas, Niyogi, Dale, Sereno, & Tootell, 1997; Shulman, Schwartz, Miezin, & Petersen, 1998; Van Oostende et al., 1997) suggest that neither V5 nor V3 play a significant role in the processing of motion-defined boundaries.

However, humans do appear to possess a cortical region (area KO) that is specialised for processing motion-defined boundaries. Imaging work by Orban and colleagues (Dupont et al., 1997; Orban et al., 1995; Van Oostende et al., 1997) has shown that this area is significantly more activated by motion stimuli composed of adjoining regions of coherent motion displaying differing directions, than by the same coherent directions of motion separated in space or superimposed in a motion transparent RDK. The retinotopy of this region has yet to be mapped. Thus, psychophyical evidence of vertical hemifield differences in the perception of motion contrast might usefully contribute to the physiological data.

It seems likely, however, that discrimination of motion-defined boundaries is mediated by mechanisms housed within both the dorsal and ventral pathways. Single cell monkey data show both V4 and inferotemporal cortex to contain small numbers of neurons sensitive to contours defined solely by motion cues (Sary, Vogels, & Orban, 1993; Sary, Vogels, Kovacs, & Orban, 1995). Furthermore, Van Oostende et al (1997) interpret their human data as indicating that KO's main projections are to ventral regions of cortex. Thus, the lack of reliance on LVF-biased dorsal subregions for detecting motion-defined boundaries makes it less likely that a LVF advantage will be found for the detection of contrasting motions.

To determine whether the vertical hemifields differ in susceptibility or resilience to motion-capture effects, I presented rectangular, multisegmented, horizontally oriented RDKs. In the central test region, both the direction of motion and the coherence level were determined by a psychophysical staircase procedure. Motion-inducer regions were located on each side of this test region. The inducer regions displayed an identical direction of motion (rightward or leftward), at a consistent 50% level of coherence. Two directions of motion were presented in the central region. One was the test direction, which was always opponent to the direction of the inducers and the other was identical with the inducer direction. Both directions could only be ascertained by virtue of motion cues; contributions from non-motion sources such as luminance, colour or disparity were purposely excluded. This stimulus was adapted from those previously employed in studies of the spatiotemporal factors producing motion capture effects at fixation (e.g. Ido, Ohtani, & Ejima, 2000; Møller & Hurlbert, 1996; Nawrot & Sekuler, 1990).

Only horizontal axis motion was presented in both test and inducer regions. This arrangement was chosen as the majority of antagonistic centre-surround cells in MT are maximally excited by opponent motion, rather than by othogonal, or shearing motion (Born, 2000). Although MT does not appear to play a major role in detecting motion discontinuities, these cells are theoretically able to detect motion-defined boundaries (Born & Tootell, 1992; Born, 2000). This class of motion stimulus is also found to be ideal for producing activation in area KO (G. Orban – personal communication).

The inducer motion was intended to promote a motion capture effect in the test region. Thus higher thresholds in one vertical hemifield would indicate a relative susceptibility to motion capture effects. Conversely, lower thresholds would indicate a relative resilience to motion capture, implying a greater degree of detection of the motion-defined boundaries.

11.2 Method

11.2.1 Participants

Ten undergraduate students, eight female and two male, participated for partial course credit. Their mean age was 22.6 years (s.d. = 3.6 years). All had normal or corrected to normal visual acuity, no known neurological condition, and were naïve to the purpose of the study.

11.2.2. Apparatus and Stimuli

The apparatus was identical to that employed in all previous experiments.

The fixation spot was a 0.1^{O} white square presented for 1000 msecs either 5^{O} above (for LVF presentations), or below (for UVF presentations) the centre of the monitor. Each RDK was rectangular, 6^{O} wide and 2^{O} high. It was divided, without vertical demarcating lines or gaps, into three separate regions. The width of the central 'test' region, to which all responses were made, was 1.6^{O}. This region contained an average of 144 white dots each of which was 1.31 minarc in diameter. Both flanking motion inducer regions were 2.2^{O} wide and contained an average of 180 dots of identical composition. Dot density across the whole stimulus was 45 dots/deg^{2}.

The inducer regions displayed, in separate blocks, either rightward or leftward motion at a fixed coherence level of 50%. Regardless of the direction of motion displayed by the inducers, the test region displayed either rightward or leftward motion, chosen at random on each trial. One direction of motion was always opponent to that of the inducer direction. The second direction of motion in the test region (identical to that of the inducer motion) was included to prevent observers from biasing responses in favour of the opponent direction of motion. Data from the direction of motion identical to that of the inducers was discarded.

The level of coherence for both directions of motion in the test region was determined by the same psychophysical staircase procedure employed in Experiment 1. Dots within all regions of the RDK were displaced by 10.48 minarc across each video frame, giving an effective velocity of 10.5^0/sec. Mean luminance values were homogenous across the three regions and identical for both stimulus and background to those reported in Experiment 1. Stimulus duration was 5-frames (83 msecs).

The RDKs were presented to each of the visual quadrants, in separate blocks. The centre of the test region was positioned at the exact location as the centre of each of the RDKs employed in Experiments 1, 1A and 2 (refer Figure 4a). The left and right boundaries of each RDK were therefore either 2.2^0 or 8.2^0 from the vertical meridian, depending on lwhether the left or right quadrant was used. The upper and lower edges were similarly either 4^0 or 6^0 from the horizontal meridian, depending on whether testing took place in the UVF or LVF.

11.2.3 Procedure

Before data collection began, observers were tested for the ability to unambiguously perceive the global direction of motion in an RDK measuring 2.18 deg^2 and containing rightward and leftward motion at a 50% level of coherence. This was presented alone, at fixation. Next, practice trials were presented and data collection began when observers indicated that they fully understood the procedure. Testing took place in a dimly lit room at a monitor to observer distance of 92 cm. Trials were initiated by observers via a mouse click which produced the fixation spot and, immediately upon its offset, an RDK. The task was to report the global direction of motion (rightward or leftward) within the central test region.

Observers responded verbally. Responses were entered into the computer by the experimenter, who was blind to all stimuli. No feedback was given. Eight visual quadrant x inducer direction (rightward and leftward) blocks were presented in random order.

11.3 Results

Motion coherence thresholds derived from the opponent motion directions in each visual quadrant are plotted in Figure 11. These data were subject to a three-way ANOVA employing vertical hemifield (UVF, LVF), horizontal hemifield (left, right) and test (opponent motion) direction (rightward, leftward) as within-factors. Again, performance in the LVF was superior to that of the UVF, producing a main effect of vertical hemifield F (1, 9) = 5.15, p < .05. However, there was also a significant interaction between vertical hemifield and horizontal hemifield, F (1, 9) = 6.77, p < .05, due to apparently poor performance in the upper-left visual quadrant. This

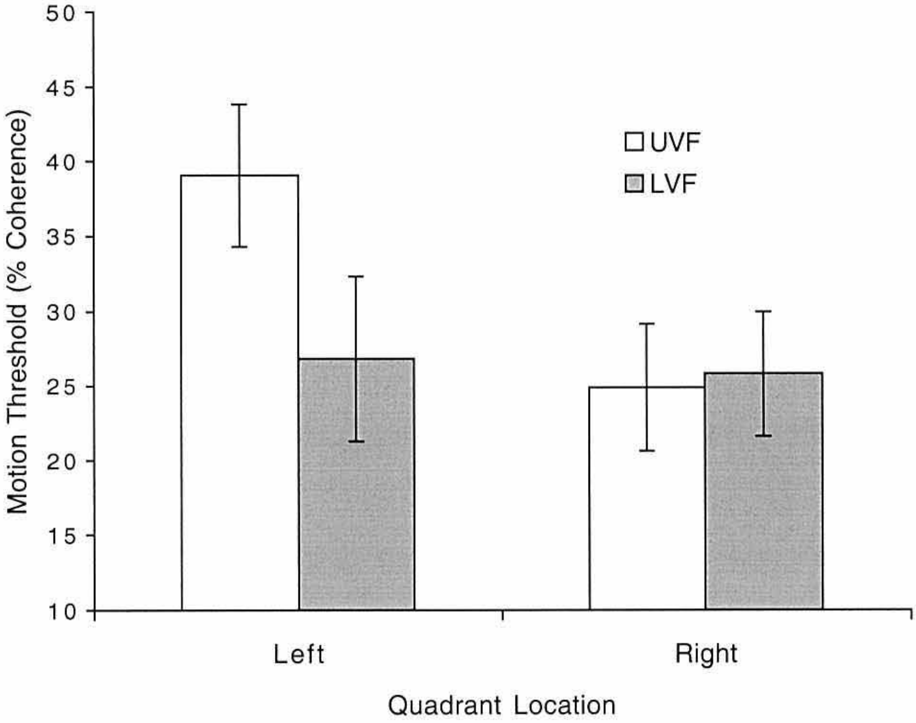

Figure 11. Coherence thresholds for opponent motion obtained in the UVF and LVF as a function of visual quadrant. Vertical bars represent +/- 1 standard error of the mean.

view was confirmed by means comparisons, which revealed the upper-left quadrant to produce a deficit performance relative to both the upper-right and lower-left quadrants (both $p < .05$). The comparision with the lower-right quadrant only narrowly missed statistical significance ($p = .052$).

11.4 Discussion

This experiment investigated the possibility that observers might demonstrate vertical hemifield differences in susceptibility or resilience to motion capture effects. At face value, findings indicate that the LVF is less susceptible than the UVF to motion capture effects, implying that motion-defined boundaries are better perceived in the LVF than in the UVF. However, in contrast to the previously reported experiments, here, there was a significant interaction between vertical hemifield and horizontal hemifield, caused by an apparent high degree of susceptibility to motion capture in the upper-left visual quadrant. When this factor is taken into account, the evidence for the LVF being relatively resilient to motion capture is considerably reduced.

A number of factors such as stimulus eccentricity, the immediate adjacent locations of the test and inducer regions, the smaller size of the test vs. inducer regions, and the lack of luminance contrast between test and inducer regions might be expected to have produced generally strong motion capture effects (e.g., Lorenceau & Zago, 1999; Mikami & Shimojo, 1993; Nawrot & Sekuler, 1990). Thus, when the percent motion coherence in the test region dropped below the 50% coherence level of the inducers there should have been a strong tendency for the flanking motion to 'capture', and so influence the perception of the signal direction of motion in the test region of the RDK.

A comparison of the motion coherence thresholds obtained here and those obtained from horizontal axis motion in the no-distractor group in Experiment 1 (UVF, 31.98% vs. 20.63%; LVF, 26.32% vs. 17.40%) strongly suggests that the present data reflect the presence of motion capture effects. However, there was a higher degree of statistical error in the present data. This suggests that the task was more difficult than discriminating a unidirectional RDK presented in isolation.

Despite the statistical noise, there does appear to be one consistent pattern in the data. Seven of the ten observers produced their highest motion thresholds in the upper-left visual quadrant while, by comparison, none produced their highest thresholds in the upper-right quadrant. Thus, although the current task might have been more difficult than that of previous experiments, the methodology nevertheless appears to have been sensitive enough to reveal inherent visual field differences in the perception of contrasting motion. In contrast to the previous studies, these differences appear to manifest between the visual quadrants, rather than between the vertical hemifields.

Why might the mechanisms used to perceive contrasting motion fail more easily in the upper-left visual quadrant? One possibility is that the upper-left quadrant relies more heavily on region-based segmentation processes, which rely on the effectiveness of spatial integration mechanisms. With poor spatial integration of motion signals, detection of the discontinuity between the contrasting motions would also be less effective (Møller & Hurlbert, 1996). The generally weaker spatial integration of motion signals in the UVF vs. LVF might be offset in the upper-right quadrant by a more effective mechanism for detecting the local differences in motion attributes that signify motion edges.

However, the pattern of difficulty displayed by two brain lesion patients suggests there is a double dissociation between computations of motion coherence and the motion discontinuity between two regions defined by motion coherence (Vaina, Grzywacz, & Kikinis, 1994). If the two motion processes are subserved by distinct mechanisms, the inferior ability to perceive contrasting motion in the upper-left quadrant cannot be attributed simply to the generally poorer UVF vs. LVF performance on motion integration tasks. Rather, there might be an additional weakness in the upper-left quadrant specific to motion segmentation.

The processing weakness may lie in the spatial allocation of attention. One way in which to facilitate the processing of coherent motion signals within the test region of the RDK would be to focus a spotlight of attention onto the central band, thus inhibiting the processing of the two inducer regions. This could not have been observed in the previous experiments. In Experiment 1A, where the static dots were located similarly to the RDK presented here, an inability to spotlight attntion onto the motion signals might have actually aided motion perception, possibly by allowing the static dots to be used asa stationary referent. However, in the present study a wide spotlight of attention, encompassing the flanker regions, might more likely bias motion integration mechanisms to be influenced by the signal direction in the inducer region.

The brain mechanisms activated in response to motion contrast stimuli appear to be highly susceptible to certain stimulus parameters. For example, using MRI, Reppas et al., (1997) found little activation in either V5, or its satellite regions, when motion-defined boundaries were continuously present throughout the lifetime of the stimulus. As this was the case with the present stimulus, it is possible that the comparable performance between the two LVF quadrants and the upper-right quadrant might be due to a relative underactivation within the presumably LVF-biased V5. Supplementing Reppas et al.'s (1997) finding, Shulman et al., (1998) reported strong activation in V5 to only the onset and offset of motion-defined boundaries. Thus, if the present stimulus had alternated between displaying contrasting and unidirectional motion, it might be speculated that a LVF advantage in both visual quadrants might have resulted.

The stimulus size may also have played some role in the results obtained. Both Dupont et al. (1997) and Van Oostende et al. (1997) report maximal activation within KO with circular kinetic gratings of only a 3^{O} diameter. When the stimuli were increased in size, activation decreased, and ceased altogether when stimulus diameters reached between 7^{O} and 14^{O}. Reppas et al. (1998) similarly found no activity within KO with much larger (26^{O} x 26^{O}) stimuli. Comparing these results, Shulman et al. (1998) noted that small-field motion contrast stimuli tend to produce activation within KO, but not in V5. Large-field stimuli produce the opposite pattern of activation. The present stimulus (encompassing 12 deg^2 of visual field) was much closer in area to a 3^{O} diameter (7.06 deg^2) than the 7^{O} diameter (38.47 deg^2) stimulus. Thus, it might be further speculated that the two motion-defined boundaries within the present stimulus activated KO to a greater degree than V5, resulting in less convincing evidence of a LVF processing bias.

Experiment 4: Perception of Global Texture

Abstract

The results obtained from the previous experiments can be interpreted as supporting the notion that the LVF is functionally specialised for processing global motion. However, the possibility remains that the LVF advantage observed thus far might simply reflect a processing advantage for the global level of any class of stimulus. The purpose of this experiment was to test this hypothesis. The stimulus employed here was analogous in many respects to the RDK paradigm. In place of moving dots were multiple line elements displaying a varying distribution of orientations. Observers viewed these stimuli both in isolation, and with a distractor stimulus at fixation, while discriminating the global orientation of the line elements. No vertical hemifield effect was found in either condition, supporting the view that the LVF is functionally specialised for processing global motion.

Chapter 12:
Experiment 4: Perception of Global Texture

12.1 Introduction

In all of the experiments reported thus far, observers were required to make global discriminations of motion direction. In each case, a LVF advantage was obtained, with the sole exception of the static-distractor condition in Experiments 1 and 1A, in which no hemifield effect was evident. Christman (1993) also found a LVF advantage, for both response accuracy and latency, when observers were required to discriminate the global level of static Navon-type letter stimuli. The possibility arises, therefore, that the LVF advantage for global motion perception may result from a general advantage for processing the global level of any stimuli, and not necessarily result from any functional specialisation for global motion. The purpose of this experiment was to test this hypothesis.

There is a fundamental methodological difference between perception of the global level of motion within an RDK and perception of the global level of a Navon stimulus. Due to their hierarchical nature, the local level of Navon stimuli is discriminated when attention is focused on any single individual element. This strategy is not possible with RDKs. Similarly the global level of a Navon stimulus is perceived when the total configuration of the local elements is perceived. This strategy would also be ineffectual for processing the coherent direction of motion within an RDK as the individual dot trajectories must be spatially integrated in order to derive some central tendency of motion direction. Thus, a more appropriate method by which the LVF advantage for global motion can be compared with the global processing of static stimuli would be to evaluate vertical hemifield performance on a task requiring the spatial integration of multiple static elements, which might differ in a single attribute, yet as a group, exhibit some global tendency.

The ability to derive a global percept from a textured surface comprising heterogenous featural elements appears to meet this need. A real-world example of such a percept might be a patch of grass, which although containing individual blades facing multiple directions nevertheless has a global appearance of pointing upward. As with global motion perception, the orientation of any single element would be an unreliable source of information for this process. Rather, some pooling algorithm must extract an average from a wide distribution of orientations.

The stimulus employed in this experiment consisted of a borderless patch containing numerous line elements displaying a varying distribution of orientations. As with a unidirectional RDK, some of the elements were labelled as 'signal' by virtue of their shared orientation, while the remaining diversely oriented elements functioned as 'noise'. The signal to noise ratio was then manipulated across trials. Reductions in signal to noise ratios meant that individual line elements were increasingly less likely to signify the global orientation of the texture. Thus, in common with RDKs, the orientations of all line elements must be perceptually integrated across space for the global orientation to be accurately discriminated. Previous work in this laboratory has shown that when viewed at fixation, the texture thresholds derived from this task are similar in magnitude to those produced in response to RDK stimuli.

Observers judged the global orientation of each stimulus and accuracy was assessed as a function of the proportion of signal lines. This yielded an orientation threshold, defined as the minimum percentage of signal lines necessary for just accurate identification of the signal, or global orientation. To better mimic the conditions that elicited a LVF advantage in Experiment 1, observers made judgements to the peripheral stimuli both with and without foveal distractor stimuli comprised entirely of randomly oriented lines.

12.2 Method

12.2.1 Participants

Seven females and three males, with a mean age of 21.0 years (s.d. = 2.2 years) participated for partial course credit. Nine were right-handed. All were inexperienced psychophysical observers, naïve to the aims of the study. All reported no prior ophthalmological or neurological disorder and had normal or corrected to normal vision.

12.2.2 Apparatus

The stimuli were generated by a Cambridge Research Systems Visual Stimulus Generator 2/3 graphics card housed in a Dell P133 computer and displayed on a 17" Eizo T562-T Flexiscan monitor with a refresh rate of 100 Hz. Head position was stabilised with an opthalomologic viewing brace and a height adjustable chair.

12.2.3 Stimuli

The fixation marker comprised two black lines, each subtending 34.8 minarc, and presented in a '+' configuration. It was located either 5^0 above (for LVF locations) or 5^0 below (for UVF locations) the centre of the monitor for 1500 msecs.

Both the test and distractor stimuli were composed of 100 black line segments, each measuring 1.34 minarc x 13.4 minarc and contained within a borderless region subtending 3.6 deg^2 of visual field. Stimuli were presented against a uniform grey field, giving a Michelson contrast of 50%. In order to ensure that no line segments overlapped each was spatially constrained within single cells (each 21.6 $minarc^2$) of an invisible 10 x 10 cell-positioning grid. To minimise vertical or horizontal collinearity, which can positively influence perception of texture elements (Field Hayes, & Hesse, 1993; Polat & Sagi, 1993), the position of each line segment was 'jittered' by being randomly offset from the centre of the cell by +/- 6.6 minarc along the *x* and *y* axes.

The orientation of the line segments around their centre points varied from a possible 16 orientations ranging from 0^0 to 168.75^0 in 11.25^0 increments, using Cartesian coordinates. Thus, signal line segments were oriented either 0^0 (vertically) or 90^0 (horizontally) while noise segments were randomly assigned one of the 16 possible orientations, including either signal orientation. Separate, intermingled 1-up, 2-down psychophysical staircases determined the percentage of signal lines (horizontal and vertical) displayed in the test stimulus on any single trial. The staircases always commenced at 100% coherence (i.e., with all line segments oriented in a single direction) and descended by 50% coherence after two correct responses. If an incorrect response was made, the staircase ascended by 50% coherence. Each staircase terminated after six such response reversals, producing a mean threshold for global orientation that converged on the 71% correct point. The distractor stimulus was identical to the test stimulus but displayed random distributions of line orientation, the pattern of which differed on every trial. The stimulus is detailed in Figure 12.

The test stimuli were presented in each of the four visual quadrants. As in all previous experiments, the centre of the test stimulus was located 7.07^0 from the fixation marker. Thus, the upper, lower, leftward, and rightward boundaries were located either 3.2^0 or 6.8^0 from the horizontal and vertical meridians, depending on the quadrant. The distractor stimuli were always centred on the prior location of the fixation marker. Both test and the distractor stimuli were presented simultaneously for 180 msecs. Previous work had indicated that, with foveal viewing, performance on these tasks asymptotes at this duration.

The pattern mask was identical in size, and located in the same location as the test stimulus. Each was composed of identical line segments, conforming to the same rules as the test and distractor stimuli, however, the lines overlapped to produce 50 elements in a '+' sign configuration whose arrangement differed on every trial. The mask was also presented for 180 msecs.

12.2.4 Procedure

The display was viewed binocularly at a distance of 92 cm. Trials were initiated by the experimenter and began with the presentation of the fixation marker. Upon its offset, either test stimuli alone, or both test and distractor stimuli, were presented without an interstimulus interval. This was followed, again without interval by the pattern mask. The observer's task was to judge the perceived global orientation of the test stimulus, either vertical or horizontal. Responses were made verbally and keyed into the computer by the experimenter who was blind to the stimuli. No feedback was given. Each session began with practice trials and data collection commenced only when participants indicated that they understood and felt comfortable with the procedure.

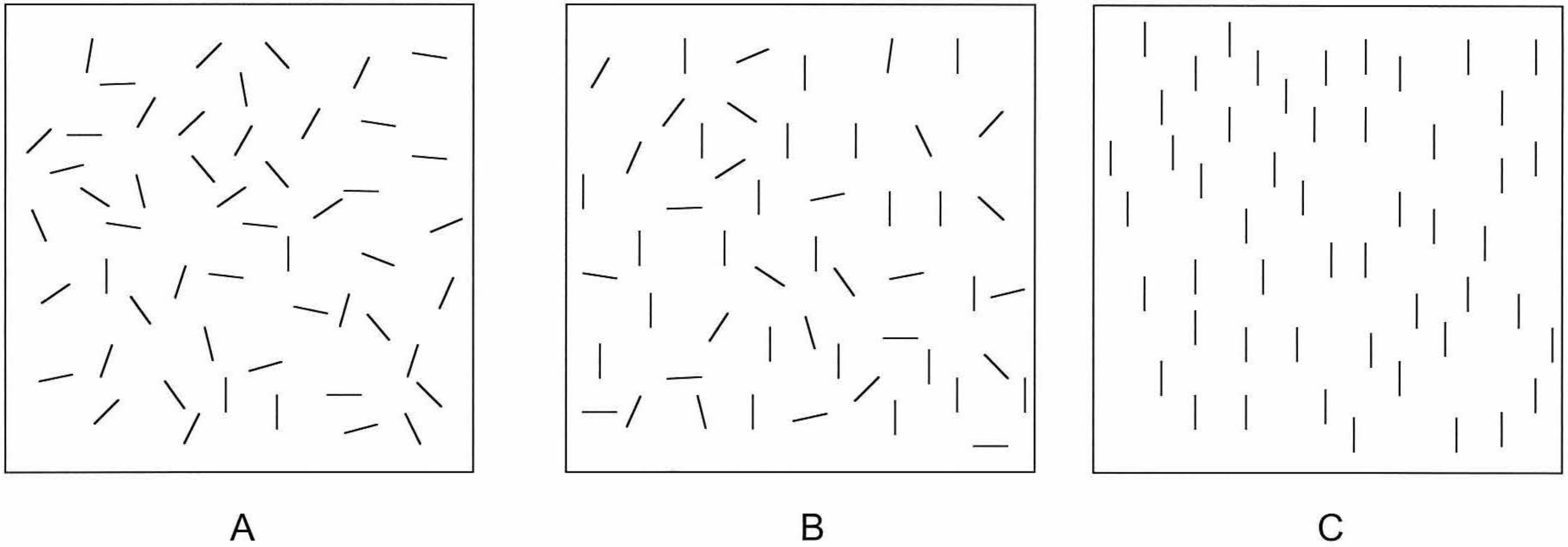

Figure 12. Schematic of the global texture paradigm. In block A, the orientation of the line segments is wholly random (i.e., a coherence level of 0%). In block B, half of the line segments are randomly oriented (noise elements) while the remainder are oriented vertically (signal elements). In this case the coherence level is 50%. In block C, all line segments are oriented vertically, displaying an orientation coherence level of 100%.

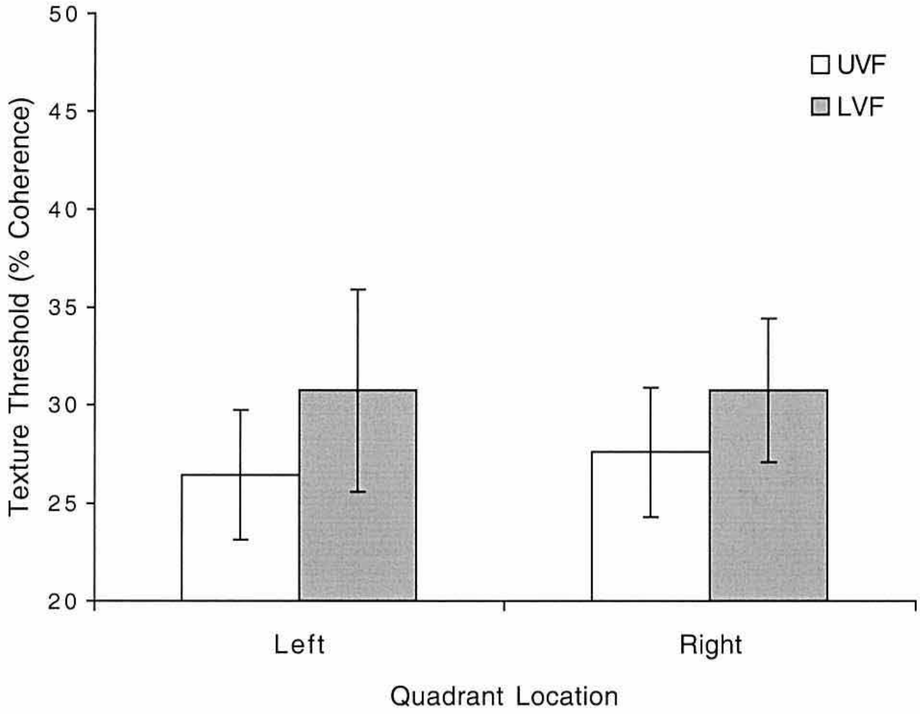

Figure 13. Texture thresholds obtained in the UVF and LVF in the no-distractor condition as a function of visual quadrant. Vertical bars represent +/- 1 standard error of the mean.

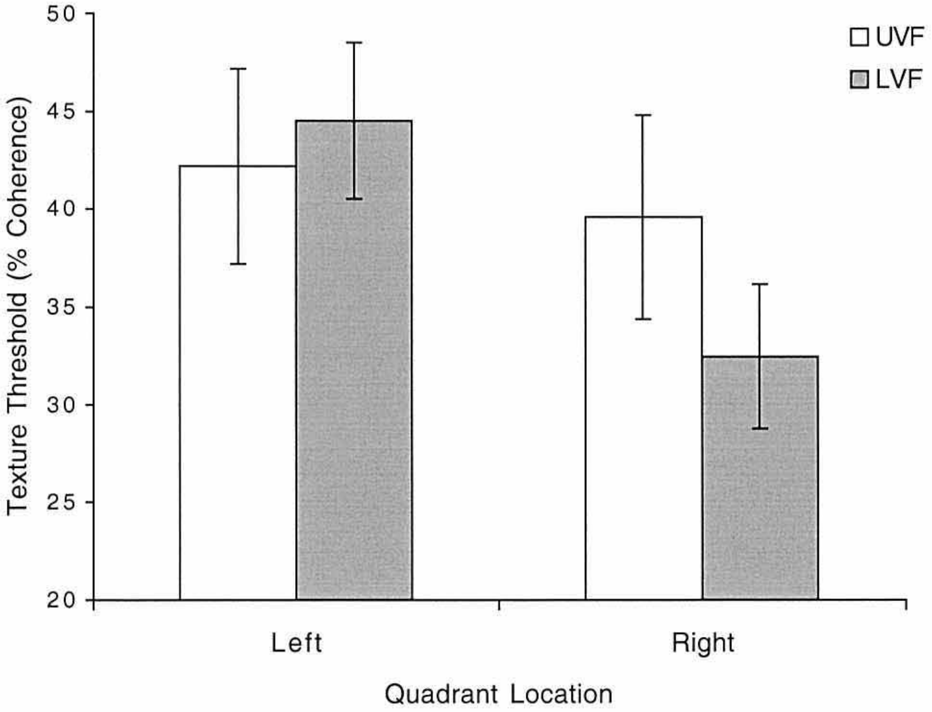

Figure 14. Texture thresholds obtained in the UVF and LVF in the distractor condition as a function of visual quadrant. Vertical bars represent +/- 1 standard error of the mean.

12.3 Results

The data obtained from the no-distractor and distractor conditions, collapsed across orientation, are plotted separately in Figures 13 and 14. A three-way, within-subjects ANOVA, with vertical hemifield (UVF, LVF), horizontal hemifield (left, right) and distractor condition (absent, present) as factors showed that performance in the vertical hemifields did not differ on this task. The only significant effect was that of distractor condition, $F(1, 9) = 15.64$, $p < .01$, which reflects the adverse effect the distractor had on texture thresholds in both vertical hemifields.

12.4 Discussion

In this experiment I presented a static stimulus, which like the RDK paradigm, is hypothesised to require the spatial integration of local elements, in order to achieve a global analysis of, in this case, orientation. The aim was to determine whether the LVF advantage observed for global motion perception represents a processing advantage for the global level of all stimuli. If the LVF demonstrated a performance advantage for this task, the notion of the LVF having a functional specialisation for processing global motion (Previc, 1990) could be questioned. On the other hand, a UVF performance advantage, or no vertical hemifield effect, would suggest that the LVF advantage observed thus far might reflect a processing specialisation for global motion.

Contrary to findings from the RDK tasks, no vertical hemifield effect was found on this task. Thus the LVF appears to demonstrate an advantage for the spatial integration of diverse motion signals but does not have a processing advantage for spatially integrating diversely oriented line elements. An additional finding was that the distractor stimulus produced a significant performance decrement in both vertical hemifields.

Despite previous observations that the present stimulus, and RDK stimuli, produce similar threshold levels when viewed at fixation, a comparison of the difference in thresholds obtained in the present experiment (see Figures 15 and 16) and the motion coherence thresholds obtained in the no-distractor and motion-distractor groups in Experiment 1

(10-frame duration) suggest that the spatial integration of oriented elements in the visual periphery is the more difficult task. However the magnitude of the distractor effect appears to be similar in both experiments. In Experiment 1, the addition of a motion distractor (10-frame duration) raised thresholds by a ratio of 1:1.4 in the UVF and 1: 1.09 in the LVF. Similarly, the texture distractor increased thresholds by a ratio of 1:1.5 in the UVF and 1:1.25 in the LVF. Thus, the task was not made relatively more difficult than was the motion task, when viewing random noise at fixation.

The physiological structures underlying the spatial integration of orientation appear, unlike the structures underlying motion perception, to not be biased toward either vertical hemifield.

As with motion signals, the initial detection of orientation is presumed to occur in V1 and V2, probably via the parallel processing of local variations in luminance and spatial frequency (Landy & Bergen, 1991; Graham, Beck, & Sutter, 1992). Few psychophysical studies have specifically investigated the mechanisms involved in the perceptual grouping of textures composed of diverse orientations (though see Keeble, Kingdom & Morgan, 1997; Keeble, Kingdom, Moulden & Morgan, 1995; Kingdom, Keeble & Moulden, 1995). Nevertheless, all have come to the conclusion that discrete texture elements are able, like motion signals, to be spatially integrated over large regions of the visual field. Analogous with motion processing, this implies the action of nonlinear, cooperative mechanisms, linking cells with wide-band orientation tuning and large receptive fields (Or & Zucker, 1989; Sha'shua & Ullman, 1988).

However, because both oriented lines and Gabor patches produce similar psychophysical results it is deemed unlikely that neural cooperativity within V1 alone would be sufficient to account for global percepts of texture (Keeble et al, 1997), suggesting that judgements of global orientation are not mediated by low-level sensory orientation detection mechanisms.

Studies of global pattern recognition in response to Glass patterns indicate that the process of spatial integration might commence in V4 (Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Assad, 1997). When V4 is selectively lesioned, leaving V1 intact, identification of individual texture defined stimuli remains possible, but the ability to segregate particular stimuli embedded in an array of competing stimuli is impaired (Merigan, 1996; Schiller, 1993). A ventral pathway locus for processing global orientation is further suggested by Rudolph and Pasternak (1999) who after lesioning MT found the expected increased susceptibility to motion noise in RDKs, relative to intact control animals, but no effect of decreased signal to noise ratios for multi-oriented stimuli.

It would appear, therefore, that the evidence of a lack of dorsal pathway involvement in the spatial integration of multi-oriented texture has resulted in the lack of a vertical hemifield effect on this task. Hence, the view that the LVF is functionally specialised for processing global motion, and not the global level of all stimuli, enjoys some support.

Experiment 5: Perception of a Single Moving Element and the Representational Momentum Effect

Abstract

To date, no studies have compared vertical hemifield sensitivity to a single moving element. Discriminating the movement of a single element requires fundamentally different mechanisms than those used to spatially integrate multiple elements displaying diverse trajectories. Therefore, it would be premature to assume that a LVF advantage exists for all types of motion stimuli. To test whether these two motion mechanisms operate to different effect in the vertical hemifields, ten observers covertly tracked the trajectory of a single dot, moving horizontally in either the UVF or LVF at a rapid velocity. At an indeterminate point, the stimulus abruptly vanished and observers then localised the vanishing point. Responses were significantly more accurate when made to UVF vs. LVF stimuli. Mislocalisations were characterised by both small underestimations and overestimations (the representational momentum effect) of the actual vanishing point. Although the distribution of mislocalisations did not differ between the vertical hemifields, overestimations were observed to be significantly larger in the LVF. These findings suggest that the motion mechanisms used to process single element and global motion operate to different effect according to vertical hemifield.

Chapter 13:

Experiment 5: Perception of a Single Moving Element and the Representational Momentum Effect

13.1 Introduction

Experiments 1, 2 and 3 demonstrated a LVF advantage for processing stimuli in which multiple moving elements are subject to a process of spatial integration. However, no studies have compared vertical hemifield sensitivity in response to a single moving element. Unlike partially coherent global, or textured motion stimuli, movement of a single object is characterised by homogeneity of motion vectors at all edges and so analysis of the leading edge alone is sufficient to compute the direction of motion of the whole object. Because of the fundamentally different processing requirements for global and single element motion, it would be premature to assume that a LVF advantage may exist for all types of motion stimuli.

Representational momentum (RM) refers to the phenomenon by which the reported final position of a single moving target appears to be displaced in the direction of travel immediately prior to its offset (Freyd, 1987). The effect has been reported for all directions of motion including rotation, translation and size change, as well as for implied motion in static scenes (see Hubbard, 1994 for a review). Again, the magnitude of this effect has yet to be compared in the vertical hemifields.

There is considerable debate as to the nature of the mechanism responsible for the RM effect. Early theories suggested that mental representations of movement were analogous to the momentum of physical stimuli, which normally continue to exhibit some forward momentum after the application of a stopping agent (e.g., Finke, Freyd, & Shyi, 1986). However, the RM effect is cognitively penetrable. For example, judged forward displacements for upward moving targets are invariably smaller than those for downward moving targets, believed to signify gravitational effects (Hubbard, 1995). Furthermore, the magnitude of the effect differs significantly when an ambiguous stimulus is prelabelled as either a church steeple or a rocket (Reed & Vinson, 1996). Thus, because the RM effect can be altered by expectations and beliefs, the 'naïve physics' metaphor is no longer considered tenable as a comprehensive explanation. Instead, in contrast to perceptual 'low-level' illusions such as apparent motion and motion after-effects, the RM effect is widely considered as evidence for the cognitive representation of motion (Hubbard, 1994).

The majority of studies agree that the RM effect reflects a bias in memory for the final position of a moving stimulus. However, recent evidence suggests that this memory bias is not confined to the final location, but can extend to the initial position of the stimulus, which is often judged as being displaced backward. Hence, the RM effect has more recently been conceived as a distortion of the entire length of the stimulus trajectory, rather than simply an overestimation of forward displacement (Hubbard and Motes, 2002).

In this experiment I investigated whether (i) spatial localisation of a single moving element differs between the vertical hemifields and (ii) whether the vertical hemifields produce RM effects of differing magnitudes. To this end, I designed an expanded version of the spatial localisation paradigm first employed by Hubbard and Bharucha (1988; Experiment 1). In the present experiment, observers covertly tracked the trajectory of a single dot that moved horizontally in either the UVF or LVF at a rapid velocity. At an indeterminate point, the stimulus abruptly vanished. The task was to localise, using a forced choice procedure, the dots vanishing point, or spatial offset.

13.2 Method

13.2.1 Participants

Nine female and one male undergraduate (mean age = 22.7 years, s.d. = 4.3 years) participated for partial course credit. They were inexperienced psychophysical observers, naïve to the study's goal. None were colour-blind, reported any current neurological disorder, or had undergone eye surgery. Prescribed optical corrections were worn if needed.

13.2.2 Apparatus

Stimuli were generated by a Power Macintosh 8500/120 computer and displayed on a 17" Applevision 1710 monitor with a vertical refresh rate of 60 Hz. A height-adjustable chair and chin and forehead restraint were provided to maintain a steady viewing posture.

13.2.3 Stimuli

All stimulus events were presented on a white background with a luminance of 76.2 cd/m^2. Fixation markers were randomly presented 8^{O} above (for LVF stimuli) or below (for UVF stimuli) the centre of the monitor. They were randomly selected on each trial from a pool of 24 black capital letters (Arial 24 point; Q and I were not used). The test stimulus was a red circular dot with a diameter of 30 minarc and a luminance of 17.7 cd/m^2, giving a Michelson ratio between test dot and background of 62.3%. The dot appeared sequentially for the duration of one screen refresh (16.6 ms), without interstimulus intervals, within an invisible array of seven possible locations along the horizontal plane in the central region of the monitor. Effective velocity was 120^{O}/sec. Although this velocity may be considered to be unusually fast, pilot data indicated that some observers were able to perform at ceiling with slower speeds. The middle location within the array was situated at the monitor's vertical midline, 8^{O} above or below the appropriate fixation marker. This location was flanked on either side by three outer locations. Each location was separated from the next by a centre-to-centre distance of 2^{O}. The array is henceforth labelled from left to right as locations 1-7 (refer Figure 15).

Four stimulus conditions were presented randomly to each vertical hemifield. The vanishing point of the dot was also randomised. In the "rightward short" condition, the dot appeared at location 1, moved rightward and vanished after appearing at either locations 3 (50 ms), 4 (66 ms), or 5 (83 ms). In the "leftward short" condition the dot would start at location 7, move leftward and vanish after appearing at either locations 5 (50 ms), 4 (66 ms) or 3 (83 ms). In the "rightward long" condition, the dot started at location 7, travelled leftward and, after appearing at location 1, reversed direction and vanished after reappearing at either locations 3 (150

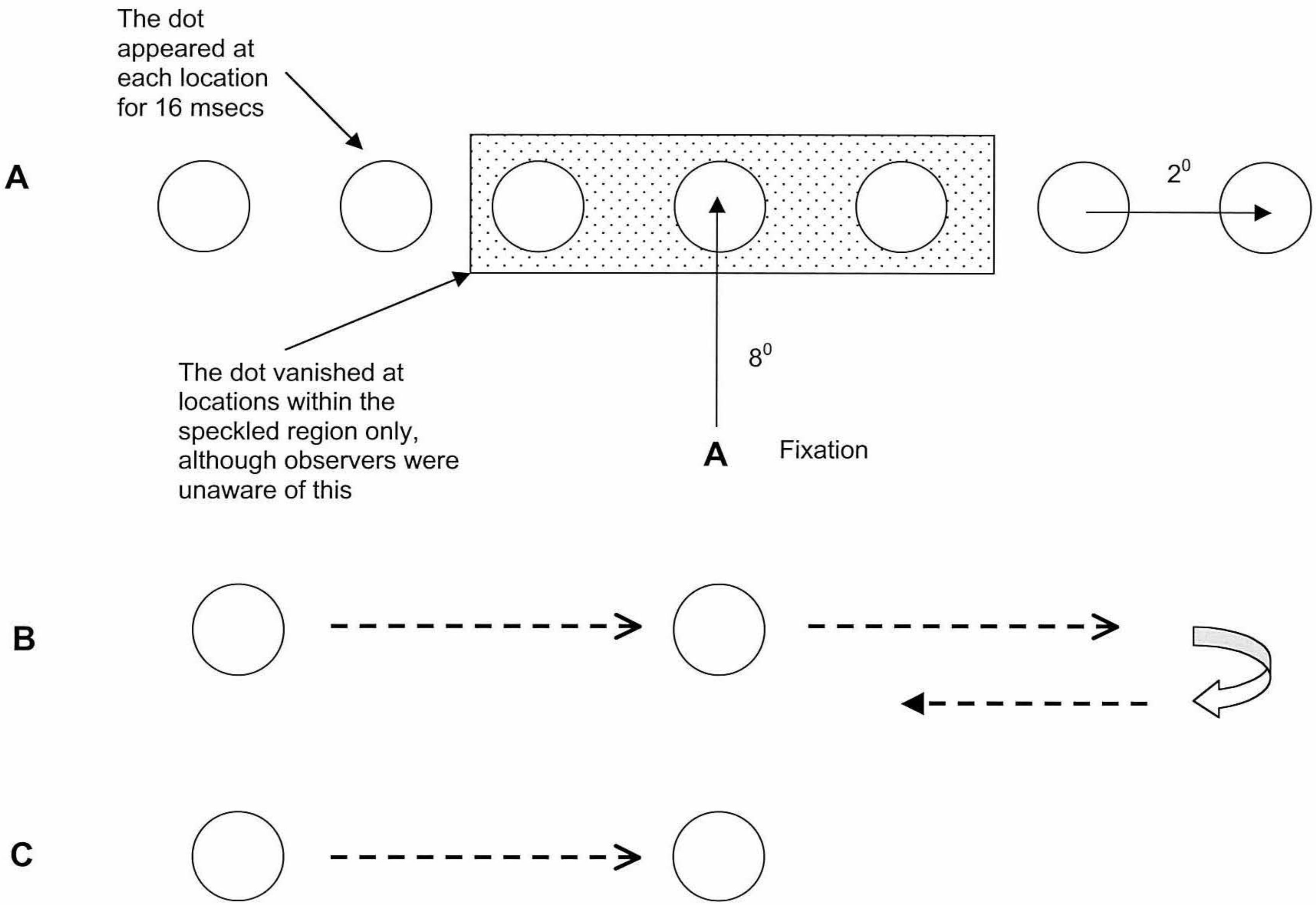

Figure 15. Schematic of the single element motion stimulus. A: The stimulus array. B: An example of a ‘leftward long’ trial. C: An example of a ‘rightward short’ trial.

msecs), 4 (166 ms) or 5 (183 ms). The “leftward long” condition was a mirror image, starting at location 1, reversing direction after appearing at location 7, and vanishing after reappearing at either locations 5 (150 msecs), 4 (166 ms) or 3 (183 ms). Thus, unknown to observers, the dot vanished only at either the middle, or the two flanking locations. Its direction of motion was always defined by the trajectory undertaken at the vanishing point.

The response screen contained seven stationary dots, identical to the test dots, which appeared simultaneously at locations 1-7. Observers judged which of the seven locations matched the dot’s final location and made a verbal report. The chance performance level for accurate response was therefore .14.

13.2.4 Procedure

Observers were positioned 57cm from the monitor in a dimly lit room. All sessions began with practice trials and data collection commenced only when observers indicated that they fully understood the procedure. Trials were initiated by the experimenter and commenced with a 500 ms presentation of the fixation marker. The test stimulus appeared simultaneously with its offset. After the test dot had vanished, there was a 250 ms blank screen, followed by the response screen. Responses were keyed into the computer by the experimenter, who was blind to stimulus presentation.

For each observer, data were collected from 240 trials, 120 each in the UVF and LVF. These consisted of 30 trials for each of the four direction x duration conditions, i.e., 10 trials for each of the three locations at which the dot vanished.

13.3 Results

The proportion of correct responses for each of the three vanishing points was calculated for each observer, in each direction x duration condition, for both the UVF and LVF. Proportion correct scores for each vanishing point were then collapsed across subjects within each condition, giving a single proportion correct score for each condition, in both vertical hemifields. Figure 16 displays these data.

As Figure 16 shows, the vanishing point was correctly identified on a higher proportion of trials when the dot travelled within the UVF, regardless of its direction or duration. This observation was confirmed by a three-way ANOVA employing vertical hemifield (UVF, LVF), motion direction (rightward, leftward), and duration (short, long) as within-factors. There was a main effect of vertical hemifield, F (1, 9) = 40.26, p < .01, as well as a main effect of direction, F (1, 9) = 18.46, p < .01, with more accurate responses to the rightward moving dots. A main effect of duration,

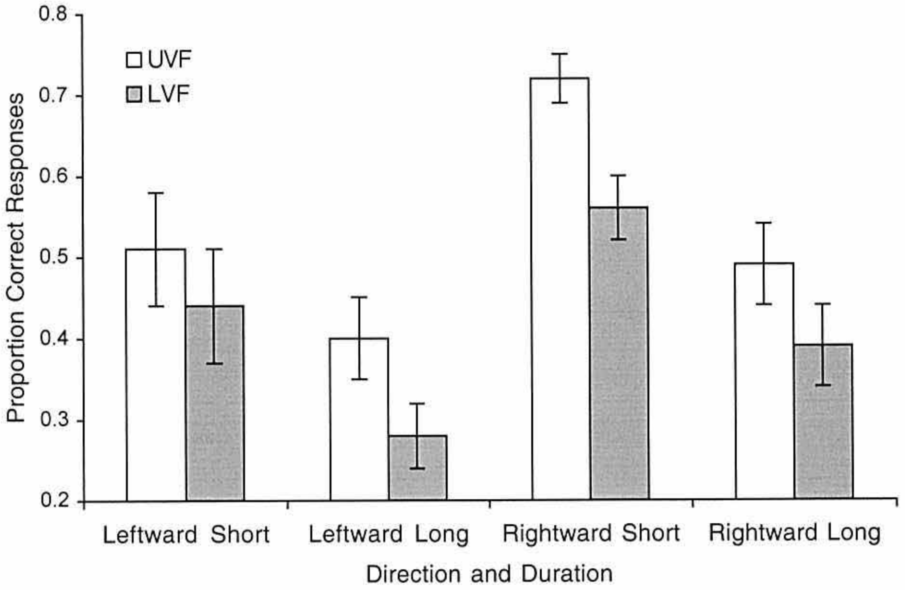

Figure 16. Proportion correct responses obtained from the UVF and LVF as a function of motion direction and stimulus duration. Vertical bars represent +/- 1 standard error of the mean.

F (1, 9) = 19.21, p < .01, was also observed, evidenced by greater accuracy at the shorter durations, i.e., in those trials in which the dot did not change direction. There were no significant interactions.

In order to quantify the spread of responses, and thus determine the magnitude of the RM effect in each vertical hemifield, mean response effect sizes were calculated for each observer. These were defined as the mean of the proportion of responses made to locations 1-7 inclusive, measured in degrees of visual angle. Figure 17 plots the response distribution as a function of vertical hemifield.

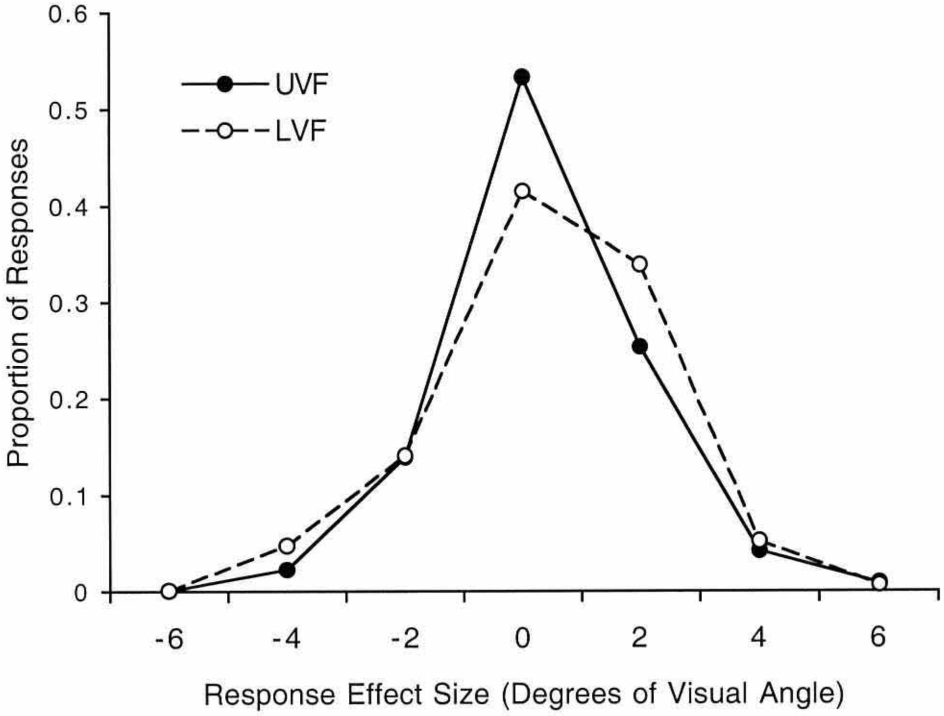

Figure 17. Distribution of responses made in the UVF and LVF converted to degree of visual field from the correct vanishing point. Negative numbers on the x-axis represents underestimations of the vanishing point, zero represents the veridical vanishing point and positive numbers represent overestimations of the vanishing point, or the RM effect.

Mean proportion correct responses are plotted at zero on the horizontal axis. Each positive coordinate (to the right of zero) plots the proportion of responses made at each location in the direction forward of the actual vanishing point. These responses constitute a representational momentum effect. Minus coordinates (to the left of zero) plot the proportion of responses to those locations sited before the actual vanishing point, i.e., an underestimation, or negative representational momentum effect. The group mean response effect size was $+0.53^{\circ}$ in the UVF and $+0.42^{\circ}$ in the LVF.

A second three-way ANOVA (vertical hemifield x direction x duration) was performed on these effect size data. There was no main effect of hemifield and, again, no interaction effects. This analysis did reveal main effects of both direction, F (1, 9) = 7.85, p < .05, and duration, F (1,9) = 5.51, p < .05. There was a significant tendency to estimate the vanishing point forward of its true position during leftward vs. rightward motion in both the short (+0.97^{O} vs. +0.04^{O} in the UVF; +1.10^{O} vs. +0.35^{O} in the LVF) and long duration (+0.64^{O} vs. –0.21^{O} in the UVF; 0.58^{O} vs. –0.24^{O} in the LVF). However, when underestimations of the vanishing point were excluded from the analysis and judged forward displacements only were compared in each vertical hemifield, the RM effect, albeit much smaller (+0.1^{O} in the UVF and +0.14^{O} in the LVF), was nonetheless found to be significantly larger in the LVF (p < .01).

13.4 Discussion

This experiment addressed two questions concerned with the processing of single-element motion. Firstly, does the ability to covertly track the movement of this type of stimulus differ in the UVF and LVF? Secondly, does the RM effect differ in magnitude between the vertical hemifields? The principal finding was that observers covertly tracked a single, rapidly moving object more accurately in the UVF than the LVF, up to 183 ms of its onset. In both hemifields, the ability to localise the vanishing point was most accurate in response to a rightward moving stimulus that had not undergone any directional change, and was weakest for a leftward moving object that had previously moved rightward. Although no vertical hemifield asymmetry was observed for the overall distribution of localisation errors, judged forward displacements were larger when made to stimuli in the LVF.

The higher level of accuracy for spatially localising the stimulus in the UVF might be argued to be due to low-level visual, rather than higher-level motion mechanisms. This could be due, for example, to enhanced detection of luminance changes, or a superior ability to temporally resolve the onsets and offsets of the stimuli. However, such an explanation would be incongruent with findings of heightened luminance and temporal sensitivity in the LVF vs. UVF (Hylkema, 1942; Phillips, 1933; Riopelle & Bevan, 1953; Skrandies, 1985b; Sloan, 1947). The fact that observers were better able to localise the offset of a flickering dot in an apparent motion sequence in the UVF therefore suggests that performance on this task was due to a superior ability to track the movement of the stimulus. Alternatively, the cause of the vertical hemifield performance difference may lie in the superior ability of memorial mechanisms in the UVF.

The dot motion paradigm employed here differs markedly from the RDK paradigm employed in previous experiments. With an RDK, the spatiotemporal features alone define the stimulus. An RDK does not exist independently of its kinetic properties, i.e., its dot trajectories, speeds, etc. In contrast, the stimulus employed in this experiment has an identity independently of its motion attributes. It can be perceived primarily as an object and secondarily as an object with kinetic properties. Furthermore, while multi-element RDKs continuously occupy a single region of space, the present stimulus comprised a single moving object traversing up to 12^{O} of the visual field.

The present task required that observers make a rapid deployment of attention to the initial onset of the stimulus. This need be followed by a rapid disengagement from that location, followed by covert tracking both in response to, and possibly in anticipation of the target's trajectory. On the 50% of trials in which a direction reversal occurred, an entirely separate subset of cortical direction-selective cells would need to be recruited. These computations require a motion mechanism that is fundamentally distinct from the mechanism used to integrate diverse trajectories within a single, unchanging region of space.

A large body of evidence suggests that the mechanism governing the rapid computation of two-dimensional spatial metrics for the covert reallocation of attention is the same as that underlying the programming of eye movements (e.g., Corbetta, 1998; Konderink, 1990). Thus, the UVF advantage on this task is conceivably due to a superior ability to continually deploy covert attention to an object traversing the visual field. It is interesting to note, therefore, that the cortical region believed to be crucial for determining the spatial metrics for the reallocation of attention, *whether an ocular motor response occurs or not,* is the lateral intraparietal region, or LIP (Snyder et al., 1997). This cortical region is somewhat anomalous within the primate dorsal stream as it has a strong representational bias toward the UVF (Li et al., 1999; Thier & Andersen, 1996).

Viewed in this way, the results obtained in this study are in broad agreement with Previc's (1990; 1998) view that the visual mechanisms coding for the UVF might preferentially process objects, as opposed to the spatiotemporal aspects of the visual array. The present study might further suggest that the visual mechanisms coding for the UVF preferentially process moving objects, as opposed to movement within a single, unchanging region of space.

A comparison of the present stimulus parameters with those of Hubbard and Bharucha (1988; Experiment 1) reveal several differences. In the original experiment, the dot was viewed freely without an initial fixation marker, thus allowing pursuit eye movements. Their stimulus was larger (50 minarc vs. 30 minarc diameter), and its fastest velocity was much lower (34.8^{O}/sec vs. 120^{O}/sec). The original stimulus was also displaced a much smaller distance (approx. 15 minarc vs. 2^{O}), and vanished at any of five, rather than three locations. Responses were made by the positioning of a cross hair, rather than by a forced choice method [13].

Regardless of these differences, peripheral viewing alone might suggest that the present task was the more onerous. However, a comparison of the mean response effect size obtained by Hubbard and Bharucha (1988; 2^{O} for rightward motion and 2.6^{O} for leftward motion) and those obtained here suggest otherwise as the present study obtained much smaller RM effects in both vertical hemifields. Surprisingly, then, covert tracking of a fast moving, small dot appears able to be performed more accurately in the vertical periphery than tracking a larger slower moving dot while it is being continuously foveated.

Bearing in mind these differences in stimulus parameters, some aspects of the results obtained here might be explained by the notion of 'naïve physics'. For example, with an increase in the distance travelled by

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[13] A forced-choice response mode was employed by Hubbard and Bharucha (1988) in a further experiment. However, a comparison with the present study was not possible as only two choices of location were provided, so a mean response effect was not calculated.

the stimulus, the RM effect tends to decrease due, partly, to expectations of the effects of friction (Hubbard, 1995). Similarly, the tendency to underestimate the vanishing point of rightward moving dots that had undergone a directional change might be attributed to a perceived loss of momentum as the result of 'bouncing off' (rather than 'crashing through') an invisible boundary. This explanation would not, however, predict the larger RM effect found for leftward moving dots that had undergone a similar directional change.

A more recent theory of RM considers the effect to be determined by the rate of decay of supraliminal processing after the target has vanished (Kerzel, 2000). The responsible agent is argued to be pursuit eye movements made during and after presentation of the target. This factor might explain the relatively large RM effect found in Hubbard and Bharucha's (1988) study. As is the case with the majority of RM experiments, Hubbard and Bharucha (1988) did not control for eye movements and so it is possible that observers made smooth pursuit movements in an attempt to continuously foveate the stimulus. When Kerzel (2000) had observers maintain fixation at a single location, the magnitude of the RM effect was considerably reduced. Thus, the lack of opportunity to make pursuit movements might explain the relatively small RM effect observed in the present study.

Nonetheless, neither theory explains why, when forward judgements were made, they were significantly larger in the LVF vs. UVF. A possible explanation derives from the perceptual phenomenon of 'boundary extension' (see Intraub, 2002 for a discussion). When recalling visual scenes from memory, subjects demonstrate a robust tendency to draw, or otherwise report, a wider-angle view than was actually depicted in the original scene. Objects are remembered as being both smaller, and displaced in depth away from the observer (Intraub, 2002). Importantly, the upper half of remembered scenes appear to be particularly susceptible to this illusion (Intraub, 2002; Previc & Intraub, 1997).

Unlike RDK stimuli, which require dimmed lighting to enable the moving dots to be perceived, this experiment was performed under bright lighting conditions, which would have enabled the monitor surround to be construed as a scene boundary. The RM effect is contingent on the memorising of the spatial aspects of a scene before responses are made (Hubbard, 1994; Hubbard & Motes, 2002). Thus, when the stimulus appeared in the UVF, it may have been recalled as having been subtly displaced in depth, resulting in a perceived shorter trajectory, eliciting smaller judged forward displacements.

The most important finding from this study, however, was the UVF advantage for spatially localising the vanishing point of a single moving element. This finding suggests that the motion mechanisms used to compute global motion and single-element motion operate to differing effect according to vertical hemifield, and therefore offers further support for the notion that the LVF is functionally specialised for processing global motion.

Case Study: Albinism

Abstract

The question of whether functional differences between the vertical hemifields are genetically or environmentally determined was addressed here. The higher photoreceptor and ganglion cell densities in the upper hemiretinae of normal adults develops during infancy. However, albinos suffer arrested development of the retina during infancy. It is known that the quality of sensory inputs during infancy can impact on cortical development, and there is also evidence to suggest that the dorsal pathway is particularly sensitive to developmental disorder. Thus, it was hypothesised that an adult albino (JK) might exhibit anomalous functional asymmetry in the vertical hemifields on dorsal pathway mediated global motion tasks. This view was confirmed. JK demonstrated no performance asymmetry in the vertical hemifields with short duration stimuli, and a clear UVF advantage at longer durations. Thus, it would appear that the quality of sensory inputs in early life might influence the development of the functional asymmetry for global motion perception.

Chapter 14:
Case Study: Albinism

14.1 Introduction

Albinism represents a heterogenous group of inherited disorders resulting from mutations in one or more of the genes associated with melanin synthesis. Its most visible symptom is hypopigmentation of the skin, hair and eyes. However, while both the skin and hair develop otherwise normally, concurrent severe abnormalities in the visual system are found. Clinically, photophobia, low acuity, horizontal nystagmus, and a lack of stereopsis are most commonly observed (King, Hearing, Creel, & Oetting, 1995).

Retinal examination invariably shows foveal hypoplasia, evidenced by cone densities approximately 10% that of normal. In contrast, the peripheral retina shows normal cone densities (King et al., 1995). Hence, discrimination of high spatial frequencies, and acuity on vernier and oriented grating tasks is found to be deficit at fixation (Wildsoet, Oswald, & Clark, 2000; Wilson, Mets, Nagy, & Ferrera, 1988a; Wilson, Mets, Nagy, & Kressel, 1988b) yet normal at 10^{O} eccentricity (Wilson et al., 1988a).

The density and distribution of cone cells in the adult albino appears to be similar to that of infants. They also lack a foveal pit, and have central cone densities between 5-15% of adult values (Hendrickson & Yuodelis, 1984; Yuodelis & Hendrickson, 1986), but normal cone densities beyond 5^{O} eccentricity (Abramov, Gordon, Hendrickson, Hainline, Dobson, & LaBossiere, 1982). The performance of adult albinos on spatial discrimination tasks is therefore observed to be approximately equal to 10-month old infants (Wilson et al, 1988b). Thus, the albino retina is considered to suffer arrested development during infancy (King et al., 1995; Oetting, Summers, & King, 1994; Wilson et al., 1988a,b).

Schwartz et al. (1987) observed that the higher ganglion cell densities in the upper hemiretinae of adults are not present at two months of age, and so must develop during infancy. Cases in which post-natal maldevelopment of photoreceptors has occurred can limit the development of both individual cortical neurons and their connectivity. This has been found in a number of species, including humans (Garey & DeCourten, 1983; Kingsbury & Finlay, 2001). Of particular relevance to the present thesis are a growing number of studies suggesting that dorsal pathway functioning is particularly susceptible to adverse effects from genetic disorders (e.g., Atkinson, Anker, Braddick, Nokes, Mason, & Braddick, 2001; Mitchell et al., 1999; Spencer, O'Brien, Riggs, Braddick, Atkinson, & Wattam-Bell, 2000).

Support for the notion that the quality of sensory input in early life might produce anomalous vertical asymmetry in high-level visual processing comes from Goldberg (2000). She was concerned with the influence of binocular deprivation, caused by congenital cataracts during infancy, on the development of attention. In one experiment, data was collected from a visual search task employing either valid or invalid cues at fixation, followed 400 msecs later by a peripheral target surrounded by either compatible or incompatible distractors. With monocular viewing, former patients (mean deprivation during infancy of 4.5 months, then aged 8-20 years) produced response times to targets in the UVF that were particularly hampered by invalid spatial cues, whereas the relationship between valid and invalid cues in the LVF was similar to that of normals.

Albinism provides an opportunity to explore the notion that the quality of sensory input during infancy might contribute to the functional asymmetries that can be observed in the vertical hemifields. In particular, if the arrested development of the albino retina impacts on the development of dorsal extrastriate regions, a reduction or absence of the LVF sensitivity advantage for global motion might be observed.

The RDK paradigm appears particularly suitable for this purpose, as performance on these tasks does not rely on the ability to perceive stereoscopically (Hibbard, Bradshaw & DeBruyn, 1999) [14] and the sensitivity

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[14] Albinos, uniquely, suffer a congential decussation of the optic chiasm, with fibres from the temporal retinae projecting anomalously to the contralateral visual cortex

shift toward low spatial frequencies exhibited by albinos (Wilson et al., 1988a) would have little effect on discriminations of global direction (Morgan, 1992; Smith et al., 1994). Furthermore, because flicker sensitivity is unimpaired in albinos (Wilson et al., 1988b), stimulus duration need not be adjusted. Indeed, before being considered for testing in the vertical hemifields, I assessed the albino observer (JK) for sensitivity to global motion at fixation and her performance was only slightly, and nonsignificantly, inferior to a control group of similar age.

Albino vs. control group performance was compared on three tasks previously described; the 'no-distractor', 'motion-distractor' and 'static-distractor' conditions from Experiment 1. As discussed, performance on global motion tasks is thought to be crucially dependent on the integrity of motion mechanisms located in extrastriate dorsal cortex (e.g., Braddick et al., 2001). Therefore, if an albino observer consistently demonstrated the same vertical hemifield effect as normal observers, it might be concluded that the cortical machinery underlying the vertical hemifield asymmetry for processing global motion, has been unaffected by retinal maldevelopment. Conversely, if the LVF sensitivity advantage for global motion was found to be reduced, absent, or reversed, this might indicate that the impoverished visual input has detrimentally affected the development of global motion mechanisms. This result would suggest the importance of the quality of early visual input in the genesis of functional specialisation in the vertical hemifields.

The value of data collected from a single subject might be questioned. However, given findings from previous studies of visual performance in albinos, this approach can be justified. Although albinos demonstrate diverse sensitivity profiles for luminance detection (Abadi & Pascal, 1993), performance differences across genetic subtypes have yet to be observed on any spatial processing tasks (Wildsoet et al., 2000; Wilson et al., 1988a,b). The albino observer tested here demonstrated a typical pattern of visual

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(Apkarian & Shallo-Hoffman, 1992). Accordingly, they demonstrate a profound loss of stereopsis, though depth perception is possible using other visual cues such as size-deficits and suffered no physical or neurological condition unrelated to albinism. Thus, the results obtained here should be similarly generalisable to other albino individuals with a similar ophthalmological profile.

14.2 Method

14.2.1 Participant

JK is a 22 year-old undergraduate student with tyrosinase negative albinism (i.e., she has normal tyrosinase levels but is unable to convert the enzyme to the skin pigment, melanin). Four years prior to participating in this study she received a complete ophthalomological examination at the Medical School of Ruprecht-Karls University, Heidelberg, Germany. Fundoscopic examination confirmed the absence of a fovea and macular hypopigmentation. Visual acuity was found to be considerably impaired. When tested at 3 metres, the right eye was assessed at 0.4 LogMAR units (6/15 Snellen) and the left eye at 0.3 LogMAR (6/12 Snellen). However, when tested at a distance of 40 cm both eyes were rated at > 1 LogMAR, equivalent to Snellen values above 6/60 which, in the United Kingdom, provides the legal basis for blindness. A horizontal, gaze-evoked, seesaw nystagmus was also observed, though strabismus was absent. During data collection prescribed optics were worn, though no telescopic low-vision aid was used.

When tested she was unaware of the aims of the study. However, she was aware that her performance on each task would be compared with a non-albino control group and gave an informed consent on this basis. She received a mixture of partial course credit and payment for participation. The three groups tested in Experiment 1 acted as controls.

14.2.2 Apparatus, Stimuli & Procedure

JK was tested on the same apparatus as described in Experiment 1. Because her nystagmus was laterally gaze-dependent, and did not manifest unless the eye was positioned eccentrically in the orbit, she did not produce

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constancy (Cobo-Lewis, Siatkowski, Lavina, & Marquez, 1997).

head oscillations when fixating forward. She was therefore able to use an opthalmic viewing brace and maintain central fixation for extended lengths of time.

The motion stimuli she viewed were also identical to those employed in Experiment 1. The relatively low mean luminance of both the RDKs and the monitor background ensured that the risk of photophobia was eliminated. However, the high level of luminance contrast between component dots and background compensated for the poor contrast sensitivity normally found in albinos (Abadi & Pascal, 1993). Accordingly, in all experimental conditions, JK reported that she was able to adequately perceive the stimuli.

The experimental procedure was identical to that of the control group. Testing took place over a three-month period.

14.3 Results

JK's motion coherence thresholds obtained both at fixation and in the vertical hemifields were compared statistically with those of the control groups using the Crawford-Howell SignificanceTest (Crawford & Howell, 1998). This test is designed to compare an individual test score against a group mean. All comparisons are two-tailed.

JK's motion coherence thresholds at fixation were 25.71% at the 5-frame, and 15.25% at the 10-frame duration. Neither threshold differed significantly from an age-matched control group of ten undergraduates, whose thresholds were 21.65% and 14.08%, respectively. However, when measured in the vertical hemifields, JK's thresholds were consistently higher than those of the relevant control group from Experiment 1, with the notable exception of the 10-frame duration in the motion-distractor condition.

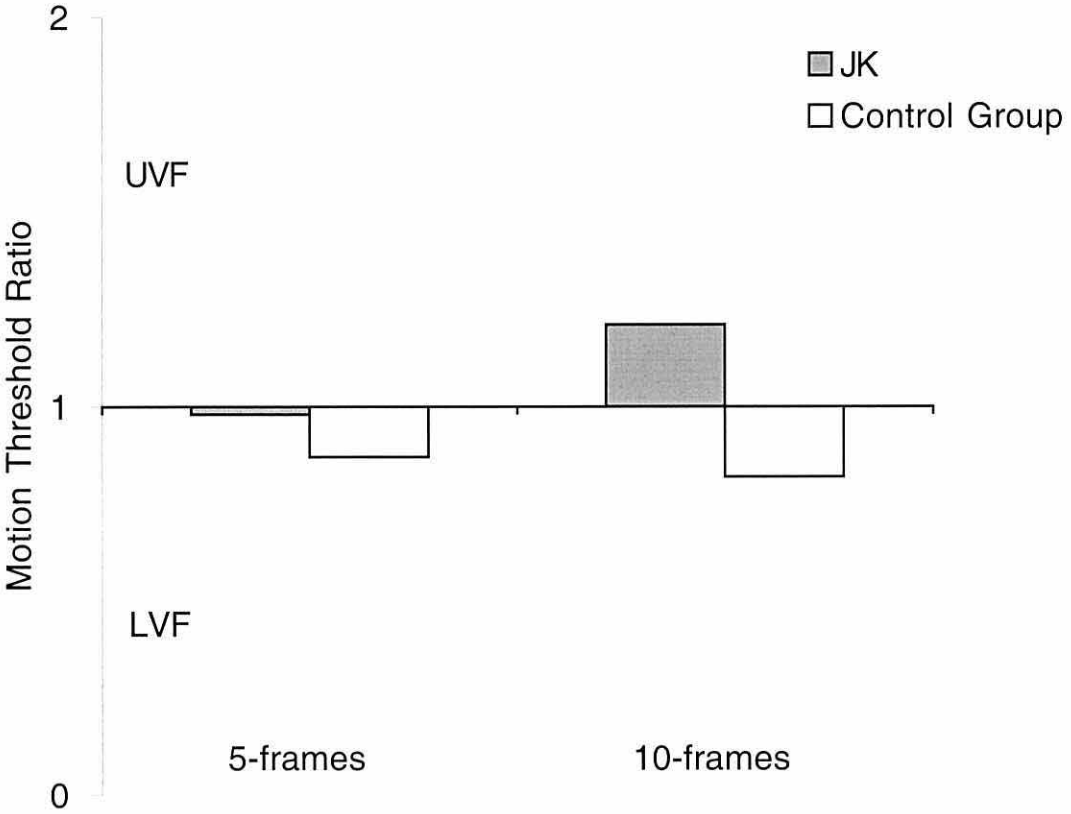

Figure 18. UVF and LVF motion threshold ratios, collapsed across distractor condition as a function of stimulus duration. These were obtained from JK and the three distractor groups in Experiment 1. The vertical position of the x-axis represents equal motion thresholds in the UVF and LVF. Ratios greater than 1 on the y-axis represent lower thresholds in the UVF vs. LVF. Ratios of less than 1 represent lower thresholds in the LVF vs. UVF.

In the no-distractor condition, her 5-frame motion thresholds were 53.89% in the UVF and 51.20% in the LVF. Both thresholds proved to be significantly inferior to those of the control group ($p < .01$ in both vertical hemifields). At the 10-frame duration, JK's thresholds dropped to 32.04% in the UVF and 37.42% in the LVF. Again, these thresholds differed significantly to those obtained in the control group ($p < .01$ in both cases).

In the static-distractor condition JK produced thresholds of 46.98% in the UVF and 46.95% in the LVF. Again, both comparisons with the control group proved significant ($p < .01$ in both vertical hemifields). Although these thresholds were substantially reduced at the 10-frame duration, comparisons with the control group remained significantly different, being 17.10% in the UVF ($p < .05$) and 22.45% in the LVF ($p < .01$).

The exception was observed in the motion-distractor condition. Here, JK's deficit performance was confined to the 5-frame duration, her thresholds being 45.86% in the UVF, and 46.07% in the LVF (both comparisons $p < .01$). However, at the 10-frame duration JK's motion thresholds (17.33% in the UVF and 19.75% in the LVF) were not significantly different from those obtained in the control group.

A consistent trend can be observed in these data, across the distractor conditions. At the 5-frame duration, JK tends to show no vertical hemifield asymmetry, although a small LVF advantage is evident in the no-distractor condition. However, at the 10-frame duration, a relative performance advantage in favour of the UVF is found in all distractor conditions. In contrast, the control group demonstrate relative performance advantages in the LVF, in all distractor conditions and at both durations.

The motion thresholds obtained from JK and the three control groups were collapsed across the distractor conditions and are plotted in Figure 18. In order to focus on the relative performance difference between the UVF and LVF, rather than the actual motion thresholds, these data are presented in terms of ratios. One on the y-axis represents equal motion sensitivity in the vertical hemifields, ratios greater than one (above the x-axis) represent a relative performance advantage in favour of the UVF, while ratios less than one (below the x-axis) represent a relative performance advantage in favour of the LVF.

One of the main findings from Experiment 1 was the vertical hemifield-specific anisotropy for motion along the vertical axis, which was observed independently of both distractor condition and stimulus duration. These data, plotted as upward vs. downward motion threshold ratios, are compared to the same ratios obtained from JK in Figure 19a (for the UVF) and Figure 19b (for the LVF). The figures show that JK displays the same vertical directional anisotropy as the controls at the 10-frame duration only.

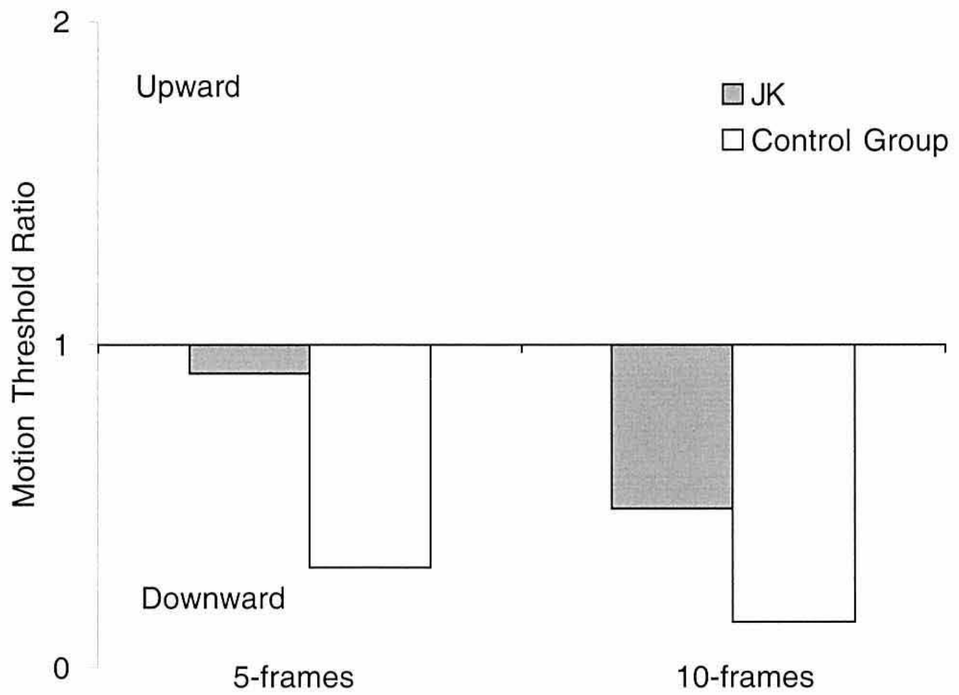

Figure 19a. Motion threshold ratios for vertical axis motion in the UVF obtained from JK and the control groups (n = 33), collapsed across distractor condition. The vertical position of the x-axis represents isotropy. Ratios greater than 1 represent lower thresholds for upward vs. downward motion and ratios of less than one represent lower thresholds for downward vs. upward motion.

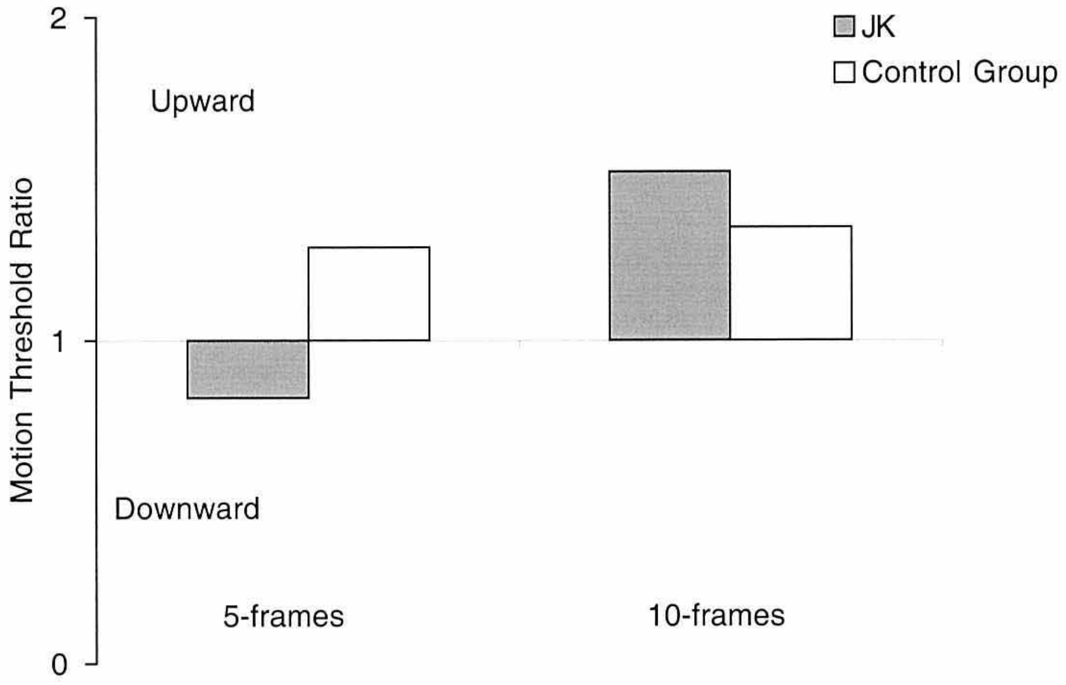

Figure. 19b. Motion threshold ratios for vertical axis motion in the LVF, obtained from JK and the control groups (n = 33), collapsed across distractor condition. The vertical position of the x-axis represents isotropy. Ratios greater than 1 represent lower thresholds for upward vs. downward motion and ratios of less than 1 represent lower thresholds for downward vs. upward motion.

14.4 Discussion

Because albinos suffer arrested development of the retina during infancy, it was hypothesised that, as adults, they may fail to demonstrate the LVF processing advantage for global motion found in normals. To ascertain whether this is the case, I compared sensitivity to global motion in the vertical hemifields of an albino adult in the three distractor conditions employed in Experiment 1, and compared these data with that of age-matched control groups.

Despite JK's motion thresholds at fixation being statistically indistinguishable from age-matched normals, her performance was clearly inferior to that of controls when tested in the vertical hemifields. There was, however, a notable exception to this finding; when tested at the 10-frame (166 ms) duration with a motion-distractor at fixation, her performance matched that of the control group. This was an unexpected finding and is discussed in more detail later.

Most important to the present study was the clear lack of evidence that JK has a LVF sensitivity bias for global motion. Her pattern of sensitivity observed showed a very small motion threshold advantage for the LVF at the 5-frame duration in all distractor conditions. This was followed, at the 10-frame duration, by much larger motion threshold advantages for the UVF. In contrast, the control groups demonstrated significantly lower motion thresholds in the LVF vs. UVF in both the no-distractor and motion-distractor conditions, at both stimulus durations. JK's relative performance in the three distractor conditions also distinguished her from controls. An additional finding concerned the directional anisotropies for downward motion in the UVF and upward motion in the LVF. Although this pattern was present in all control groups at both the 5- and 10-frame durations, JK failed to manifest the same anisotropies until tested with 10-frames.

Had JK shown no trend toward superior performance in either hemifield, a sensory level explanation might have been indicated. Photoreceptor and ganglion cell densities in the albino retina resemble that of a normal infant (Hendrickson & Yuodelis, 1984; Yuodelis & Hendrickson, 1986; Scwartz et al., 1987), and should therefore show no evidence of a vertical asymmetry. If a sensory level explanation for the global motion processing advantage in the LVF of normals was viable, JK should have shown no hemifield effect on the same tasks. JK's tendency toward better performance in the UVF acts to further confirm the view that performance on global motion tasks is not determined by retinal morphology.

The notion that JK's performance simply reflects an inability to adequately perceive the stimuli is also easily dismissed. Her performance at fixation, at both the 5- and 10-frame durations was comparable to that of an age-matched control group. This is not surprising given that none of the visual problems encountered in dyslexia (primarily lack of stereopsis and poor acuity), would not be expected to adversely affect discriminations of global motion (e.g., Hibbard, et al., 1999; Morgan, 1992; Smith et al., 1994). Furthermore, the short stimulus durations employed here should not, in themselves, have been a problem as albinos have normal temporal sensitivity (Wilson et al., 1988b). Indeed, at the 10-frame duration in the 'motion-distractor' condition, JK's motion thresholds were not only on par with those of the control group, but did not differ markedly from her performance at fixation.

The present findings indicate, therefore, that not only was JK able to perceive the stimulus adequately but she was also capable of producing normal performance under specific (though anomalous relative to controls) experimental conditions. Thus these data suggest that JK's extrastriate motion mechanisms, particularly those mechanisms involved with reducing motion noise, operate effectively.

At the 5-frame duration, the lowest thresholds produced by the control groups, in both the UVF and LVF, were found in the 'no-distractor' condition. This result was predicted, as making discriminations of a peripheral stimulus should involve less computational demand than when distractors were simultaneously present at fixation. Despite this, JK was observed to produce her highest motion thresholds in this condition, in both vertical hemifields, at both the 5- and 10-frame durations. In contrast to the control groups, JK produced her most sensitive performance in the 'motion-distractor' condition, in which she appears to have performed comparably with the control group. This condition was rightly predicted to most adversely affect motion thresholds in Experiment 1, due to the additional motion noise presented at fixation.

Thus, the mechanisms responsible for JK's sensitivity to global motion in the vertical hemifields appear to operate most effectively when random motion is present, rather than absent, from the centre of the visual field. Indeed, a comparison of JK's motion thresholds across distractor conditions and stimulus durations suggests that the presence of distractor stimuli generally result in a performance increment, relative to the 'no-distractor' condition.

Some speculation: For the normally sighted, fixating on a target would be the preferred strategy when making visual discriminations. However, resolution in the central region of the visual field is poor in albinos, necessitating greater reliance on peripheral cues. JK is hyperopic, demonstrating superior, albeit deficient, visual acuity for stimuli presented in far rather than near space. Because stimuli located in far space tend to be elevated in the visual field (e.g., Cutting & Vishton, 1995; Previc, 1990), JK's hyperopia may have resulted in a learned response to preferentially attend to stimuli presenting in the UVF, without refixating. Because JK's UVF advantage was only observed at the 10-frame duration, this might reflect the time needed to shift attention toward the UVF. This might also explain why JK's normal pattern of hemifield-specific directional anisotropy also took time to develop.

Poor acuity at fixation might also explain why JK produced lower motion thresholds when distractor stimuli were present vs. absent from the fovea. It was expected that the motion mechanisms in normally sighted observers would act to inhibit the distractor stimuli, so as to facilitate processing of the peripheral test stimulus. Because albinos lack a fovea and so have poor central vision, it might be argued that they have learned to adopt this strategy for visual processing as a matter of course. By inhibiting stimuli within central vision, they would be theoretically better able to attend to stimuli in those regions of the visual field in which their acuity is best.

It cannot be concluded, therefore, that JK's tendency to superior performance in the UVF is a natural consequence of retinal maldevelopment in all albinos. A myopic albino, for example, might show the opposite trend, and so preferentially process closer stimuli, which might produce preferential attendance to LVF stimuli. Because motion integration mechanisms in albinos appear to operate normally under suitable conditions, a myopic albino might therefore demonstrate a sensitivity advantage for global motion in the LVF.

Previc (1990) has postulated that the functional specialisation within the vertical hemifields is hard-wired, and so develops largely independently of the quality of sensory inputs. Breitmeyer (1990) argues the opposite; that the visual inputs provided by the environment will better determine which processing asymmetries are observed in the vertical hemifields. JK's data would only have offered support for Previc's (1990) view if she had shown clear evidence of a LVF processing advantage for sensitivity to global motion. Bearing in mind that she performed comparably with controls at fixation and in the motion-distractor condition, her lack of a clear hemifield effect at the 5-frame duration, followed by a UVF advantage at the 10-frame duration, suggests that retinal maldevelopment adversely affects the development of vertical hemifield asymmetries rather than global motion processing *per se.* Thus, the present data lend more support to Breitmeyer (1990) than to Previc (1990).

Chapter 15: General Discussion

15.1 Background to the Research

In recent years, physiological evidence from monkeys and imaging work with humans has uncovered multiple brain regions that either code exclusively for one vertical hemifield or have a pronounced retinotopic bias toward a vertical hemifield. The strongest evidence of this kind is for a LVF bias, found in a number of regions within the dorsal pathway, especially V3, which codes for the LVF only (Burkhalter et al., 1986; Felleman & Van Essen, 1987; Smith et al., 1998) and MT, which has a pronounced representational bias toward the LVF (Gattas & Gross, 1981; Maunsell & Van Essen, 1987). Given that the bulk of evidence points to global motion perception in humans being critically dependent on processing within these, and other regions within the dorsal pathway (e.g., Braddick et al., 2001; Smith et al., 1998), it was predicted that the LVF would prove to be more sensitive to, and therefore functionally specialised, for the processing global motion.

A few studies had previously taken measures of global motion sensitivity in the vertical hemifields. All had used the RDK paradigm, a well-established procedure for measuring sensitivity to global motion. However, only one study had explictly compared motion sensitivity in the UVF and LVF (Rezec et al., 2000), and they reported a LVF advantage only under conditions of uncertainty as to the forthcoming location of the stimulus. As discussed in Experiment 1 there are, arguably, doubts as to whether the stimulus parameters they employed were suitable to fully engage motion integration mechanisms and so elicit hemifield performance differences.

Two further studies were primarily concerned with the presence of directional anisotropies (Edwards & Badcock, 1993; Raymond, 1994). In both cases, the data suggest heightened motion sensitivity in the LVF. The fourth study had a clinical orientation and collected data from normals only for control purposes (Joffe et al., 1997). Thus, the stimulus parameters appear to have been chosen with the visual abilities of glaucoma patients, rather than a normal population in mind. No vertical hemifield effect is evident in their data.

In contrast, the stimulus parameters employed in Experiment 1 of this thesis were purposely chosen to elicit performance asymmetries between the vertical hemifields in a normal adult population. For example, to fully engage motion integration mechanisms, the RDKs presented contained small, densely packed component dots. Further, dot speed was within 0.5^{O}/sec of the optimal response of V5 cells (Chawla et al., 1998), and within the bandwidth of 80% of V3 cells (Felleman & Van Essen, 1987). Sensitivity to global motion was further explored under a number of stimulus conditions, including the presence of both kinetic and static distractor dot stimuli at fixation, with static dot distractors placed adjacent to the test stimulus (Experiment 1A), with superimposed transparent directions of motion (Experiment 2), and for opposing directions of motion (Experiment 3).

15.2 Summary of Results with Implications for Further Research

The experiments conducted are summarised in Table 2. In support of the primary experimental hypothesis, the LVF was found to be significantly more sensitive to unidirectional global motion as assessed in Experiment 1, in all stimulus conditions, at two separate durations, with one notable exception: when static dots were simultaneously present in the visual field, either at fixation or adjacent to the moving dots, no vertical hemifield effect was found. Although previous studies had suggested that the LVF might be more sensitive to unidirectional global motion viewed in isolation (e.g., Edwards & Badcock, 1993; Raymond, 1994), none had previously shown that the quality of visual input at the fovea might be a further determining factor in eliciting the sensitivity advantage. The lack of a vertical hemifield effect for temporal recruitment ability also provides an important addition to the literature.

It was suggested in that the LVF sensitivity advantage for unidirectional global motion might depend crucially on some interaction between the stimulus variables of dot speed and density. Indeed, ecological

Experiment No.	**Task**	**Condition**	**Stimulus Location**	**n**	**Finding**
1	Discrimination of unidirectional global motion in RDK	No distractor at fixation: 5-frame (83 ms) duration	5° on vertical meridian and 7° in visual quadrants	11	LVF advantage
1	"	No distractor at fixation: 10-frame (166 ms) duration	"	11	LVF advantage
1	"	Motion-distractor at fixation: 5-frame duration	"	11	LVF advantage
1	"	Motion-distractor at fixation: 10-frame duration	"	11	LVF advantage
1	"	Static-distractor at fixation: 5-frame duration	"	11	No vertical hemifield effect
1	"	Static-distractor at fixation: 10-frame duration	"	11	No vertical hemifield effect
1A	"	Adjacent static-distractors	"	11	No vertical hemifield effect
2	Discrimination of direction in transparent RDK	8-frame (133 ms) duration	"	10	LVF advantage
2	"	12-frame (200 ms) duration	Visual quadrants	7	No vertical hemifield effect
3	Discrimination of motion contrast in multisegmented RDK	5-frame duration	Visual quadrants	10	LVF advantage
4	Discrimination of global orientation in texture	180 ms.	Visual quadrants	10	No vertical hemifield effect
5	Spatial localisation of single moving element	50-183 ms	12° horizontal trajectory centred 8° on vertical meridian	10	UVF advantage

Table 2. A brief summary of the experiments performed and the results obtained. The case study is not included.

approaches to visual processing in the vertical hemifields, as expounded by Gibson (1961) and Previc (1990; 1998), would suggest that the LVF advantage would be observed most obviously as high dot densities, due to the more textured appearance encountered in the ground plane, rather than in the UVF. The LVF advantage might also manifest at higher dot speeds, due to the higher optic flow rates normally found in the LVF vs. UVF (Lee, 1980; Young & Oman, 1974). Because this prediction was not further explored in subsequent investigations, this remains a potentially fruitful avenue for further research.

The LVF sensitivity advantage found for transparent (bidirectional) motion (Experiment 2) constitutes a further addition to the motion literature. The ability to perceive transparent motion in the absence of non-motion cues has proven problematical for current models of motion perception as the noise reduction algorithms hypothesised to extract unidirectional motion act to prevent the perception of superimposed bidirectional motions (Qian & Andersen, 1994b). Nevertheless, the LVF advantage for discriminating two directions of motion in a transparent RDK was predictable for two reasons. Firstly, single-cell recordings in monkey had indicated that the computation of transparency was critically determined by neural activity within MT and possibly, MST (Qian & Andersen, 1994a; Snowden et al., 1991). Secondly, transparent, or semi-occluded conditions are more likely to be experienced in the LVF than the UVF (Gibson, 1961; Lee, 1980).

Because the perception of the two directions of motion seems to involve a serial process (Cobo et al., 1999; Pinilla et al., 2001; Valdes-Sosa et al., 1998; 2000), it was conjectured that the LVF advantage might be due to an enhanced ability to disengage and reallocate attention from one sheet of dots to the other. This view is supported by an equal level of sensitivity in each vertical hemifield to the horizontal component within the RDKs. The LVF advantage was therefore determined by heightened sensitivity to the vertical component of the bidirectional display. However, this pattern of sensitivity was characterised by a reversal of the upward vs. downward sensitivity bias found in the LVF in Experiment 1. Thus, directional biases in the vertical hemifields appear not to be ubiquitous, but rather to be task-specific, and dependent on the type of motion mechanism activated by the stimulus. This finding offers a further challenge to current models of motion perception.

Testing whether the LVF advantage was due to an enhanced ability to disengage and reallocate attention between the two sheets of dots could be better ascertained by requiring observers to attend (and report) firstly to either the vertical or the horizontal component of the transparent display. If motion mechanisms in the vertical hemifields do differ in the ability to reallocate attention from one direction of motion to the other, the direction of motion attended to initially should have little effect on performance in the LVF. However, in the UVF, attending to the vertical component initially should produce a reversal of the sensitivity pattern found in the present study, i.e., equal sensitivity for vertical axis motion in both vertical hemifields, accompanied by a UVF vs. LVF deficit for the horizontal motion component.

The LVF also proved to be more sensitive to opposing global directions of motion, and therefore to be less susceptible to motion capture effects (Experiment 3). Murakami and Shimojo (1993) had previously tested the influence of moving inducer dots on stationary recipient dots within the lower-left visual quadrant only. Thus, the present study was novel in two ways. Firstly, by measuring motion capture effects in all four visual quadrants and secondly, by employing moving dots as both the inducer and test stimuli. The most striking finding in this experiment was the pattern of sensitivity between the visual quadrants. This finding differed from the previous experiments, as deficit performance was found at a single quadrant location only, i.e., the upper-left quadrant, and was the only instance in which performance in the horizontal hemifields was observed to influence performance in a vertical hemifield.

The ability to perceive contrasting motion appears to depend on several distinct motion mechanisms acting in unison; detection of local differences in motion signals (Braddick, 1993), complemented by a region-based segmentation process (Møller & Hurlbert, 1996). Further, Orban and co-workers report a brain region in humans seemingly specialised for processing the motion-defined boundary between two contrasting motions (Dupont et al., 1997; Orban et al., 1995; Van Oostende et al., 1997). The poor performance in the upper-left quadrant found here might have been due to deficits in any one of these hypothesised mechanisms. Thus, further psychophysical testing of motion contrast stimuli in the visual quadrants, aimed at isolating the effects of the differing motion contrast mechanisms is indicated for future study.

One related possibility is that superior performance in the upper-right vs. upper left quadrant may be due to the more frequent movement of the arm and hand on the right side of space. The upward (and backward) sweep of the arm would produce contrasting motion against a moving background in many situations. Thus, left-handed people might tend to show the opposite pattern of sensitivity to contrasting motion in the UVF. It would be a relatively easy task to test this hypothesis.

It is interesting to note, however, that data from both monkeys and humans suggest that neither MT/V5 nor V3 play a significant role in the processing of contrasting motions (Dupont et al., 1997; Lauwyers et al., 1995; Marcar, et al., 1995; Orban et al., 1995, Reppas et al., 1997; Shulman et al., 1998; Van Oostende et al., 1997). Thus, the equivalent performance between the two LVF quadrants and the upper-right quadrant might also reflect the lack of involvement of those brain regions with a representational bias toward the LVF.

The final two experiments acted to further confirm the notion that the LVF is functionally specialised for processing global motion. The static global texture task presented in Experiment 4 was analogous in many respects to the RDK paradigm, requiring the spatial integration of diversely oriented line elements across the whole stimulus. The lack of a hemifield effect, both with and without the presence of a foveal distractor, points to the global analysis of diverse motion signals as a specific strength of the LVF. Because evidence from the perception of Glass patterns Wilson & Wilkinson, 1998; Wilson et al., 1997) and monkey lesion work (Rudolph & Pasternak, 1999) suggests that the spatial integration of oriented stimuli is performed primarily by ventral pathway mechanisms, this study further supports the notion of functional links between the dorsal pathway, global motion processing, and the LVF (e.g., Previc, 1990).

Nevertheless, these functional links might have been placed in doubt had a LVF performance advantage been found on a task assessing the ability to compute the movement of a single element, which engages a fundamentally different motion mechanism from that involved in processing RDK stimuli. Thus, greater accuracy in the UVF for judging the end-point of the stimulus trajectory, once again points to the specific nature of the LVF's performance advantage for motion processing. It is also feasible, given the results of this study that the vertical hemifields hold fundamentally different functional specialisations; for global motion in the LVF and for local motion in the UVF.

The question of whether vertical hemifield effects in motion processing emanate from some genetic process, and thus not able to be modified by experience, or whether they are acquired by the visual system as the result of experience, was also addressed. The data obtained from JK, an albino adult who had suffered arrested development of the retina during infancy, indicate that her cortical motion processing mechanisms are unaffected by her sensory losses, provided certain stimulus conditions are met. However, she demonstrates the reverse vertical hemifield asymmetry, with a clear trend toward superior performance in the UVF on global motion tasks.

JK's reverse asymmetry suggests that the LVF sensitivity advantage for global motion processing is not hard-wired, as Previc (1990) has proposed. Nevertheless, given the longer stimulus duration, she did demonstrate a normal pattern of hemifield-specific directional anisotropy. If there is a tendency for the environment to produce particular directions of motion more often (due e.g., to the effects of gravity) it is conceivable that it is the directional anisotropies, rather than the vertical hemifield asymmetries, that are hard-wired.

15.3 Possible physiological mechanisms underlying the LVF motion sensitivity advantage

It is not possible, given the psychophysical methodologies employed, to accurately isolate which aspects of motion processing mechanisms might have been responsible for the LVF sensitivity advantage for discriminating unidirectional global motion. However, four biologically plausible candidate mechanisms deserve mention. Note however, that none of these mechanisms necessarily operates exclusively. Some, or all, may operate synergistically to have produced the LVF sensitivity advantage.

Firstly, dorsal subregions coding for the LVF may contain a larger proportion of motion-selective cells with facilitatory centre-surround receptive fields, as opposed to antagonistic centre-surround mechanisms. This arrangement does appears to exist in V3. Here, imaging work has shown that single element motion is largely ignored (Smith et al., 1998). However, partially coherent random dot stimuli produce considerable activation, equivalent to that observed in V5 (Braddick et al., 2001; Smith et al., 1998), suggesting that the majority of V3's direction-selective cells have facilitatory centre-surround mechanisms.

A corollary of this view is that subregions coding for the UVF may contain a higher proportion of cells with antagonistic centre-surround receptive fields, which are able to signal the moving edges of single components (Born & Tootell, 1992; Born, 2000). The data obtained from Experiment 5, in which the movement of a single dot was more accurately tracked in the UVF, arguably offers some support for this speculation.

Secondly, subregions coding for the LVF may generally contain cells with larger receptive fields than subregions coding for the UVF. Larger receptive fields are able to better integrate numerous, diverse motion vectors simply because they are able to encompass a greater number of motion inputs. However, when the density of motion inputs is low, the ability to average multiple vectors across space becomes compromised (Braddick et al., 2001). This might explain why high density RDKs, such as those employed by Raymond (1994) and in the present thesis, appear to elicit a LVF advantage for global motion, while low-density RDKs, such as those employed by Joffe et al. (1997) and Rezec et al. (2000) do not.

A third possibility is that motion-selective cells representing the LVF have a denser lateral connectivity than those representing the UVF. This would afford greater computational power, as the output of cells with partial or barely overlapping receptive fields would be better combined, permitting the integration of motion signals across a larger cell population.

Finally, the algorithm used to integrate diverse motion inputs may differ according to visual field location, operating more effectively in the LVF vs. UVF. This possibility has previously been suggested with regard to motion processing in foveal vs. peripheral regions (Mackay, 1982; Pantle, 1992) but may need to be further elaborated given evidence of motion sensitivity differences between the vertical hemifields.

15.4 Theoretical Consequences for Current Models of Motion Perception

The present data impact on two assumptions commonly made in current models of motion perception. Firstly, although it is widely acknowledged that sensitivity to motion signals differs between the fovea and the visual periphery, there appears to be little appreciation that motion sensitivity might differ at mirror locations within the visual periphery. Although data obtained from the horizontal hemifields support this view (Bosworth & Dobkins, 1999; Raymond, 1994), data from the vertical hemifields obtained here would disagree.

The picture is further complicated by the lack of a vertical hemifield effect, observed when a static dot texture was simultaneously present within the visual field. The opportunity for motion mechanisms to make a perceptual comparison with the stationary dots, or an enhanced ability to direct attention toward motion in the UVF were both mooted, however the data do not allow any definitive conclusion to be made. What was ascertained is that under this condition, sensitivity to global motion was modified only in the UVF. Motion processing in the LVF does not appear to have been affected any differently than it was by the motion-distractor. Thus it might be that, although sensitivity to global motion can be positively influenced by the presence of other stimuli in the visual field, motion mechanisms in the UVF are more strongly influenced, in this case, positively, than in the LVF.

According to the second assumption, sensitivity to each direction of motion is isotropic within all regions of the visual field. Although this has been demonstrated at the fovea (Raymond, 1994) the present data clearly indicate that vertical hemifield-specific directional anisotropies exist for motion along the vertical axis. This is evidenced by a robust sensitivity to upward vs. downward motion in the LVF and to downward vs. upward motion in the UVF. Both anistropies were present in all foveal distractor conditions in Experiment 1. Thus, simply factoring in sensitivity differences for different regions of the visual field would be insufficient to update current models of human motion perception. Such an approach would not, for example, be able to account for the heightened sensitivity to downward motion in the UVF, as the mechanism responsible for this directional sensitivity bias appears to demonstrate a level of motion sensitivity on par with the motion mechanisms operating in the LVF.

There is little evidence to suggest that the centripetal motion biases found in each vertical hemifield is the result of distortions in direction perception. Indeed, both the upward bias in the LVF and the downward bias in the UVF can be argued to have ecological advantage and to result from physiological biases.

Raymond (1994) has suggested that the upward bias in the LVF might supplement optic flow computations, facilitating figure/ground segmentation against a centrifugally moving background, normally encountered during forward locomotion. The same bias may also play a role in the visual control of the forward sweep of the arm toward a target object, which is invariably perceived as upward motion (Previc, 1990). This particular bias seems expecially robust, as it was maintained in the adjacent distractor condition in

Experiment 1A, whereas the downward bias in the UVF was lost under this condition.

Naito et al. (2000) have suggested that the downward bias in the UVF might be due to the effects of gravity, as objects in free-fall are encountered more often than upward moving objects. Similarly, because the horizontal plane is slanted downward from the horizon to the observer, objects approaching from far space also tend to move progressively lower in the visual field (Cutting & Vishton, 1995). All these notions suggest that the visual system acquires a heightened sensitivity to those directions of motion encountered most often.

A physiological bias for centripetal motion has been reported in the central 12^{O} of the visual field in MT (Albright, 1984). It would be interesting, therefore, to replicate Experiment 1, with the test RDKs presented at an eccentricity greater than 12^{O}. The loss of a centripetal bias would suggest that the effect found here was physiological, rather than attentional, in nature.

15.6 Possible Applications of the Findings

The data obtained in behavioural studies of visual processing in the vertical hemifields have potentially greater import than, for example, informing future models of motion processing. Findings from experimental psychology, including those concerned with processing differences between the UVF and LVF, are being increasingly cited in journals concerned with functional design. This field has traditionally been informed primarily by aesthetic, rather than functional principles. It is becoming increasingly recognised, for example, that the majority of critical workstations are not designed with the natural proclivity of the operator to process visual information, in mind. This is especially the case for aircraft cockpits and car dashboards, where poor allocation of visual resources and inappropriate attentional load is considered a major cause of the transient losses of situational awareness that often result in accidents (e.g., Lamble et al., 1999; Previc, 2000; Wierwille & Tijerina, 1996). Thus, in order to better investigate vertical hemifield effects, laboratory paradigms normally used to explore processing abilities in the visual periphery might usefully be supplemented by studies in which human performance is tested in more ecologically valid situations.

The application of psychophysical findings for practical puposes such as this appears inevitable, given that the environment encountered by humans is essentially three-dimensional. Not surprisingly, it has long been recognised that many visuomotor abilities are biased in terms of left-right and near-far coordinates. It seems natural, then, that physiological and perceptual mechanisms in the human visual system are proving to be similarly biased in terms of upper and lower space. The data presented here provide additional evidence that mechanisms of motion perception are similarly constrained.

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