Binocular interactions in human vision

Midgley, Caroline Ann

Midgley, Caroline Ann (1998) *Binocular interactions in human vision*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/4839/

Binocular Interactions in Human Vision

By

Caroline Ann Midgley

Submitted for the degree of Doctor of Philosophy
University of Durham Psychology Department
March 1998

DECLARATION

This thesis reports the research that was undertaken by the author between October 1994 and August 1997 while a postgraduate student in the Department of Psychology at the University of Durham. None of the work contained in this thesis has been submitted in candidature for any other degree.

STATEMENT OF COPYRIGHT

ABSTRACT

Early visual processing is subject to binocular interactions because cells in striate cortex show binocular responses and ocular dominance (Hubel & Weisel, 1968). The work presented in this thesis suggests that these physiological interactions can be revealed in psychophysical experiments using normal human observers.

In the region corresponding to the blind spot, where binocular interactions differ from areas of the visual field which are represented by two eyes, monocular contrast sensitivity is increased. This finding can be partially explained by an absence of normal binocular interactions in this location (Chapter 2). A hemianopic patient was studied in an attempt to discover whether the effect in normal observers was mediated by either a mechanism in striate cortex or via a subcortical pathway. However, the results were unable to distinguish between these two explanations (Chapter 3).

In a visual search task, no difference in reaction time was observed for targets presented to the region corresponding to the blind spot compared with targets presented to adjacent binocularly represented areas of the visual field. Since performance was unaffected by the monocularity of the region corresponding to the blind, pop-out for orientation may be mediated beyond striate cortex where cells are binocularly balanced (Chapter 5). Further support for this contention was provided by studies of orientation pop-out in central vision which found that dichoptic presentation of stimuli did not affect the degree of pop-out obtained and that in general, visual search for a target based solely on eye of origin is impossible (Chapter 6). However, a task that measured orientation difference sensitivity more directly than the search experiments, found that thresholds were higher for dichoptically presented stimuli. This suggests the involvement of neurons that receive a weighted input from each eye. A model of orientation difference coding can account for the results by assuming that the range of inhibition across which orientation differences are coded is narrower for dichoptic stimuli leading to a greater resolvable orientation difference (Chapter 7).

ACKNOWLEDGEMENTS

I would like to thank Charles Heywood for supervising the first half of this thesis and John Findlay for supervising the remainder. I am grateful for the encouragement and advice my supervisors provided throughout my Ph.D. The discussions concerning my work I had with Harvey Smallman, Ian Gilchrist and Bob Kentridge are greatly appreciated and I am thankful to Ariella Popple for her advice on the setting-up of a mirror stereoscope.

Help provided by Paul Young enabled me to learn a programming language at a much faster rate than I would have done on my own. Paul was also extremely supportive, especially during my second year, and I value our friendship highly. In addition, I am grateful to my parents for their love and encouragement over the years. Finally I would like to thank Katy Fulford, for being such a calming presence in the office and for always knowing the right thing to say.

I dedicate this thesis to my parents with love

CONTENTS

Contrast Sensitivity in the Sighted and Blind Hemifields of a hemianope 56

FIGURES

TABLES

1

Introduction

This chapter provides an introduction to the topic of binocular vision in general and to the subject of this thesis in particular. The first section provides a context to the thesis by discussing some major issues in binocular vision research and concludes with a description of the subject of the thesis and its aim. Subsequent sections elaborate on the major themes within the thesis and include reviews of physiological and psychophysical evidence for binocular interactions in human vision.

INTRODUCTION TO BINOCULAR VISION AND AIM OF THESIS

Binocular vision refers to the overlap of the visual fields and to the neural and psychological integration that occur as a result. Much of the research in binocular vision has focused on the sensory consequences of binocular stimulation and therefore to place this thesis in context it is necessary to review research in the areas of binocular fusion, diplopia, rivalry and stereopsis. Such visual phenomenon might be considered a direct functional outcome of the binocular organisation of the human visual cortex. In contrast, this thesis aims to investigate more indirect consequences of this neural machinary. Specifically it seeks to discover whether the binocular convergence of signals in primary visual cortex affects the limits of vision for visual tasks that do not require binocular stimulation. Such an approach is important since it may have implications for the way in which these tasks are mediated at the level of the striate cortex. Before discussing the topics of investigation further, a review of some of the major issues in binocular vision will be presented starting with the benefits of binocular vision.

Benefits associated with binocular vision

Perhaps the most basic question in binocular vision is that of why we possess two eyes. There are several advantages are associated with binocular vision. The most obvious benefit is that it enables stereopsis, the impression of depth arising from binocular disparity. Binocular disparity is the difference in the positions and shapes of the images in the two eyes due to the difference in vantage points from which the eyes view the world. Stereopsis greatly enhances the ability to discriminate differences in depth and provides a performance advantage for many different jobs, especially those requiring eye-hand co-ordination such as putting sticks in holes and needle threading (Sheedy et al 1989). However there are other benefits of binocular vision not attributable to enhanced depth perception. Performance in basic visual tasks, such as detection, resolution and discrimination is slightly better with both eyes open. Many complex visual tasks such as reading, detecting camouflaged objects and eye-hand co-ordination are performed more effectively with both eyes than with one even when the visual display contains no depth (Jones & Lee, 1981; Sheedy et al. 1986). A final benefit is that in the case of injury to one eye there is an eye in reserve.

The geometry of stereoscopic space and the horopter

A pre-requisite for understanding depth perception is an analysis of the geometry of stereoscopic space and hence this is a significant research topic in binocular vision. It is important to examine the relations between the images projected onto the two retinas and the objects to which they refer in the physical world since these geometric relations provide the inputs from which the binocular system extracts depth information (Arditi, 1986). The term horoptor was coined by Aquilonius (1613) and used to describe the locus of points having zero retinal disparity. The precise definition of the horoptor has prompted great debate and is important because it is the baseline to which all other aspects of sterescopic perception are tied.

The Vieth-Muller circle (see Figure 1.1), which passes through the point of fixation and nodal point of each eye, demarcates the set of corresponding points along the horizontal meridian. This horoptor assumes that the eyes are perfect spheres, that the optics are perfectly spherical and that the eyes rotate about axes passing only through their optical nodes (Arditi, 1986). Empirical studies produce estimates which deviate from this theoretical horoptor (Ogle, 1950). Some of the discrepancy may be due to opthalmic considerations such as the location of the optical nodes relative to the rotation of the eyes and the displacement of the nodes with eye rotation (Fry & Hill, 1962). Despite difficulties in its measurement, the concept of the horoptor is useful because it defines the locations in the third dimension where objects must lie in order to be in the region of maximal stereoacuity and thus not elicit fusional disjunctive eye movements. However, Arditi (1986) asserts that it has been applied with rather limited scope since little work has determined the horoptor for fixations off the horizontal plane (the vertical horoptor is an exception) or under conditions of asymmetric convergence. Furthermore, the horoptor has never been described for nonzero disparities. Arditi suggests that the traditional horoptor should be viewed more generally as one in a family of contours, each corresponding to a different disparity. These iso disparity contours would more richly describe the structure of binocular space.

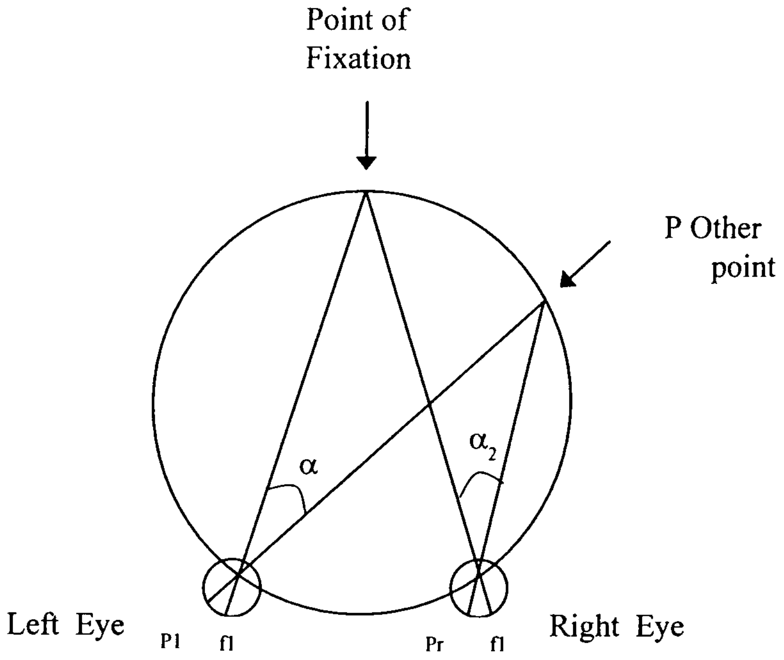


Figure 1.1 The Vieth-Muller Circle. If the eyes are assumed to be perfect spheres that rotate about axes passing through their optical nodes and have perfectly spherical optics, all points in space with zero retinal disparity will fall on this circle. This analysis applies only to the horizontal plane through the eyes and symmetric convergence. Reproduced from Arditi (1986).

Binocular fusion

Objects around the horopter give rise to small disparities which are seen as fused while objects further away give rise to large disparities which may be seen as diplopic (double). The area around the horoptor in which objects are seen as single is referred to as Panum's fusional area. Research has shown that Panum's fusional area is not fixed but increases with eccentricity and is affected by the spatial and temporal properties of the stimulus (Tyler, 1983).

A classic question in binocular vision research asks how it is that normally sighted individuals see only one outside world even though the images in the left and right eyes are slightly different. In response to this question, Tyler & Scott (1979) have suggested a physiological basis for fusion and diplopia. Physiological evidence (Hubel & Wiesel, 1962; Barlow et al, 1967; Hubel & Wiesel 1970) implies there are four different classes of neurons having binocular corresponding, binocular disparate, monocular right and monocular left receptive fields. The model assumes each neuron is labelled for a specific visual direction which is unambiguous for all classes except the binocular disparate where it is assumed to fall midway between the visual directions of the monocular receptive fields for that neuron.

When sets of stimuli are presented to each of the two eyes so that they project to corresponding points, the binocular corresponding neurons and monocular right and monocular left neurons with the same local sign are stimulated. Since all three types have the same visual direction label, there is no conflict and the stimulus, encoded as the sum of all neurons responding is seen as single (Figure 1.2a). The introduction of a small disparity stimulates the binocular disparate neurons and prevents the binocular corresponding neurons from responding. Now the monocular neurons have visual directions that are to either side of the mean visual direction signalled by the binocular disparate neurons. It is assumed that the two monocular visual directions, which would be discriminably different if presented alone, are integrated with that signaled by the binocular disparate neurons (Figure 1.2b). There should therefore be a small range of disparities that gives rise to a unitary perception of a fused stimulus. Finally, if the diparity between the sets of points is increased beyond the range in which the binocular disparate neurons can respond, each monocular response is associated with a different visual direction and two diplopic sets of stimuli are perceived (Figure 1.2c). Tyler & Scott stress that from this view, the basic disparity in binocular receptive fields forms a basis for fusion and diplopia rather than a basis for stereopsis.

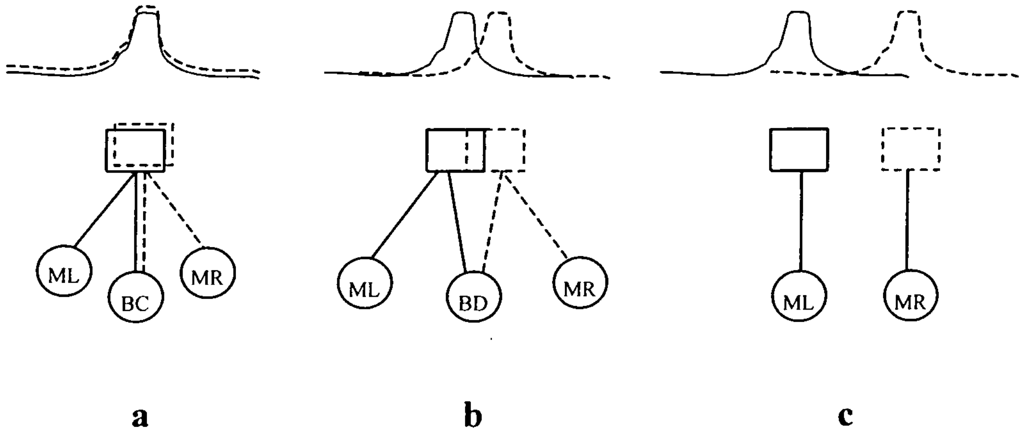


Figure 1.2 Model of binocular fusion and diplopia, considered from the point of view of four classes of cortical neuronal receptive fields with similar visual directions: monocular left eye (ML), monocular right eye (MR), binocular corresponding (BC), and binocular disparate (BD). Monocular stimulus inputs to these receptive fields are shown as solid (L) and dashed (R) lines: **a** = zero, **b** = small and **c** = large binocular disparities. Reproduced from Tyler (1983).

Binocular suppression and rivalry

Under conditions of natural viewing, objects that are well off the fixation plane may give rise to grossly different images in corresponding regions of the two retinas. This type of stimulation may give rise to rivalry in which the image in one eye dominates over the other, the dominant eye alternating from time to time. The study of binocular suppression and rivalry is important because it may shed light on how binocular vision remains single despite grossly different images in corresponding locations.

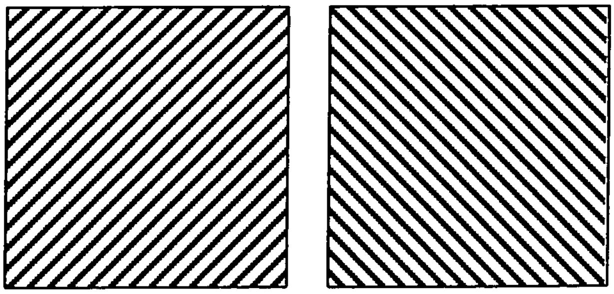


Figure 1.3 Stimulus demonstrating strong binocular rivalry when left panel is viewed by left eye and right panel is viewed by right eye in the same retinal location. Reproduced from Tyler (1983).

Under experimental conditions rivalry can be demonstrated using a stereogram consisting of lines orthogonally oriented in the two eyes (see Figure 1.3). When stereoscopically combined, the pattern at any given instant may appear to be composed of only one of the half-images, the other being suppressed. Over time the two half images alternate in phases of dominance or suppression whose periods are in the order of 1-4 seconds. There seems to be very little voluntary control over which eye appears dominant at any one time (Blake et al, 1971) and during rivalry, visual sensitivity is reduced in the suppressed eye, by an amount equal to about 0.5 log units according to the subject and stimulus conditions. Research suggests that binocular rivalry may occur at a high level in the visual system. Perceptual occlusion of a stimulus during binocular rivalry had no effect on the strength of the motion after-effect (Lehmkuhle & Fox, 1975) threshold elevation or spatial frequency shift after adaptation to a grating (Blake & Fox, 1974). In contrast, equivalent physical occlusion of the stimulus greatly diminished these effects. This shows that adapatation can occur even when the stimulus is rendered invisible by suppression and suggests that rivalry occurs at a higher level than these effects which are almost certainly cortical.

Limits of stereopsis

The range of disparities giving rise to stereopsis is an issue that has also received considerable attention. This topic is not synonymous with the problem of single vision since very small disparities may provide no sensation of depth while very large disparities may give rise to a perception of depth despite the stimuli being seen as diplopic. The smallest disparity yielding valid apparent depth is the threshold for stereoacuity and interest in this subject stems from the observation that thresholds can be just a few arc seconds. Stereoacuity is maximal at the fovea and declines as the test stimulus is moved to eccentric locations (Tyler, 1983) or in depth in the crossed or uncrossed direction (Badcock & Schor, 1985). Thresholds are also low with small stimuli composed of high spatial frequencies (Ogle, 1964) and stereoacuity is maximal under photopic conditions (Graham, 1965) with stimuli that are well above threshold (Ogle, 1964).

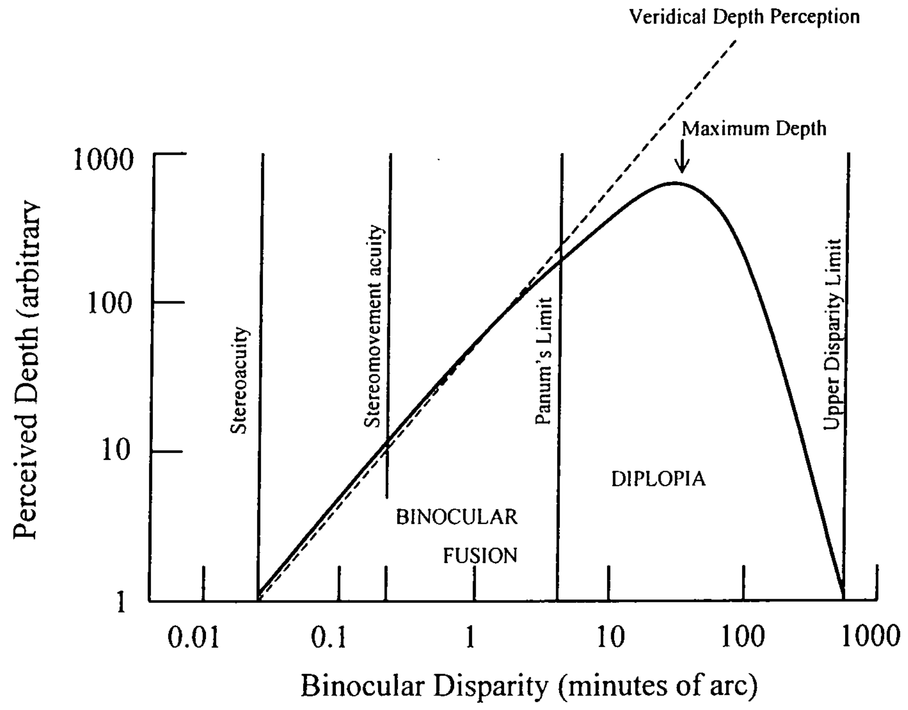


Figure 1.4 Schematic of some stereoscopic limits of perceived depth and fusion as a function of binocular disparity. Reproduced from Tyler (1983).

Figure 1.4 is a summary of the relationship between disparity and depth perception. It is based on experiments by Richards (1971) and Richards & Kaye (1974) in which the perceived depth of briefly flashed disparate images were matched to full scale depth stimuli or determined by magnitude estimation. This diagram shows the threshold for stereoacuity below which there is no sensation of depth. Above this limit, depth perception is veridical in that the sensation of depth is congruent with that implied by the disparity. Veridical depth perception breaks down at Panum's fusional limit and at greater disparities, images are seen as diplopic. However, it is still in this region that the greatest apparent depth is experienced. Finally, at very large disparities, the sensation of depth diminishes and eventually disappears altogether. While this diagram provides a useful summary of the relationship between disparity and perceived depth, the actual limits will vary according to the stimulus conditions.

Neurophysiology of stereopsis

Work on stereopsis undertaken by Poggio and others (Maunsell & Van Essen, 1983; Poggio & Fischer, 1977; Poggio et al, 1985; Poggio & Poggio, 1984; Poggio & Talbot, 1981) has examined the binocular responses of neurons in area 17 of awake behaving monkeys and cats. These studies have demonstrated the existence of four different classes of neurons tuned to disparity. Near and far neurons are coarsely tuned for crossed and uncrossed disparities respectively and are inhibited by stimulation in the opposite direction. Tuned excitatory and tuned inhibitory are excited and inhibited respectively for stimuli around the horoptor. It has been argued that these disparity sensitive neurons found at lower levels of the visual system provide the substrate for the initial processing of retinal disparity (Poggio & Poggio, 1984).

More recent work has attempted to explain stereopsis in terms of parvocellular and magnocellular processing streams. The parvocellular system originates with type B retinal ganglion cells and projects via the parvocellular layers of the dorsolateral geniculate nucleus to the temporal cortex. The magnocellular system begins with type A retinal ganglion cells and projects via the magnocellular layers of the dorsolateral geniculate nucleus to areas of the parietal cortex. Controversy surrounds which pathway is most critical for stereopsis. Livingstone & Hubel (1988) suggested that the magnocellular system plays a vital role in stereopsis and motion since many cells in this pathway at the level of the cortex are sensitive to moving stimuli and disparity. However, De Yoe & Van Essen (1985) argued that the substrate could be parvocellular since they found neurons with strong binocular interaction at cortical levels of the parvocellular pathway. Logothetis et al (1990) recently showed that, in primates parvocellular lesions impaired color vision, fine detail form vision and fine stereopsis while magnocellular lesions impaired high temporal frequency flicker and motion perception but not stereopsis. This suggests that the perception of fine details, colour and fine depth perception is mediated by the parvocellular system while the perception of flicker and motion is mediated by the magnocellular pathway. Coarse form vision and coarse stereopsis were not affected by either kind of lesion suggesting that these perceptual abilities can be mediated by either pathway.

Theoretical aspects of stereopsis

The most influential development in binocular vision techniques has been the introduction of the random-dot stereogram by Julesz (1960) because it allows the study of processes occuring after binocular convergence. A random dot stereogram is composed of two arrays of thousands of randomly ordered dots; each array is presented to one eye of an observer. Disparity is created by shifting laterally a subset of dots in one eye's view, and leaving unshifted corresponding dots in the other eye's view. An observer with stereopsis perceives the sterescopic stimulus defined by the shifted dots as a form appearing in a depth plane different from that of the background dots. A stimulus created from disparity embedded in a random-dot stereogram has been referred to as cyclopean since its form is not apparent from viewing either of the monocular images separately.

The advent of the random-dot stereogram has highlighted the problem of correspondence. How is a correct match between stimuli across each eye achieved when in principle a dot in one eye could be matched with any dot in the opposite eye? According to the network hypothesis, disparity sensitive mechanisms operate in a co-operative and competitive way. Units tuned to the same disparity in different parts of the visual field excite each other while units tuned to different disparities in the same part of the visual field inhibit each other (Julesz, 1971). McKee & Mitchison (1988) have shown that the establishment of binocular correspondence is governed primarily by the disparity in the edges of stimuli. Employing an array of dots, they found that the edges of the array are first matched by the visual system over a duration of several seconds, followed by changes in vergence angle from the plane of initial fixation to that associated with the edges. Mckee & Mitchison suggested that binocular correspondence is achieved via a coarse to fine strategy because only coarse spatial channels would detect the edges of the stimulus.

Once correspondence is established, the binocular visual system must compute the magnitude of the disparity. This apparently involves the metrical coding of signals from the two eyes. Once disparity is computed, depth must be derived from it. This is not a trivial task since disparity is an inherently ambiguous depth cue. There is no one-to-one correspondence between disparity and depth: the same value of disparity will yield different magnitudes of depth depending on viewing distance. Disparity information must be calibrated differently for different distances in order for veridical depth to be computed by the visual system - a process termed depth constancy. There are several possible cues that could enter into the computation of perceived depth. One set of cues involves proprioceptive information from accomodation, vergence or both. Another set of cues may be environmental or field cues such as perspective and texture (Fox, 1985). Research has still to establish the relative contribution of these cues to veridical depth perception.

Subject, approach and aim of thesis

The preceding review highlights the major themes of research in binocular vision. This research addresses different aspects of the sensory consequences of binocular stimulation such as fusion, diplopia, rivalry and stereopsis. Stereopsis in particular seems the most prominent field of research in binocular vision and this review has highlighted related topics which include the geometry of visual space, the relationship between disparity and perceived depth, the physiology of stereopsis and theoretical issues.

It has been argued that the starting point for the analysis of retinal disparity is the binocular convergence of signals in V1 (Poggio & Poggio, 1984). However, the behavioural effects of binocular interaction in striate cortex go beyond the analysis of disparity and its role in stereopsis. The aim of this thesis is to establish how this neural machinary affects the limits of vision in normal human observers on tasks which do not require binocular stimulation. Therefore the emphasis is not on the role of binocularity in stereoscopic depth perception but on how visual performance in other functional domains is affected.

The assumption is that if a task is mediated at an early level of the visual system, it may be affected by the binocular structure of V1. Compared to other visual areas, V1 is unique in that most of its cells show ocular dominance, a preference for the input of one eye. Perhaps the effect of this unique binocular organisation can be revealed in psychophysical experiments in normal human observers. If this were possible, it would provide a useful tool for identifying processes that occur at the level of the striate cortex. A further benefit is that the results of such behavioural experiments may shed light on cortical organisation and the processes occurring within striate cortex.

Evidence for a relationship between visual sensitivity and the binocularity of striate cortex comes from research into the development of the visual system. Research in both humans and other animals has demonstrated that if binocular interactions are disrupted early in development, performance on visual tasks such as acuity and contrast sensitivity may be affected. Human observers who have lost an eye early in development have a monocular contrast sensitivity that is equal to that obtained binocularly in normal individuals (Nicholas et al, 1996). This suggests that a change in the binocular structure of the visual cortex can alter the limits of visual sensitivity. Evidence relating to the anatomical and functional changes following visual deprivation will be reviewed more fully later in this chapter. If it is possible to show psychophysically the difference in binocular interactions in monocular and binocular humans, perhaps a similar difference can be demonstrated in normal observers between binocular and monocular areas of the visual field. This possibility is explored experimentally in the next two chapters of this thesis.

Since neurons encode multiple visual attributes, it is important to establish how ocular dominance affects the processing of information in other visual domains. Physiological evidence concerning ocular dominance and lateral interactions suggests that the strength of these interactions may be affected by stimulus eye of origin. Since evidence suggests that orientation pop-out and orientation difference sensitivity may be mediated by these lateral connections, these tasks may be affected by the binocular structure of V1. Such an investigation would reveal at what level of the visual system these tasks are mediated and whether ocular dominance affects their limits of sensitivity. A review of evidence concerning orientation pop-out and the role of lateral interactions is presented in Chapter 4. Investigations reported in subsequent chapters utilise dichoptic tasks that require the comparison of information in each eye, the rationale being that if neurons showing ocular dominance are involved, there should be a cost (in speed or accuracy) associated with integrating the information across the two eyes.

If there really were a close correspondence between the processing of information in striate cortex and visual perception then it ought to be possible to detect the eye of origin of information. Neurons in V1 are selective for a number of different visual characteristics including spatial frequency, temporal frequency, wavelength, orientation and disparity (See DeVelois & DeVelois, 1990 for a review). According to one theory of visual processing, these attributes form the input to later levels of the visual system, which extract colour, form and depth from these visual primatives. In contrast, the eye of origin of information, which is necessary to determine whether a disparity is crossed or uncrossed should be directly available to consciousness since monocular stimulation in one position in the visual field will result in a distribution of responses biased towards that eye. A review of evidence on this controversial debate is presented later in this chapter and an experimental investigation is reported in Chapter 6. This represents another attempt to demonstrate the effects of the binocular structure of V1 on visual perception.

In summary, the aim of this thesis is to investigate the relationship between the binocular structure of V1 and aspects of visual perception not associated with stereoscopic depth perception. The approach adopted is reductionist in that it seeks to explain psychophysical data in terms of the organisation of a single anatomical structure, V1. The next section will review physiological evidence for binocular interactions in striate cortex.

PHYSIOLOGICAL EVIDENCE FOR BINOCULAR INTERACTIONS IN VISION

Binocularity in primary visual cortex and ocular dominance

David Hubel and Torsten Wiesel did pioneering work on the nature of binocular interactions in the primary visual cortex. In the monkey, ipsilateral and contralateral inputs from the dorsal lateral geniculate nucleus are segregated and the first cortical layer (IV) is exclusively monocular (Hubel & Wiesel, 1968). A binocular cell was defined as one that responded to a stimulus presented to either eye alone. Such cells were found to respond to stimuli at corresponding points in each eye and had the same orientation and direction preference. However, cells differed in terms of their strength of eye preference, ranging from complete dominance by one eye, through equality, to complete dominance by the other eye. To describe this, Hubel and Wiesel defined a 7 point ocular dominance scale. Although this has proved to be a useful classificatory system, these authors were aware that it did not capture the full range of possible binocular interactions. For example, it was noted that while some cells did not respond to monocular stimulation they did respond when both eyes were stimulated simultaneously.

The columnar nature of ocular dominance was revealed in the monkey using electrophysiology (Hubel & Wiesel, 1968). In a perpendicular electrode penetration from the cortical surface to the white matter, cells typically shared the same eye preference. While in an oblique penetration, eye dominance alternated. The anatomical segregation of inputs from the LGN was confirmed to underlie this columnar organisation by making lesions in single laminae of the LGN in monkeys and staining the resulting terminal degeneration in layer IV of striate cortex with the Nauta method (Hubel & Wiesel, 1972). In tangential view, this revealed bands about 400 m wide separated by bands of the same width that were free of degenerating terminals. It was concluded that afferents serving the left and right eyes terminate in alternating non-overlapping bands in layer IV.

Later, methods became available with which to examine the large-scale structure of ocular dominance columns. One useful method has been an autoradiographic procedure that depends on the transneural transport of proline or fucose from the eye through the LGN to the cortex. When applied to the macaque monkey this produces a pattern of labelled and unlabelled bands, corresponding to the ocular dominance stripes for the injected and non-injected eyes (Wiesel et al., 1974). Studies employing this technique have shown that the bands are more or less constant within the central portion of the visual field but that beyond 15-20 degs there is an attenuation and fragmentation of the bands representing the ipsilateral eye. This may reflect the imbalance in the numbers of retinal ganglion cells at equivalent eccentricities in nasal and temporal retina.

Other imaging techniques that enable the visualisation of large areas of cortex rely on detecting differential levels of activity. Radiolabelled 2-deoxyglucose (2DG) is actively absorbed by cells metabolising glucose and neurons showing greater activity absorb more 2DG. Ocular dominance columns have been revealed in the macaque monkey using this technique by exposing the animal to monocular stimulation for about 45 mins after injection of 2DG. After sacrifice, the distribution of 2DG can then be examined autoradiographically (Hubel & Wiesel, 1977). Also widely used is the cytochrome oxidase method, which stains for the metabolic enzyme cytochrome oxidase, found in the mitochondria of cells. Following enucleation this reveals the ocular dominance bands for the remaining eye as densely stained and those for the missing eye bleached out (Rosa et al.,1992). Both these techniques have revealed that ocular dominance stripes in the monkey pervade all layers of striate cortex, but that in the monkey they stop abruptly at the V1/V2 border. Ocular dominance columns are also present in humans though they tend to be wider (1 mm) reflecting the greater surface area of the human cortex compared to the monkey (Horton & Hedley-White, 1984).

Other physiological work has examined the neurochemical basis of ocular dominance and in particular, the role of GABA mediated inhibition. In a study of inhibitory interactions contributing to ocular dominance in cat striate cortex (Sillito et al.,1980), the GABA antagonist bicuculine was applied to cells to produce a block of inhibitory mechanisms acting upon them. While only those cells that showed a strong eye preference were studied, it was found that 50% of these cells showed varying degrees of increased sensitivity to the nondominant eye without any concomitant reduction in sensitivity to input from the dominant eye. It was concluded that inhibitory processes make a large contribution to the ocular dominance of cat striate neurons and that ocular dominance is not a hard-wired feature of cortical architecture.

Although ocular dominance columns have been known to exist for over 30 years, their function in the cortex is still debated. In general, there are several processes that binocularity in the visual cortex might enable. These include binocular fusion, stereoscopy, binocular rivalry and interocular transfer. The most widely advocated hypothesis is that ocular dominance columns are part of the neural mechanism for stereoscopy (LeVay & Nelson, 1991). In support of this notion, manipulations that disrupt ocular dominance columns also disrupt stereoscopy (see Livingstone et al. 1995). In addition, during development, stereopsis and ocular dominance mature with similar time courses (see Livingstone et. al. 1995). Furthermore, several studies have indicated a relationship between disparity coding and ocular dominance. Cells broadly tuned to near and far disparities tend to have the strongest ocular dominance while binocularly balanced cells tend to code for the horopter. This relationship has been found in both the cat (Gardner & Raiten, 1986) and rhesus monkey (Poggio & Fisher, 1977).

In the cat, there appears to be a clear functional architecture relating ocular dominance to stereoscopy. Cells on the borders of ocular dominance columns tend to be binocularly balanced in that they can be driven equally well by either eye (Shatz & Stryker, 1978). Such cells are most sensitive to stimuli that are on or near the horopter. This arises because the receptive fields of cortical cells have mutually antagonistic excitatory and inhibitory zones. Binocularly balanced cells presumably have inputs from spatially corresponding receptive fields. Stimuli that are nearer or farther away will fail to activate corresponding excitatory regions. Therefore an excitatory response to one eye's receptive field will be blocked by inhibition in the other eye (Ferster, 1981).

Conversely, cells situated in the centres of ocular dominance columns tend to receive excitatory inputs largely from one eye. However, many also receive inhibitory inputs from the non-dominant eye (see Sillito et al 1980 above). The function of this inhibition is related to selectivity for disparity and cells strongly dominated by one eye tend to be broadly tuned for crossed and uncrossed disparities (Ferster, 1981). Thus Ferster suggested there was a clear functional architecture to the cat striate cortex with respect to disparity coding with cells coding for the horopter located on the boundaries of ocular dominance columns and cells broadly tuned to near and far disparities centred within the columns. Whether a similar functional architecture exists for the monkey remains to be established.

A recent study which measured evoked potentials to cyclopean patterns in random dot stereograms in an alert squirrel monkey (Livingstone et al., 1995) casts doubt on the necessity of ocular dominance for stereoscopy. There is considerable anatomical evidence showing the squirrel monkey lacks ocular dominance columns and its ocular dominance distribution in V1 is much more binocular (i.e. most cells receive input from both eyes rather than being strongly activated by one). Yet this monkey showed evoked responses both to changes in disparity and to shifts between correlation and uncorrelation. The responses to these two types of stimuli were clearly different suggesting that there was true sensitivity to disparity and not simply to correlation between the two eyes. In addition, the magnitude of the evoked potential became larger with increasing disparity. This strongly suggests that the squirrel monkey can detect stereoscopic depth and questions the assumption that ocular dominance columns bear an important relation to stereopsis.

A further paper by this author showed that it was possible to induce ocular dominance columns in layer IVCß of V1 of the squirrel monkey by making the animal strabismic within a few weeks of birth (Livingstone, 1996). The idea is that strabismus prevents correlated visual inputs from each eye and thereby ensures that the geniculate-cortical afferents remain segregated. Livingstone hypotheses that variations in ocular dominance expression may be related to differences in the maturation of geniculo-cortical inputs and intracortical lateral connectivity rather than reflecting functional variation.

The most recent paper to address this issue has found positive evidence for ocular dominance columns in the squirrel monkey (Horton & Hocking 1996). In two animals columns in layer IVC were labelled by putting [^{3}H] proline into one eye and WGA-HRP into the other eye. Comparison of the adjacent sections showed interdigitation of the two cortical labels, establishing that squirrel monkeys have ocular dominance columns.

However, the columns were much smaller than those seen in any other animal and they were organised in a fractured irregular mosaic. It may be concluded then, that while the function of ocular dominance columns remains unknown, their existence is widespread. In addition, the theory that they are important for stereopsis cannot be refuted.

Although this discussion has focused on stereopsis, it is clear that not all binocular cells carry information about depth. Many cells found within layer V of cat striate cortex are binocular but respond without strong summation or any spatially coded interaction between the two eyes. Binocularity may be important for interocular transfer and provide information about the two dimensional position of a stimulus. LeVay & Nelson (1991) argue such information would be appropriate for the superior colliculus (the major target of layer V cells) since the superior colliculus might be involved in the control of conjugate saccades.

It is also important to stress that binocular interactions are an important feature not just of striate cortex, but of other cortical areas. Although prestriate cortex in primates cannot be segregated into ocular dominance columns and the majority of cells are driven equally well by either eye (Zeki, 1979), the activity of cells in these areas may be modified (i.e. suppressed or enhanced) by various binocular combinations of stimuli.

The effects of monocular deprivation on the developing visual system

The previous section reviewed evidence concerning the structure and function of normal binocular interactions in the visual cortex. This part of the review will examine the effects of interrupting binocular interactions through enucleation or monocular pattern deprivation early in development. Preventing normal binocular interactions has been shown to have dramatic consequences on the development of the visual system because the remaining eye expands its connections into the neural territory normally innervated by the other eye. Monocular deprivation has been an invaluable tool to the neurobiologist and has led to many insights into how the mature pattern of organisation of the visual system is established. It has also demonstrated the considerable plasticity of the developing nervous system and indicated the importance of binocular interactions in normal development. This section will begin by looking at the anatomical and physiological effects of enucleation and pattern deprivation on the retina, LGN and cortex and conclude with some animal studies of visual performance in the remaining or non-deprived eye.

During development, there is an initial overproduction of ganglion cell axons which is then followed by a loss due to the death of ganglion cells. This process occurs in many mammalian species including the rhesus monkey (Rakic & Riley, 1983) and human (Provis et al.,1985). In terms of the proportion of the interval between conception and natural eye opening (CP), all mammalian species studied thus far follow a similar pattern. Typically axon numbers increase very rapidly around 40% CP, peak at 55% CP and then decline rapidly until about 85% CP, by which time the numbers of axons is only slightly higher than that in the adult optic nerve (Robinson & Dreher, 1990). It has been argued that many of the extra axons in the initial overproduction innervate inappropriate targets and that it is through competition with the other eye that these aberrant connections are removed (White & Chalupa, 1991). If this is correct, it should be possible to prevent the normal death of ganglion cells by interrupting binocular interactions either before or shortly after birth.

This was confirmed by a study in the cat in which prenatal enucleation was done before the projections to the LGN had become segregated. The retina of the remaining eye was found to have a higher number of retinal ganglion cells than normal (Chalupa et al.,1984) leading to an increase in cell density in the retina. This is presumably why, for at least one class of ganglion cell, the alpha cell, the dendritic fields are smaller than normal in prenatally enucleated cats (Kirby & Chalupa, 1986). In addition, monocular enucleation results in a widespread projection from the remaining eye to the entire ipsilateral and contralateral dorsal lateral geniculate nucleus in both the cat (Chalupa & Williams, 1984) and macaque monkey (Rakic, 1981). This means that the area innervated in the dorsal lateral geniculate nucleus by the remaining eye of enucleates is roughly twice that of the eye of a normal animal. Thus binocular interactions are crucial for the normal ocular segregation of layers in the lateral geniculate nucleus.

There is also evidence that monocular deprivation affects cortical organisation. (Wiesel & Hubel, 1963). These authors created an animal model of amblyopia by raising kittens with one eyelid sutured. Upon recording from the striate cortex it was found that cells could be driven only via the normal, open eye. The anatomical correlate of this shift in ocular preference was shown later in cats and monkeys by injection of proline into one eye (Hubel et al., 1977; Shatz & Stryker, 1978; LeVay et al.,1980). Autoradiographs of the cortex showed a marked shrinkage of the ocular dominance columns serving the amblyopic eye. Unfortunately, equivalent studies in humans are lacking. Post-mortem analysis of human ocular dominance columns in a case of anisometropic amblyopia (Horton & Stryker, 1993) and strabismic amblyopia (Horton & Hocking, 1996) has failed to find any shrinkage in the columns of the deprived eye. However, these authors suggest that both these forms of amblyopia may develop in infancy when the columns have matured enough to resist shrinkage induced by visual deprivation.

Given the widespread anatomical changes to the visual system that follow early enucleation and pattern deprivation, many authors have sought to determine the functional consequences of interrupting binocular interactions. In one study, recordings were made from single neurons in the visual cortex of adult cats that had one eye enucleated at least two weeks before birth (Shook et. al.,1985). In the cats with prenatal enucleation, the remaining eye drove all of the neurons. As in normal animals, the majority of neurons were orientation selective. In addition, there were sequences of neurons containing a full 180-degree cycle of orientation preferences, a finding characteristic of hypercolumns. This suggests that orientation columns can develop independently of ocular dominance columns. A further finding was a change in the distribution of receptive field sizes. In the enucleates, there was an increase in the proportion of cells with small receptive fields but a concomitant decrease in the number of cells with large receptive fields. This finding led the authors to propose that the remaining eye of the prenatally enucleated cat could have supernormal vision, especially with respect to acuity.

This issue was addressed in a study that measured contrast thresholds electrophysiologically at the cortex of rats that had been enucleated on the day of birth (Heywood et al., 1988). In the enucleates, in hemispheres both ipsilateral and contralateral to the eye removal, VECPs were found to be of a greater amplitude than controls tested monocularly. The effect was proportionally greater for the ipsilateral response. Furthermore, contrast thresholds derived from VECPs were lower for the ipsilateral projection in the enucleates and were similar in sensitivity to the contralateral projection in normal animals. Presumably the supersensitivity was largely restricted to the ipsilateral pathway because the rat's retino-geniculate system is predominantly crossed. Consequently, loss of one eye in a rat favours the ipsilateral projection in the remaining eye, which can innervate the large area that would normally receive the contralateral projection of the lost eye.

Another study relevant to this issue looked at the visual performance in the remaining eye of cats unilaterally enucleated three weeks before birth (Bisti & Trimarchi, 1993). While the enucleated cats had normal visual fields and normal grating acuity, changes in the contrast sensitivity function were observed. Specifically, in the enucleated cats, the optimum spatial frequency was substantially higher than in normal cats tested monocularly. In addition, there was an increased maximum contrast sensitivity and attenuation in sensitivity at low spatial frequencies. Cells with large receptive fields presumably mediate sensitivity at low spatial frequencies. The loss of sensitivity is consistent with single unit recordings in area 17 in prenatal unilaterally enucleated cats, which have failed to reveal cells with large receptive fields (Shook et al., 1985). Cells with large receptive fields correspond physiologically to Y cells. After prenatal unilateral enucleation the Y ganglion cells of the remaining eye develop abnormally large terminal axons (Sur, 1988). However, despite the increased axonal arborisation, fewer Y-ganglion cells are recorded in the lateral geniculate nucleus of these animals (White et al., 1989). This suggests that in prenatally enucleated cats, the Y system may be functionally impaired leading to a loss of sensitivity at low spatial frequencies.

Support for this notion came from a study in which visually evoked potentials were recorded from the 17-18 border of cats who had either undergone prenatal or early postnatal enucleation or had undergone a surgical removal of Y ganglion fibres (Bisti et al.,1995). The results showed that prenatal enucleation reduces the contrast response to low spatial frequencies with no effect on the contrast sensitivity response to moderate and high frequencies. Similarly, VEPs recorded in animals with the Y-ganglion input removed were strongly attenuated in response to stimuli of low spatial frequencies. This supports the notion that the loss of sensitivity seen in prenatal enucleation in the cat is due to the selective loss of function of the Y system. Enucleation just after birth had no effect on the normal development of the contrast sensitivity function. This is consistent with the observation that by this time the optic radiation has started to synapse with cortical neurons. It was concluded that normal development of the Y ganglion cell system in cats depends strongly on correct binocular interactions during prenatal life.

BINOCULAR INTERACTIONS IN HUMAN VISION

Overview of perspectives

There have been a number of different approaches to the psychophysical study of binocular interactions in human vision. One approach has been to study the interocular transfer of visual adaptation effects. The rationale behind this approach is that if a given effect shows interocular transfer, it implies the involvement of binocular neurons. There is a large body of evidence concerning such effects, coverage of which, is unfortunately beyond the scope of this review (see Chapter 9 of Howard & Rogers, 1995).

A second approach to studying binocular interactions in human vision has been to examine binocular summation, the superiority of binocular over monocular viewing on visual threshold tasks. Tasks which show this superiority include increment detection, form recognition, contrast sensitivity and flicker detection (for reviews see Blake & Fox, 1973; Blake et al., 1981; Arditi, 1986). Controversy in this area surrounds whether binocular summation arises from probability summation, the fact that possessing two eyes provides two opportunities to detect a weak signal, or whether a form of neural interaction between the two eyes is involved. This issue is considered further in the discussion of Chapter 2.

Thirdly, binocular interactions in human vision have been examined by studying visual anomalies. Amblyopia is a condition in which an uncorrectable loss of visual function occurs in an eye (which has no overt pathology) that was strabismic or anisometropic early in life (Hess & Pointer, 1985). Anisometropia refers to a large difference in refractive error between each eye. One model of amblyopia holds that it results from an imbalance between binocular *neuronal interactions* resulting from the strabismus or amblyopia (Wiesel & Hubel, 1965). An alternative model suggests that the competitive imbalance develops from the direct non competitive deprivation effects of the blurred retinal image present early in life (Ikeda & Wright, 1976). Unfortunately space does not permit a full discussion of amblyopia but a more extensive review of the nature of the visual deficit can be found in Hess et al (1991).

Another group of individuals who have a deficit in binocular interactions are those with stereodeficits. Such observers have been studied to see whether they show normal interocular transfer (Mohn & Van Hof-van Duin, 1983; McColl & Mitchell, 1997) and binocular summation (Westendorf et al, 1978). Stereoblindness is associated with a history of visual abnormalities and amblyopia is not uncommon. Arguably, the most extreme disruption to binocular interactions occurs in those who have lost an eye early in development either through trauma or disease. The effect of monocular deprivation on visual sensitivity, arising from either enucleation or amblyopia, will now be reviewed.

The effects of monocular deprivation on visual sensitivity

Nicholas et al. (1996) measured the contrast sensitivity of individuals who had had an eye removed for retinoblastoma (<4 years) or trauma (11-13 years). This study found that the enucleates had a higher contrast sensitivity than normal subjects tested through their better eye but only at intermediate spatial frequencies. At high and low frequencies the enucleates and normal subjects performed similarly. In addition, the earlier the eye had been lost, the lower the spatial frequency and the larger the range of spatial frequencies over which contrast sensitivity was enhanced. This reflects the difference in rate at which sensitivity to different spatial frequencies develops. Surprisingly, those subjects who had lost their eye early on (<4 years) had a peak contrast sensitivity at 4c/deg that exceeded that of normal subjects tested binocularly. This increase over normal binocular viewing was attributed to a loss of binocular inhibition. Other mechanisms that were advanced to explain the hypersensitivity included a possible increase in the ganglion cell population in the remaining eye and practice at monocular viewing.

There have been other investigations of the visual performance of the remaining eye of subjects who have had monocular deprivation, although not all have found enhancements. For example, one study examined vernier acuity in the functional eye of subjects who had experienced monocular deprivation mainly from anisometropic amblyopia (Freeman & Bradley, 1980). In the vernier task, subjects had to detect the misalignment of the upper and lower halves of a bar. The monocularly deprived subjects had lower vernier thresholds in their functional eye than normal subjects tested monocularly and this improvement was very close to a value of $\sqrt{2}$. It was also shown that the improvement from monocular to binocular vernier acuity in normal subjects is $\sqrt{2}$. This implies that in terms of vernier acuity, the monocularly deprived subjects were able to fully compensate for their visual deprivation. However other studies which have examined vernier acuity have failed to replicate this finding (Johnson et al., 1982; Gonzalez et al., 1992).

Recently, Reed et al (1997) used Regan letter charts to compare the recognition acuity of individuals who had had an eye removed during childhood (4-47 mths) with that of normal subjects. It was found that the performance of the enucleates was equivalent to that obtained by the control subjects viewing binocularly, suggesting that the enucleates were able to fully compensate for their loss of an eye.

The demonstration that monocular deprivation can improve the functioning of the non-deprived eye suggests the possibility that in normal subjects, monocular areas of the visual field will be similarly enhanced. The blind spot is a naturally occurring region of visual deprivation and the suggestion that such deprivation improves the sensitivity of the corresponding location in the other eye is assessed in Chapter 2. This is followed-up in Chapter 3 with a similar study in a patient with a homonymous hemianopia.

Utrocular identification

A number of investigators have suggested that ocular dominance might support utrocular identification, the ability to identify the eye of origin of a visual stimulus. This debate began in the nineteenth century, when Helmholtz (1866) considered whether it was possible to "distinguish the impressions of one eye from those of another" (cited in Ono & Barbeito, 1985). While Helmholtz knew that eye of origin information was preserved at some level of the visual system (for example, it was required to distinguish between crossed and uncrossed disparities), he wanted to know whether such information was open to conscious scrutiny. From his investigations he concluded that conscious access to eye of origin information is denied. Yet subsequent investigations have shown that under certain circumstances, eye of origin information is available. However, whether this represents true utrocular identification has been disputed.

Recent interest in utrocular identification was catalysed by a greater understanding of the nature of binocularity in primary visual cortex. Blake & Cormack (1979a; 1979b) suggested that monocularly driven cells carry eye of origin information and that a population of cells with varying degrees of ocular dominance might support utrocular identification in normal observers. Furthermore, since stereoblind individuals may have a paucity of binocularly driven cells, they may also possess a superior ability to discriminate eye of origin than individuals with normal stereo acuity[1]. To test these hypotheses, observers judged whether a grating (equated for apparent contrast) had been presented to the left or right eye. The eye of the target was chosen at random on each trial and the non-target eye received a blank field of the same space averaged luminance. Without any feedback about the accuracy of their response, normal observers could correctly identify the eye-of-origin of the grating at low but not high spatial frequencies whereas utrocular identification by the stereodeficient observers was above chance at all spatial frequencies. The superior performance of the stereoblind observers seemed to support the notion that monocular cells carry eye of origin information that is available to consciousness.

In a follow-up study, Martens et al (1981) suggested that ocular origin may be denoted by an afferent signal emanating from the eye containing the stimulus which reflects the increased activity of ocular dominance neurons predominantly tuned to that eye. The same methods as Blake & Cormack (1979a;1979b) were used except that the test grating could be embedded in a binocular display of one-dimensional noise. Utrocular identification in the presence of the noise was reduced to chance when the contrast of the grating was lowered to a certain point (reduction in contrast per se had no effect on

---

[1] This also implies that utrocular identification should be superior in monocular areas of the visual field. However this would be difficult to test as stimulus eye of origin would be correlated with stimulus position.

utrocular identification) but only when the noise contained power at the spatial frequency of the test grating. In addition, utrocular identification was more impaired by a binocular noise background with a rapid onset and transient presentation, than one with a gradual onset and sustained presentation. This led the authors to conclude that the utrocular identification cue is based on temporal transience. Martens et al. suggested that since the transient system is less sensitive to high spatial frequencies, this accounts for the absence of utrocular identification at high spatial frequencies.

Others (Ono & Barbeito, 1985; Barbeito et al 1985; Porac & Coren, 1986) take a somewhat different view of the accessibility of eye of origin information to consciousness. Essentially, these authors assert that any utrocular identification is the manifestation of a peripheral cue rather than a central mechanism that relies on a pool of neurons with different degrees of ocular dominance. Ono & Barbeito (1985) point out that reliable discrimination between the two eyes views is often possible because of the multitude of ways in which the appearance of stimuli presented to the two eyes can differ. Cues listed by Ono & Barbeito that are mentioned in the literature include: (a) asymmetry of apparent size, clarity or brightness in the two eyes (Coren & Porac, 1979); (b) ocular motor adjustment (Smith, 1945); (c) a difference in visual directions of an object seen by the two eyes due to fixation disparity (Templeton & Green, 1968) and (d) a difference in 'feelings' in the eyes (Enoch et al., 1969; Blake & Cormack, 1979a; 1979b).

Ono & Barbeito (1985) argue that many of these cues can be used to distinguish between stimuli presented to each eye. However, none of these cues are valid cues to utrocular discrimination in the sense that they uniquely specify the identity of the eye to which a stimulus has been presented. Many of these cues can be manipulated such that the cue is correlated with the 'wrong' eye i.e. perfect discrimination in the wrong direction. With feedback, subjects can associate subtle available cues with the eye to which a stimulus has been presented and hence produce reliable discrimination. The importance of feedback is emphasised by Porac & Coren (1986) who found that without feedback, performance (for detecting the eye of origin of a small square surrounding a binocular fixation point) was at chance even with extensive familiarity with the display. It can be argued that feedback calls a subject's attention to subtle differences between the appearance of stimuli presented to each eye, which can then be used to mediate reliable discrimination in the desired direction.

How can the above chance performance of Blake & Cormack's subjects, which occurred in the absence of feedback be explained? These authors comment that for those subjects who could identify the eye to which the grating had been presented (and there was wide individual variation), the presentation of the grating was accompanied by a poorly defined 'feeling in the eye' that received the grating. Ono & Barbeito (1985) argue that this 'feeling in the eye' is not a valid cue to utrocular discrimination since utrocular identification was reduced to chance when the presentation of the grating was accompanied by a luminance change in the other eye. Ono & Barbeito suggest that the 'local' changes in luminance variation produced by the onset of the grating are responsible for the 'feeling in the eye' and that the change in luminance in the other eye produced an equivalent feeling, rendering the feeling produced by the test grating non unique. Not all stereoblind observers showed utrocular identification using Blake and Cormack's paradigm and, like normal observers, identification was abolished when accompanied by a luminance change in the other eye. This led Barbeito et al (1985) to conclude that neither stereo normal or stereoblind observers have conscious access to eye of origin information. Referring to Martens et al (1981) study, which also rendered responses unreliable by manipulating time and luminance, it is argued that the experimental manipulation equated the 'feeling in the eye', also making the responses unreliable.

The crux of the debate seems to be whether the 'feeling in the eye' represents intrinsic eye of origin information or whether it is a spurious cue such as that provided by a luminance difference between the two eyes or a fixation disparity. Ono & Barbeito (1985) adopt the latter position. They argue this phenomenon should not be examined in the context of utrocular discrimination or identification because they claim to experience 'feeling in the eye' binocularly when entering a normally lit room after dark adaptation. To demonstrate utrocular identification, one must find a cue that cannot be dissociated from the stimulated eye or a cue that provides the correct information about the stimulated eye across different conditions.

However, a more recent demonstration of utrocular identification seems harder to dismiss as the manifestation of a peripheral cue. Timney et al (1997) replicated and extended Blake & Cormack's original study. It was shown that subjects can identify the eye of origin of a low frequency vertically oriented grating when accompanied in the other eye by a low frequency horizontally oriented grating (orientation and contrast jitter were added to mask appearance cues). Timney et al argue that the finding of utrocular discrimination even with simultaneous stimulation of each eye strongly supports a 'labelled line' hypothesis as opposed to utrocular discrimination based on peripheral recognition cues. Finally, superior utrocular discrimination was found with low spatial frequency and high temporal frequency stimuli supporting the possibility of a greater involvement of the magnocellular pathway.

It has recently been suggested that human observers may be able to access ocularity information if extrastriate areas are functionally anaesthetised (Dobbins & Kolb, 1995). To test this possibility, subjects were asked to report the eye of origin of stimuli known to suppress MT neurons in macaques. In all experiments a target was presented to one eye while a noise stimulus was presented to the other. The MT suppressing target was a bidirectional field of paired moving dots while the MT exciting target was a unidirectional field of moving dots. Subjects were better at identifying the eye of origin of the MT suppressing target than the MT exciting target suggesting that access to eye of origin information is possible when MT is functionally anaesthetised. This implies there are circumstances under which one is aware of information available only in V1.

This discussion relates specifically to Chapter 6, which investigates binocular interactions in visual search and considers whether eye of origin information is available to the search process. The aim of investigating binocular interactions in visual search is to localise the point in the information flow at which preattentive vision occurs.

2

Contrast Sensitivity in the Region Corresponding to the Blind Spot in the Other Eye

ABSTRACT

Studies of the effects of monocular deprivation suggest that areas of the visual field, which are monocular in their neural representation, are capable of mediating supernormal performance. A series of experiments is reported in which the photopic achromatic contrast sensitivity of normal human observers was measured in several areas of the visual field including the region corresponding to the blind spot in the other eye. The contrast sensitivity of this region was significantly higher than the monocular contrast sensitivity obtained in a comparable region at the same eccentricity for all spatial frequencies tested (0.2-3.2 c/deg). Foveal measures of contrast sensitivity were used to calculate the contrast sensitivity expected along the horizontal meridian at the same eccentricity as the blind spot. The expected values were found to be significantly lower than the contrast sensitivity actually observed in the homonymous region of the blind spot. The elevation in contrast sensitivity was not significantly different from measures obtained binocularly in a comparable region of the visual field at the same eccentricity as the blind spot. This suggests that the area of the visual field, which lies homonymous to the blind spot, has a perceptual sensitivity equivalent to binocular viewing. The possible neural mechanisms underlying this phenomenon are discussed.

INTRODUCTION

The blind spot is the region of the visual field, which corresponds to the papilla, or entrance of the optic nerve. Since it is a region devoid of photoreceptors and thus insensitive to light, it is a naturally occurring scotoma or retinal lesion. It was discovered by Mariotte (1668) (cited in LeGrand, 1967) when he found the entrance of the optic nerve while dissecting the eye. It seems quite surprising that it was not discovered until the 17th century given its size; at a distance of two metres, a human head fits easily into the scotoma. However, the blind spot is not generally apparent to the observer even when viewing is monocular and the mechanism responsible for this perceptual 'filling in' has been studied extensively (Ramachandran & Gregory, 1991; DeWeerd et al., 1995; Durgin et al., 1995). Reports of a faint light sensitivity within the blind spot (Wolf & Morandi, 1962 cited in LeGrand, 1967) can be attributed to light scatter by the papilla. The blind spot is roughly oval in shape and has a vertical diameter of 7-8° and a horizontal extent of 5-6°. The internal edge of the spot lies 12-13° from the fovea and its centre is vertically displaced below the horizontal meridian by 2-3° (LeGrand, 1967). Very precise mapping of the blind spot is difficult since across the boundary there is a gradual transition from sensitivity to insensitivity that is about 1° in width and the overall size is subject to vascular changes of the optic nerve.

The blind spot in each eye is situated on the nasal hemi-retina and its representation in the brain is mapped topographically onto the LGN and cortex. In the LGN of primates there are 6 layers; layers 1,3 and 5 receive input from the ipsilateral eye (temporal retina) while layers 2,4 and 6 receive input from the contralateral eye (nasal retina). Thus the blind spot 'projects' only to the contralateral layers. Electrophysiological investigations have revealed that the region of the LGN corresponding topographically to the optic disc in the retina is completely cell free. This is true in general for all layers of the LGN receiving a contralateral projection and has been demonstrated in a wide variety of carnivores and primates (Kaas et al., 1973). However, at the cortex, there is no discontinuity corresponding to the locus of the blind spot, which is completely innervated by the ipsilateral eye. The cortical representation of the blind spot is thus monocular[2] and ocular dominance columns are absent. This has been shown in many studies in the monkey employing both glucose autoradiography (Kennedy et al., 1975; Kennedy et al., 1976; Horton, 1984) and cytochrome oxidase histochemistry (Rosa et al., 1992). For example, in a series of sections from layer 1 to white matter, Horton (1984) could find no trace of any pattern in the optic disk representation in deoxyglucose autoradiographs. Given the monocularity of the region corresponding to the blind spot, could perceptual sensitivity be altered as a consequence?

There is some evidence to show that supernormal monocular perceptual performance can arise following monocular deprivation when it occurs early in development. As reviewed in Chapter 1, the effect of early monocular pattern deprivation and enucleation is that the non deprived or remaining eye preserves and expands its connections into the neural territory normally innervated by the contralateral eye. This change in the normal pattern of connectivity has been shown to have functional consequences. For example, prenatal enucleation in the cat results in all neurons sampled being driven by the remaining eye. There is also an increase in the number of cells with small receptive fields suggesting that acuity could be enhanced (Shook et al, 1985).

Positive evidence of supernormal perceptual ability comes from a study which showed a reduction in monocular contrast thresholds measured eletrophysiologically in rats who had been enucleated on the day of birth (Heywood et al, 1985). In partial agreement with this study, cats with prenatal enucleation tested monocularly were found to have a higher optimum spatial frequency, an increased maximum contrast sensitivity but an attenuation in sensitivity at low spatial frequencies (Bisti & Trimarchi, 1993).

Several studies with human participants have also reported an increase in perceptual sensitivity in the unimpaired eye following either monocular deprivation or the loss of an eye early in development (see Chapter 1). Visual functions which have been found to

---

[2] While all physiological studies to date show that the cortical representation of the blind spot is monocular, there is some psychophysical evidence which suggests the existence of binocular mechanisms sensitive to stimuli surrounding the blind spot and the corresponding region in the other eye (Tripathy & Levy, 1994).

be increased compared to monocular control measures include contrast sensitivity (Freeman et al., 1989; Nicholas et al., 1996), vernier acuity (Freeman & Bradley, 1980) and recognition acuity (Reed et al., 1997). However, two studies have failed to replicate the finding of reduced vernier acuity thresholds in monocularly deprived humans (Johnson et al., 1982; Gonzalez et al., 1992).

Since the contrast sensitivity of monocular humans can be increased, perhaps areas of the visual field in normal humans, which are monocular in their neural representation, will be similarly enhanced. Although there have been numerous studies of the contrast sensitivity profile of the normal human peripheral visual field (Rovamo, 1978; Rijsdijk et al., 1980; Robson & Graham, 1981; Pointer & Hess, 1989; Pointer & Hess, 1990), these studies have not been specifically concerned with sensitivity in the region corresponding to the blind spot. Some data from Rovamo & Virsu (1979) (cited in Drasdo, 1991) suggest that sensitivity could be enhanced within the homonymous region of the blind spot. These authors found that contrast sensitivity along the horizontal meridian is the same, irrespective of eccentricity, when the size of the stimuli are scaled by the cortical magnification factor so that they project to equally sized cortical areas. This suggests that the decline in contrast sensitivity normally observed when sensitivity is measured with stimuli of the same size is due to the decrease in the amount of cortex available for processing a given region of the visual field. However, when contrast sensitivity was measured along the horizontal nasal visual field using the scaled stimuli, sensitivity was conspicuously higher for a location 14° eccentric than any other eccentricity, but only for a restricted range of spatial frequencies (0.8-3.0 c/deg).

GENERAL METHODS

Subjects

In total eleven subjects took part in the investigations reported in this chapter. At least half of the subjects had no prior experience of psychophysical tests and were naive to the purpose of the study. None of the subjects had any known binocular abnormalities and all scored within the normal range on a test of stereopsis and the Maddox Wing test for muscle balance. All subjects except KF required optical correction to achieve normal acuity. During procedures that were done monocularly, the left eye was covered with an opaque occluder. For those subjects who used glasses, care was taken to ensure that the frame did not obscure the screen surround.

Equipment

All stimuli were generated using the VSG 2/2 (Cambridge Research Systems) graphics board using the accompanying PSYCHO software. The stimuli were displayed on a monitor (32cm*24cm) with a P4 phosphor, a screen resolution of 768 lines (with 1024 pixels per line) driven at a frame rate of 70Hz. The voltage/luminance relationship was linearised using gamma correction and the accuracy of the calibration was then checked photometrically. The mean screen luminance was 47cd/m , the viewing distance was 57cm and the only light sources were the test monitor and the experimenter's monitor. Head movements were restricted via the use of a chin rest incorporating a head clamp.

Stimuli

The stimuli employed in all experiments were circular patches of one-dimensional sine wave gratings in zero phase. They were horizontally orientated and their mean luminance equalled that of the screen background. Temporal modulation of 1Hz sinusoidal contrast reversal was employed to prevent the intrusion of afterimages. The stimulus onset and offset transition envelope followed a raised cosine function (which approximates a gaussian). The onset is the time taken for the stimulus to increase from the background luminance to full envelope. The offset is the time taken for the stimulus to decrease from the maximum to the background luminance. The total stimulus presentation time of 750 ms included 250 ms for the onset, 250 ms of the stimulus at full envelope followed by 250 ms for the offset.

Stimuli of five different spatial frequencies were employed (0.2, 0.4, 0.8, 1.6, and 3.2 c/deg) and their size was varied to allow the presentation of just one period of each grating. Thus the diameter of the stimuli were 5°, 2.5°, 1.25°, 0.625° and 0.3125° respectively. Control of the number of cycles present is important because increasing the number of cycles of a grating improves sensitivity via spatial summation (Findlay, 1969; Estevez & Cavonius, 1976; Howell & Hess, 1978; Robson & Graham, 1981).

Thus if the stimuli are of a constant size, spuriously high measures of sensitivity will be obtained for high spatial frequencies. Since the intention was to present stimuli which were smaller than the region corresponding to the blind spot (RCBS), the size of the largest stimulus was restricted to 5°. This limited the lowest spatial frequency that could be tested to 0.2c/deg.

Contrast sensitivity measurements

Contrast sensitivity was defined as the reciprocal of the contrast threshold where contrast is defined as:

$$C = \frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}} \tag{2.1}$$

where $L_{\max}$ is the maximum luminance of the grating and $L_{\min}$ is the minimum luminance of the grating.

Contrast thresholds were measured in blocks, each block providing one threshold estimate for a single spatial frequency and retinal position. The order of presentation of the blocks for each subject was always counterbalanced. Each block comprised either 50 or 60 trials and yielded one threshold estimate. Each trial consisted of two time slots indicated by different tones, separated by a temporal interval of 1 second. The subject had to indicate, by pressing one of two buttons, the time slot in which the stimulus appeared. A maximum of 5 seconds was allowed in which to make a response but in practice the time required was much less. The response terminated the end of the trial and triggered the onset of the next. The contrast of the stimulus at the beginning of each block was always well above threshold. For each correct response, the contrast was multiplied by 0.85 so that the amount by which the contrast was reduced became progressively smaller as threshold was approached. A correct response followed by an incorrect response was defined as a reversal and produced a doubling of contrast. Each block typically yielded 6 reversals and the contrast threshold was calculated as the mean of the log contrasts at reversal. The experimenter was able to continuously monitor the subject's response to each contrast. This meant that when subjects made a mistake i.e.

produced a reversal that was clearly above threshold, the block could be restarted. Thus contrast thresholds were not overestimated by the inclusion of one or two atypical values at reversal. Every subject was tested twice for each spatial frequency and visual field position so the raw data was the mean of two thresholds. All subjects were allowed to practice the psychophysical procedure before data collection commenced and were able to take breaks between blocks if desired.

Blind spot mapping

The observed size and location of the blind spot varies according to how it is measured. It depends on the target size, direction of target motion into or out of the blind spot and the level of luminance. Indeed it is possible to obtain above zero measures of sensitivity in the blind spot if a target of sufficient size and luminance is used. This arises either because the stimulus directly stimulates receptors on the edge of the blind spot or gives rise to sufficient scattered light to be detected indirectly. It has been argued that while the proximal edge is little influenced by the above factors, the distal edge may easily vary between 2-3° (Wolf & Zigler, 1959). With this in mind, the blind spot was mapped using a small circular spot 0.5° in diameter, the spot itself was black on a light background to minimise scattered light effects, and measurements of the boundaries were based on movements both into and out of the blind spot.

The subject was informed of the aim of this procedure and told they would be required to indicate the presence or absence of a small dot, which would be moved through their blind spot. They were also made aware of Troxler's fading phenomenon and advised to move their eyes away from the fixation point every few seconds to refresh the image. However, it was emphasised that all judgements of visibility must be based on what could be seen when fixating the centre of the fixation cross.

PSYCHO's position co-ordinates are specified in terms of an eccentricity and meridional angle in relation to the screen centre. The experimenter positioned a dark fixation cross (0.5° diameter) at the left of the screen and moved the small black dot in steps of 0.5° out from the screen centre along a meridian which on average would intersect the centre of the blind spot. The subject was required to indicate when the spot disappeared and reappeared. The spot was moved several times both backwards and forwards over these boundaries to ensure they were accurately located. If there were locations where the spot could be only partially seen, then the midpoint of these locations was taken as the boundary. Next, the experimenter varied the meridional angle of the dot keeping the eccentricity constant (at a value midway between that of the first boundaries). Again the boundaries of the blind spot on these axes was recorded. The measurements were translated into linear co-ordinates and the boundaries plotted on squared paper. To find the centre, it was first assumed that the blind spot is circular. Then any two pairs of different boundary points were chosen and each pair was connected by a straight line. The centre of that line was found and another line drawn perpendicular to the original line. The point of intersection of lines perpendicular to the original ones gave the centre of the circle that would fit these boundary points.

RESULTS

Blind spot centres

The central location of each subject's blind spot is shown in Table 2.1. This shows that on average, the centre of the blind spot was horizontally located approximately 16° eccentric from the fovea and vertically displaced below the horizontal meridian by almost half a degree. The variability in the location of the central region of the blind spot, as indicated by the standard deviation, was quite small; just over a degree horizontally and slightly less than a degree vertically.

Subject	Distance along horizontal meridian (degrees)	Distance above/below horizontal meridian (degrees)
CF	17.8	- 1.6
JT	17.4	- 0.4
AH	14.6	+0.9
KF	16.2	+0.2
HS	15.2	- 0.2
CH	13.8	- 0.8
DH	16.4	- 0.4
VV	16.6	0.0
JF	17.8	- 0.2
CM	16.0	-1.6
Mean	16.2	-0.4
SD	1.3	0.73

Table 2.1. Blind spot centres for 10 subjects given in terms of horizontal eccentricity and vertical displacement. Positive numbers indicate displacement above the horizontal meridian.

To check the accuracy with which this procedure had located the centre of the blind spot, a large stimulus was presented to the measured centre, to see if it was visible to the subject. The stimulus used was a circular (5° diameter) and sinusoidal grating patch of 0.8 c/deg, 30% contrast and 1 Hz counterphase reversal. The subject was asked to indicate whether the stimulus was visible when fixating the centre of the fixation cross. By trial and error, the experimenter varied the position and size of the stimulus so that the subject could not see it. The results of this procedure are shown in Table 2.2 for the five subjects who participated in this procedure. It may be seen by comparison with Table 2.1 that the difference between the first and second measurements is quite small. The size of the largest discrepancy in the central point of the blind spot was just over a degree horizontally and just under a degree vertically. Thus the blind spot can be mapped quite consistently.

Subject	Horizontal eccentricity (degrees)	Vertical displacement above/below horizontal meridian (degrees)	Size of target invisible when located in the blind spot (degrees)
AH	14.8	+ 0.8	5.0
VV	16.1	0.0	5.2
DH	17.5	- 1.0	5.0
CM	16.7	- 0.8	5.0
JT	16.9	- 0.6	4.8

Table 2.2. Central locations of the blind spot and sizes of target which were invisible when located in the blind spot

Monocular contrast sensitivity in the RCBS and control regions

Contrast sensitivity measurements were taken monocularly for 10 subjects in the region corresponding to the blind spot (RCBS) and at a control point at the same eccentricity along a meridian 45° above. The results are summarised in Figure 2.1. A two-way repeated measures ANOVA was performed using Retinal Position and Spatial Frequency as Factors. The dependent variable used in all the inferential analyses presented in this chapter was log contrast sensitivity. This ensured the data were normally distributed. Not surprisingly there was a highly significant main effect of spatial frequency (epsilon corrected F = 326.56, df = 2,16, P < 0.01) reflecting the inverse relationship between spatial frequency and contrast sensitivity. Contrast sensitivity was also found to be significantly higher in the RCBS than in the control region (F = 53.23, df = 1,9, P < 0.01), with a mean contrast sensitivity in these areas of 28.0 (SE = 8.65) and 19.2 (SE = 6.42) respectively. This effect did not depend on the spatial frequency tested and thus there was no significant interaction between retinal position and spatial frequency (F = 1.48, df = 4,36, P > 0.05). The highest contrast sensitivity was found at the lowest spatial frequency (0.2 c/deg) which in the RCBS was 52.0 (SE = 8.01) compared with 36.3 (SE = 4.88) in the control region. The lowest contrast sensitivity was found at the highest spatial frequency (3.2c/deg) which was 5.65

(SE = 0.75) and 3.1 (SE = 0.51) for the RCBS and control areas respectively. Thus it appears that acuity is higher in the RCBS.

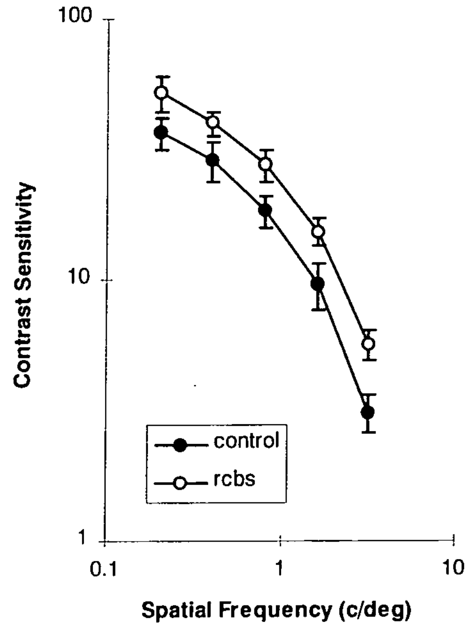


Figure 2.1. Monocular contrast sensitivity in the RCBS and a region at the same eccentricity on a meridian 45 above it. Each datum is the mean of 10 subjects' measurements (in this and all following investigations, each subject's measurement was the mean of two threshold estimates). Subjects = CF, JT, AH, KF, HS, CH, DH, JF, VM & CM. All error bars shown in the graphs in this chapter represent +/- 1 S.E of the mean.

Expected contrast sensitivity values

It is important to show that the increase in sensitivity in the RCBS cannot be attributed to regional variation in contrast sensitivity across the visual field. Specifically, the effect would be more convincing if it could be shown that sensitivity in the RCBS is significantly higher than expected given the known decline in contrast sensitivity away from the fovea.

It has been shown that under photopic conditions, contrast sensitivity (on logarithmic axes) is maximal at the fovea (for all spatial frequencies tested) and declines linearly across the visual field when plotted against eccentricity scaled by the spatial frequency of the stimulus (Pointer & Hess, 1989; Pointer & Hess, 1990). Hess and Pointer found that there were just three gradient values which described the decline in contrast sensitivity for high (>1c/deg), medium and low (<0.2 c/deg) spatial frequencies and that the value of the gradient depended on the meridian tested. The decline in contrast sensitivity along the vertical meridian was found to be significantly greater than that observed along the horizontal meridian. However, the decline along the nasal and temporal horizontal hemi-meridians did not differ significantly from each other, or from the decline observed along any of the four major oblique meridians.

The existence of rules governing the decline in contrast sensitivity indicates it is possible to calculate an expected value for any eccentricity along any of the principal or oblique meridians, given a measurement at the fovea. Specifically, if it could be shown that the measurement in the control region accords with Hess & Pointer's rules while that in the RCBS does not, it would provide additional evidence that the RCBS is hypersensitive. To see how the contrast sensitivity measurements obtained above compared with expected values, foveal contrast sensitivity measurements were made for 5 of the subjects tested previously. These measures were obtained under the same testing conditions as above and used to calculate the sensitivity that would be expected in the region corresponding to the blind spot and control region for each spatial frequency.

The logarithmic scaling function described by Hess and Pointer implies that the expected contrast sensitivity, *ex,* can be calculated using the following equation (using the gradient values supplied in their papers).

$$ex = 10^{(f - fgse)} \tag{2.2}$$

where f is the log contrast sensitivity observed at the fovea, g is the gradient, s is the spatial frequency and e is the eccentricity of the expected value. The value of g depends on the spatial frequency and meridian tested. Along the horizontal/oblique meridians: at spatial frequencies >1 c/deg, g = 0.0165/log contrast sensitivity; at spatial frequencies 0.2-0.8 c/deg, g = 0.0335/log contrast sensitivity.

The observed contrast sensitivity measures at the fovea have been plotted in Figure 2.2 together with the data from Figure 2.1 to enable a comparison. It may be noted that sensitivity in the RCBS is actually higher than that observed in the fovea for 0.2 c/deg. Figure 2.3 shows the contrast sensitivity observed in the control region together with the sensitivity which might be expected in the RCBS given the sensitivity observed at the fovea. It is apparent that these two sets of data are almost identical. However, a repeated measures ANOVA on the log contrast sensitivity measurements revealed a significant interaction between spatial frequency and the observed and expected values ($F = 198.59$, $df = 4,16$ $p < 0.01$). A post hoc comparison of means revealed that this interaction was due to the fact that the expected value at 3.2 c/deg was significantly lower ($p < 0.01$) than the observed value at this spatial frequency. However, in general, the data from the control region closely agree with the expected values. Showing that the measurements in the control region agree with those predicted from measures at the fovea, provides further support for the notion that sensitivity is higher in the RCBS than expected for its position in the visual field. In Figure 2.4, the same expected contrast sensitivity values are plotted against those obtained in the RCBS for comparison. It is clear that sensitivity in the RCBS is higher than expected.

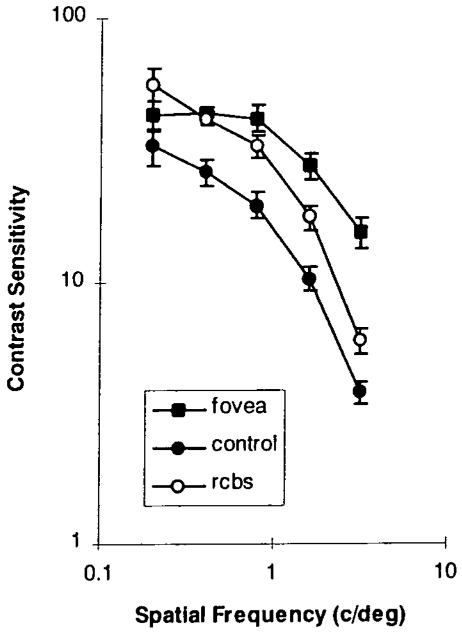


Figure 2.2. Monocular contrast sensitivity of the RCBS and control region (obtained previously) and the fovea. All data shown are from the same 5 subjects (AH, CM, DH, JT & VM).

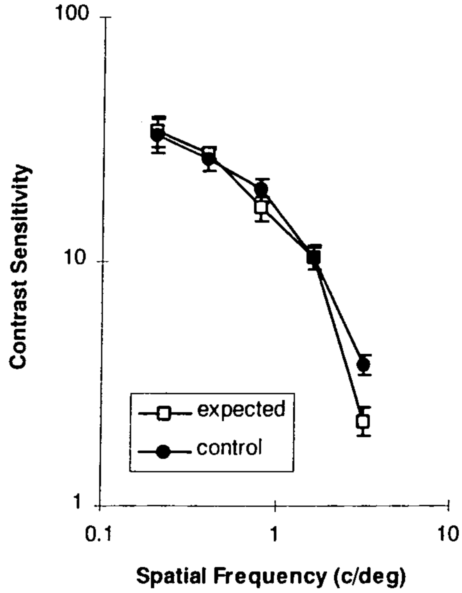


Figure 2.3. Expected monocular contrast sensitivity (derived from foveal measurements using equation 2.1) plotted against data from the control region for comparison. All data shown are from the same 5 subjects (AH, CM, DH, JT, VM). Each expected value is the mean of the individual expected values.

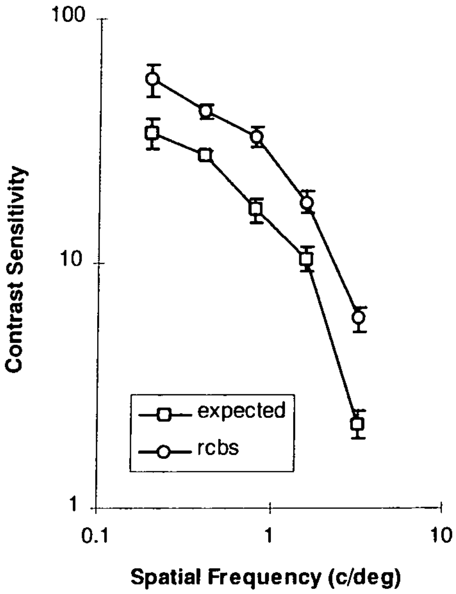


Figure 2.4. The expected monocular contrast sensitivity shown in Figure 2.3 plotted against data obtained previously for the RCBS. All data shown are from the same 5 subjects (AH, CM, DH, JT, VM).

Using the inverse of the above procedure, it is also possible to calculate the eccentricity, *e*, at which one would expect to observe the contrast sensitivity actually gained in the RCBS. This was calculated using the following equation:

$$e = \frac{(f - o)/g}{s} \tag{2.3}$$

where f is the log contrast sensitivity at the fovea, o is the observed log contrast sensitivity, g is the slope gradient and s is the spatial frequency. These values are shown in Table 2.3.

Spatial Frequency (c/deg)	Eccentricity (degrees)
0.2	better than fovea
0.4	1.74
0.8	4.06
1.6	7.29
3.2	7.87

Table 2.3. The eccentricity at which one would expect to obtain the sensitivity actually observed in RCBS given similar measurements at the fovea.

Comparison with normal binocular measures

Binocular measures of contrast sensitivity were taken for 5 subjects in the control region to see how these compared to the contrast sensitivity of the RCBS. These measures are given in Figure 2.5. In general, the contrast sensitivity of the RCBS equals that of the control region tested binocularly. A repeated measures ANOVA on log contrast sensitivity revealed no significant difference between sensitivity in the RCBS and measures obtained binocularly in the control region ($F = 0.46$, $df = 1,4$, $P > 0.05$). As expected there was a significant effect of spatial frequency ($F = 364.07$, $df = 4,16$, $P < 0.01$) but no significant interaction ($F = 1.75$, $df = 4,16$, $P > 0.05$).

The ratios of improvement from monocular to binocular viewing were 1.564, 1.968, 1.798, 1.624 and 1.272 for the spatial frequencies 0.2-3.2 c/deg respectively. This yields a mean improvement of 1.65 (SE = 0.105). This value is slightly higher than the improvement seen by Campbell & Green (1965) who reported a reduction in contrast thresholds for binocular viewing by a factor of 1.4 (that did not depend on spatial frequency) and Legge (1984) who reported a decrease in contrast thresholds for binocular viewing of 1.5. However, since contrast thresholds decrease with practice, the increase in binocular over monocular sensitivity observed here may be slightly exaggerated.

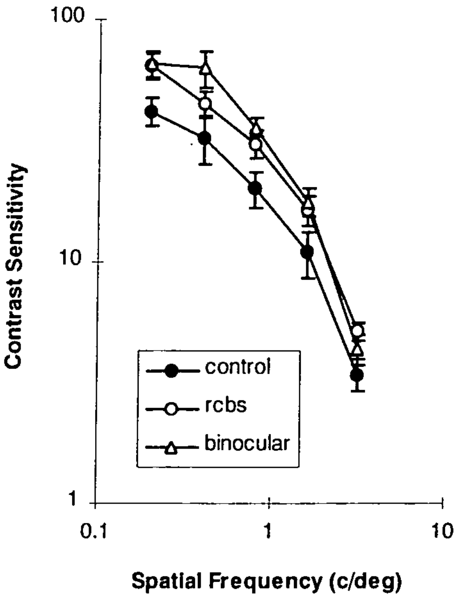


Figure 2.5. Binocular contrast sensitivity measurements for the control region plotted against data obtained monocularly for the control region and RCBS. All data were taken from the same 5 subjects (JT, CH, CM, VV & HS).

Contrast sensitivity along the arc intersecting the RCBS

Contrast sensitivity measurements were taken for 5 subjects along an arc, which intersected the centre of the RCBS, using a single stimulus 5° in diameter and a spatial frequency of 0.2 c/deg. The outcome of this investigation is shown in Figure 2.6. Zero on the abscissa is the centre of the RCBS. The two measurements on either side of this point (on average +/- 11°) were centred on the boundary of the RCBS while the two measurements beyond this (on average +/- 22°) were located just outside the RCBS. All points sampled were at the same eccentricity.

There is some indication of an increase in sensitivity in the RCBS. However as shown in the graph, the measurements for the RCBS are actually lower (mean = 51.7, SE = 2.76) than those obtained in this region at 0.2 c/deg for the same five subjects in the original experiment (mean = 64.55, SE = 4.86). This serves to reduce the observed difference in sensitivity between the area homonymous to the blind spot and surrounding regions of a similar eccentricity. A one way repeated measures ANOVA revealed that the log contrast sensitivity was not significantly different in any of the positions tested (F = 1.8, df = 4,16, P > 0.05). Note that the data from the previous run (open symbols) were not included in the analysis.

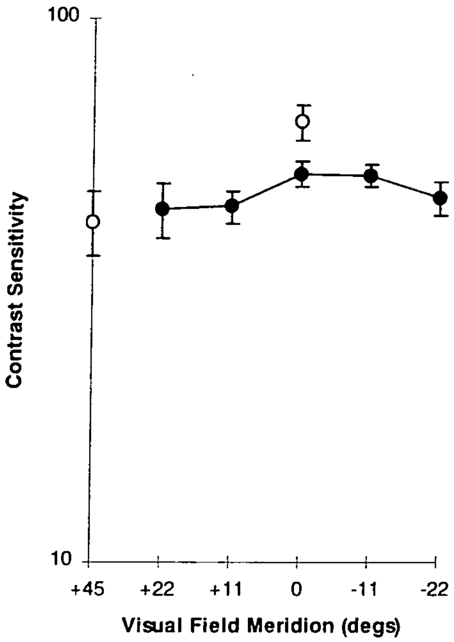


Figure 2.6. Contrast sensitivity along an arc intersecting the RCBS. Zero represents the centre of the RCBS. Positive meridianal angles are positions above the RCBS. The open symbols are taken from results obtained previously using the same five subjects (JT, CH, CM, VV & HS).

Contrast sensitivity along the meridian intersecting the RCBS

In the final investigation, contrast sensitivity was examined along the meridian passing through the centre of the blind spot so that measurements were taken at a constant eccentricity from the fovea. This rules out an explanation of the effect based on the radial organisation of the visual lobe which describes the superiority in motion detection and the resolution of gratings when the motion of stimuli or the orientation of the grating is aligned with a meridian passing through the fovea (Rovamo et al, 1982). Since the gratings in this study were horizontal, this could have produced spuriously high measures in the RCBS. Comparing sensitivity in the RCBS to a position closer to the fovea provides a measure of hypersensitivity not affected by the radial organisation of the visual lobe. Before taking contrast sensitivity measurements, the locus of the blind spot was checked. All 6 subjects who participated were unable to detect a 5° diameter target of 30% contrast flickering at 1Hz counterphase when presented to their blind spot. As a further control for any spatial nonlinearity of the monitor, the stimulus was always presented to the same screen location and eccentricity was varied by moving the fixation point. The stimulus used was a grating of a single period with a spatial frequency of 0.2 c/deg.

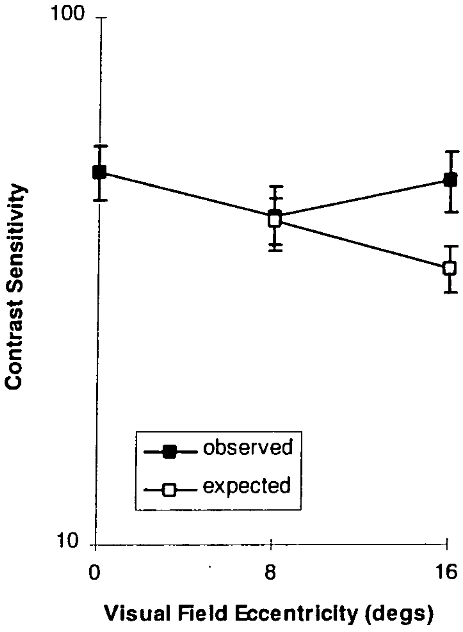


Figure 2.7. Contrast sensitivity measurements taken at the fovea, 8° eccentric and the RCBS (mean eccentricity = 16°). The expected values were calculated from the observed sensitivity at the fovea using equation 2.2. Data from 6 Subjects (BY, AH, JT, CM, JF, DH).

It is apparent from Figure 2.7 that the contrast sensitivity observed at 8 degrees eccentric is almost identical to that which might be expected given the known decline in sensitivity under photopic conditions. However, contrast sensitivity in the RCBS was significantly higher than expected ($F = 22.98$, $df = 1,5$, $P < 0.01$). This represents an increase in sensitivity for the homonymous region (mean = 49.01, SE = 6.5) over the expected sensitivity (mean = 33.30, SE = 3.31) by a factor of 1.471.

DISCUSSION

Summary of results

The main finding of this chapter was that the contrast sensitivity of the region corresponding to the blind spot (which lies in the nasal visual field) is higher than that observed monocularly at the same eccentricity along a meridian in the upper nasal field 45° above. The possibility that this is merely due to normal regional variation in contrast sensitivity across the visual field was ruled out by demonstrating that the contrast sensitivity of the control region was congruent with that expected for its position in the visual field while sensitivity in the region corresponding to the blind spot was higher than expected. The magnitude of the supersensitivity was shown to be equivalent to binocular measures in the control region. While the size of the effect appeared to be equal for all spatial frequencies tested, it may be that the stimuli employed contained too few cycles to detect any possible spatial frequency difference.

Measurement of contrast sensitivity along an arc passing through the centre of the region corresponding to the blind spot failed to demonstrate a discontinuity in sensitivity but this may be because the supersensitive area extends beyond this region. Also the stimuli used were large (5° diameter) and hence would have stimulated very large overlapping receptive fields thereby not providing a particularly localised measure of sensitivity. Finally it was shown that the contrast sensitivity in the region homonymous to the blind spot was higher than expected based on values taken along the horizontal meridian. Taken together, these results suggest that the region corresponding to the blind spot can support a contrast sensitivity, which is equal to binocular viewing.

Comparison with other studies

The results of this study are consistent with those which have looked at scotopic luminance thresholds in the peripheral visual field. In one study it was noted that when thresholds were measured along the horizontal meridian and along a parallel line 1.5° below, there appeared to be a dip in thresholds in the nasal portion of the visual field corresponding to the location of the blind spot in the other eye (Wolf & Zigler, 1959). This was confirmed in a subsequent study in which thresholds were measured monocularly for six observers on one vertical and three horizontal lines running through the region corresponding to the blind spot (Wolf & Gardner, 1963). The test field was a square, 1° wide which was presented for 40 msecs. Thresholds were found to be lower in the region corresponding to the blind spot compared with adjacent retinal regions, yielding a mean increase in sensitivity of 0.25 log units (a factor of 1.8). The increase in sensitivity extended over an area which was wider than the optic disk itself both horizontally and vertically. This is consistent with the failure of this study to demonstrate an increase in contrast sensitivity when large targets were used to map sensitivity along an arc through the region corresponding to the blind spot.

However, there is another study which has failed to find an advantage for the region corresponding to the blind spot (Westheimer, 1982). This investigation compared monocular hyperacuity thresholds for an area just inside the area homonymous to the blind spot in the left eye with a position closer to the fovea just outside. When thresholds were measured for the detection of the tilt of a line away from vertical, they were found to be lower for the more fovealward measurement by a factor that could be accounted for by the smaller eccentricity. The spatial integration area of hyperacuity processing was also estimated by measuring thresholds for the vertical alignment of two small squares as a function of their separation. The shapes of the resulting functions were the same for the two locations and again the difference in thresholds was consistent with the difference in eccentricity. Vernier acuity thresholds are lower for binocular viewing by a factor equal to $\sqrt{2}$ (Freeman & Bradley, 1982) an observation which is inconsistent with the argument that the region corresponding to the blind spot has an effective binocular sensitivity. However, the mechanisms underlying contrast sensitivity and hyperacuity are almost certainly different and this could underlie the lack of a hyperacuity advantage for the region corresponding to the blind spot. Whereas contrast sensitivity may be based on a mechanism that summates information over a population of detectors, hyperacuity seems to be based on a mechanism that interpolates the position of stimuli. Hyperacuity thresholds are much smaller than the upper limit for acuity predicted by the spacing of the photoreceptors on the retina. If it is assumed that the point spread function is sufficiently broad for several receptors to be stimulated simultaneously, then differencing the outputs of these receptors could derive the position of a stimulus. This would allow the resolution of differences smaller than the spacing of receptors in the retinal mosaic (DeValois & DeValois, 1990).

Is the number of cortical detectors increased?

Since the region corresponding to the blind spot is monocular, during development of the visual nervous system this region has no competition from the other eye. Hence one might expect the ipsilateral eye to expand its connections into the cortical area that corresponds topographically to the blind spot in the contralateral eye. According to LeVay (cited in Westheimer, 1982), the area in monkey visual cortex devoted to the visual field containing the blind spot is about what may be expected if both eyes projected to it. That is, twice as much cortical surface is available to one eye per unit area of the visual field as in the adjoining field where its ocular dominance columns must share the cortical surface area with those of the other eye. Moreover, in the striate cortex of the monkey, the cytochrome oxidase patches observed in the optic disk representation are larger and rounder than patches in adjacent binocular cortex (Horton, 1984). In addition, the density of the patches in the optic disk representation is slightly more than half the density of patches in surrounding binocular cortex. These changes in the cortical representation of the blind spot suggest there may be more cells available to mediate detection under monocular viewing conditions compared with binocular cortex.

On statistical grounds it could be argued that possessing twice as many cells doubles the opportunity for detecting a stimulus, assuming these cells operate independently of each other. This notion of probability summation has been discussed in relation to both binocular (for review see Blake & Fox, 1973; Blake et al., 1981) and spatial summation (Howell & Hess, 1978; Robson & Graham, 1981). To look at predictions made on the basis of probability summation it is useful to assume that doubling the number of cortical cells available for detection is equivalent to the improvement gained from possessing two eyes over one. The probability summation model holds that in binocular viewing, the two eyes act as independent detectors, each with a threshold. The stimulus is detected if either one or both thresholds is exceeded. If neither monocular threshold is exceeded when the stimulus is presented in a forced choice trial, the observer is forced to guess. Assuming equal sensitivities for the two eyes, the following relationship exists between the monocular proportion correct P_M and the binocular proportion correct P_B for two alternative forced choice.

$$P_B = 1 - 2(1 - P_M)^2 \tag{2.4}$$

It should be noted that this equation relates monocular and binocular probabilities or d'[3] values and says nothing about the relation between d' and contrast for monocular viewing (Legge, 1984). Unfortunately, d' values are not available for the data from this study. It is possible however, to make predictions about contrast thresholds, based on other studies of the relation between contrast and d'. The relationship between these two parameters approximates a straight line when expressed on log-log axes and has been found by several authors to have a slope of about 2 (Foley & Legge, 1981; Rubin, 1983; Legge, 1984). This means that d' is directly proportional to squared contrast. According to Legge (1984), applying this assumption to the above equation leads to a predicted monocular/binocular ratio of about 1.3. This is clearly lower than the ratio of expected to observed contrast thresholds reported here which is 0.0300/0.0204 = 1.471. Therefore this formulation of probability summation cannot fully account either for the increase in

---

[3] d' is a signal detection parameter which refers to detectability. It is given by the difference between the observers response to the mean of the noise distribution and the mean of the signal plus noise distribution in units of the standard deviation of the noise distribution. In 2AFC experiments, sensitivity is indexed by percentage correct *P(c)*. d' is related to *P(c)* in the following way

$$d' = \sqrt{2}z(c)$$

using normal curve tables to find the z-score, *z(c)* , above which the area *P(c)* lies (see p64 (McNicol, 1972).

performance observed in the region corresponding to the blind spot, or for the superiority of binocular over monocular viewing which is also greater than 1.3 (Campbell & Green, 1965).

Calculations based on signal detection theory lead to even lower estimates of expected improvement. This view asserts that information processed by each detector can be thought of as a signal in a noisy channel. The standard error of the sum of these signals is reduced by the square root of the number of channels. Thus doubling the number of cortical cells available to mediate detection might be expected to produce a $\sqrt{2} = 1.414$ increase in detectability (assuming that d' is limited by noise in the nervous system rather than external noise). If d' is proportional to squared contrast, a $\sqrt{2}$ increase in d' predicts a reduction in contrast thresholds of just $2^{1/4} = 1.189$. Thus a simple consideration of doubling the number of detectors available based on either probability summation or signal detection theory cannot fully explain the observed increase in contrast sensitivity in the region corresponding to the blind spot.

Release from interocular suppression?

Another theory of binocular contrast sensitivity relevant to this discussion asserts that the superiority of binocular over monocular viewing arises not from probability summation or physiological summation but from a release of tonic interocular suppression. This view is based on experiments in which monocular contrast sensitivity was measured while the contralateral eye was adapted to large homogenous fields with different luminance values (Denny et al., 1991). It was found that luminance adaptation (>1 cd/m^2) in the contralateral eye produced an increase in contrast sensitivity (for spatial frequencies > 2c/deg) compared to when the contralateral eye was dark adapted. An adapting field presented to the same eye as the test grating, or presented binocularly was ineffective. Whether the effect was due to a release of inhibition was examined by pressure blinding the non-tested eye. Pressure blinding removes the blood supply to the retinal ganglion cells hence removing their signal to the brain. By pressure blinding the non-tested eye it was possible to make a subthreshold grating visible, suggesting that with monocular viewing, a dark-adapted eye tonically suppresses vision in the contralateral eye. Moreover, the contrast sensitivity of binocular viewing was almost identical to that produced by combining monocular viewing with interocular light adaptation suggesting that the improvement seen in two-eyed viewing may be attributable to the removal of tonic interocular suppression. Finally, luminance adaptation in the non-tested eye has been shown to increase the amplitude of visually evoked potentials indicating that the interocular adaptation effect is present at the level of the cortex (Eysteinsson et al., 1993).

Presumably the region corresponding to the blind spot is not subject to tonic interocular inhibition and it is this which accounts for its equivalence to binocular contrast sensitivity. To account for the data presented here, which showed an increase in contrast sensitivity over a wide range of spatial frequencies (0.2-3.2c/deg), the effect must operate at low spatial frequencies. Data on tonic interocular suppression at spatial frequencies less than 1 c/deg has not been published. This theory predicts that the increase in contrast sensitivity in the region corresponding to the blind spot ought to disappear if the luminance of the non-tested eye is sufficiently increased. It also suggests that monocular contrast sensitivity should differ according to whether the non-tested eye is covered by an opaque occluder or one that is translucent. However, authors who have examined this have concluded that it makes no difference whether no light or a diffuse light enters the non-viewing eye (Campbell & Green, 1965). This observation is difficult to reconcile with the contention that monocular contrast sensitivity depends on the luminance adaptation state of the non-tested eye.

A similar but physiologically based argument has been offered to account for the superior contrast sensitivity of monocular humans, which at their peak spatial frequency was even higher than control subjects tested binocularly (Nicholas et al., 1996) This explanation is based on the view that cells in binocular cortex are subject to interocular suppression which underlies their ocular dominance. This interocular inhibition may be mediated by GABA since in the cat, application of the GABA antagonist bicuculine results in an increase in responsiveness by the non dominant eye (Sillito et al, 1980). It can be argued that an absence of interocular inhibition in monocular humans or in the cortical representation of the region corresponding to the blind spot could lower the threshold firing rate for cells resulting in lower detection thresholds. It remains to be seen whether pharmacological removal of interocular inhibition results in increased perceptual sensitivity.

If normal monocular contrast sensitivity is limited by interocular inhibition then one might expect observers who lack normal binocular interactions to have a monocular contrast sensitivity equal to that obtained binocularly in normal observers. It has been claimed that individuals who lack stereopsis have fewer binocular neurons. It therefore seems logical that their perceptual sensitivity would not be restricted by interocular suppression. In a study which examined luminance detection, non-amblyopic stereoblind observers were found to lack normal binocular summation; the observed summation could be accounted for by probability summation (Westendorf, 1978). This finding has been replicated by other authors (Lema & Blake, 1977; Levi et al., 1979). However, there was no evidence that their monocular sensitivity was as good as the binocular sensitivity of the normal subjects (Westendorf, 1978).

The Sprague effect

A further explanation for hypersensitivity in the region corresponding to the blind spot concerns possible interhemispheric interactions. Before looking at how this relates to the region corresponding to the blind spot, it is necessary to examine the evidence for the interhemispheric interactions known as the Sprague effect.

Sprague (1966) demonstrated that in a cat rendered hemianopic by an occipito-temporal lesion, vision is restored by removal of the contralateral superior colliculus or section of the tectal commissure. Others have replicated this finding in both rats and cats (Goodale 1973; Sherman 1974; Sherman 1977). It has been argued this is due in part, to reciprocal inhibitory connections between the two colliculi. A unilateral cortical lesion produces a loss of facilitation in the ipsilateral colliculus (via a descending cortico-tectal pathway) and a consequent loss of inhibition in the contralateral colliculus. Vision is restored when this colliculus is removed because the colliculus ipsilateral to the lesion is released from inhibition. What is the anatomical and physiological evidence for tecto-tectal and cortico-tectal projections?

Evidence from field analysis and extracellular unit recordings suggests that the connections between the two colliculi are inhibitory (Maeda et al., 1979; Fish & Rhoades, 1981; Moshovakis & Karabelas, 1982) and that they are roughly organised in a point-to-point fashion. The origin of the inhibitory commisural projection is not clear since the tectal commisure contains a multitude of fibres, some of which originate in the pars reticulata of the substantia nigra. Consistent with this, the Sprague effect can also be obtained by destruction of the contralateral substantia nigra (Wallace & Rosenquist, 1986). In terms of cortico-tectal projections, in the monkey, ablation or reversible cooling of visual cortex renders single cells in the deeper layers of the tectum unresponsive to visual stimulation (Schiller et al., 1974) and on the basis of studies of the receptive field properties of cortico-tectal cells, Finlay (1976) concluded that the cortical input to the superior colliculus has a gating function in contributing to the control of the excitation from the superficial to the deep layers of the colliculus. Thus the anatomical and physiological evidence is consistent with the Sprague effect.

Several behavioural demonstrations in humans of interhemispheric interactions have been interpreted terms of the Sprague effect (Pöppel & Richards, 1974; Zihl et. al., 1979; Holtzman, 1984). For example, it has been suggested that visual orienting depends at least in part on interactions between cortical and subcortical areas (Holtzman, 1984). This notion is based on a study of two patients who had undergone surgical transection of the corpus callosum for the control of intractable epilepsy. Their ability to make saccades to a target whose location was cued by a stimulus in the opposite hemifield was examined. The split brain patients could saccade to the target with only a small decrement in performance suggesting they were able to integrate visual information between the two hemifields. Moreover, it was argued that the result could not be attributed to collicular vision per se unmediated by occipital cortex because a patient with unilateral occipital damage was unable to localise targets in her hemianopic field despite intact superior colliculi. It was concluded that these findings reflect interactions between cortical and subcortical areas in humans.

Further evidence for such interactions comes from a study of two hemianopic patients, in which there were islands of residual vision in a large scotoma which were located in a mirror image position to a small scotoma in the contralateral hemi-field (Pöppel &

Richards, 1974). This effect was explained in terms of inhibitory interactions between the two colliculi and facilitatory cortico-tectal and tecto-cortical pathways. It also suggested that the tecto-tectal connections were organised in a mirror symmetric fashion.

In normal observers, mirror symmetrical effects have been observed for visual adaptation and the resetting of thresholds (Zihl & Von Cramon, 1979a; Zihl & Von Cramon, 1979b; Zihl et al., 1979). Repeated measurements of decremental light thresholds for localised stimuli at 30° eccentricity lead to an increase in threshold by as much as 0.5 log units. This adaptation shows almost complete interocular transfer demonstrating it is centrally mediated. Measurement of thresholds mirror symmetric to the adapted area (either in the same or contralateral eye) produced a resetting of threshold to its original preadaptation level or even lower. Such a resetting did not occur when thresholds were determined in non-symmetric areas. This adaptation was explained in terms of intertectal inhibition. A functional lesion in one area may result in the facilitation of a group of neurons in the other tectum sub-serving the previously adapted area. Further evidence that adaptation is mediated by a subcortical pathway is given by the observation that adaptation produced in the sighted field of a hemianope could be reset by stimulation in the unsighted hemifield (Zihl et. al., 1979). Moreover, in a patient with a congenital malformation of the right superior colliculus, neither adaptation or resetting of thresholds could be achieved in the contralateral visual field. Together this evidence suggests that interhemispheric interactions can occur in normal observers, that they can be mediated by a subcortical pathway and that the connections are organised in a mirror symmetric fashion.

Can an explanation based on these interhemispheric interactions explain the increase in contrast sensitivity in the region corresponding to the blind spot? The Sprague effect predicts that the blind spot in one hemifield, disinhibits the collicular representation of the homonymous region of the visual field which in turn produces facilitation via a backward projection to the cortex. Empirical support that this could occur was provided by one of Pöppel & Richard's patients who was able to detect a moving stimulus in a scotoma in a position mirror symmetric to the blind spot. However, it is important to note that this explanation is mutually exclusive with the above suggestion that the cortical representation of the blind spot can support a contrast sensitivity that is effectively binocular. Presumably if striate cortex fully compensated for its monocularity it would not produce a loss of facilitation in the ipsilateral colliculus and there would be no corresponding release from inhibition for the homonymous region.

3

Contrast Sensitivity in the Sighted and Blind Hemifields of a hemianope

ABSTRACT

The region corresponding to the blind spot has a contrast sensitivity that is effectively binocular. To shed light on the underlying neurological substrate, predictions were made concerning the contrast sensitivity of the sighted and blind hemifields of a hemianope (GY). The contrast sensitivity of the region corresponding to the blind spot was measured together with control regions closer (8°) and further (24°) from the fovea. The control regions were sampled both temporally and nasally in the sighted and blind hemifields. In the sighted hemifield, there was no evidence of an increase in sensitivity in the region corresponding to the blind spot but contrast sensitivity was at the high end of the range of values observed in normal control subjects, especially at 8° eccentric where GY scored at the 95th percentile. This opposes the results of Hess & Pointer (1989) who found a deficit in contrast sensitivity in the sighted hemifield of three hemianopes including GY. Consistent with other findings, there was evidence of residual vision in the blind hemifield. However, there was no evidence that this was localised to, or increased in the region corresponding to the blind spot. Thus this study did not replicate Pöppel & Richards (1974) finding of an area of increased sensitivity in a scotoma contralateral to the blind spot.

INTRODUCTION

In Chapter 2 it was shown that the region corresponding to the blind spot in the other eye can support a monocular contrast sensitivity which is equivalent to binocular viewing. In the discussion of the previous chapter, several mechanisms were proposed to account for this increase in sensitivity. These mechanisms included probability summation, which is based on the notion that in the cortical representation of the region corresponding to the blind spot, there are twice as many cells available to mediate detection compared to adjacent areas of the visual field where the input must be shared between two eyes (LeVay cited in Westheimer, 1982). A further cortical mechanism is release from interocular suppression which asserts that sensitivity may be increased because cells in the cortical representation of the blind spot are monocular and not subject to the interocular suppression that underlies ocular dominance (Kennedy et al., 1975; Kennedy et al.,1976; Horton, 1984). These two explanations are not mutually exclusive. Not only may there be more cells available to mediate detection via probability summation, but the threshold firing rates of the cells themselves may be lower because they are not subject to interocular inhibition. Thus probability summation or release from interocular suppression or both may be responsible for the increase in sensitivity in the region corresponding to the blind spot.

For the purpose of this chapter, these two explanations, which occur solely at the level of the cortex, will be referred to as 'cortical' explanations. They may be contrasted with the Sprague hypothesis, which accounts for the monocular hypersensitivity of the region corresponding to the blind spot in terms of inhibitory tecto-tectal and facilitatory cortico-tectal and tecto-cortical connections. The Sprague hypothesis will be referred to as a 'subcortical' explanation. Using this dichotomy, the aim of this study was to obtain evidence to rule out either the 'cortical' or 'subcortical' explanation for the increase in sensitivity in the region corresponding to the blind spot in normal observers. This entailed making predictions about the contrast sensitivity in the sighted and blind hemifields of a subject with a homonymous hemianopia, arising from a unilateral cortical lesion.

Predictions for the sighted hemifield

In the sighted hemifield, on the basis of Pöppel & Richard's (1974) paper, it can be argued that if it is only the Sprague effect which underlies the effective binocularity of the region corresponding to the blind spot, then it should not be possible to demonstrate an enhancement for this region relative to the rest of the visual field. This is because a unilateral cortical lesion, giving rise to a hemianopia, should produce a loss of facilitation for the entire ipsilateral colliculus, releasing the contralateral colliculus from inhibition and facilitating the contralateral prestriate and striate cortex via an ascending tecto-cortical pathway. Thus there is no advantage for the region corresponding to the blind spot because the whole of the sighted hemifield is released from inhibition.

However, if the effect in normal observers is due only to a cortical mechanism, then if the hemianope's intact striate cortex functions like that of a normal observer, there should be an advantage for the region corresponding to the blind spot in the sighted hemifield. In the subject studied here (GY), the unilateral lesion was sustained in late childhood (8 years), which is beyond an age at which developmental plasticity is likely to produce a reorganisation of the visual system. While it is noted that both retrograde and anterograde degeneration are known to follow damage to the striate cortex (Cowey & Stoereg, 1991), there is no evidence that this extends as far as the striate cortex contralateral to the lesion. In addition, magnetic resonance imaging (MRI) scans and computerised tomographic (CT) x-ray scans demonstrate that in the case of GY, the lesion is entirely restricted to the left hemisphere (Barbur et al., 1994). Therefore it seems reasonable to assume that in GY, the striate cortex contralateral to the lesion is organised like that of a normal subject.

Predictions for the blind hemifield

According to the Sprague effect, in the blind hemifield, the region corresponding to the blind spot should be facilitated compared to adjacent areas of the blind hemifield which are inhibited. The whole of the blind hemifield is inhibited because a unilateral cortical lesion should produce a loss of facilitation for the entire ipsilateral colliculus leading to a depression of collicular functions. This explanation has been offered to account for the depression of pupillary response to light in areas of homonymous scotoma (Koerner & Teuber, 1973).

How is the region corresponding to the blind spot in the blind hemifield facilitated? According to Pöppel & Richards (1974) explanation of the Sprague effect, the blind spot in the sighted hemifield, is an effective lesion in the contralateral colliculus. Thus the mirror symmetric location, represented in the colliculus ipsilateral to the blind spot in the sighted hemifield, is released from intertectal inhibition. This release from inhibition should facilitate the representation of the region corresponding to the blind spot in prestriate cortex, via an ascending tecto-cortical pathway. This study provides a rigorous test of the Sprague hypothesis since any residual vision in the blind hemifield cannot be attributed to sparing of striate cortex.

Finally, if the effect in normal observers is due to a purely cortical mechanism like probability summation or release from interocular suppression then there should be no advantage for the region corresponding to the blind spot in the blind hemifield, because there is no striate cortex present to mediate the effect.

These predictions were tested in the hemianopic patient GY by measuring contrast sensitivity in the sighted and blind hemifields at several visual field positions including the region corresponding to the blind spot. A summary of the predictions for the sighted and blind hemifields is given below in Table 3.1.

Summary of predictions

Mechanism	Position	Sighted Hemifield	Blind Hemifield
Subcortical	RCBS	Facilitation	Facilitation
	Whole Field	Facilitation	Inhibition
Cortical	RCBS	Facilitation	No Effect
	Whole Field	No Effect	No Effect

Table 3.1. Summary of predictions for the sighted and blind hemifields for the subcortical and cortical theories concerning the monocular sensitivity of the region corresponding to the blind spot compared to the rest of the visual field.

GENERAL METHODS

Subject

GY was aged 36 at the time of testing. At the age of 8 he was involved in a road traffic accident which resulted in damage to the left hemisphere. Ophthalmic investigation carried out immediately after the accident revealed an almost complete right homonymous hemianopia which was found to be virtually unchanged fourteen months later. Subsequent to the accident GY was unable to detect or recognise objects presented in his right field and regards himself as blind in that area (Barbur et al., 1980). Computerised Tomographic (CT) x-ray scans and more recent magnetic resonance imaging (MRI) scans show complete unilateral damage to the left striate cortex except for tissue corresponding to macular sparing (Barbur et al., 1994) of which there is approximately 2-3°.

In the sighted hemifield, visual function is normal for rod and cone threshold illumination levels and foveal colour matches. GY also shows the contrast elevation effect whereby the threshold contrast level for detection of a grating is increased by adaptation to a grating of similar spatial characteristics. As in normal observers, this effect is reduced if a conditioning grating of appropriate spatial frequency is presented to the opposite eye (binocular inhibition). While GY has fine stereoscopic discrimination, he cannot identify the 3-D image structure of random dot stereograms which implies a lack of global stereoscopy (Barbur et al., 1980). Cognition, memory, attention and speech are normal. GY is an experienced observer having participated in many psychophysical investigations. Corrected Snellen acuity is 6/6 in each eye.

Apparatus

The stimuli were generated using the VSG 2/2 Cambridge Research Systems graphics board using accompanying PSYCHO software (v.4) and displayed on a Taxan monitor (32cm x 24cm). The voltage luminance relationship was linearised using the same correction as employed in Chapter 2. The mean screen luminance was 47cd/m^2, the viewing distance was 57 cm and the only light sources were the test monitor and the experimenter's monitor. Head movements were restricted via the use of a chin rest incorporating a head clamp. The stability of GY's fixation was checked by imaging GY's eyes on a monitor using a JVC TK128E colour camera. This established that no significant eye movements occurred during the testing sessions.

Mapping the blind spot

The blind spot in GY's left eye (sighted hemifield) was mapped using the procedure outlined in Chapter 2. The stimulus used initially was a 0.5° diameter unstructured spot of 100% contrast temporally modulated sinusoidally at 1 Hz counterphase. However, the use of this stimulus yielded inconsistent results when trying to map the blind spot in its vertical extent. Therefore the blind spot mapping procedure was repeated using the same stimulus but with 2 Hz square wave contrast reversal. GY found this much easier to detect. Use of this stimulus placed the centre of the blind spot at 15.9° eccentric along the horizontal meridian and 1.4° below the horizontal meridian. GY was unable to detect a 5° diameter circular stimulus of 80% contrast, temporally modulated at 1 Hz counterphase, when presented to this locus.

Design of study

The aim of this investigation was to examine contrast sensitivity in the sighted and blind hemifields of GY to see if there was an enhancement in the region corresponding to the blind spot. Control measures were taken at 8° and 24° eccentric along the horizontal meridian in the nasal and temporal hemifields of each eye. Measures were also taken binocularly and this included the RCBS to check the stimuli in this area had been accurately positioned. Thus if the blind spot has been mapped correctly, contrast sensitivity in the RCBS should be the same whether obtained monocularly or binocularly. A schematic diagram of the areas of the visual field sampled is shown in Figure 3.1 below.

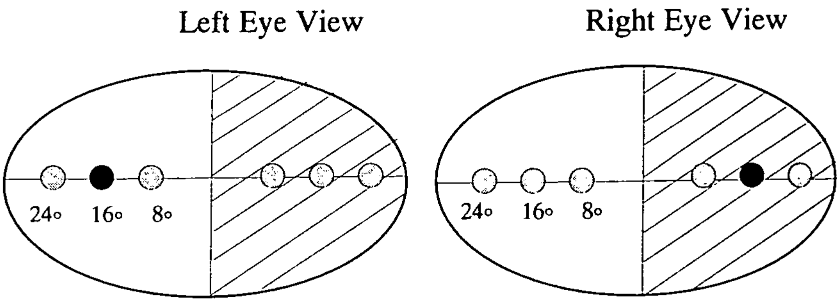


Figure 3.1. Schematic diagram of the areas of the visual field sampled. Hatched areas indicate the visual field defect.

Procedures

All the data presented in this chapter were collected over four days of testing (31-10-95, 1-11-95, 3-12-95 and 5-12-95). The same temporal 2AFC procedure outlined in Chapter 2 was used to measure contrast thresholds. Thresholds were measured in blocks of 50 trials each yielding one threshold estimate for a single stimulus at a particular visual field location. The temporal interval between stimulus presentations was 500 ms and trials were separated by a 1000 ms gap. Stimuli were always presented to the same position of the screen and eccentricity varied by moving the fixation point. The monitor was also moved left or right so that the fixation point was centred directly on GY's eye. During monocular testing, the non-tested eye was covered with an opaque occluder.

Blocks were grouped into testing sessions according to the eye tested. Each testing session comprised 6-10 blocks and GY was allowed to rest between testing sessions. Each condition was repeated twice during a testing session and the order of presentation of blocks was counterbalanced ABBA. Towards the end of the first day of testing, a fault developed on the monitor used to display the stimuli. It was apparent that contrast reversal was not confined to the stimulus but was visible across the rest of the screen. Testing was discontinued immediately. It was found the fault only arose when stimuli were presented to the right half of the screen so to test the blind hemifield, the monitor was turned upside down. The monitor was subsequently mended and used for the rest of the data collection.

Stimuli

All the stimuli used to measure contrast sensitivity in the sighted hemifield were circular one-dimensional grating patches that were horizontally oriented. They had a sinusoidal luminance profile and contained a single cycle of the nominal spatial frequency (zero phase). The stimuli were also counterphased at 1 Hz with sinusoidal temporal modulation. For all stimuli (including those presented to the blind hemifield), the stimulus onset and offset transition envelope followed a raised cosine function (which approximates a gaussian). The onset is the time taken for the stimulus to increase from the background to full envelope. The offset if the time taken for the stimulus to decrease from full envelope to the background luminance. Unless indicated otherwise, the onset and offset time was 250 ms. Thus a presentation time of 750 ms included 250 ms for the onset, 250 ms of the stimulus at full envelope followed by 250 ms for the offset. Further details of the stimuli used in the sighted and blind hemifields are given in the results section.

RESULTS I: THE SIGHTED HEMIFIELD

Is the RCBS hypersensitive?

Contrast sensitivity was measured in the sighted hemifield using a spatial frequency of 0.2 c/deg (5° diameter). The stimulus duration was 750 ms. Figure 3.2 shows the results of contrast sensitivity measurements taken monocularly and binocularly at three visual field locations in the sighted hemifield. The monocular and binocular measures of sensitivity taken in the RCBS (about 16° eccentric), are almost identical indicating that the placement of stimuli in the RCBS was accurate. Initial inspection of Figure 3.2 suggests that there is both a reduction of binocular contrast sensitivity in the region corresponding to the blind spot, and an enhancement of this region compared to monocular right eye measures. To examine this further, observed and expected contrast sensitivity values were compared.

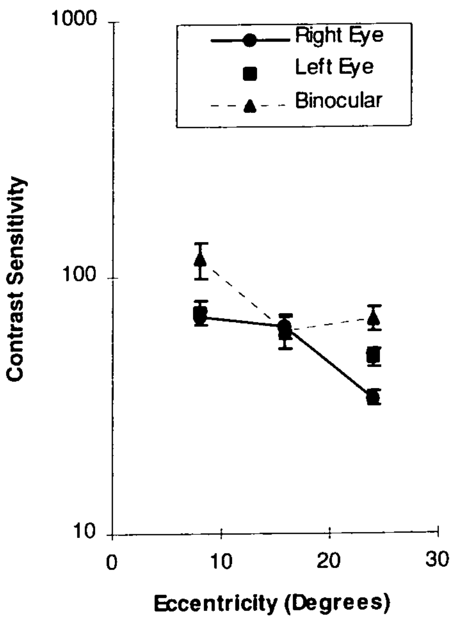


Figure 3.2. Contrast sensitivity at three visual field positions under monocular and binocular viewing conditions for a grating patch of 0.2c/deg. Measures were taken in the nasal hemifield of the right eye and the temporal hemifield of the left eye. Monocular data points are the mean of 6 threshold estimates. Binocular data points are the mean of 2-4 threshold measurements. Error bars on this and subsequent graphs represent +/- 1 S.E. of mean.

In Chapter 2 it was noted that the relationship between eccentricity and log contrast sensitivity is linear when eccentricity is scaled by the spatial frequency of the stimulus. It was also shown that an expected value can be calculated for any eccentricity given an observed value at another eccentricity, the spatial frequency of the stimulus and the gradient of the slope. Using the observed contrast sensitivity at 8° eccentric and equation 2.2, expected contrast sensitivity values were calculated for the RCBS and 24° eccentric. Since several threshold estimates were obtained at 8° eccentric, an expected value was calculated for each threshold estimate. Mean and standard error estimates for the observed and expected values are presented graphically in Figure 3.3 for the right eye (a.), left eye (b.) and binocular measures (c.).

Two tailed independent measures 't' tests were made to statistically compare observed and expected values. Independent measures 't' tests were considered appropriate because the expected values are based on observed values taken at 8° which can be considered to be uncorrelated with observations taken at other eccentricities. That is, any spurious correlations should be controlled for by counterbalancing the order of presentation of the stimuli. Since the aim is to make inferences about the population of

GY's behaviour, the observations in the sample can be considered to be independent of each other.

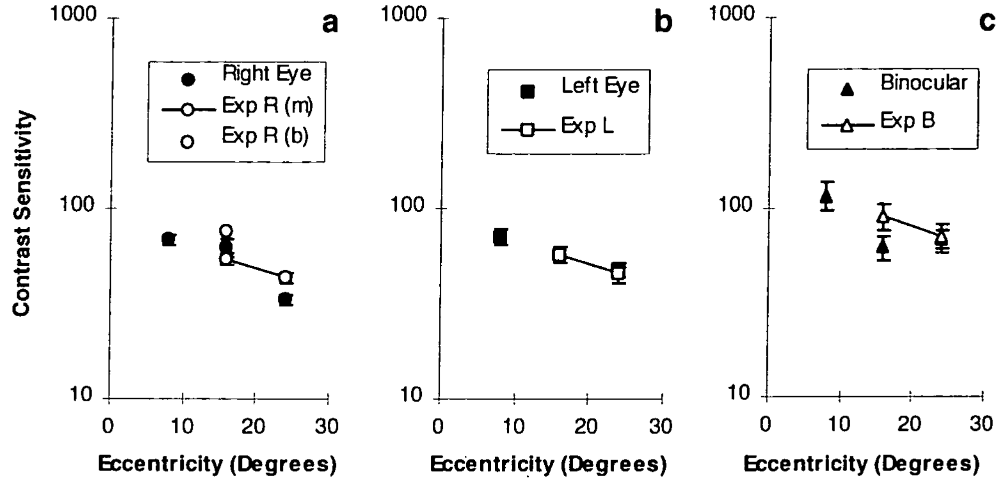


Figure 3.3. Comparison of observed and expected contrast sensitivity values obtained for the right eye (a), left eye (b) and binocularly (c.) Expected contrast sensitivity values were calculated using the sensitivity at 8° and equation 2.2. Note that the expected R eye measurement for binocular viewing in 3.3(a) is calculated from the expected monocular sensitivity and assumes reduction in contrast thresholds from monocular to binocular viewing by a factor of 1.414.

Eye	Pos. (degs)	Obs. mean	Obs. SE	Origin of Exp value	Exp. mean	Exp. SE	Value of 't' (obs-exp)	d.f.	P.
Right	RCBS	1.786	0.047	r, 8°	1.735 (m)	0.03	+0.92	10	0.38 (N.S.)
Right	RCBS	as above	as above	r, 8° * 1.414	1.885 (b)	0.03	-1.79	10	0.103 (N.S.)
Right	RCBS	as above	as above	b, 8°	1.939	0.06	-2.05	8	0.075 (N.S.)
Right	24	1.518	0.034	r, 8°	1.635	0.028	-2.65	10	0.02 *
Left	24	1.673	0.043	l, 8°	1.647	0.044	+0.42	10	0.68 (N.S.)
Binocular	RCBS	1.785	0.065	b, 8°	1.939	0.060	-1.57	4	0.19 (N.S.)
Binocular	24	1.828	0.048	b, 8°	1.828	0.056	0.0	6	1.00 (N.S.)

Table 3.2. Summary of the comparisons of observed and expected log contrast sensitivity measurements together with independent 't' test results for GY's sighted hemifield. All inferential statistics reported in this chapter were made using the log of each contrast sensitivity at threshold as the raw data. The origin of the expected value is the observed value from which the expected value was calculated. (N.S. = $P > 0.05$; * = $P < 0.05$).

The results of the statistical comparisons between the observed and expected values are presented in Table 3.2. This shows there was no significant difference between the contrast sensitivity of the RCBS and the expected monocular value for the right eye ($t = +0.92$, df = 10, $P > 0.05$). This suggests that there is no hypersensitivity in the region corresponding to the blind spot. However, this is not supported by the failure to find a significant difference between the expected binocular estimate (based on the monocular estimate and the assumption that binocular thresholds are lower by a factor of $\sqrt{2}$) and the RCBS ($t = -1.79$, df = 10, $P > 0.05$). While the difference between the monocular

RCBS and expected binocular estimate (based on binocular measures taken at 8°) eccentric approached significance ($t = -2.05$, $df = 8$, $P > 0.05$), the binocular RCBS measure was not significantly different from the expected binocular RCBS measure ($t = -1.57$, $df = 4$, $P > 0.05$). However, in the case of the latter comparison, the fewer degrees of freedom available make the test less sensitive to the difference.

Further support for an absence of hypersensitivity in the RCBS comes from an analysis of contrast thresholds. The ratio of the monocular RCBS contrast threshold ($1/10^{1.7856} = 0.0164$) to the expected binocular contrast threshold ($1/10^{1.9393} = 0.0115$) is 1.426 (the latter being calculated from the binocular measures of contrast sensitivity). This is very close to the traditionally observed ratio of monocular to binocular contrast thresholds of $\sqrt{2}$ and suggests there is no compensation for the monocularity of the RCBS.

The previous argument concerning the $\sqrt{2}$ difference between the expected binocular contrast threshold and the observed monocular contrast threshold in the RCBS is only valid if expected values correspond to observed ones for other areas of the visual field. Supporting this, there was no difference between the observed and expected log contrast sensitivity measures for GY's left eye at 24° for either the monocular ($t = +0.42$, $df = 10$, $P > 0.05$) or binocular measures ($t = 0.0$, $df = 6$, $P = > 0.05$). However, GY's log contrast sensitivity was significantly lower than expected for his right eye at 24° eccentric ($t = -2.65$, $df = 10$, $P < 0.05$).

Taken together, the results suggest that in the sighted hemifield, the monocular contrast sensitivity of the region corresponding to the blind spot is not equivalent to values expected on the basis of binocular viewing. The lack of evidence of monocular hypersensitivity in the region corresponding to the blind spot is consistent though with the Sprague hypothesis outlined in the introduction, which predicts that the sensitivity of the whole hemifield is increased. To examine this, the results of GY were compared with those of normal observers in the following section.

The contrast sensitivity of GY's sighted hemifield compared to normal

To establish whether the contrast sensitivity of GY's sighted hemifield is normal it is necessary to consider the range of contrast sensitivity observed in a normal population.

Figure 3.4 shows data obtained for GY using the same experimental procedures as those employed in the previous chapter for 6 normal subjects (with a lower mean age than GY), whose data have been reproduced from Figure 2.7 for comparison. An estimate of GY's sensitivity compared to these subjects was derived by calculating a z score, which expresses the difference between GY's mean and the control mean in terms of standard deviations of the control mean.

At 8° eccentric, the log contrast sensitivity for GY's right eye was higher (mean = 1.831) than the normal observers (mean = 1.612, SD = 0.136). This difference (0.22 log units) corresponds to a z score of +1.6 (equal to the 95th percentile). At the same eccentricity, the sensitivity of GY's left eye (mean = 1.844) was also higher than that of the normal observers (z = +1.708, 96th percentile). The magnitude of this difference was 0.23 log units. For the RCBS, the log contrast sensitivity was only slightly higher for GY (mean = 1.7856) compared to normal observers (mean = 1.6711, SD = 0.141, z = +0.812, 79th percentile). According to the z scores, GY's sensitivity lies at the high end of the range of normal sensitivity observed in this study. If the sighted hemifield of GY were increased in sensitivity it would support the explanation outlined in the introduction based on the Sprague effect.

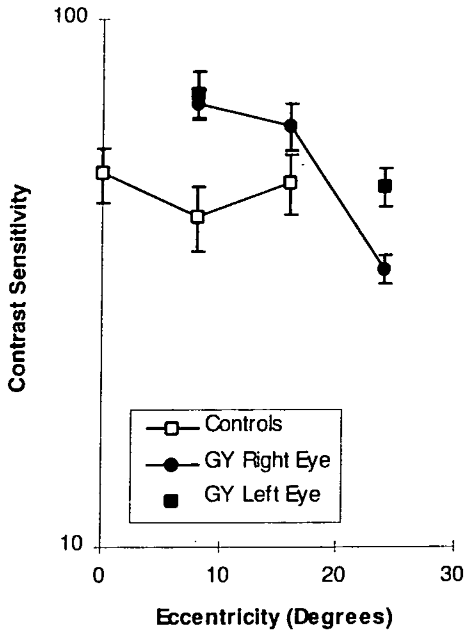


Figure 3.4. The contrast sensitivity of GY's sighted hemifield compared to normal observers (n=6) for a 0.2 c/deg grating. The data for the normal observers is reproduced from Figure 2.7. Each datum is the mean of 2x6 threshold measurements for normal observers and 6 threshold measurements for GY.

RESULTS II: THE BLIND HEMIFIELD

Contrast sensitivity in the RCBS

Is the region corresponding to the blind spot hypersensitive? The most important stimulus parameters for eliciting residual vision in GY's blind hemifield are temporal transience and a large stimulus area over which summation can occur (Weiskrantz et al., 1991). Thus the stimulus parameters were chosen to optimise these attributes. The stimulus used was a 5° diameter circular grating patch containing a single cycle of a 0.2 c/deg square wave grating, counterphasing at 4 Hz (square waveform). The stimulus duration was 1000 ms and a two-alternative forced choice paradigm employed. The results of monocular and binocular contrast sensitivity measurements in the perimetrically blind field with this stimulus are shown in Figure 3.5(a). While there is clear evidence of residual visual function, there is little evidence that the RCBS is hypersensitive.

There is evidence though that sensitivity is better in the right eye (temporal hemifield) compared to the left eye (nasal hemifield). Rafal (1989,1990,1991) has suggested that the retino-collicular pathway is predominantly crossed compared with the retino-geniculate projection and that any temporal hemifield advantage observed in the blind fields of a hemianope can be attributed to this anatomic asymmetry. More recent evidence, however, casts doubt on this proposal. Cowey (1995) retrogradely labelled the retinal ganglion cells of both eyes of the macaque using horseradish peroxidase. He found that the ratio of labelled cells in the contralateral retina was no different from the ratio found after implants in the optic nerve, which label the entire afferent pathway. This suggests differences in blindsight between the nasal and temporal visual fields cannot be attributed to differences in the projection from the nasal and temporal retina to the midbrain.

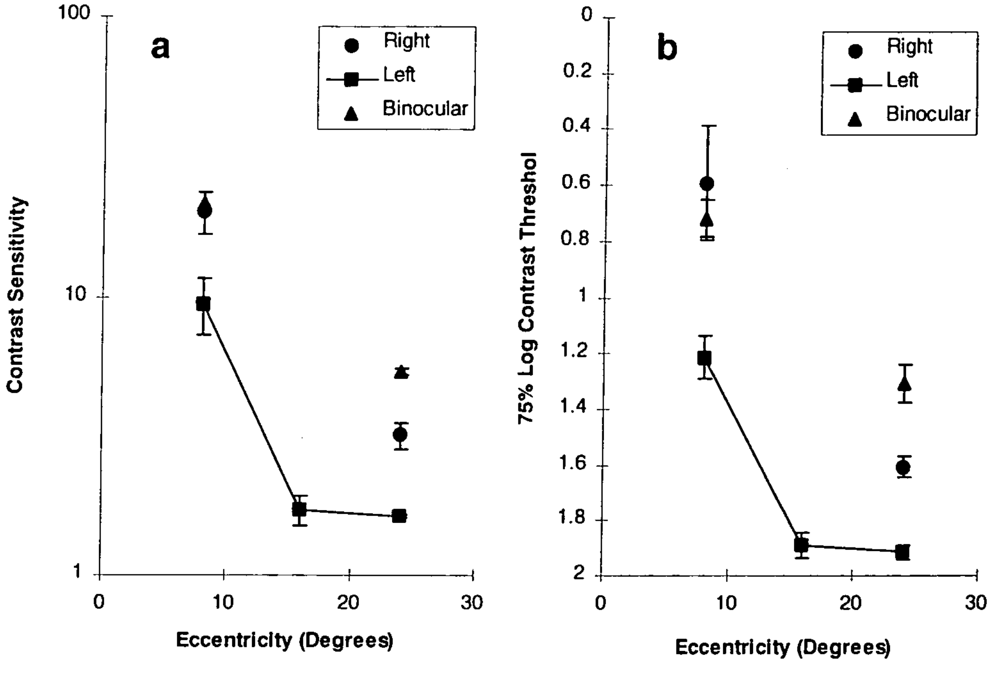


Figure 3.5. (a) Monocular and binocular contrast sensitivity in the blind hemifield at three visual field loci including the region corresponding to the blind spot. Each datum is the mean of 1-4 threshold measurements. (b) 75% log contrast thresholds for three visual field loci in the blind hemifield. S.E. estimates were given by Probit. Note that the two scales are equivalent.

Since contrast sensitivity was so low in the blind hemifield and in particular the RCBS, there is a danger that the staircase method used to calculate thresholds could have overestimated sensitivity. This is because even if there were no sensitivity, a contrast sensitivity of 1 would still be recorded. Therefore to check that sensitivity was not over estimated, 75% threshold estimates were calculated using probit. Since staircase procedures result in stimuli of many different contrasts being presented, the log contrasts were rounded to the nearest 0.1 log unit. This resulted in enough responses per log contrast to use probit (see the Appendix at the end of this chapter for psychometric functions). The 75% log contrast thresholds are plotted in Figure 3.5(b). Although estimates of sensitivity are slightly lower (for the lowest sensitivity measures) when obtained using probit, the pattern of results is essentially the same.

Light difference thresholds in the RCBS.

In a final investigation into sensitivity in the RCBS, a light difference threshold was measured using a 5° diameter unstructured stimulus (zero spatial frequency). The luminance of the target was initially well above that of the background and decreased until threshold was reached. The stimulus presentation time was short with an abrupt onset and offset (stimulus duration = 300 ms, onset = 100 ms, offset = 100 ms). Figure 3.6 shows the luminance threshold obtained for the left and right eyes. Although there is obviously some residual function, there is little evidence that it is particularly high in the RCBS.

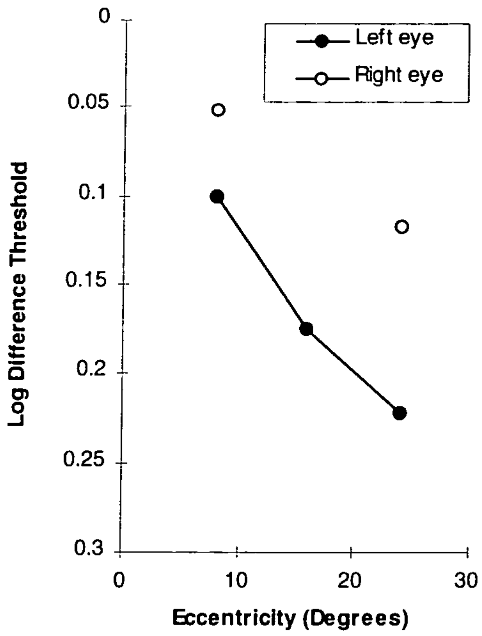


Figure 3.6. Light difference thresholds for stimuli at three retinal locations including the RCBS. Log difference threshold (*T*) is $T = \frac{B - S}{S}$ where *B* is the log screen luminance and *S* is the log stimulus luminance. Each datum is the mean of two threshold measurements.

Thus the results from the blind hemifield offer no evidence for an increase in monocular sensitivity in the region corresponding to the blind spot compared to the rest of the visual field.

RESULTS III: CONTROL EXPERIMENTS IN THE SIGHTED HEMIFIELD

In summary, there is little or no evidence of monocular hypersensitivity in the region corresponding to the blind spot compared to adjacent areas of the visual field, in either the sighted or the blind hemifield. It also appears that the sighted hemifield is increased in contrast sensitivity compared to normal observers. This latter finding is in disagreement with Hess & Pointer (1989) who found a deficit in contrast sensitivity in three hemianopes including GY compared to normal controls. The possible basis of this latter contradiction is examined in the following section. In the final section, the relationship between observed and predicted values in the sighted hemifield is further examined.

Mean luminance change?

One reason for the discrepancy concerns differences between the stimuli employed in the two studies. Whereas the stimuli employed by Hess & Pointer (1989) were equally modulated above and below the mean level in both the spatial and temporal domains, our stimuli had an overall change in mean luminance in the temporal domain. This was because our stimuli contained an incomplete temporal cycle (i.e. the presentation time was 750 ms allowing presentation only ¾ of a 1 Hz cycle). To see if this was responsible for the discrepancy, contrast thresholds were measured in the nasal field of GY's right eye using a 0.2 c/deg stimulus with a presentation time of 1000 ms allowing the presentation of a complete temporal cycle. A comparison of the results from these two different stimuli is shown in Figure 3.7. Although there is too little data to make a statistical comparison by position, collapsing the data across all positions leads to no significant difference in sensitivity obtained using the stimulus with the incomplete temporal cycle (mean = 1.723, S.E. = 0.066), and that obtained using the stimulus with the complete temporal cycle (mean = 1.711, S.E. = 0.058). The difference between the two means is not significant according to a two-tailed related t test on log contrast sensitivity ($t = -0.27$, $df = 5$, $P > 0.05$). Thus the difference cannot be explained by an overall change in luminance.

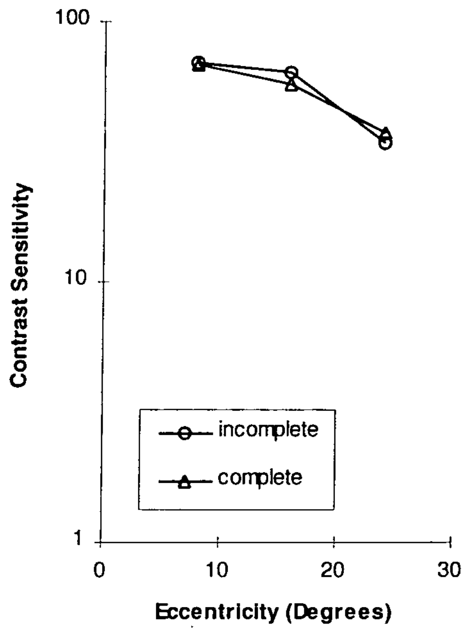


Figure 3.7. Contrast sensitivity of GY's right eye for a 0.2 c/deg stimulus obtained with an incomplete temporal cycle and a complete temporal cycle. In the former, each datum is the mean of 6 threshold estimates, in the latter each datum is the mean of 2 threshold estimates.

A further comparison of observed and expected values in the RCBS

To examine further the relation between observed and expected values, monocular contrast sensitivity was measured in the sighted hemifield of GY's right eye using a 0.8 c/deg grating patch (1.25° diameter). The presentation time was 1000 ms. Four positions along the horizontal meridian of the nasal visual field were sampled at 0°, 8°, RCBS and 24°. The results of this together with expected values calculated from the sensitivity at the fovea and equation 2.2 are shown in Figure 3.8. It is clear that the expected values do not provide a good model of the observed sensitivity. However too few measurements were available to confirm this statistically as there was only time to obtain 4 threshold measurements for each position. Since expected values do not predict sensitivity, it is not clear whether there is an absence of hypersensitivity in the RCBS.

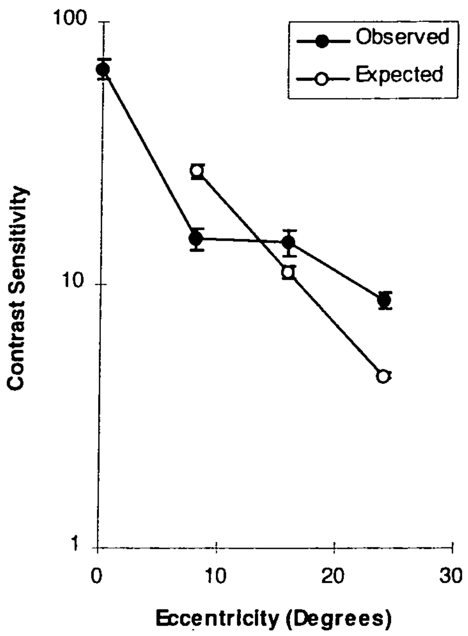


Figure 3.8. Observed and expected monocular contrast sensitivity for GY's R eye along the nasal hemifield for a 0.8 c/deg grating patch. Each datum is the mean of four threshold estimates.

DISCUSSION

Summary of results and implications for predictions

There was no evidence of hypersensitivity in the region corresponding to the blind spot in either the sighted hemifield or the blind hemifield of GY. In the sighted hemifield, using stimuli of 0.2 c/deg, expected values calculated using rules derived from empirical studies of normal observers (Pointer & Hess 1989; Pointer & Hess 1990) were able to account fairly well for the observed sensitivity. However, when a spatial frequency of 0.8 c/deg was used, observed and expected values were not congruent. This suggests that rules which govern sensitivity in normal observers may not provide a good model of the contrast sensitivity of the sighted hemifield of a hemianope. In addition to possible differences in the pattern of contrast sensitivity, there was also evidence of a quantitative difference since GY actually had a higher sensitivity than the normal observers. This difference was statistically significant for GY's left and right eyes at 8° eccentric. While there was evidence of residual vision in the blind hemifield, there was no evidence that it was localised to, or increased in, the region corresponding to the blind spot. This was true for a stimulus with no overall change in mean luminance and one with an overall change in light levels.

Thus in terms of the predictions outlined in the introduction, this study yielded contradictory results. In the sighted hemifield, the absence of hypersensitivity in the region corresponding to the blind spot, together with the apparent superiority over normal observers, supports the Sprague effect but is inconsistent with the cortical theories of probability summation and release from interocular suppression. Conversely, in the blind hemifield, the absence of hypersensitivity in the region corresponding to the blind spot is consistent with the cortical theories and contradicts the Sprague effect.

Why was there no increase in the RCBS in the blind hemifield?

The results of this study contradict those obtained by Pöppel & Richards (1974) who performed extensive perimetry on two patients with a large scotoma in one hemifield and a small scotoma in the opposite hemifield. In one patient a static target was visible in the large scotoma in a position mirror symmetric to the small scotoma. A moving target was also visible in the region corresponding to the blind spot. In the second patient, some residual vision could be demonstrated, also in a mirror symmetric location by measuring an increment threshold (increasing the intensity until the patient could detect the target). Since no anatomical evidence concerning the locus of the damage is presented, the possibility that the result was due to spared cortex rather than a subcortical pathway cannot be ruled out. Although it seems unlikely that by chance, there would be sparing in a mirror symmetric position, it is unknown whether the patients presented in the study were randomly selected.

One slightly puzzling aspect of Pöppel & Richards explanation is their claim that the residual vision is mediated by a backward projection from the colliculus to the visual cortex. Since their subjects had lesions of the visual cortex, one wonders how this facilitation might arise. Even when lesions are restricted to V1 in the monkey, evidence suggests that prestriate cortical areas are affected. For example, visual sensitivity in V2 is temporarily abolished by cooling the striate cortex (Girard & Bullier, 1989) and the inferotemporal cortex is visually unresponsive after striate cortical ablation (Rocha-Miranda, 1975).

If the lesions were restricted to V1, then one anatomical candidate for the residual vision would be the projection from the superior colliculus to MT via the pulvinar (see Benevento & Standage, 1983; Maunsell & Van Essen, 1983; Standage & Benevento, 1983). Consistent with this, in the monkey, cells in MT may remain functional after striate cortex damage (Rodman et al., 1989). However, the receptive fields of MT are less retinotopically organised than those in V1 (Zeki, 1993 p. 151) and thus could not account for the discretely localised areas of mirror symmetric facilitation observed by Pöppel & Richards. In addition, one would only expect to find sensitivity to moving stimuli since the overwhelming majority of cells in MT are directional and unresponsive to stationary spots of light (Zeki, 1974). Thus this pathway does not seem a likely candidate for the residual vision of Pöppel & Richards patients.

An alternative explanation would be to propose that the residual vision is mediated by the colliculus. The receptive fields of cells in the superior colliculus of the primate are retinotopically organised and cells in its superficial layers respond well to stationary or flashing spots of light (Goldberg & Wurtz, 1972). However, since it tends to have larger receptive fields than those in V1, it is also difficult to see how a lesion in V1 would result in a similarly sized area of facilitation in the contralateral hemifield. Therefore it is difficult to explain Pöppel & Richard's findings in terms of the Sprague effect.

Comparison with other studies of the perimetrically blind field of GY

Hess & Pointer (1989) found no evidence of residual vision in the blind fields of three hemianopes including GY. However, Weiskrantz et al (1991) showed that the effective stimulus size they used was too small and the onset-offset transition too gradual to elicit residual vision. These authors showed that the detectability of a stimulus in GY's blind hemifield depends on the slope of the onset and offset transition, the effective stimulus size, and the form of the spatial and temporal modulation. As expected, performance was also related to the contrast of the stimulus. Essentially, performance increased with temporal and spatial transience. Thus the more rapid the stimulus onset (the smaller the SD of the temporal gaussian), the better the stimulus was detected. While changing the SD of the temporal gaussian envelope necessarily alters the presentation time, presentation time per se had no effect on performance. Performance was also improved by increasing stimulus size (or the SD of the spatial gaussian envelope). Similarly, both square wave temporal and square wave spatial modulation were more effective than sinusoidal modulation.

Considering these findings, Barbur et al. (1994) made a study of the response properties of the residual vision of GY's hemifield using stimuli that could not be detected on the basis of transience provided by the spatial and temporal onset and offset. Evidence for two channels was found. One channel was spatially tuned with a peak sensitivity of about 1 c/deg with sensitivity falling off rapidly with increasing or decreasing spatial frequency. The other channel was sensitive to overall changes in light flux levels on the retina and showed extensive spatial summation. Both channels required transient inputs with a peak sensitivity at 10 Hz.

In this study, the stimuli presented to the blind field were hard- edged and the onset was more rapid than that employed by Hess & Pointer (1989). The temporal modulation at 4 Hz was square, as was the luminance profile across space (0.2 c/deg). Given the spatial and temporal transience of the stimuli employed, the finding of residual vision in the blind hemifield is fully consistent with the findings of other authors who have studied the residual vision of GY.

Why was there no increase in the RCBS in the sighted hemifield?

It is not clear why GY failed to show any increase in sensitivity in the region corresponding to the blind spot. The result is difficult to interpret given that the extent of normal variation in the effect size is unknown. It may be that the effect is present but masked by the higher overall sensitivity of the sighted hemifield.

Comparison with other studies of the perimetrically normal field

This section will discuss other studies of the visual capacity of the perimetrically sighted field of patients with visual field defects. It will begin by considering the discrepancy between the results of Hess & Pointer (1989) and the present study and conclude with a general discussion of other studies of the perimetrically normal hemifield.

GY may have scored at the high end of the normal range of contrast sensitivity because of extensive practice at psychophysics. However this explanation is inconsistent with Hess & Pointer's (1989) finding of a deficit in contrast sensitivity in the sighted hemifield of three hemianopes (including GY) compared to *naive* normal observers. The deficit was found in both spatial and temporal contrast sensitivity and for the spatially structured stimuli, the magnitude of the deficit was 0.25-0.75 log units. The effect was observed at all spatial frequencies tested (0.2-30c/deg), temporal frequencies (1 & 15 Hz) and locations (0° and 20° eccentric along the horizontal meridian). It is clear that the disagreement must be due to differences in contrast sensitivity measurement, because their control subject had a lower sensitivity than the normal observers in this study by 0.22 log units at the fovea (see their Figure 5, p. 880).

While both studies employed a 2AFC procedure, there are differences between the stimuli used that might be responsible for the results. The stimuli used by Hess & Pointer were weighted with gaussian envelopes of time and space. The SD of the spatial envelope was 2°, the SD of the temporal envelope was 250 ms and the stimuli were truncated in the spatial and temporal domains at +/- 2 SDs. This means that the onset and offset of stimuli employed in this experiment was more transient in both the spatial and temporal domain. In the temporal domain, the onset of the stimulus in this study was more rapid (250 ms) than in Hess & Pointer's (500 ms). In the space domain, our stimuli were hard-edged. However, the notion that temporal transience is important is not supported by the finding of no difference in sensitivity obtained between a stimulus containing a complete and an incomplete temporal cycle.

From a comparison of the spatial and temporal weighting functions employed in the two studies, it is clear that the effective stimulus presentation time was shorter, and the stimulus size smaller, in Hess & Pointer's study. Thus the opportunity for spatial and temporal summation was greater in this study. Yet this explanation is inconsistent with the failure to find any improvement in performance when the stimulus presentation time was increased from 750 ms to 1000 ms.

Perhaps the greater spatial transience and potential for spatial summation provided by the stimuli employed in this study are responsible for the apparent contradiction in findings. In view of the above inconsistency, future work must characterise the response properties of the sighted hemifield in a manner similar to that already done in the blind hemifield. Only by careful control of the stimulus parameters will such discrepancies be resolved.

There have been other reports of perceptual changes in the perimetrically sighted fields of hemianopic subjects but typically these have found a deficit rather than an enhancement of function. Several investigators have found a reduction in critical flicker frequency (the rate of flicker at which subjective fusion occurs) in the perimetrically intact field of patients with field defects (Teuber & Bender, 1949; Battersby, 1951; Teuber et al 1960; Goldman 1968). Only one study has failed to find such a reduction (Koerner & Teuber, 1973). Hemianopes with field losses arising from trauma to the geniculo-calcerine system have been found to have a reduced CFF across the visual field, a deficit not seen in frontal lobe patients. (Battersby, 1951). Teuber et al (1960) also found a decline in CFF in his analysis of patients with field defects arising from gun shot wounds to the occipital lobe. According to Goldman et al. (1968), these results cannot be attributed to diffuse damage outside the focal lesion responsible for the field defect.

Goldman et al studied a group of patients who had undergone temporal lobe resection for epilepsy. The patients were divided into those with quadrantanopia (produced by accidental invasion of the optic radiations during surgery) and those without. While CFF was slightly impaired by temporal lobe lesions (without field defects), especially those of the left hemisphere, it was more impaired in patients with field defects irrespective of the side of the lesion. The deficit was not only apparent in the lower intact quadrant contralateral to the lesion but also in the hemifield ipsilateral to the lesion. The results were attributed to the disruption of interactions both within and between the hemispheres.

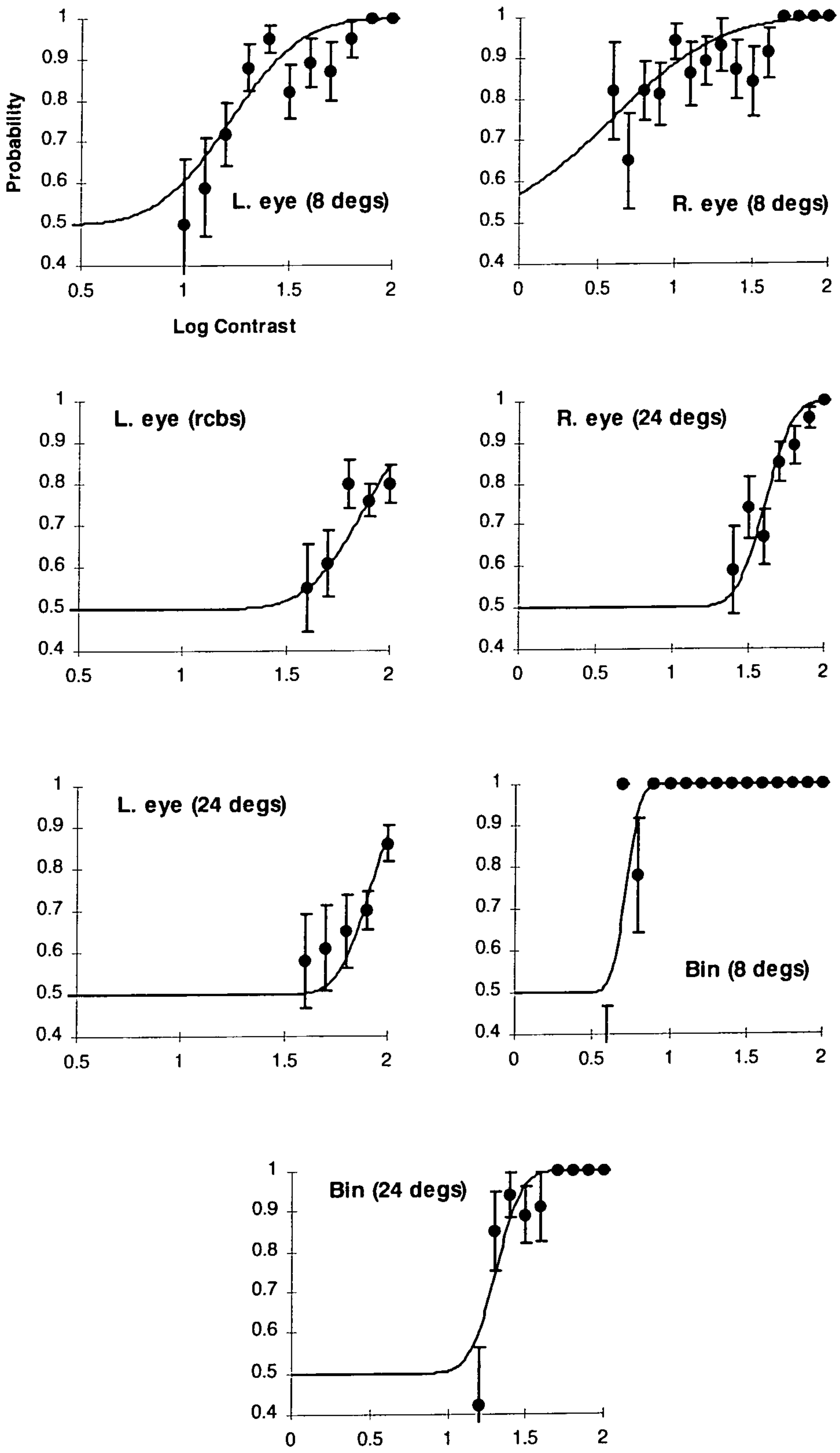
This latter point is further elaborated by Rizzo & Robin (1996) who claim that few (if any) pathological lesions affect human V1 alone. They at least disrupt the underlying white matter and U-fibre connections to adjacent occipital areas. As noted above, even when lesions are restricted to striate cortex, the functioning of extrastriate areas is affected (Girard & Bullier, 1989; Rocha-Miranda, 1975). This suggests that lesions of the striate cortex will also affect visual functions that depend on the functional integrity of prestriate cortex. Rizzo & Robin (1996) argue that extrastriate areas play a crucial role in attention and that consequently attentional deficits could follow striate cortex damage in the ipsilesional sighted field of patients with field defects

This hypothesis was confirmed in a group of patients with unilateral visual cortex lesions whose performance was found to be impaired on tasks with high attentional demands. For example, the patients were slower and less accurate at detecting the spatially and temporally unpredictable onset/offset of a light spot in a field of random spots. The authors note that the poorer performance was not mirror symmetrical to the perimetrically defined field loss, thus the deficit was diffuse rather than localised. It was concluded that the deficits are due to damage to white matter underlying connections to prestriate cortex and a concomitant disruption of function in heterotopic callosal projections between prestriate cortical areas. However, to be certain that the deficit is due to a dysfunction in the visual system, it should be established that patients with damage arising from non visual areas are not as impaired as patients with damage to the striate cortex.

Conclusion

This chapter reports several findings concerning the sighted and blind hemifields of GY. No increase in monocular contrast sensitivity in the region corresponding to the blind spot in the sighted hemifield was found. However, it is impossible to accept the hypothesis that this effect is not present in GY, because of the higher overall sensitivity of the sighted hemifield. This finding is consistent with the Sprague hypothesis that predicts an increase in monocular contrast sensitivity across the whole of the sighted hemifield. Yet, if the Sprague effect were operating, it should have been possible to demonstrate an increase in contrast sensitivity in the blind hemifield. No evidence of such an increase was found. Hence the results of this study are contradictory and do not help to explain the physiological basis of the effect observed in normal observers in the previous chapter.

PSYCHOMETRIC FUNCTIONS FOR GY'S BLIND HEMIFIELD.



The continous lines represent the fit obtained from probit.

4

Pop-out, Lateral Inhibition and Other Related Perceptual Phenomena

INTRODUCTION

This chapter is a literature review that deals with orientation pop-out and provides a context for the experimental work presented in Chapters 5, 6 and 7. The focus of this review is preattentive vision (with respect to orientation) and its place in the information processing stream. It is important to establish the role of V1 in preattentive vision. If processes in striate cortex play an overwhelming role in preattentive vision, it might be possible to demonstrate binocular interactions in visual search, a topic investigated in subsequent chapters. This review will begin by contrasting two quite different approaches to the understanding of preattentive vision. The first approach is embodied in the work of Treisman and Julesz, who emphasised the importance of features in visual search and texture segregation. Researchers such as Nothdurft and Sagi, who emphasise the importance of local feature differences and link their theory to the physiology of V1, exemplify the second approach.

This review will begin by discussing psychophysical evidence on pop-out and texture segregation relating to the different approaches outlined above. Next, evidence for orientation dependent physiological inhibition will be offered as a physiological correlate of pop-out and texture segregation. The possibility that long-range lateral interactions are the anatomical substrate of this inhibition is then considered. Finally, general psychophysical evidence relating to orientation dependent lateral interactions is reviewed.

POP-OUT AND TEXTURE DISCRIMINATION: THEORY AND PSYCHOPHYSICS

The starting point for this discussion is orientation pop-out. This occurs when an individual line element at an orientation different to that of the background elements appears to be particularly salient and is instantly detected in search experiments (Treisman 1985, 1986; Treisman & Gormican, 1988). The line is just as detectable regardless of the number of line elements (distracters) in the background and the search is said to occur in parallel or preattentively. This may be contrasted with serial search in which the time to find the target increases with the number of items in the background (see Figure 4.1). Texture segregation can be described as the segmentation of a pattern into two distinct areas, each of which appears to be separated from neighbouring areas by a clearly visible (but physically non-existent) texture border.

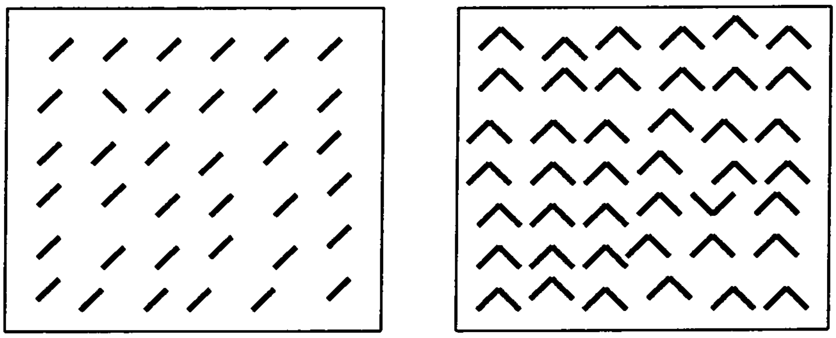


Figure 4.1 Parallel search (left). The reaction time to detect the target is independent of the number of distracters. Serial search (right). The reaction time to detect the target increases with the number of items in the display.

Although pop-out and texture segregation have been studied for other visual attributes such as colour, motion (Nothdurft, 1993; Treisman and Gormican, 1988) and disparity (Nakayama and Silverman 1986 cited in Treisman and Gormican 1988), consideration of these is beyond the scope of this discussion which will be confined to orientation.

Early work on pop-out and texture segregation used them as paradigms to investigate attention. Treisman and Gelade (1980) proposed the feature integration theory of attention in which features are registered early, automatically and in parallel across the visual field while objects are identified separately at a later stage which requires focused attention. Part of the evidence for this theory came from these authors demonstration that in visual search, simple features can be detected in parallel and that the search for such features (i.e. red or vertical) is little influenced by the number of the distracters in the display. Treisman and Gelade (1980) also found that texture segregation only occurs between areas of stimuli differing in separable features and not by discontinuities defined by conjunctions of features. An important aspect of this approach was that it offered techniques for establishing which visual dimensions (e.g. colour and orientation) were separable.

Like Treisman, Julesz (1984) also viewed human vision as operating in two modes; a preattentive mode in which features are detected in parallel and an attentive mode enabling serial search by focal attention in steps of 50 msecs. Julesz argued that all existing textures and patterns can be reduced to the simple combination of a few local features called textons. With reference to two dimensional monochrome images, three types of texton were proposed: the orientation of elongated shapes (lines, bars and ellipses), line crossings and line terminations. Thus textures comprised of elements which differ in their orientation, number of line elements or line endings should yield preattentive discrimination and texture segregation. Julesz (1984) demonstrated that this was indeed the case.

Bergen & Adelson (1988) have cast doubt on the notion that texture patches comprised of 'L's and 'X's segregate because they differ in feature properties such as terminators, crossings and intersections. This paper shows that manipulating the size of the oriented line elements making up each pattern can either make segregation easier or more difficult. This manipulation of texture discrimination is consistent with a mechanism based on simple linear filters tuned to different sizes. From this view, segregation is based on an analysis of local energy in the pattern rather than on the distribution of features. A similar point is made by Nothdurft (1990) below.

Nothdurft has published a series of papers criticising the texton theory of human vision. One problem is that textons can only be defined posthoc by studying the segregation of a presumed texture border. In addition, the application of the theory to natural scenes is difficult as texton features are not well defined in such patterns. Many textures may segregate because of unintended variation of other visual cues rather than differences in the spatial distribution of textons. For example, blobs of different sizes segregate because the two texture areas differ in their mean luminance. When the luminance contrast of the larger elements is reduced so that both texture areas display a similar luminance, segregation is reduced (Nothdurft, 1990). This suggests segregation is not based purely on the distribution of textons.

Another artefact that may be partially responsible for the apparent segregation of textons is the luminance distribution across the two segregating areas. For instance, a texture comprised of line crossings and non crossings differs in its power spectra across the two segmenting areas especially at low spatial frequencies. Differences in the power spectra or luminance distribution in the pattern can be partially masked by randomising element position, varying element density and size and randomising the luminance of elements in the display. While orientation is particularly insensitive to these manipulations, the fact that other textons are affected suggests that segregation is not due to the spatial distribution of these discrete features alone (Nothdurft, 1990).

Further evidence against the texton theory comes from the observation that for some textons, perceptual segregation is independent of the detection and discrimination of the texton. To some extent, texture segregation and the identification of textons are mediated by different mechanisms. In masking experiments with band limited visual noise, performance in texture segregation and texton analysis were predominantly affected at different spatial frequency bands, indicating that these tasks are mediated by different groups of cells with different sensitivities (Nothdurft, 1991a). Although it should be noted that for oriented lines, masking curves were similar in the texture segregation and texton detection tasks.

Nothdurft argues that texture segregation is based on local discontinuities. Continuous changes in texture do not segregate even though the individual features can be recognised. Further evidence that segregation is based on local feature contrast rather than the distribution of features themselves is provided by Nothdurft's (1991b) feature map paradox. The line pattern in Figure 4.2(a) spontaneously segregates into two areas, a (foreground) square-like figure and a surrounding background. However, if the spatial distribution of a typical texton such as a vertical line is plotted, the pattern in Figure 4.2(b) is obtained. Other textons (i.e. lines of different orientations produce even less regular spatial distributions). Thus if perception were based on first-order differences within specific texton maps, a rhomboid but not the square like-figure should be seen. Lastly, the finding of orientation difference cells (discussed below) suggests that it is not the detection of orientation per se that enables the segregation of oriented lines.

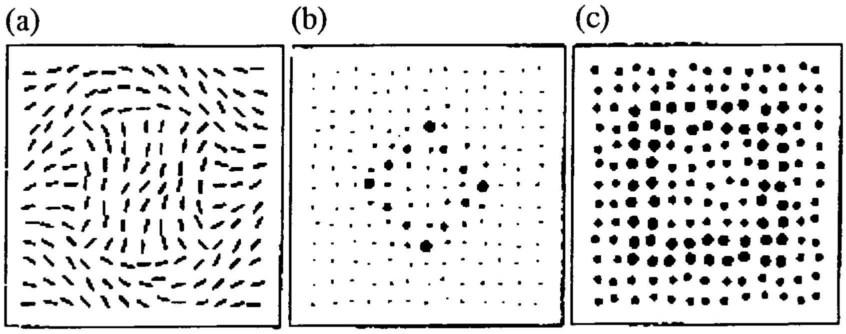


Figure 4.2. A Feature map paradox. (a) Line pattern from which a square-shaped texture area segregates. (b) Assumed response distribution in a supposed texton map for vertical line detectors. Response strength is assumed to be modulated by neighbouring orientation difference. (c). Assumed response distribution of pools of neurones with different orientation preferences but similar orientation difference sensitivity as neurones in (b). Texture borders could be evaluated from non-specific summation over many orientation selective cells. Reproduced from Nothdurft (1991b).

It is also likely that pop-out depends on the detection of feature differences. In a series of experiments, Nothdurft, (1991b;1992) systematically investigated the role of orientation differences in both pop-out and texture segmentation. He conjectured that textures segregate because of local dissimilarities between elements rather than the similarity within texture areas. Because these two aspects would be indistinguishable with the use of texture patterns in which all lines had the same orientation, measurements were extended to patterns with nonuniform texture areas in which the line elements varied systematically with line orientation. This means that elements within the texture bar have the same orientation as those in the background while the texture itself is defined by the orientation difference between neighbouring elements (see Figure 4.3). The textures were constructed such that the difference in local orientation at the texture border was always larger than the background orientation shift. As the background variation increased, the local orientation difference required to achieve texture segregation became greater. Similar results were obtained in pop-out and grouping experiments. These results cannot be explained by theories in which texture segmentation is based on element similarity. It was concluded that sensitivity to local dissimilarities (orientation difference) could be achieved from pooling the responses of all orientation sensitive V1 cells, which have been found to increase with local orientation difference (Knierim & Van Essen, 1992).

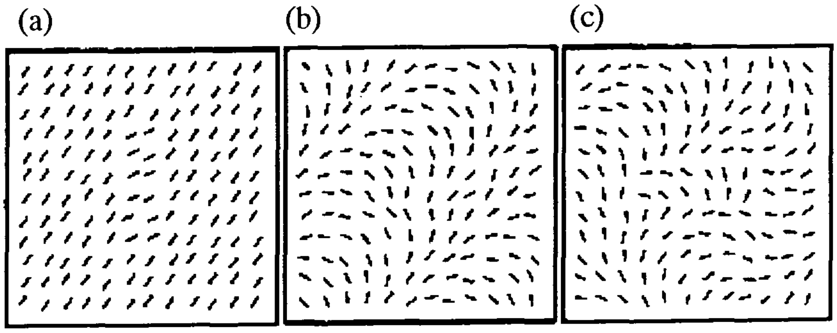


Figure 4.3 The detection of a texture bar depends on the signal to noise ratio of the texture border over background variation (a) Homegenous textures with zero orientation shift between neighbouring lines. Orientation difference at border is 30°. Texture bar is vertical. (b) Same border difference with a background variation of 20°. Texture bar is horizontal. (c) Maximum orientation difference (90°) with same background variation as in (b). Despite similar orientation difference in (a) and (b), the bar can hardly be seen on the increased background noise in (b). Only when the border difference is increased and signals lie well above background noise does the bar become visible (c). Reproduced from Nothdurft (1991b).

Dov Sagi has also emphasised the importance of the detection of feature differences in preattentive vision. If the preattentive detection of a target embedded in an array of distracters were based on the representation of different features in feature maps in which the target is defined by the total (global) activity at the corresponding map (Triesman, 1985), detection of the target should not be influenced by the presence of distracters and their number. This arises because targets and distracters activate different maps. According to this view, preattentive vision operates in feature space and does not have access to information concerning spatial position (Treisman & Gelade, 1980). Sagi (1990) contrasts this view of preattentive processing with a mechanism that detects local differences in some feature maps where targets and distracters are mapped according to their spatial locations. According to this view, preattentive detection is only possible if the target generates a strong local difference signal in comparison with local difference signals generated by the distracters. It is argued that all local difference signals are combined according to their spatial location, regardless of their label (orientation, colour etc.). This view is supported by evidence which shows that the detection of orientation differences improves with increasing element density both in texture discrimination tasks (Nothdurft, 1985) and in search tasks (Sagi & Julesz, 1987). Presumably, the closer items are, the stronger the difference signal obtained.

Sagi (1990) extended these findings to examine the number of cycles over which interactions between stimuli occur by using gabor patches of differing wave-lengths to examine visual search for an orientation singularity as a function of the spatial separation between target and distracters. The task was to detect the presence or absence of a vertically oriented gabor patch amid horizontal distracters. The presentation time was brief (40 ms) and masked by a full screen of Gabor patches. It was found that increasing distractor density improved target detection dramatically. Best performance was achieved when the spatial separation between signals was larger than 3 times their centre wavelength but smaller than nine times their wavelength. This supports the notion that the mechanism underlying the detection of feature differences operates through local interactions.

PHYSIOLOGICAL EVIDENCE FOR THE DETECTION OF ORIENTATION DIFFERENCES

Evidence for a physiological basis of pop-out and texture segregation comes from the observation that cells in striate cortex show orientation dependent inhibition. The first relevant evidence in primates came from Born & Tootell (1991) who recorded from cells in the interblob regions of layers 2 and 3 of the macaque striate cortex.

The motivation for their study was a preliminary finding that a high proportion of cells in this area responded poorly to full-field gratings, compared with responses to single bars, edges or delimited gratings. This was most often due to side inhibition in which increasing the number of cycles of a grating placed within a the cell's receptive field caused progressive inhibition of the response. A similar finding had been reported by De Valois et al (cited in Born and Tootell, 1991) who also noted a progressive inhibition of response of striate cortex cells in the macaque as more cycles of a grating were added. This property was termed side-stopping. It is important to note that side inhibition occurs well beyond the classical responsive region or classical receptive field (the area over which the cell gives an excitatory response to a single bar of light). Looking at the spatial extent of side inhibition, Born and Tootell noted that on average, just over 1 cycle of a grating gave the maximal response while adding about 2 further cycles reduced the firing rate by 50%. Deoxyglucose experiments confirmed that side inhibition is very widespread in the interblobs of layers 2 and 3 but is reduced or lacking in layers 4A through 6.

Another aim of this study was to examine whether the inhibition beyond the bar responsive region was orientation selective. To investigate this, a stimulus that consisted of two grating patches, a centre and a surround, was used. It was found that the inhibition was maximal when the orientation of the surround grating was parallel to the centre grating, diminished or absent when the orientation was perpendicular and moderate at intermediate orientations. Although only 6 cells were tested for this property, some degree of surround orientation selectivity was seen in all of these neurons. Such cells might be specialised to signal orientation difference. For example, the presence of side inhibition may mean the response of a cell to a single horizontal bar might be inhibited less when it is flanked by vertical bars than when it is surrounded by other horizontal bars. Although too few cells were identified to make generalisations about the population of cells, these authors suggested that such cells might help to signal the presence of contours by filtering out redundant information in noisy or textured surfaces. Born & Tootell (1991) cite masking illusions and the tilt illusion as phenomena which may arise because of side inhibition.

Similar inhibitory surround effects were reported by Grinvald et al (1994) in the primary visual cortex of the monkey using optical imaging. In vivo real-time optical imaging of sensory evoked activity is based on the use of voltage sensitive dyes. In contrast to single-unit recordings which can only measure spike discharge rates, optical signals primarily measure the change in transmembrane potential of a population of neuronal elements, including the subthreshold synaptic potentials that impinge on the extensive arborisation of cortical cells. Whereas single unit recording examines the points in the visual image that a single cell responds to, optical imaging is concerned with the inverse problem. It aims to identify the smearing of cortical activity that arises from a single point in visual space.

An area of cortex 6 mm x 6 mm was imaged, centred on receptive fields that responded to 6.6° below the horizontal meridian and 2° away from the vertical meridian. To demonstrate the long-range spread of visually evoked activity, a large grating (6° x 9°) with a 2° x 3° “hole” was used as a surround stimulus, while a small 1° x 0.5° stimulus was used to stimulate the centre. The orientation of the gratings was the same in the centre and surround. When the cortical activity to either of these stimuli presented alone was imaged, it was found to extend beyond that observed with traditional single unit recordings. To determine whether the spread of activity had an inhibitory component, the surround and centre stimuli were presented simultaneously. The observed response to the surround and centre stimulus was found to be much less than the linear combination of each presented alone. This suggested the presence of a large suppressive effect between the centre and the surround and vice versa.

The next step was to determine whether the inhibition was at least partly cortical in origin. It was reasoned that if the lateral inhibition depended on the orientation of the surround grating then it was probably cortically mediated. This study used a surround stimulus which did not extend along the long axis of the bars of the centre stimulus to avoid confusion with end-stopping. The difference between the response pattern produced by the centre plus an orthogonal surround and that produced by the centre plus a parallel surround was compared. It was found that the “parallel” surround produced a stronger attenuation of response than the “orthogonal” surround. This finding of orientation specific lateral inhibition is consistent with the findings of Born and Tootell reported above.

A link between orientation specific inhibition and pop-out was made explicitly by Knierim and Van Essen (1992) who recorded from neurones in V1 of alert monkeys using stimuli like those used in psychophysical pop-out experiments (see Figure 4.4). Neuronal responses to a single oriented line segment placed within a cell’s classical receptive field were compared with responses in which surround elements were either orthogonal or parallel with the centre element. The main finding was that the population response to orientation contrast textures was 15% larger than the response to a uniform contrast texture. Interestingly, a random orientation surround was just as effective at suppressing a cell's response as a surround of elements at the same orientation as the centre element. The effect of changing the spatial organisation of the surround was also examined. While both flanking and end quadrant surrounds produced orientation difference effects neither was as effective as the whole surround. Lastly, the general suppressive effect diminished as the density of the elements decreased. Unfortunately, too few cells showed orientation contrast to look at the effect of texture density on them. Knierim and Van Essen proposed a tentative link between the properties of their cells and the psychophysical phenomenon of pop-out but suggested that further evidence be sought before firm conclusions are made. For example, it should be examined whether cells in the attentional control system also show the orientation difference effect.

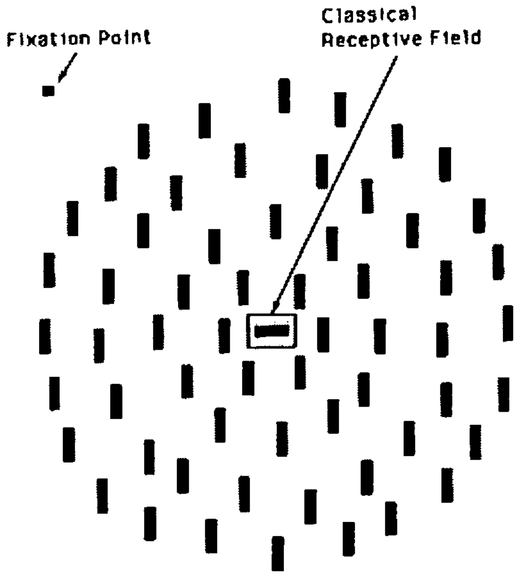


Figure 4.4. Orientation difference stimulus. A centre bar was placed within the cell's classical receptive field and rings of elements placed outside the classical receptive field. For a uniform orientation stimulus, both centre and surround elements had the same orientation. Reproduced from Knierim & Van Essen (1992).

Hegdé and Felleman (1996), who also used pop-out type stimuli (coloured oriented lines), failed to find orientation dependent inhibition in the macaque. However, since this work has only been published in abstract form, the details of the study are not known and hence cannot be evaluated. Taken together then, the evidence for the existence of orientation specific inhibition in striate cortex is compelling. Evidence from three different physiological techniques; single cell recording, optical imaging and deoxyglucose have demonstrated the existence of orientation dependent inhibition which is a physiological correlate of pop-out. The basis of this inhibition, however, still remains uncertain. It could arise from subcortical activity, end-stopping, activity in higher cortical areas or long-range lateral connections.

THE ORIGIN OF ORIENTATION DIFFERENCE SENSITIVITY

Subcortical activity, end-stopping and higher cortical areas

According to Kneirim & Van Essen, evidence for a subcortical origin for general suppression, comes partly from the demonstration of modulatory effects from stimuli well outside the classical receptive field in the retina and LGN of cats (McIlwain 1964) and monkeys (Kruger 1977; Kruger et al. 1975; Marrocco et al. 1982). There is also a massive feedback projection from V1 to the LGN (Hollander, 1974; Lund et al., 1975) whose function is poorly understood. However, since cells in the LGN are non-oriented, they are unlikely to be responsible for orientation dependent suppression. A more probable candidate is end-stopping. The end-stopped regions of cells in both striate cortex (Orban et al., 1979) and area 18 (Hubel and Wiesel, 1965) of cats have been shown to be orientation dependent, such that the suppressive effects of these regions are greater if the orientation of the stimulus in the end-zone matches the orientation of the stimulus in the excitatory receptive field centre. However, Knierim and Van Essen found no clear relationship between end-stopping and orientation dependent suppression. Grinvald et al. concluded there was a role for end-stopping in iso orientation suppression because it was observed that the attenuation of the centre response was larger when the surround stimuli had shorter bars. However, it could not explain orientation dependent inhibition because this was seen when the surround stimuli were placed along an axis perpendicular to the orientation of the centre grating. Thus while it is plausible that end-stopping may contribute to orientation dependent inhibition, it cannot be the sole mechanism.

Knierim and Van Essen have suggested that orientation difference effects may originate from higher cortical areas. DeYoe et al. (1986) showed that cells in V2 of anaesthetised monkeys show similar surround effects to those reported above. DeYoe et al (1986) argue that feedback connections from V2 may generate the surround effects in V1 which then pass the surround effect back up V2. Yet it is equally plausible that the activity in V2 is merely a reflection of that in V1. This view is consistent with Born and Tootell's observation that orientation dependent inhibition is confined to layers 2 and 3 of V1 since these layers are the major source of projections to V2.

Long-range horizontal connections in striate cortex

The final substrate to be considered is long-range lateral connections. Anatomic studies have revealed the existence of long-range horizontal connections within macaque striate cortex that can reach distances of up to 4 mm (Blasdel et al., 1985). Obviously the extent of the visual field covered by such connections depends on the cortical magnification factor. According to figures given by Hubel & Wiesel (1977, p.14), in layer III of macaque striate cortex, a 4 mm traversal of cortex covers approximately 0.2° at the fovea, 1° at 7° eccentric, 3° at 22° eccentric and 6° at 45° eccentric.

Ts'o et al. (1986) used cross-correlation analysis to determine whether there was any relationship between these horizontal connections and the cortical columns in layers 2 and 3 of cat striate cortex. Cross-correlation provides a measure of the type and strength of interactions between neurons. Using one cell as a reference, these authors recorded from other cells with a second electrode and looked for correlated firing between the two recording sites. Cells whose firing rates are highly correlated are assumed to share a common input. Evidence was found for excitatory connections between cells with like orientation preferences (<30°). In addition, cells with similar orientation tuning were more likely to show correlated activity if they shared the same eye preference. Although no evidence was found for inhibitory connections, it is has been shown that this technique may be incapable of detecting weak inhibitory interactions. Similar evidence for excitatory connections between cells of like orientation has been found in the monkey and these are also related to eye preference. (Ts'o and Gilbert, 1988).

How can the observation that long-range connections are excitatory be reconciled with the physiological inhibition discussed above? Recently, the electron microscopy studies of McGuire et al. (1991) have shown in the macaque, that a significant number of excitatory synapses actually terminate on inhibitory neurones. Finally in a study of long-range connections in the ferret, Weliky et al (cited in Derrington, 1996) showed that not only are these connections more prolific between iso-orientation columns but that blocking (excitatory) glutamate synapses also blocked inhibition indicating that the lateral excitatory connections are also responsible for inhibition. The typical pattern of responses was a rapid low-threshold excitation followed by a slower, higher threshold inhibition. Therefore, long-range horizontal connections appear capable of mediating the orientation dependent inhibition discussed above.

MODELLING OF POP-OUT AND TEXTURE SEGREGATION

Having established that physiological mechanisms exist which could underlie pop-out and texture segregation, it is necessary to examine their computational plausibility. Stemmler et al. (1995) have devised a model of orientation tuned neurones to explore the role of lateral connections in the suppression and enhancement of signals in primary visual cortex. This model views both pop-out and the perceptual completion of lines as arising from excitatory lateral interactions. The model assumes that direct inputs from the LGN and indirect excitation arising between horizontal connections activate both excitatory and inhibitory neurones. Excitation has a lower threshold of activation than inhibition so when input to the LGN is weak, the effect of a high contrast surround is to boost the signal. This is a physiological correlate of the perceptual phenomenon of line completion. However, when input to the LGN is strong, the effect of the surround becomes inhibitory and the signal is damped down. Crucial to the explanation of pop-out is the assumption that the lateral connections occur predominantly between cells tuned to the same orientation. Thus the response to a target is inhibited less in the presence of an orthogonal surround than in the presence of a parallel one. The success of this approach was demonstrated by the fact that the response of model neurons were very similar to those measured empirically by Knierim and Van Essen.

While Stemmler et. al. aimed to model the activity of individual neurones, Schofield and Foster (1995) were interested in accounting for the performance of human observers in texture segmentation and line-target-detection tasks. Their artificial neural networks were designed to process line element images by mimicking the properties of orientation difference sensitive cells identified by Knierim and Van Essen. Processing took place in three stages: first the orientation of individual line elements in the image were estimated; secondly the degree of orientation difference at each location in the image was computed; finally the target region of the image was classified as either horizontal or vertical, or if the task was line detection, as either left or right. The model could contain two types of orientation module, both of which responded well to single elements and to single elements with an orthogonal surround. However, uniform suppressed units were suppressed when there was a parallel surround while the random suppressed units were inhibited by a surround comprised of line elements at random orientations. Only a model which contained both types of modules produced an output similar to that of human observers. This suggests that the physiological mechanisms identified by Knierim Van Essen have the computational requirements to mediate pop-out and texture segregation.

The discussion thus far suggests that pop-out and texture segregation for orientation depend on the detection of local feature differences rather than the features themselves and that a physiological correlate of this may be the orientation dependent inhibition identified in V1. The origin of this orientation dependent physiological inhibition may be long-range horizontal connections which primarily link cells with the same orientation preferences. Model neurons based on such connections produce an output similar to the orientation difference cells identified by Kneirim and Van Essen (Stemmler et al, 1995) while a neural network model adds computational plausibility to the notion that orientation difference cells underlie performance in pop-out and texture segregation tasks (Schofield & Foster, 1995). The following evidence places this discussion in a wider context by considering other psychophysical phenomena that appear to reflect spatial interactions that arise within and beyond the classical receptive field.

OTHER PERCEPTUAL PHENOMENA RELATED TO ORIENTATION DEPENDENT SURROUND EFFECTS

This section will examine several psychophysical effects that depend on the orientation of elements in the surround. Firstly there is the reduction in apparent contrast of a central stimulus in the presence of a surround. Secondly, two relevant visual illusions will be discussed: the masking of contours by parallel lines and simultaneous orientation contrast (the tilt illusion). Finally evidence will be examined for the suppression and facilitation of threshold contrast by lateral masking, which offers evidence for both within filter and across filter integration processes.

Changes in apparent contrast (suprathreshold experiments)

Direct evidence for orientation dependent inhibition in humans comes from experiments by Cannon and Fullencamp (1991). These studies show that the apparent contrast of a central grating patch is reduced by a surrounding patch of the same spatial frequency. This inhibition occurred regardless of whether the surround was of a higher or lower contrast than the central patch and extended over spatial distances equivalent to more than 12 cycles of the central grating. Inhibition of the central patch showed a sharp decline as surround orientation increased to a difference of 15° and a much slower decline for further orientation increases. This suggested the existence of two components to the inhibition and it is noteworthy that inhibition was not abolished even for the orthogonal surround. Using bow-tie stimuli it was shown that the spatial organisation of the inhibition is roughly isotropic. This may be a psychophysical correlate of the orientation dependent lateral inhibition reviewed above.

Visual illusions

Two visual illusions which also suggest the existence of orientation related inhibition are masking illusions and the tilt illusion. The former were discovered by Galli and Zama (1931 cited in (Born and Tootell, 1991) who observed that a contour is effectively hidden when flanked by additional contrasts of the same orientation. For example, the image in Figure 4.5. appears to be a large square whose corners are covered by four smaller striped squares, even though it is actually an octagon whose oblique lines have been flanked by multiple parallel lines. Without the flanking gratings, these sides would be perceived as part of the octagon. One explanation for this is that the boundaries are masked by the presence of the striped surround. Although it is also possible that attention is not drawn to the octogon in the picture because of the tendancy to group the striped surrounds into squares occluding a larger square underneath. Born and Tootell suggest that cells sensitive to orientation difference may operate as "contour-pass" filters, enabling the identification of object boundaries.

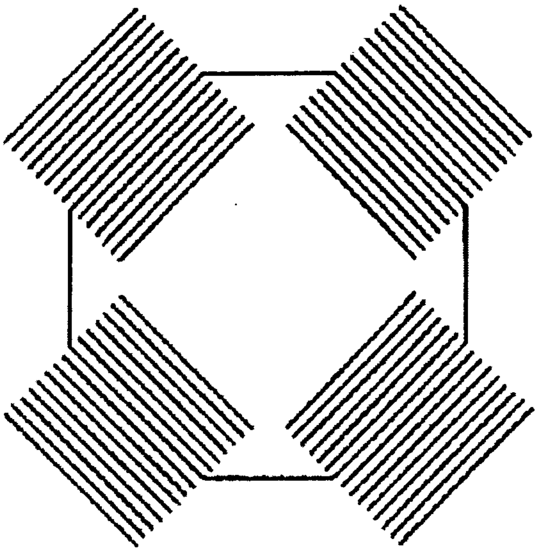


Figure 4.5. Masking of contours by parallel lines (Galli & Zama, 1931). The oblique sides of the octagon are swallowed up by the textured squares that overlie the four corners of the octagon. Side inhibition at different spatial scales may account for this type of illusion. Reproduced from Born & Tootell (1991).

Simultaneous orientation contrast (or tilt illusion) refers to the change in the apparent tilt of a central test line when flanked by similar lines. Westheimer (1990) found that the test line appeared tilted in a direction opposite to that of the inducing lines and that to null the orientation shift (i.e give an appearance of vertical), the test line had to be presented with a tilt in the same direction as the inducing lines. The magnitude of the induced orientation shift was 1-3.5 degs, peaked at contrasts of 15-30 degs and was absent when the inducing lines were parallel or orthogonal. The shift declined with distance between the test and inducing lines until it was no longer apparent at 50 mins of arc. The introduction of a difference in depth plane had little impact, but the effect was diminished when the presentation of the test and surround line was dichoptic.

Simultaneous orientation contrast could be induced in a variety of oriented features, including illusory contours, an ellipse, a moving dot and a row of dots or lines.

Gilbert and Wiesel (1990) looked for neural activity that might be related to the tilt illusion at the level of single cells in the cat striate cortex. Single cell recording of complex cells in the superficial layers revealed several influences of visual context (i.e. oriented bars) on the properties of the receptive field centre. Inhibition or facilitation which was dependent on the orientation of the surround was found. In addition there were shifts in orientation preference and changes in the bandwidth of orientation tuning. To relate these changes to perceptual changes in orientation, a neural ensemble encoding orientation was modelled.

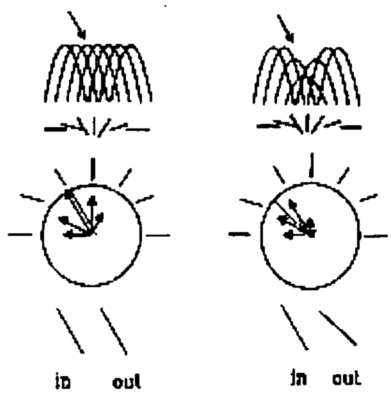


Figure 4.6. Model for estimation of line orientation based on an ensemble of orientation selective cells/ filters. When the cells are activated by a line of a given orientation, the cells are activated to different levels of excitation, depending on the peak position and breadth of their tuning curves. The firing rate of each cell is represented as a vector pointing in its preferred location with a length proportional to its firing rate. The estimation of orientation is taken as the vector sum (straight line within circle without arrow). When the filters are spaced at constant intervals and have the same height and width (left), the estimation of orientation is equivalent to the stimulus orientation (bottom left). When some of the filters are inhibited (right), the vectors change in length and consequently the estimate of orientation is shifted away from the stimulus orientation. Reproduced from Gilbert & Wiesel (1990).

The model consisted of a set of gaussian filters broadly tuned to different orientations in which perceived orientation depended on the ratio of firing of the different filters. As shown in Figure 4.6, an oblique line causes the filters to fire at different rates. The contribution of each filter to the estimation of orientation is represented as a vector pointing in the direction of its preferred orientation with a length proportional to its firing rate. The vector sum of the ensemble is taken as the estimated orientation. The difference between the input orientation and the estimated output represents the orientation shift perceived by the system. When the tuning of all cells is equivalent, there is no difference between the input and the output. However, when a few of the filters are suppressed (right-hand part of Figure 4.6), the resultant vector shifts away from the original estimate and there is a discrepancy between the input orientation and the output estimate. Using this model, it was possible to identify those physiological effects that could bias the perceived orientation of a central line away from that of surrounding lines. These included surround inhibition tuned to the same orientation as the centre, shifts in orientation tuning towards the orientation of the surround and changing the breadth of orientation tuning. Essentially these results show that the sensitivity of the ensemble of striate cortical cells is not fixed but can change according to the visual context.

Suppression and facilitation of threshold contrast by lateral masking

Another set of psychophysical experiments that have been held to reflect horizontal interactions between orientation sensitive cells in V1 have been reported by Polat & Sagi (1993;1994). These authors employed a paradigm in which local contrast sensitivity was measured for a foveal Gabor target in the presence of two spatially adjacent, high contrast 'masking' Gabor patches. Gabor patches are sinusoidal luminance signals with gaussian envelopes. Since they approximate the receptive field structure of simple cells in V1, it is assumed that they can activate a limited set of early cortical neurons (Kovacs, 1996). Specifically, it is argued that the use of such band-limited stimuli can distinguish between two major contributions to lateral masking. The first comes from within filter integration processes (which are assumed to be linear) while the second concerns interactions between spatially adjacent filters (following some nonlinearity at the filter output). It is argued that the use of low pass and broad band stimuli such as letters, line elements or light spots probe mainly within filter processes since they stimulate large (lower frequency) filters that cover both the test and the mask. Thus the use of Gabor patches are more suitable for studying interactions between spatially adjacent filters.

Varying the distance between the test and masks revealed the existence of two spatially separate zones. An inner zone of threshold elevation was observed for a separation less than twice the target wavelength, while an outer zone of threshold reduction was seen when the distance ranged between two and ten wavelengths. The threshold reduction also occurred when the test and masks were of opposite sign suggesting that the enhancement is not due to linear integration. Increasing target and mask size (SD of gaussian) by a factor of two did not affect the interaction range suggesting that the size of the zones depends on wavelength. In general, the decrease in threshold was of equal or higher magnitude when compared with the increase in threshold, and more sensitive to differences between target and mask spectra. No significant effects were found when target and mask orientations differed by more than 45° and their spatial frequency by more than two octaves (Polat & Sagi, 1993). This latter point is important since the filter width of simple cells in V1 is assumed to be about two times its most sensitive wavelength (Watson et al.,1983; Wilson, 1983).

These results were interpreted as evidence for excitatory and inhibitory interactions in the space domain. Specifically Sagi & Polat argue that threshold elevation reflects physiological excitation and, since it occurs within a range that overlaps with known filter size, may largely reflect spatial integration within the filter receptive field. Conversely, threshold reduction is held to reflect physiological inhibition and, since it occurs well beyond the known filter size, may represent interactions between spatially adjacent filters.

The identification of physiological inhibition with threshold reduction is not necessarily paradoxical. Barfield & Tolhurst (cited in Polat & Sagi, 1993) suggest that direct inhibition on the target area may reduce spontaneous activity (noise) at or near the area of detection and thus improve detection. Since intrinsic noise in the system is only a limiting factor at threshold, the effect should reverse for contrast judgements made on suprathreshold targets. Such an explanation is consistent with the studies in apparent contrast outlined above by Cannon & Fullenkamp (1991) who found a reduction in apparent contrast for a target surrounded by a high contrast surrounding grating that was still apparent at target to mask separations of up to ten wavelengths.

In a follow-up to their initial paper, Polat & Sagi (1994) examined how the reduction in threshold (enhancement effect) varied with the spatial configuration of the Gabor patches. The largest enhancement occurred when the Gabor patches were co-linear, a smaller enhancement occurred when the target was orthogonal to the masks while the effect was almost absent for diagonal orientations. This relationship between local and global orientations was independent of the absolute local and global orientations. These results shed light on the architecture of lateral connections in terms of a cell's preferred axis. In interpreting these results these authors cite two physiological studies. Single cell recordings from cat striate cortex indicate the existence of facilitatory interactions along the cell's main axis and inhibitory interactions in other directions (Nelson & Frost, 1985). Responses of orientation selective neurons in monkey V1 can be suppressed by presenting flanking line segments of similar orientation, on either direction from the cell's location (Van Essen et al., 1989). Thus coaxial enhancement may be a result of disinhibition, and the absence of diagonal interactions may be a result of an inhibitory-excitatory balance.

This work places the notion of lateral interactions in a broader context of information processing channels. The existence of channels in the human visual system which are selectively sensitive to different ranges of spatial frequencies and orientations is indicated by increasing evidence (see Polat & Sagi, 1993 for refs). However these channels are not completely independent and receive inhibitory inputs from channels coding for neighbouring spatial frequencies or orientations and disinihibitory inputs from channels beyond this inhibitory region. Polat & Sagi suggest that analogous channels also exist in the space domain in which channels are excited by channels within a distance of two wavelengths from their location and are inhibited by channels from larger distances.

The experiments presented in the following chapters are founded on the premise that the detection of orientation difference is based on lateral interactions in V1. If orientation difference sensitivity depends crucially on these processes then given the ocular dominance of cells in striate cortex, it may be possible to demonstrate binocular interactions in orientation difference sensitivity. Binocular interactions in visual search are first examined in the next chapter in a pilot experiment that compares orientation pop-out in monocular and binocularly represented areas of the visual field. Chapter 6 looks at dichoptic interactions by assessing whether the eye of origin of information affects the search process. The final experimental chapter examines dichoptic interactions using a task which, measures orientation difference sensitivity more directly than the pop-out experiments.

5

Visual Search for Orientation in the Region Corresponding to the Blind Spot

ABSTRACT

The experiment reported in this chapter examines dichoptic interactions in visual search in the region corresponding to the blind spot. The reaction time to detect the presence or absence of a target (horizontal line) amid vertical distracters was measured. All stimuli were presented to the right hemifield and arranged in a semicircle at the same eccentricity as the blind spot. Targets presented to binocularly represented regions of the visual field could be presented to either eye while targets presented to the region corresponding to the blind spot were only presented to the left eye. The distracters could either be presented to the same eye as the target (monocular condition) or to the opposite eye (dichoptic condition). Similar reaction times to targets in monocular and dichoptic conditions were observed and the function relating reaction times to visual field position was U-shaped. Explanations offered for the U-shaped position effect include the radial organisation of the visual field, the elliptical shape of the visual lobe and the increased monocular sensitivity of the region corresponding to the blind spot. In terms of binocular interactions, the extent to which the experiment tested the predictions outlined in the introduction (validity) is assessed.

INTRODUCTION

Chapters 2 and 3 tried to establish a link between the binocular structure of V1 and behaviour by measuring monocular contrast sensitivity in monocular and binocular areas of the visual field. The rationale behind this stems from physiological evidence suggesting these areas may process information differently and therefore produce different threshold estimates. Evidence consistent with this notion was found. Since neurophysiological evidence reviewed in the previous chapter suggested that striate cortex may play a vital role in orientation pop-out, we aimed to establish whether pop-out also varied across monocular and binocular areas of the visual field. A further way of investigating the effect of ocular dominance on visual sensitivity is to examine whether there is a cost for integrating information across the two eyes. The rationale is that if a task is mediated by monocular or partially monocular neurons, there should be a cost (in terms of speed/accuracy) when stimuli are presented dichoptically compared to a solely monocular presentation. We sought to investigate this possibility for pop-out. This experiment is a pilot experiment for ideas that are pursued more fully in the next two chapters. The stimuli were presented dichoptically using red-green anaglyphs, a method that unfortunately reveals the eye of origin of stimuli to the subject. Since this technique is less than satisfactory, the aim was to repeat the experiment, if evidence of binocular interactions was found, using a more adequate method.

Before describing the experiment, it is necessary to summarise the evidence for a role of striate cortex in orientation pop-out. A number of investigators have suggested that the preattentive processing of orientation may occur in V1 (Knierim & Van Essen, 1989; 1992; Sagi, 1990; Nothdurft 1991a,1991b;1992; Stemmler, et al. 1995; Schofield & Foster 1995; Derrington, 1996). Both Stemmler et al (1995) and Derrington (1996) argue that preattentive orientation processing is mediated by the extensive network of horizontal processes that extend well beyond the representation of the classical receptive field in primary visual cortex. It is suggested that these lateral connections, which primarily link regions of cortex whose neurons prefer stimuli with similar orientations provide neurons with information about the visual context of a stimulus.

Lateral interactions may underlie the tuning properties of 'orientation difference' cells. These cells were identified in monkey V1 and formed a third of the sample of cells tested by Knierim and Van Essen (1992). Such cells are more suppressed by an orthogonal surround than a parallel surround providing a physiological correlate of pop-out. For some cells, this property was superimposed on the orientation selectivity of the cell, while other cells were selective for orientation contrast without being selective for orientation. This physiological evidence implies that a horizontal line amid vertical distracters pops out because there is more distractor-distractor inhibition than target-distractor inhibition.

As reviewed in Chapter 1, most cells in V1 show ocular dominance, but this feature is absent from cells in the cortical representation of the region corresponding to the blind spot (Rosa et al., 1992; Horton, 1984; Kennedy et al., 1975; Kennedy et al., 1976). If preattentive vision depends crucially on processes occurring in V1 then given the ocular dominance differences, different predictions can be made for binocularly represented areas of the visual field compared to the region corresponding to the blind spot.

Predicted pop-out in binocularly represented areas of the visual field

Assuming that the degree of lateral inhibition between stimuli reflects the strength of the response to each stimulus, it follows that the degree of inhibition between stimuli should depend not only on their orientation difference but also on their eye of origin. Specifically there may be more target-distractor inhibition when the target and distracters are presented to the same eye than when they are presented to opposite eyes. If greater pop-out occurs when target-distractor inhibition is reduced this would enable a target to be detected more rapidly when it is presented dichoptically compared to when it is presented monocularly.

Predicted pop-out in the RCBS

A second prediction concerns the region corresponding to the blind spot. Since this area is deprived of a signal in the opposite eye, information may be automatically treated *as if* it were binocular in origin. This is consistent with the observation of a monocular contrast sensitivity that is equivalent to that expected binocularly. Perhaps this means that when the target is in the region corresponding to the blind spot the inhibition created between the target and distractor is the same regardless of whether the stimuli are monocular or dichoptic. Hence there might be no difference in pop-out for dichoptic and monocular targets in the region corresponding to the blind spot.

This study should be distinguished from Ramachandran's (1992) demonstration of pop-out in the blind spot. In Ramachandran's study, the display consisted of a donut texture (white filled circles on a black background with a hole in the centre of each circle). When presented to the blind spot the hole is occluded and only a white circle is visible. This makes the element in the blind spot appear to pop-out from the rest of the elements. Whereas Ramachandran's study is an investigation of filling-in at the blind spot, this study is concerned with pop-out at the corresponding location in the other eye.

The above predictions were tested by measuring the time to detect the presence or absence of a target (horizontal bar) in the presence of distracters (vertical bars) located at the same eccentricity as the blind spot. The target was either in the same eye as the distracters (monocular condition) or the opposite eye (dichoptic condition). Red-green glasses were used to achieve binocular separation.

METHODS

Equipment

Stimuli were generated and presented using the framestore (GSP) of Cambridge Research Systems Visual Stimulus Generator (Version 2/2 with software version 4.05). The experimental software was written in-house using a modified version of a visual search program written by Iain Gilchrist. The stimuli were displayed on an EIZOF784 colour monitor with a screen resolution of 1024 x 768 pixels. The screen dimensions were 40 cm x 30 cm. To make the red-green glasses, the surround of a pair of eye-protector goggles was painted black and coloured filter paper attached over each eye's view. A partition down the centre ensured only one colour could be seen with each eye. The red filter was placed over the right eye, the green filter over the left eye. Goggles were used to maximise the visible field of view and had the advantage that glasses could be worn underneath.

Subjects

6 adult subjects with normal vision participated. All subjects scored within the normal range on a test of stereopsis and the Maddox Wing test. 5/6 subjects had corrected to normal visual acuity while subject KF was emmetropic.

Mapping the blind spot

The blind spot was mapped in the right eye of each subject while wearing an opaque patch over the left eye. The viewing distance was 57 cm and the head was stabilised using an adjustable chin and forehead rest. The background was light (67cd/m^2) to minimise the effects of scattered light. The mapping stimulus was a 0.5° diameter spot (2.25 cd/m^2).

The mapping procedure was a computer driven task in which the subject used the keyboard to respond 'yes' if the stimulus was visible and 'no' if it was not. At the beginning of each trial a tone was sounded to indicate that a stimulus had been presented. The extent of the blind spot was first determined along the horizontal meridian. The vertical extent of the blind spot was then established, using the results from the horizontal mapping to ensure that the vertical extent was mapped roughly through the centre of the blind spot. Along each axis the spot was presented in a pseudorandom order at each of 33 locations spaced 0.5 cm apart. The visibility of the spot was sampled 5 times at each position.

Examination of the data revealed that there was often a sharp transition between positions in the blind spot and those which were not. Positions along each axis for which the subject responded 'yes' on less than 50% of trials were deemed to be in the blind spot. A blind spot boundary was defined as the midpoint of positions that marked the transition between positions inside and outside the blind spot. Once the four blind spot boundaries had been established, an ellipse was fitted to these points using an Ndimensional fitting program from Numerical Recipes (Press et al., 1992). The fitted ellipse was always symmetrical about its horizontal and vertical axes. The accuracy of the fitted ellipse was checked by running a program to display the four observed boundary points and the fit, an example of which is shown in Figure 5.1. The ellipse fitting function provided the central co-ordinates of the blind spot together with the length of its major and minor axes. Radial co-ordinates were derived from these linear co-ordinates to position stimuli in the blind spot in the visual search experiment. The results of the blind spot mapping procedure are given in Table 5.1.

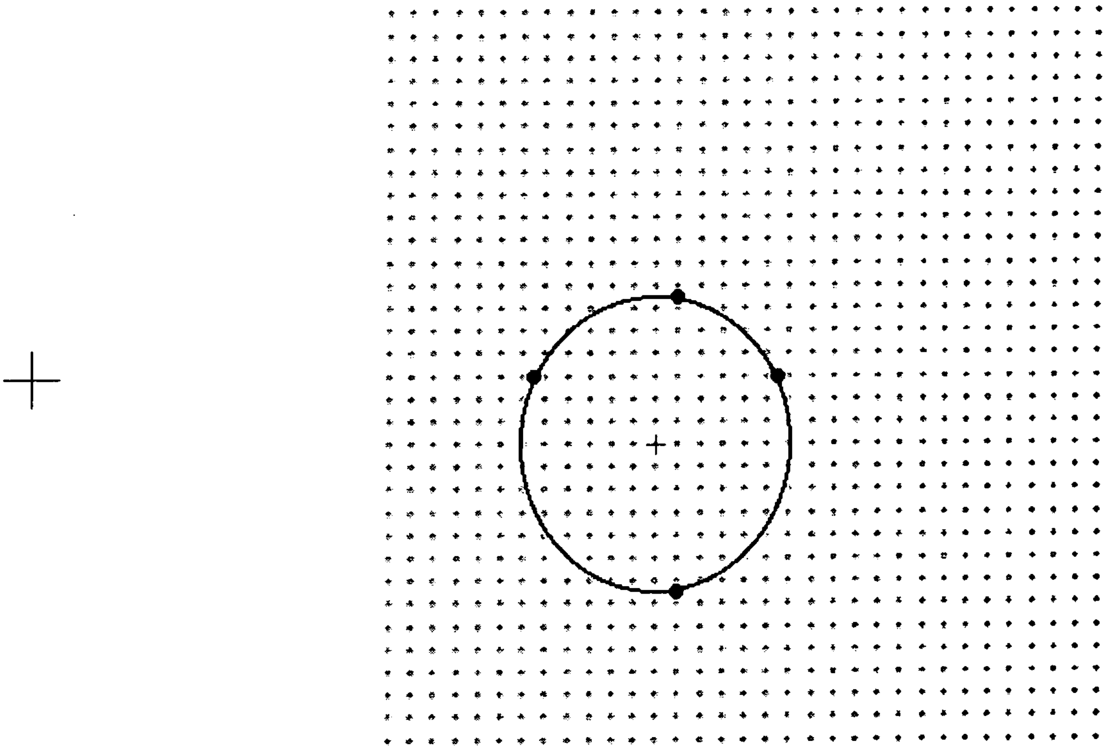


Figure 5.1. Example results of the blind spot mapping program for subject PY showing the four boundary points and the fitted ellipse. The centre of the ellipse is marked with a small cross. The points on the grid were separated by 0.5 cm.

Subject	Distance along horizontal meridian (degs)	Vertical displacement above/below horizontal meridian (degs)	Height (degs)	Width (degs)
AP	15.5	-0.5	6.1	4.7
CH	14.0	-0.2	8.6	4.7
IG	15.0	-1.3	5.6	4.1
KF	15.7	-1.5	5.2	6.1
PY	13.8	-1.5	6.2	5.5
SH	14.0	-0.3	5.7	5.7
Mean	14.7	-0.9	6.2	5.1
SD	0.7	0.6	1.1	0.7

Table 5.1. Blind spot centres for 6 subjects given in terms of horizontal and vertical displacement together with estimates of height and width. Negative numbers represent displacement below the horizontal meridian.

Calibration of the display

When using red-green glasses for binocular separation, it is important to ensure that the left eye is blind to the image intended for the right eye and vice versa. If the red and green phosphors of a colour monitor are used together with broad-band filters, then full separation will not occur. There will be 'crosstalk' which means that some red light will be transmitted through the green filter and vice versa. However, it is possible to achieve completely monocular images by adjusting the colours on the monitor of the regions that should appear light and dark using a procedure outlined by Mulligan (1986).

The aim of the matching procedure is to make four colours; monocular green, monocular red, binocular yellow and binocular brown. To make these colours a test display is set up displaying each of these four colours as shown in Figure 5.2(a). To begin with, red is the maximum value of the red phosphor and contains no green light, green is the maximum value of the green phosphor and contains no red light. Yellow is an additive mixture of the maximum value of the red and green phosphors while brown (black) contains no red or green light. These colours need to be altered such that the views shown in Figure 5.2(b) and Figure 5.2(c) are obtained.

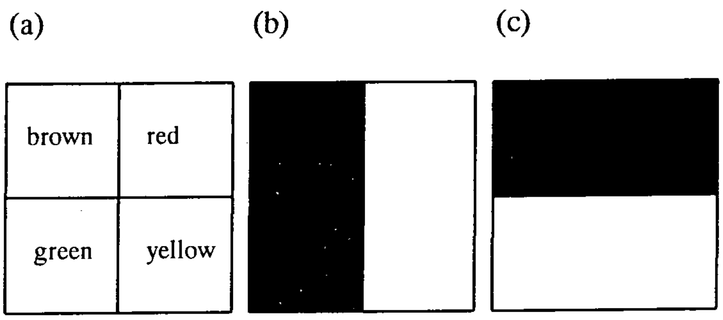


Figure 5.2. Schematic representation of the colour calibration display from Mulligan (1986). (a) The test display. (b) The test display as it should appear after matching viewed through the red filter only. (c) The test display as it should appear after matching viewed through the green filter only.

The essence of the procedure is to mask the cross-talk of the filters by increasing the luminance of the brown colour by adding red or green light to it. For example, the green patch viewed through the red filter will initially appear brighter than the brown patch because the red filter allows some green light through. To compensate for this, red light is added to the brown patch to equalise the luminance of the two patches. However as the brightness of the background patches (as seen through each filter) is increased, the complementary colour must also be added to the monocular patches to make them indistinguishable from the background colours. Thus green light must be added to the red patch so that it appears indistinguishable from brown through the green filter and red light must be added to the green patch so that it appears indistinguishable from the brown patch through the red filter. So to produce a match it is necessary to alter three colours in the display; brown, red and green in an iterative fashion.

This procedure was employed to obtain the views given in Figure 5.2 (b) and 5.2 (c) at the viewing distance required. The luminance of each patch as viewed through each filter was also measured using a photometer and these values are given in Table 5.2.

Viewing Filter	Colour of patch			
	Brown	Green	Red	Yellow
RED	1.62	1.66	2.07	2.00
GREEN	1.41	2.04	1.36	1.87

Table 5.2. Luminance values (cd/m^2) for colour patches viewed through each filter.

Design of experiment

Subjects were required to detect as quickly and accurately as possible the presence or absence of a target (horizontal line). The target was presented to the right hemifield at one of five radial positions at the same eccentricity as the blind spot. The stimulus positions were located on meridians that were separated by 30°, one at the blind spot locus, two above and two below. The bars were 4° x 0.25° and the viewing distance was 40 cm.

In the multiple item conditions, the target was accompanied by three vertically oriented distractor items arranged randomly in three of the non-target positions (excluding the blind spot). On target absent trials, an additional distractor was presented so that the total number of stimuli on each trial was always four. The target was either monocular or dichoptic with respect to the distracters and target and distractors were presented to one eye only.

Single item trials were included to examine whether choice reaction times differed by location in a manner similar to the multiple item trials. In these trials, subjects had to detect whether the single item presented was a target or a distractor. To control for the possibility that reaction times to targets in the two eyes might differ, the target was presented to either eye with equal probability. This also had the advantage of keeping the overall adaptation state of the two eyes the same throughout the course of a block of trials. In addition, in the multiple item conditions, this enabled some estimate of the stability of fixation since some targets would inevitably fall in the blind spot.

Given each possible permutation of variables, there were 1600 multiple item trials (2 target present/absent x 5 target positions x 2 eyes x 2 tasks x 40 repeats). In addition, there were 720 single item trials ((2 target present/absent x 5 target positions x 2 eyes x 40 repeats) - (2 target present/absent x 1 target position x 1 eye x 40 repeats)). The number subtracted is those trials that would have placed a single item in the blind spot. The total number of trials was 2320 which was split into 8 blocks of 290 trials. Within each block the trials were presented in pseudo-random order.

During the experiment, subjects were provided with a continuously visible binocular fixation point. Each trial began with a fixed delay of one second before the stimulus configuration was presented. The offset of the stimulus display was governed by the subject's response. Feedback was provided by accompanying incorrect responses by a tone.

RESULTS

Error rates

The error rates for the blind spot, multiple item trials and single item trials are shown in Table 5.3. The error rate for the blind spot is the percentage of 'yes' responses to targets presented to the blind spot. The error rate for the multiple and single item trials is the percentage of incorrect responses (both target present and target absent trials). The accuracy of the blind spot mapping procedure, and or stability of each subject's fixation can be checked by comparing the error rate in the blind spot with that in the multiple item trials (no targets were presented to the blind spot in the single item trials). For all subjects, the error rate in the multiple item trials was less than 5% and the error rate in the blind spot was similar. However, the blind spot error rate for subject AP was rather higher than the error rate in the multiple item trials suggesting that fixation was less reliably maintained in this subject. Since this subject's results were similar to those of other subjects, this subject's data was left in the analysis.

For all subjects, the error rate in the single item trials was higher than in the multiple item trials suggesting that the former task was more difficult. The error rates in the single item trials for subjects IG and SH are especially high and probably represent a carry-over effect. These subjects had participated in a previous search experiment where the target was a vertical rather than horizontal bar.

Error Source	Subject					
	AP	CH	IG	KF	PY	SH
Bspt	15.2	1.3	2.5	1.3	2.5	1.3
Multiple	3.5	4.2	1.6	2.1	2.6	3.7
Single	5.0	7.0	14.2	6.7	3.1	10.0

Table 5.3. Percentage error rates obtained in the blind spot, multiple and single item trials. The error rate for the blind spot is the percentage of 'yes' responses to targets presented to the blind spot. The error rate for the multiple and single item trials is the percentage of incorrect responses made on the target present and target absent trials.

Reaction times in the single and multiple item trials

For the analysis presented in this section, reaction times that were less than 200 ms or greater than 3000 ms were discarded as motor errors and incorrect responses were removed. Since target-absent trials (in the search conditions) do not provide location specific information, they were also excluded from the analysis. Trials where the target was presented to the blind spot (which are effectively target-absent trials) were also eliminated. Mean reaction times were then calculated for each subject and condition and these values constituted the raw data for the following descriptive and inferential analyses.

The mean overall reaction times for each choice RT task (single item, multiple item monocular and multiple item dichoptic) are given in Figure 5.3. This shows very little difference in RTs between the three tasks. Since nasal and temporal hemifields yielded similar reaction times, they are combined in the following charts. Figure 5.4 illustrates that the pattern of RTs by visual field position is U-shaped with fastest RTs centred on the region corresponding to the blind spot. Figure 5.5 shows the position by task interaction and there is some indication that RTs in the single item trials were less U-shaped than those in the multiple item trials.

A two-way repeated measures ANOVA was undertaken on the data using Task and Position as Factors. This showed that while there was no significant main effect of task ($F = 0.57$, df = 2,10, $P > 0.05$) there was a highly significant main effect of position ($F =$

19.61, df = 4,20, P < 0.01). The task by position interaction approached but failed to reach significance (F = 1.92, df = 8,40, P = 0.084).

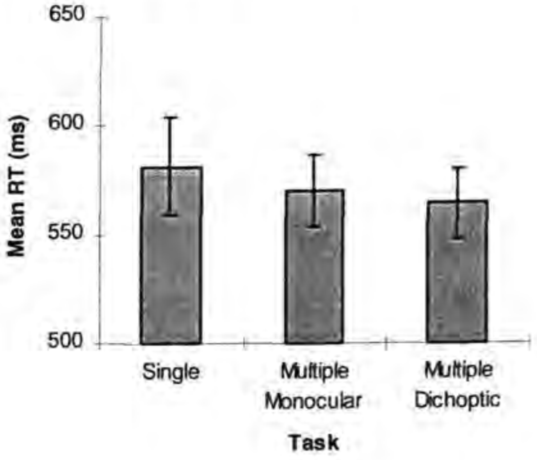


Figure 5.3. Mean reaction times to targets in the single and the multiple item trials collapsed across visual field position for 6 subjects. Error bars represent one SE +/- mean.

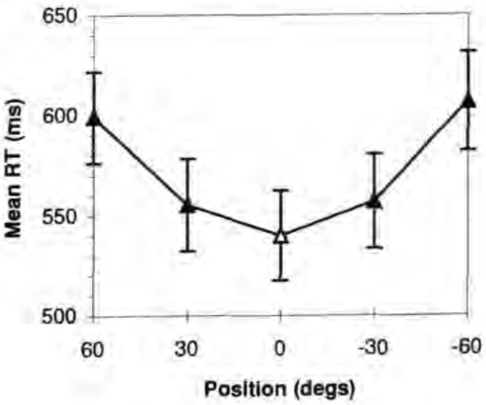


Figure 5.4. Mean reaction times to targets according to position in the visual field. Position (degs) refers to the angle of the meridian at which the target was located in relation to the blind spot. The results are shown for the upper to lower visual field from left to right on the abscissa and zero represents the region corresponding to the blind spot. The symbol for the region corresponding to the blind spot is different to highlight the fact that it is based on measurements solely from the left eye while data for the other positions is based on measurements from both eyes.

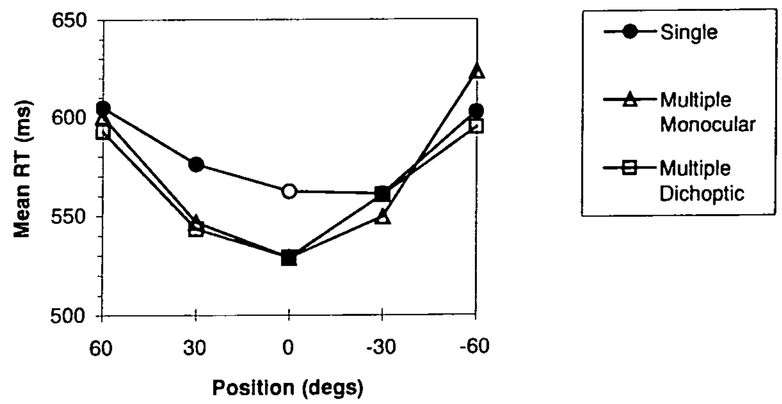


Figure 5.5. Mean reaction times for task by position for 6 subjects. The abscissa is as indicated in the legend of Figure 5.4.

To further investigate the position effect, a post hoc analysis was undertaken. The Newman-Keuls test was selected as appropriate as it is recommended by Howell (1992) for use when there are 3-5 groups and more than 2 pairwise comparisons to be made. The goal of the Newman-Keuls test is to sort treatment means into subsets of treatments which do not differ from themselves but differ from other subsets. This test revealed that the three inner positions (0, +30 and -30) were not significantly different from each other ($P > 0.05$). Similarly, the two outer positions (+60, -60) were also not significantly different from each other ($P > 0.05$). However, reaction times to targets in the three inner positions were significantly faster than reaction times to the two outer positions ($P < 0.05$).

DISCUSSION

Spatial nonuniformities in visual search

Although not central to the issues outlined in the introduction to this chapter, the spatial variation with reaction times should be discussed. This experiment found a U-shaped pattern of reaction times by visual field position that was centred on the region corresponding to the blind spot. Such a pattern of results is similar to that of Efron & Yund (1996) who examined the variation of reaction times with hemifield, position and target orientation (horizontal or vertical). As in this experiment, the stimuli were located at positions equidistant from the fovea and both bar and square wave gratings were used as targets. In multiple item conditions, using horizontally oriented targets, Efron & Yund found a U-shaped position effect in the right hemifield, which for bar stimuli was similar in magnitude to the one reported here. For vertically oriented targets, the function relating RT to position was relatively flat.

Efron & Yund argue the different shapes of the position effect for horizontal and vertical targets reflect the influence of low level factors in visual search. The effect can be interpreted in terms of the visual lobe and the radial organisation of the visual field. The visual lobe refers to the elliptical shape of isocontours for lines of equal photoreceptor density (e.g. Curcio et al., 1987) or spatial resolution (e.g. Rijsdijk et al., 1980; Pointer & Hess, 1989;1990) whose long axis is aligned with the horizontal meridian. This factor predicts faster reaction times for stimuli at the horizontal meridian than stimuli at the same eccentricity on the vertical meridian. As previously noted in Chapter 2, the visual field shows a radial effect for motion detection, the resolution of gratings (Rovamo et al, 1982) and spatial interaction zones (Toet & Levi, 1992). This factor predicts faster RTs for vertically oriented targets at the vertical meridian and faster RTs for horizontal targets on the horizontal meridian. For horizontal targets the effect of the visual lobe and radial organisation of the visual field operate in the same direction, producing a U-shaped function while for vertical targets, the two effects cancel producing a relatively flat function.

A further spatial non uniformity in this experiment, that may contribute to the position effect, is the increased sensitivity of the region corresponding to the blind spot. Both monocular contrast sensitivity (see Chapter 2) and thresholds for luminance detection (Wolf & Gardiner, 1963) appear to be increased in the region corresponding to the blind spot. In addition, Schmielau & Marzi (1983) found that simple reaction times to spots of light in the region corresponding to the blind spot were 10 ms faster than in other locations along the horizontal meridian. However, to be certain this was an influence on the position effect observed here, the shape of the position effect at other eccentricities would need to be examined to see if it was significantly less curved than the one observed here.

Binocular interactions in visual search in the RCBS

The experiment presented in this chapter showed that pop-out in the region corresponding to the blind spot is similar to that in regions of the visual field at the same eccentricity that are displaced above and below the blind spot by a meridional angle of 30°. This suggests that the monocularity of the blind spot does not affect preattentive vision. In addition, a similar degree of pop-out was obtained whether the distracters were presented monocularly or dichoptically suggesting that eye of origin also has no effect on performance. However, before concluding that the search process is unaffected by eye of origin, it is necessary to assess whether this experiment provided optimal conditions for revealing eye of origin effects.

It is possible that this experiment was dominated by high level factors in visual search, rather than low level processes occurring early in the visual system where cells are differentially weighted according to each eyes input. Bravo & Nakayama (1992) suggest that attention can be guided in two ways. Top-down guidance of attention can occur when the target identity is known, while in the absence of such information, detection of the target must rely on interactions between the target and distracters which are likely to be more effective when the density of items in the display is high.

In this experiment, subjects searched for a target of known orientation rather than a target defined by sensory pop-out and the stimuli were widely spaced. Using displays where the elements were also widely spaced, Findlay (1997) found that prior specification of the target shape improved the percentage of saccades accurately directed to the target. This may be contrasted with the results of Williams (1967) who used denser displays and found that providing subjects with information concerning the target shapes led to very little benefit in overall search times or in the ability to restrict fixations to the appropriate shape. This suggests that manipulating the density of the elements in the display will affect the extent to which performance is governed by lateral interactions between stimuli.

Accordingly, it has been shown that texture segregation and pop-out effects are reduced as the density of texture elements decreases (Nothdurft, 1985; Sagi & Julesz, 1987). Similarly, Kneirim & Van Essen (1992) found that the general suppressive effect of a surround on the response of a cell to a stimulus in its classical receptive field diminished as the density of the elements was reduced. In addition, orientation dependent suppression was stronger when the surround stimulus completely surrounded the classical receptive field as opposed to covering only the end-zone regions or flanks. This suggests that increasing the density of elements in the display and having the distracters completely surround the target might be a more effective test of whether eye of origin can affect visual search. This possibility is investigated next in Chapter 6.

Another important point is that this experiment only demonstrates an absence of binocular interactions in visual search for targets which are orthogonal to the distracters. If the effect of eye of origin on visual search is subtle, then perhaps it is only apparent at small target-distractor orientation differences. This issue is also examined in the following chapter.

6

Dichoptic Visual Search for Orientation and Eye-of-Origin in Central Vision

ABSTRACT

The studies reported in this chapter investigate binocular interactions in visual search. In total, three visual search experiments are described in which the target was either presented to the same eye as the distracters (monocular condition) or to the opposite eye (dichoptic condition). The target was defined either in terms of a difference in orientation from the distracters (Experiments A), or solely by eye of origin (Experiments B and C). In all experiments, subjects were required to identify the location of the target and thus pop-out was measured in terms of the proportion of targets correctly localised rather than the reaction time to detect the target presence or absence (as in the experiment reported in the previous chapter). In addition, a target of unpredictable orientation was employed and the display was presented in central vision.

Whereas subjects searched for a target of known orientation in Chapter 5, the target was defined by sensory pop-out in Experiment A. This experiment systematically varied the orientation difference between the target and distracters. For a range of orientation differences (7.5-21°) no difference in pop-out between the monocular and dichoptic conditions was observed. At an orientation difference where performance in the monocular condition was close to chance, performance in the dichoptic condition was significantly higher. This suggested the possibility that subjects could use eye of origin

information to guide search. This issue was examined in Experiment B which found that most subjects (4/6) could reliably identify the target when it was defined solely by eye of origin. Finally, in Experiment C, the extent to which this performance was based on a luminance cue was examined. Most subjects (2/9) were unable to perform the eye of origin search task when the luminance values of the targets and distracters were randomised. This suggests that most subjects cannot discriminate a target based on eye of origin per se and that the superior performance in the dichoptic condition of Experiment B at the smallest orientation difference is largely due to the presence of a luminance artefact. Overall, the evidence suggests eye of origin is not a basic feature available to the search process nor something which interacts with other features such as orientation. This seems to support the notion that preattentive search for orientation is mediated beyond V1.

INTRODUCTION

The experiments in this chapter pursue the issue raised in the previous chapter, that of binocular interactions in visual search. Although the experiment discussed in that chapter did not find any evidence of such interactions, for the reasons outlined in the discussion, the experiment did not seem a comprehensive test of the hypothesis. Before describing the experiments of this chapter, this introduction will review further evidence that suggests that binocular interactions could affect the search process, drawing somewhat upon the literature presented earlier.

As reviewed in Chapter 4, both Nothdurft (1991b;1992) and Sagi (1987;1990) emphasise the importance of feature differences in both pop-out and texture segregation. Nothdurft (1991b;1992) found that increasing the background orientation difference required a larger local orientation difference to detect both pop-out singularities and texture bars suggesting a mechanism which depends continuously on orientation difference. Similarly, Sagi (1990) suggests that preattentive detection is only possible if the target generates a strong local difference signal in comparison with local difference signals generated by the distracters. This view is supported by evidence showing that detection of orientation differences improves with increasing element density both in texture discrimination tasks (Nothdurft, 1985) and in search tasks (Sagi & Julesz, 1987).

Electrophysiological studies in the cat and monkey show that a substantial proportion of cells in striate cortex are selective for feature differences and this has been found for both orientation and direction of motion (Born & Tootell, 1991; Kneirim & Van Essen, 1992; Grinvald et al., 1994; Kastner et al., 1997). Studies of orientation difference have reported that some cells respond better to a line element that is surrounded by lines of the orthogonal orientation (pop-out condition) than to a line surrounded by lines of the same orientation. If this differential cell activity is to be related to perception, it would imply that the line of the different orientation pops out because there is less target-distractor inhibition than distractor-distractor inhibition. According to the physiological evidence outlined in Chapter 4, the anatomical substrate of this coding of orientation difference may be long-range inhibitory horizontal connections which primarily link regions of striate cortex whose neurons prefer stimuli with similar orientations (Weliky et al, 1995 cited in Derrington, 1996). Thus there is some evidence that the neurological substrate of orientation difference sensitivity is generated in striate cortex.

As reviewed in Chapter 1, a striking aspect of cortical architecture in V1, which is absent from prestriate cortex (Zeki, 1979), is the presence of ocular dominance columns (Hubel & Wiesel, 1977). Most cells in striate cortex show ocular dominance in that while they can be driven by either eye, most show a preference for the stimulation of one eye. Cells sharing the same ocular preference are grouped together in columns spanning all cortical layers which have been revealed using autoradiography (Hubel & Wiesel, 1977) and cytochrome histochemistry (Rosa et al., 1992) as long parallel and bifurcating stripes. The basis of ocular dominance is due at least in part to inhibitory interactions between the to eyes. This was demonstrated by Sillito et al (1980) (see Chapter 1) who found that blocking GABA mediated inhibition in the striate cortex of cats increased the responsiveness of the non-dominant eye.

Thus research highlights two different modulatory influences on the responsivity of a striate cell's input to its classical receptive field (the area over which the cell gives an excitatory response to a single bar of light). One source comes from long-range horizontal connections which extend across space and enable modulation of the visual signal by its visual context (lateral interactions). The other source is suppression for the corresponding point in space that originates from the other eye (interocular inhibition).

An important question concerns how these two forms of modulatory influence might interact. Do lateral interactions depend on eye of origin or do lateral interactions occur after interocular inhibition?

If lateral interactions in V1 are affected by the fact that cells in this area are unequally driven by the two eyes, then one might expect the strength of these interactions to differ according to the eye of origin of the stimuli. Physiological evidence that is consistent with this notion comes from cross-correlation studies in cat and monkey. These have found evidence for excitatory connections between cells with like orientation preferences (<30°) and noted that cells were more likely to show correlated activity if they shared the same eye preference (T'so et al, 1986; T'so & Gilbert, 1988). This suggests that the strength of lateral interactions between stimuli may depend on their eye-of-origin.

Psychophysical evidence for the incomplete ocular transfer of lateral interactions comes from the tilt illusion (see Chapter 4). When surrounded by two lines of a differing orientation, a test line changes its apparent orientation in a direction away from that of the surround lines. This change in apparent orientation is reduced with dichoptic presentation of test and surround lines (Westheimer, 1990). In response to this study, Gilbert & Wiesel (1990) found evidence of orientation specific lateral interactions in V1 of the cat. A neural ensemble was modelled encoding orientation with which it was shown that some of these lateral interactions could account for the tilt illusion. These studies suggest that the tilt illusion is mediated by lateral interactions whose activity may be modulated by eye of origin.

Given the previous evidence linking visual search for orientation to orientation specific lateral interactions, the degree of orientation pop-out may also differ according to the eye of origin of the stimuli. Although this issue was partially addressed in Chapter 5, the following experiments sought to reduce top-down influences in search by making the target orientation unpredictable on each trial, and using a dense display in which the distracters completely surrounded the target to maximise lateral interactions between stimuli. However, the paradigm was the same and in all experiments, the distracters were either presented to the same eye (monocular condition) or eye opposite to the distracters (dichoptic condition).

GENERAL METHODS

The following experimental details are generic to the experiments reported in this chapter.

Equipment and experimental set-up

All displays were presented using a mirror stereoscope which unlike anaglyphs do not provide the subject with a colour cue as to the eye-of-origin of stimuli. The stereoscope was composed of two EIZO Flexscan 6500 21 inch monochrome monitors with a screen resolution of 764 by 1024 pixels. The width of the visible display was approximately 35 cm and the viewing distance was about 100 cm. The frame-rate (as given by the VSG function that returns the frame period taking into account any hardware limitations) was 68 Hz. The mirrors of the stereoscope were 203 mm wide by 246 mm high and fixed at right angles to each other. The stimuli were drawn using the VSG 2/3 graphics board with accompanying software V4.062.

In setting up the stereoscope, it was first ensured that the distance between the apex of the mirrors to each monitor was identical and that the base of each monitor was aligned both vertically and horizontally. The mirrors were moved backwards and forwards in relation to the observer to change the horizontal alignment of each monitor until each view was appropriately converged. A spirit level was used to try to ensure there was no difference in tilt between the monitors in either the vertical or horizontal dimensions. Once the monitors had been physically aligned, their images were aligned on screen with the aid of a grid pattern displayed on each monitor (kindly provided by Ariella Popple). The luminance of each monitor was matched using a photometer and was indistinguishable by eye.

All experiments were conducted in a dark room where the only light sources were the monitors of the stereoscope. Subjects wore eye-protector goggles with the visor removed to prevent distraction by the sight of the monitors in peripheral vision. Thus vision was completely limited to the experimental display. Head movements were restricted by the use of a chin rest.

Subjects

In total, data from 12 subjects (8 females and 4 males) is presented in the following sections. All subjects had normal binocular functions and scored within the normal range on a test of stereopsis and the Maddox Wing test. 8 subjects had corrected to normal visual acuity while subjects BK, EM, KF and MK were emmetropic. Two further subjects were tested for whom the display induced binocular suppression. These subjects often reported seeing a hole in the display, presumably where the dichoptic target was located. The data from such subjects was not analysed.

Paradigm

The basic procedure involved presenting subjects with a 5 x 5 array of oriented lines in central vision (similar to that shown in Figure 6.4) and the task of the subject was to determine whether the target (a single line) had been presented to the left or right of the centre of the screen. Thus pop-out was quantified in terms of a percentage correct rather than a reaction time.

The target could appear in one of three different positions (one up, one down or centre) in each column adjacent to the central column. The actual position was chosen randomly on each trial. The target was defined either by its difference in orientation, or by its different eye-of-origin, or both, in relation to the distracters. Subjects responded by pressing either the left or right mouse button with either the left or right hand.

In each experiment, on equal numbers of trials the target was presented to the left or right of the screen. On equal numbers of trials, the target was presented to the left or right eye and thus the overall adaptation state of each eye was kept constant. The display was shown for about 100 ms followed by a blank field and the subject's response initiated the next trial. Trials were divided into blocks and, within a block, presented in random order using the time the block was initiated to seed the random number generator.

EXPERIMENT A: VISUAL SEARCH FOR A TARGET DEFINED BY EYE OF ORIGIN AND ORIENTATION DIFFERENCE

In the experiment reported in the previous chapter, the search task may have been unduly dominated by high level factors since subjects were searching for a target of known orientation. Any dichoptic effects of interactions between target and distracters are more likely to be revealed if the target is defined by its sensory difference in orientation from the distracters. For this reason, the orientation of the lines was randomised on each trial, while the difference in orientation between distracters and target was systematically varied.

Method

The actual position of each line element (0.4° x 1 min) in the display was jittered by up to 10% of its position as given by the regular grid spacing (+/- 4 mins). This was to prevent subjects from doing the task on the basis of a global structure (Meigen et. al., 1994) and to encourage subjects to make local orientation difference judgements. The mean angular separation of each line was approximately 0.7°. A square binocular frame was provided to help subjects maintain a stable state of convergence. The frame subtended 5.5°, was approximately 6 mins wide and was continuously visible throughout a block of trials. The luminance of the stimuli on the left monitor was 6.70 cd/m^2 and 6.71 cd/m^2 on the right monitor (mean of three measures).

Across the experiment, the difference in orientation between the target and distracters was varied from 3.5°-21° in steps of 3.5°. The target was either monocular or dichoptic, and the eye of the target was variable. Typically subjects participated in 3 blocks each consisting of 480 trials. One block consisted of 5 repeats of each permutation of orientation difference, eye and task.

On a single trial, a binocular fixation cross was presented to the centre of the screen which was displayed for about 1 sec. This was replaced by the stimulus display which was presented for 100 ms and then replaced by a blank field. The subjects response initiated the onset of the next trial.

Results

The proportion correct obtained for each search task for each subject is shown in Figure 6.1. The mean proportion correct obtained overall is shown in Figure 6.2. The most notable feature of the results is that for most subjects (AH, AP, CM, IG, KF and KP) performance in the dichoptic condition is conspicuously high at an orientation difference of 3.5° where performance in the monocular condition is close to chance. A 2-way repeated measures ANOVA was undertaken using the mean of each subject for each condition, using Task and Orientation Difference as Factors. This revealed there was no main effect of Task ($F = 1.07$, $df = 1,7$, $P > 0.05$). As expected there was a highly significant effect of Orientation Difference ($F = 178.31$, $df = 5,35$, $P < 0.01$). There was also a highly significant interaction between Task and Orientation Difference ($F = 9.8$, $df = 5,35$, $P < 0.01$). To investigate the interaction, a posthoc analysis was undertaken. The Tukey HSD (honestly significant difference) test was deemed appropriate as it is recommended for making multiple comparisons between groups (when the number of groups exceeds 6) as it fixes the family-wise error rate[4] at 0.055 (Howell, 1992, p.363). This revealed that the significant interaction between Task and Orientation Difference was entirely due to the superior performance in the dichoptic condition (Mean = 0.66, SE = 0.03) compared to the monocular condition (Mean = 0.53, SE = 0.02) at an orientation difference of 3.5° ($qHSD = 0.066 <$ Mean Diff. $= 0.132$, $P < 0.05$).

This experiment shows that search in the dichoptic condition is more accurate than in the monocular condition, but only at the smallest orientation difference tested (3.5°). At this orientation difference, performance was close to chance in the monocular condition. This difference may reflect binocular interactions in visual search for orientation or, may reflect the use of some 'peripheral' cue by subjects, such as a difference in luminance sensitivity between the two eyes. If the latter explanation is correct, wide

---

[4] The familywise error rate is the probability of making at least one type I error when making a set of comparisons between group means.

variation in the ability of subjects to perform the task might be expected and the failure of subjects CH and BK to show the dichoptic advantage could be attributed to an absence of such cues. From this view it is not surprising that CM showed the largest dichoptic advantage as the author is most familiar with the display and therefore has most experience with subtle cues associated with the target. To examine this issue the following experiment looked at whether subjects could perform at a level greater than chance when the target was defined solely by its different eye of origin from the distracters.

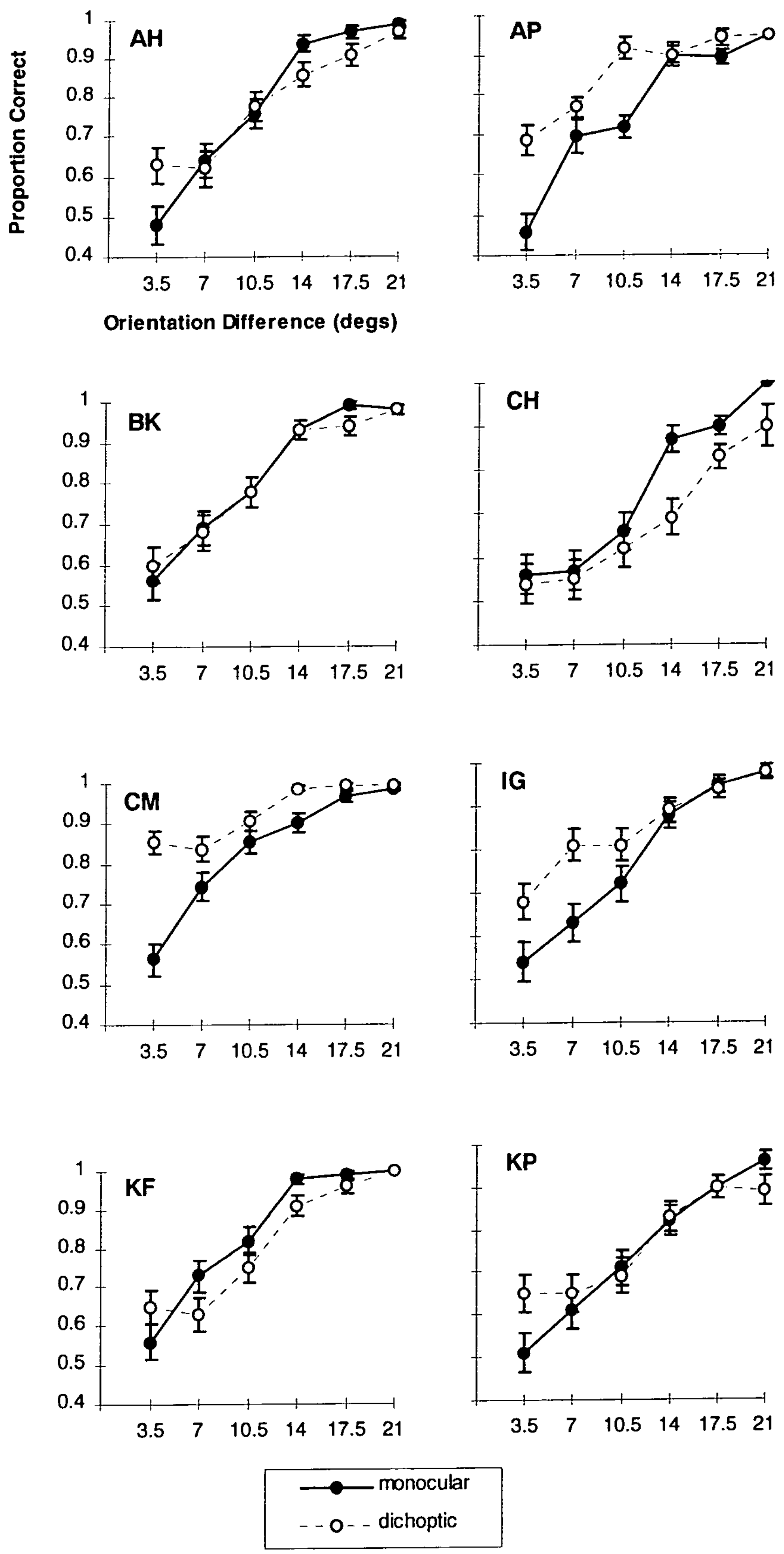


Figure 6.1. Proportion correct obtained in the monocular and dichoptic search tasks for each subject. Error bars represent +/- one S.E. for a proportion drawn from a binomial distribution. All axis labels are as for AH.

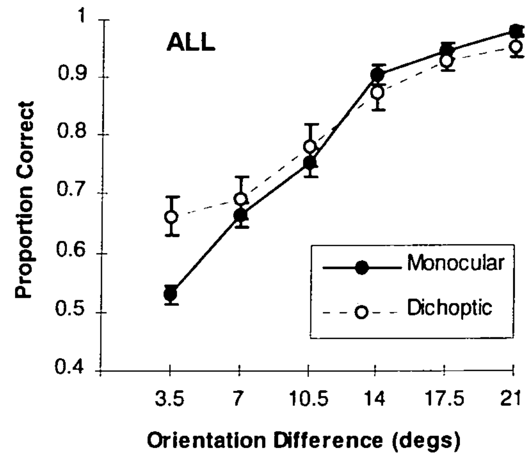


Figure 6.2. Mean proportion correct for 8 subjects. Error bars represent +/- one S.E. of mean across subjects.

EXPERIMENT B: VISUAL SEARCH FOR A TARGET DEFINED SOLEY BY EYE-OF-ORIGIN

Method

Subjects participated in 240 trials in which the target was always dichoptic, of the same orientation as the distracters and could appear on either side of fixation. Again the eye to which the target was presented varied across trials. Instead of being asked to select the line which differed in orientation from the background, subjects were asked to identify the line that appeared the 'most salient'. 6 of the subjects who had participated in the previous experiment also participated in this task. No feedback was provided. All other experimental details are as in the previous experiment.

Results

Figure 6.3 shows the proportion correct obtained for each subject. One tailed binomial probability tests were undertaken to determine whether the observed proportion correct for each subject was significantly higher than chance ($p = 0.5$). This showed that subjects AP (Obs. Prop. = 0.83, $P < 0.01$), CM (Obs. Prop. = 0.91, $P < 0.01$), KF (Obs. Prop. = 0.59, $P < 0.05$) and CH (Obs. Prop. = 0.58, $P < 0.05$) could detect the target at a level greater than chance. The scores of subjects AH (Obs. Prop. = 0.46) and BK (Obs

Prop. = 0.55) were not significantly higher than chance (P > 0.05). Overall then, most subjects (4/6) could detect the target at a level greater than chance. The mean proportion correct obtained overall was 0.65 with a standard deviation of 0.16.

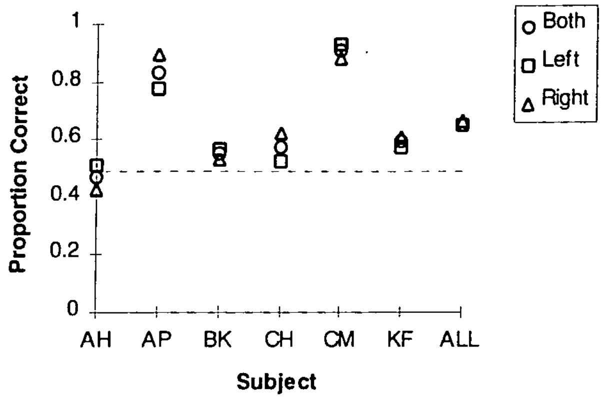


Figure 6.3. Proportion correct obtained for each subject in the task where the target was defined solely by its different eye of origin to the distracters (Ntrials = 240). Both is the mean of the left and right eye proportions. The dashed line indicates chance level of performance. ALL is the overall mean proportion correct.

EXPERIMENT C: VISUAL SEARCH FOR EYE-OF-ORIGIN WITH RANDOMISED LUMINANCE

To determine the extent to which subjects in the previous experiment were using a luminance cue to detect the target, the luminance of each line (target or distractor) could randomly assume one of four different values. As in the previous experiment, the target was defined by its dichoptic presentation to the eye contralateral to the distracters and both target and distracters were presented monocularly. Feedback was provided by accompanying errors by a low tone. Subjects were first given 20 practice trials after which they completed 160 experimental trials.

Display

The luminance of the lines on each monitor were indistinguishable by eye. Measured with a photometer and taking the mean of three measures, the luminance values of the stimuli on the right monitor were 4.38, 13.5, 34.9 and 62.0 cd/ m^2. The corresponding values for the left monitor are 4.47, 14.1, 35.0 and 61.5 cd/ m^2. To stabilise horizontal vergence and cyclovergence, the lines were drawn on a binocular background that was displayed throughout the experiment. This background, which extended over the entire screen (19.5° x 14.2°), consisted of squares (of side 0.6°) each of which were randomly filled in black (0.05 cd/m^2) or grey (1.6 cd/m^2). In the centre of the background, black filled circles were drawn in which the lines were presented on each trial. An example of the experimental display is given in Figure 6.4. The position of the lines in the display (1° x 0.1°) was jittered by up to 10% of the regular spacing of the grid (+/- 0.15°/ 9 mins arc). The mean angular separation between stimuli was 1.5°.

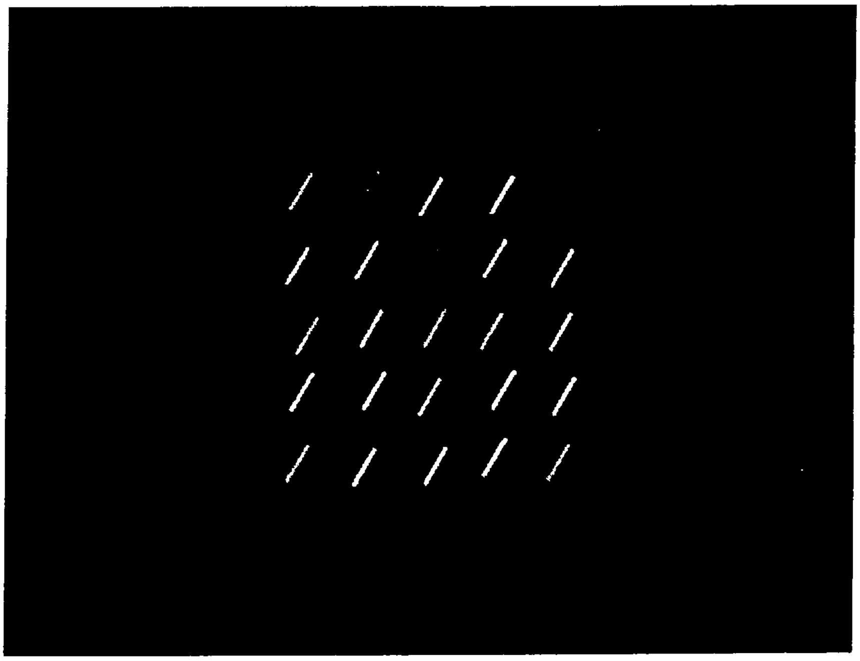


Figure 6.4. Experimental display for the search experiment in which the target is defined by its different eye-of-origin to the distracters and the luminance of the stimuli is randomised.

A single trial consisted of the presentation of a binocular fixation stimulus (a circle drawn in a line of a single pixel 0.5° in diameter) shown for about 1 sec, followed by the presentation of the display for 100 ms. The background was then shown for about 1 sec before the onset of the next trial, which was initiated by the subject's response. The actual orientation of the lines was randomised across trials (0-180°), but all lines had the same orientation within a trial.

Results

The proportion correct obtained for each subject is shown below in Figure 6.5. One-tailed binomial probability tests were undertaken on each subject's data to determine whether the observed proportion correct was significantly higher than chance (p = 0.5). Only subjects CM (Obs. Prop. = 0.74, P < 0.01) and IG (Obs. Prop. = 0.77, P < 0.01) scored significantly above chance. Subjects AH (Obs. Prop. = 0.56), BK (Obs. Prop. = 0.51), EM (Obs. Prop. = 0.50), KP (Obs. Prop. = 0.55), LS (Obs. Prop. = 0.51), MK (Obs. Prop. = 0.50) and VB (Obs. Prop.= 0.49) failed to score significantly higher than chance (P > 0.05). Although the probability of making a type I error for 9 independent comparisons is 0.45 at the 0.05 level, the results of CM and IG are so highly significant that they cannot plausibly be attributed to chance. It should be noted though that author CM had previously used this display to pilot a different experiment and was thus very familiar with the display. Overall, most subjects (7/9) were unable to reliably discriminate the target. The mean proportion correct obtained overall was 0.57 with a standard deviation of 0.11.

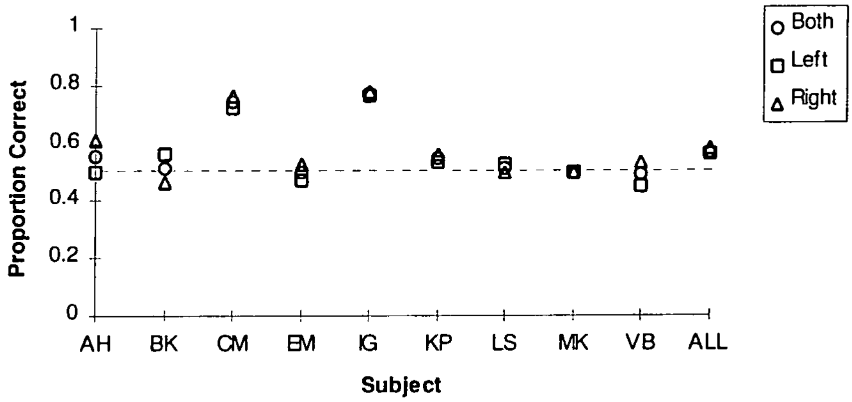


Figure 6.5. Proportion correct collapsed over both eyes (Ntrials = 160) and also shown separately for the left (Ntrials = 80) and right (Ntrials = 80) eyes for 9 subjects. ALL is the overall mean proportion correct. Chance level of responding (p=0.5) is represented by a dashed line.

The fact that a smaller number of subjects showed reliable discrimination in this experiment, and that the overall proportion of correct responses is lower when the luminance of the stimuli is randomised suggests that the superior performance in Experiment A in the dichoptic condition at an orientation difference of 3.5° is due in part to a luminance artefact rather than superior detection of the orientation difference per se.

GENERAL DISCUSSION

Summary of results

Taken together, the results of the Experiments A, B and C suggest that visual search for orientation is mediated by a mechanism that is insensitive to the eye of origin of stimuli. In Experiment A, no difference in pop-out between the monocular and dichoptic targets was observed for a range of orientation differences (7.5 - 21°). While greater pop-out was found in the dichoptic condition at the smallest orientation difference (3.5°), performance was almost at chance in the monocular condition suggesting that subjects were employing cues other than the orientation difference. This was confirmed in Experiment B, in which subjects searched for a target defined solely by its different eye-of-origin. In this experiment, most observers (4/6) were able to reliably discriminate the target. Experiment C suggested this discrimination was aided by a luminance cue since randomising the luminance of the targets and distracters reduced the proportion of subjects who could discriminate the target and the overall mean proportion correct. This suggests that in general, eye of origin information is not available for visual search.

The level of processing at which visual search for orientation occurs

In Chapter 4 evidence was reviewed which suggested that the preattentive processing of orientation was mediated early in the visual system by the lateral interactions that occur between the oriented filters of V1. However, the lack of evidence for an effect of eye of origin in search for orientation tends to support Wolfe's contention that "the orientations that are processed in parallel in visual search are derived from a relatively late, abstracted representation of orientation and not from the sort of oriented luminance contrast that might drive cells in primary visual cortex" (Wolfe, 1996). One line of evidence for this view comes from a study which showed categorical processing of orientation in visual search (Wolfe et al, 1992). While search for an oriented line among homogenous distracters is efficient or largely independent of set size, search for an oriented line among distracters with different orientations is surprisingly inefficient. However, a search task is easier if the orientations of the target can be assigned to a different orientation category from the distracters, thus it is easy to search for a 'steep' (near vertical) target among 'shallow' (near horizontal) distracters. For example, search for a -10° target among -50° and +50° distracters is more efficient than search for a +10° target amid -30° and +70° distracters. This is because in the former case, the target is the only steep item. If search were governed only by the difference in orientation between targets and distracters then these two tasks should yield similar results. Such experiments lead to the conclusion that visual search for orientation must occur at a locus in the system that has access to orientational categories and does not have direct output to orientationally tuned channels in early vision.

There is good evidence that search can proceed at a relatively high level because parallel search has been found for oriented stimuli that are defined by colour, texture, motion or depth differences (Bravo & Blake, 1990; Gurnsey et al., 1992; Cavanagh et al., 1990). The fact that these second-order stimuli support preattentive processing suggest that this stage is not confined to the oriented luminance sensitive cells of V1 and the interactions between these cells.

Further evidence that search occurs on a relatively "late" representation of the visual stimulus comes from another study by Wolfe which examined visual search for a variety of stimuli defined by their binocular properties such as items that have binocular rivalry, items that have cyclopean (but not stereoscopic) features and items that are defined by eye-of-origin information (Wolfe & Franzel, 1988). Items defined by binocular rivalry did not support parallel search. Similar to the results of Experiment C, search for a target defined by its different eye of origin was found to be impossible suggesting that purely monocular information is not available for search. Cyclopean (non stereoscopic) features could be found by parallel search implying that some purely binocular information is available for visual search.

Although eye of origin information does not appear to influence visual search for orientation, there is behavioural evidence which suggests that texture elements are processed independently in each eye, but that such processes are not ordinarily open to conscious scrutiny. Kolb & Braun (1995) presented observers with displays of gabor patches in which a square-shaped texture was defined by the orthogonal orientation of its elements to the background. In the non rivalrous display, identical images were presented to each eye while in the rivalrous displays, each eye was presented with an array of stimuli whose orientation was orthogonal to those in the other eye. The latter display gave rise to a percept comprised of small stars with no impression of there being a target present. The presentation time was short (250 ms) to avoid binocular rivalry. Performance was found to be well above chance (and similar) in both the rivalrous and non-rivalrous displays. The main difference between the two displays was that in the non-rivalrous display, accuracy was highly correlated with confidence while in the rivalrous display, accuracy was uncorrelated with confidence and observers believed they were 'guessing' on each trial. Evidence that rivalrous patterns elicit approximately half the activity of non rivalrous patterns in extrastriate areas V4 and MT (Logothetis & Schall, 1989; Leopold & Logothetis, 1995) led these authors to conclude that rivalrous displays impede the direct propagation of activity from striate to extrastriate cortex. It is argued that reduced input to extrastriate cortex produces a lack of a conscious percept corresponding to the target. Yet activity in striate cortex could still affect behaviour in extrastriate areas via the superior colliculus, the pulvinar or other subcortical nuclei. Hence a texture contrast registered in striate cortex could guide behaviour without entering subjective awareness.

If the interpretation of this evidence is correct it implies that texture elements are processed independently and in parallel in each eye and that the results of this processing are available to direct behaviour. However Morgan et al (1997) failed to find evidence of blindsight in normal observers. Using the same experimental task it was found that observer confidence ratings were predictive of performance in both rivalrous and non rivalrous displays. Observers also reported the target was defined by vague cues such as a difference in brightness or depth from the background. This suggests that observers are not being unconsciously guided by the orientation difference. While orientations may be processed independantly and in parallel in each eye the evidence thus far cannot unequivocally determine whether the results of this processing are available to influence behaviour.

Utrocular discrimination and identification.

In Chapter 1, evidence was reviewed concerning utrocular identification, the ability to identify the eye of origin of a stimulus. In this experiment, it should be noted that subjects were not required to identify the eye of the stimulus but merely to detect that one of the stimuli appeared different in some way. Thus the task was one of utrocular discrimination rather than identification. Whether true utrocular identification is possible is open to debate. Some researchers believe that it is possible with certain kinds of stimuli (Blake & Cormack, 1979a; 1979b; Martens et al, 1981; Timney et al 1997) while others argue that positive results always represent the manifestation of some peripheral cue (Ono & Barbeito, 1985; Barbeito et al 1985; Porac & Coren, 1986). A third group of researchers believe that utrocular identification is possible but that conscious access to eye of origin is only permitted under certain circumstances (Dobbins & Kolb, 1997).

What the literature on utrocular identification does illustrate is that there are numerous peripheral cues that can signal an apparent difference between the two eyes and enable reliable discrimination. Therefore it is perhaps not surprising that two subjects in Experiment C were able to perform the task despite attempts to control many of the cues described in Chapter 1. A cue based on luminance was minimised by randomising the luminance of the stimuli. The position of stimuli was jittered by an amount larger than Panum's area at the fovea so that information provided by a fixation disparity should not have been useful and horizontal and cyclovergence were stabilised with the aid of a binocular patterned background. Neither CM or IG reported any 'feeling in the eye' although subjectively their level of confidence in their decision seemed correlated with their performance as indicated by the feedback. Nonetheless, the possibility cannot be ruled out there was some subtle difference in image quality between the two eyes of these subjects that might be responsible for their above chance performance. Even with refraction, slight differences in acuity may remain. This is especially true in the case of CM whose refractive index differs across the two eyes by 1.75 dioptres. Such a large difference in refraction will also mean that with spectacles, the images to each eye are differentially magnified. Therefore there is potentially both a size cue and a blur cue available.

Conclusion

With reference to the hypotheses outlined in the introduction, it would appear that stimulus eye of origin does not influence visual search for orientation. This in turn casts doubt on the sufficiency of the detection of orientation differences as cortical substrates of the search tasks described in this chapter. Work on utrocular discrimination suggests that eye of origin information is not available to consciousness. It also demonstrates there are many potential differences between the two eyes that can mediate discrimination and hence the search paradigm is easily contaminated by these spurious cues. In the following Chapter, dichoptic interactions in the orientation domain are investigated further using a task in which performance cannot be based on the detection of small peripheral differences between the two eyes.

7

Orientation Difference Sensitivity in Central Vision

ABSTRACT

A problem with using a visual search paradigm to examine dichoptic interactions in orientation difference sensitivity is that there are often other cues available in the display that can be utilised to do the task. Therefore it is unclear from the previous experiments whether the results indicate whether dichoptic interactions exist or whether the results represent the use of cues other than orientation. The studies reported in this chapter were designed to measure orientation difference sensitivity more directly. In two experiments, subjects had to judge which of two flanking lines differed in orientation from a central line. The lines were presented in central vision and the global configuration was horizontal. In the first experiment, when the central line was presented dichoptically with respect to the two flanking lines, 75% orientation difference thresholds were significantly higher by 1.7°, and reaction times to detect the target were significantly slower by 24.6 ms (5% trimmed mean). The second experiment investigated whether performance was affected by the image quality of the stimulus presented to each eye. Randomising the luminance of the central line had no significant effect on thresholds and also replicated the original finding of an increase in threshold in the dichoptic condition, albeit of a smaller magnitude (0.9°). However, no significant difference in reaction time was found. A simple qualitative model of orientation difference coding is presented which accounts for the higher dichoptic thresholds in terms of differential orientation dependent inhibition.

INTRODUCTION

From the studies presented in the previous chapter, it was concluded that visual search for an oriented line is unaffected by the eye of origin of the distracters. This suggests that the process, which mediates visual search for orientation, operates on a representation of the stimulus that lies beyond the orientation sensitive cells of V1 whose inputs and interactions are affected by stimulus eye of origin. However, a problem with using a visual search paradigm to examine dichoptic interactions in orientation difference sensitivity is that the target can be rendered salient by cues other than orientation such as a fixation disparity or difference in image quality between the two eyes. Thus to examine this issue more carefully, a paradigm is required which cannot be contaminated by such spurious cues. The experiments in this chapter presented subjects with three oriented lines with a horizontal global configuration, in which the central line was either monocular or dichoptic with respect to the two flanking lines. The task was to select which of the two flanking lines differed in orientation from the central line.

EXPERIMENT A: ORIENTATION DIFFERENCE SENSITIVITY

Method

As in the experiments of Chapter 6, the display was presented using a mirror stereoscope (see Chapter 6 for details of the stereoscope set-up). An example of the display used is shown in Figure 7.1 and consists of three lines (each 1° x 0.1°) separated by 1.5°. Surrounding the stimulus lines was a binocular square frame of side 9° to aid vergence stability. The width of each rectangular side in the frame was 0.25°. No positional jitter was added to the spacing of the lines. The monitors were set to have the same luminance. Measured with a photometer, the luminance of each stimulus on the left monitor was 6.70 cd/m^2 while the luminance of each stimulus on the right monitor was 6.71 cd/m^2.

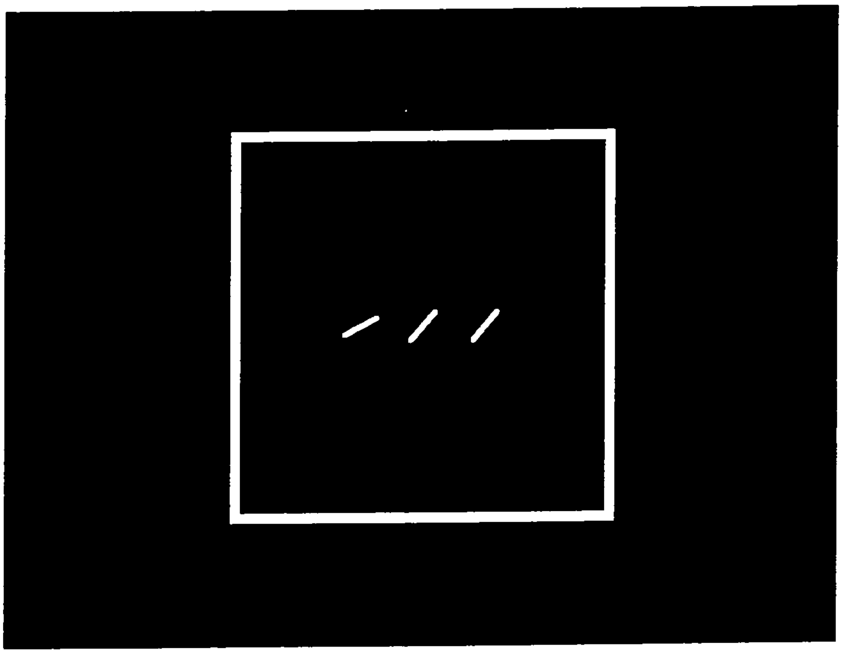


Figure 7.1 An example of the experimental display used in experiment A.

During a single trial subjects were presented with a fixation stimulus for fixed period of about 1 sec. This was followed by the stimulus display which was presented to the centre of gaze and shown for 100 ms. Immediately after this, a blank screen was shown for about 1 sec. The fixation stimulus was a circle of diameter 0.5° drawn in a line one pixel wide. The target was one of the two flanking lines that always differed in orientation from the central line. The task was to decide whether the target was the left or right flanking line. Responses were collected using a button box and reaction times were also measured.

The absolute orientation of the lines was varied randomly on each trial from 0°-180°. The orientation difference between the target and distracters on each trial varied between 3.5° - 21° inclusive in steps of 3.5°. The target could be presented to the left or right eye. 8 subjects with normal binocular vision and normal or corrected to normal acuity participated in this experiment. There were 3 blocks of 480 trials yielding 1440 trials altogether (2 eyes x 2 tasks x 6 orientation differences x 60 repeats). Subject VM was only available for 2 blocks.

Results

A small percentage of trials were removed from each subject's data set because the reaction times were unanalysable. This arose for a number of reasons. There were a few obvious outliers that were several seconds longer than the next reaction time and clearly not part of the process under study. Sometimes the subject pressed the button on the response box the wrong way (so a null response was recorded) or accidentally responded twice to a single trial. This response was automatically accepted as the response for the next trial and recorded as a zero RT. Subject VM had the most (1.4%) trials excluded for these reasons while for the other subjects the percentage of trials removed was typically 0.3%.

Orientation difference thresholds

The probability of a correct response in each condition is plotted against orientation difference for each subject in Figure 7.2. The error bars were calculated using a formula for the standard error of a proportion of size n drawn from a binomial distribution ($SE = \sqrt{P(1-P)/n}$ where P = probability of a correct response). A probit analysis was run on each subject's data to obtain the orientation difference at which a 75% correct response would be obtained. The smooth lines shown in Figure 7.2 represent the fit obtained from probit.

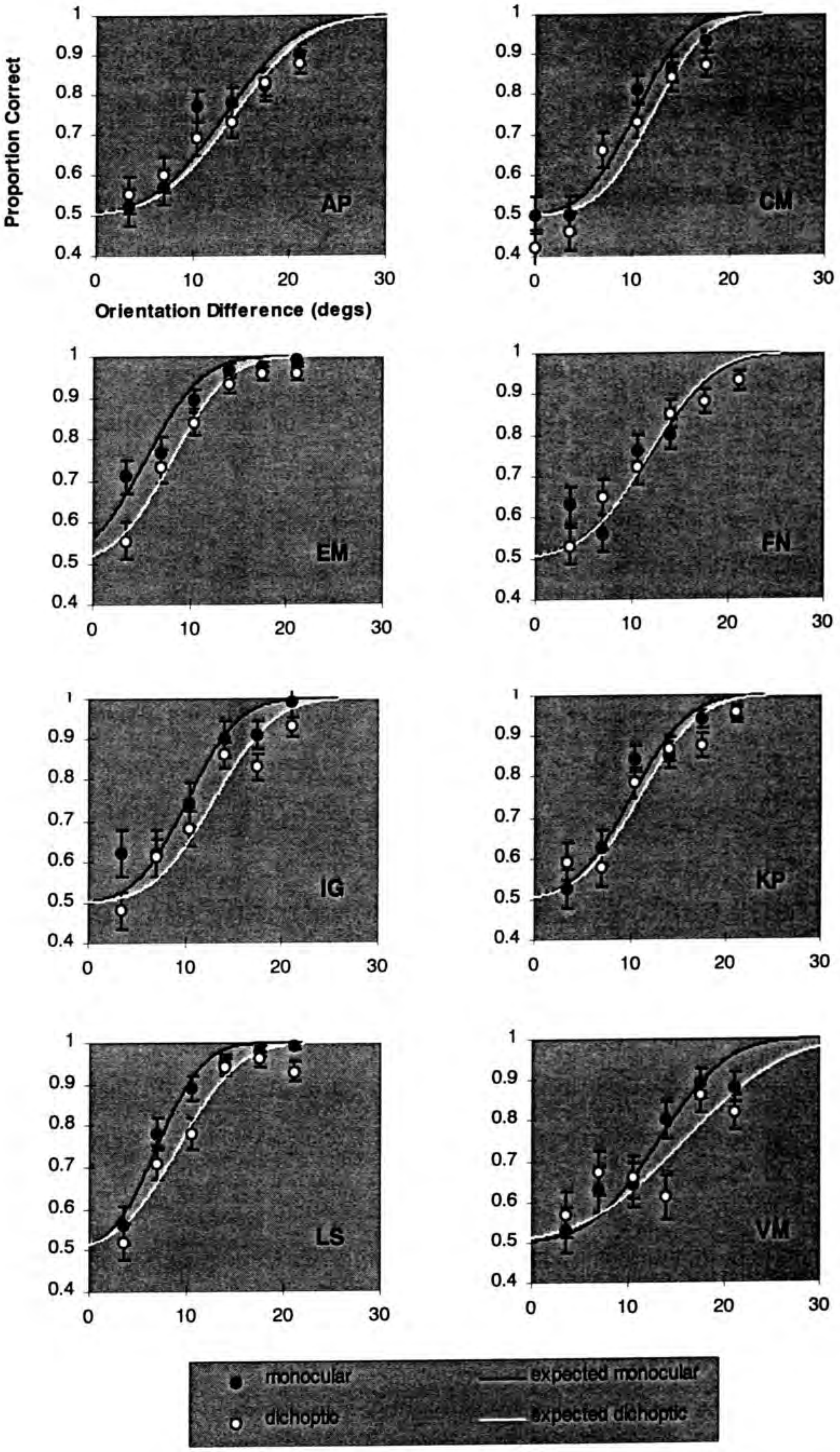


Figure 7.2. Probability of a correct response plotted against orientation difference. The fitted curves obtained from probit are represented by continuous lines.

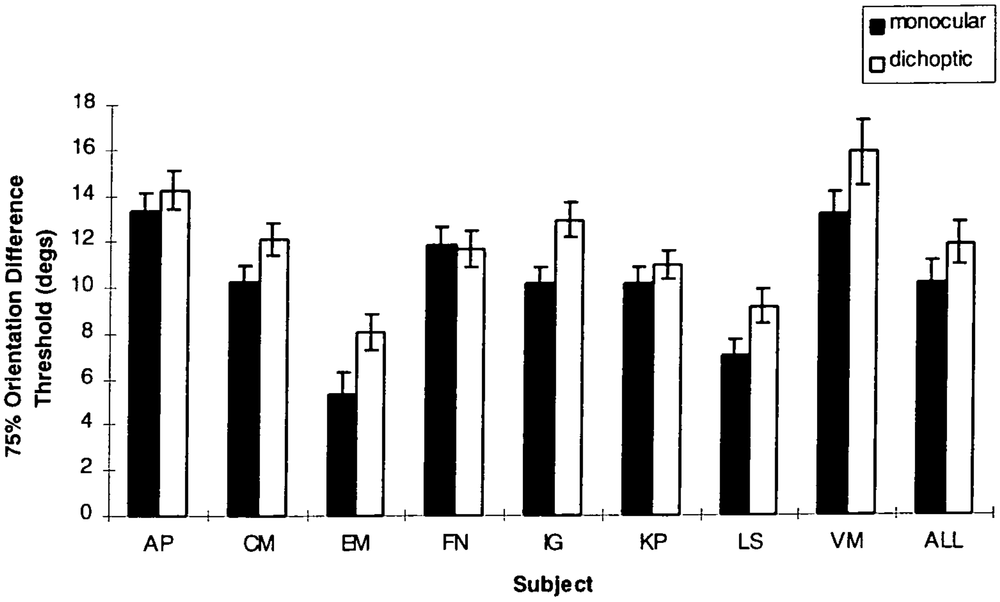


Figure 7.3. 75% threshold estimates for the monocular and dichoptic conditions for each subject. The error bars represent +/- one S.E. whose estimates were also obtained from probit. ALL represents the mean of 8 subject's data with error bars representing +/- one S.E. of the mean.

The 75% threshold estimates obtained from probit for the monocular and dichoptic conditions for each subject are shown in Figure 7.3. This shows firstly, considerable individual variation in orientation difference sensitivity. Thresholds ranged from a low of 5.40°, S.E = 0.90 (subject EM, monocular condition) to a high of 13.20°, S.E = 0.98 (subject VM, dichoptic condition). However, despite this variation, thresholds were typically lower in the monocular condition compared to the dichoptic condition. This is convincing for subjects CM, EM, IG, LS and VM where the error bars in the two conditions do not overlap. The mean threshold estimate for N = 8 subject's data was 10.18°, (SE = 1.00) in the monocular condition and 11.88°, (SE = 0.90) in the dichoptic condition. A two tailed related measures 't' test revealed that these two values were significantly different ($t = 4.52$, $df = 7$, $p < 0.01$).

Reaction times

To find out whether there was an overall difference in reaction times in the two conditions, the data were collapsed across all orientation differences. Although it is likely that correct responses would yield different reaction times from incorrect ones, to analyse this difference it would be necessary to confine the analysis to within levels of orientation difference and this would be unnecessarily complicated. Any speed/accuracy trade-off is apparent from a comparison of a subject's overall reaction time for each condition with their orientation difference threshold estimate.

Subject	Mean		Median		SD		Mean
	M	D	M	D	M	D	Total
AP	380.9	393.0	354.0	353.0	125.3	156.8	387.0
CM	538.6	598.6	451.0	473.0	282.7	370.1	568.6
EM	934.4	957.3	808.0	771.5	494.0.	574.4	945.9
FN	564.3	585.9	529.0	549.0	177.7	197.3	575.1
IG	916.8	968.2	838.0	876.5	289.2	326.4	942.5
KP	959.1	983.6	889.0	925.0	365.8	386.0	971.4
LS	735.3	775.1	642.0	679.5	311.8	371.9	755.2
VM	551.4	561.9	501.0	514.0	203.8	204.0	556.6
ALL	697.6	728.0	626.5	642.7	205.7	210.5	712.8

Table 7.1. Means, medians and standard deviations for reaction times (msecs) obtained in each condition together with the mean total response time for each subject. Values for ALL are the mean of the means, mean of the medians and SD of the mean of the means. M = monocular, D = dichoptic.

Table 7.1 shows that like the threshold estimate, there is a wide variation in response speed across subjects. This may be partly indicative of a speed accuracy trade-off as subject EM, who produced the lowest thresholds produced on average, long reaction times (mean = 945.9) while subject AP who typically responded much quicker (mean = 387.0) was less accurate. It is also interesting to note that subject FN, who showed no difference between thresholds for each condition, still showed slower reaction times in the dichoptic condition, a difference of 20 ms in both the means and medians. All subjects showed larger means and standard deviations in the dichoptic condition.

A problem with analysing reaction time data is that such data are typically not normally distributed but skewed with a long right hand tail (see Ratcliff, (1993) for a discussion of the use of different summary statistics and their consequences for the power of ANOVA). 5% trimmed means were calculated for each subject condition and means calculated for each condition overall. A 5% trimmed mean removes 5% of the data from the tails of the distribution, restricting the extent to which the mean is skewed by data in the tails. Using this technique, the mean in the dichoptic condition was 694.9 ms while the mean in the monocular condition was 670.3 ms, a difference of 24.6 ms. This difference was significant ($t = 4.34$, $df = 7$, $P = < 0.01$).

In summary, orientation difference judgements were worse by 1.7° when the central reference line was dichoptic with respect to the two flanking lines and subjects were slower to respond, by a 5% trimmed mean of 24.6 ms.

EXPERIMENT B: ORIENTATION DIFFERENCE SENSITIVITY WITH RANDOMISED LUMINANCE

Introduction

The discussion on utrocular discrimination in Chapter 1 emphasises that stimuli presented to each eye can differ in image quality in several subtle ways. For example, subjects report that stimuli presented to one eye may appear brighter, clearer or larger than stimuli presented to the contralateral eye (Porac & Coren, 1984). Perhaps subjects were performing the task by looking for the flanking line that was of the same orientation as the central line and a difference in image quality between the two lines made this matching task harder. It is conceivable that a subtle difference in the appearance of the central and the flanking lines was enough to degrade performance even though it was irrelevant to the task. For example, visual search for a target is more difficult when the stimuli in the display differ in luminance (cited in Duncan, 1995). Subjects were asked to decide whether the letter A was present in a 2-8 letter array. In some conditions the luminance of all the letters was the same while in other conditions half the letters were bright and the other half were dim. While changing the luminance of all the stimuli in the display had little effect on performance, search for the letter in the mixed luminance displays was slower and less accurate. This implies that subjects were unable to ignore the difference in luminance of the stimuli even though it was irrelevant to the task.

The aim of this experiment was to look at the effect of changing the luminance of the central line. If it can be shown that this has no effect on performance in either the monocular or dichoptic conditions then this would suggest that a subtle difference in image quality between the two eyes is not responsible for the higher dichoptic orientation difference thresholds observed in the previous experiment.

Method

The luminance of the central line could assume one of three different brightness values. In the 'same' condition, the flankers were the same luminance as the central line. In the 'different' condition, the flankers assumed one of the other two luminance values (see Table 7.2). Same and different luminance conditions occurred with equal frequency in a block of trials.

Same			Different		
1 1 1	2 2 2	3 3 3	2 1 2	1 2 1	1 3 1
1 1 1	2 2 2	3 3 3	3 1 3	3 2 3	2 3 2

Table 7.2. Each permutation of same and different luminance conditions with three different absolute luminance levels.

As in the previous experiment, the central line was either monocular or dichoptic with respect to the flanking lines and the task was to select the flanking line which differed in orientation from the central line. 120 trials were obtained for each Luminance x Task x Orientation Difference, yielding 2880 trials altogether. 7 subjects wearing their normal refraction were tested. Subject AP was only available for 4/5 blocks.

Responses were obtained using mouse buttons. This is a better method of collecting reaction times since the button box buttons of the CRS system have to be pushed some way before registering a response. The luminance of the two monitors was adjusted manually so they appeared equal. Measured with a photometer, stimuli on the left monitor were 7.30, 4.04 and 2.15 cd/m^2. On the right monitor the luminance of the stimuli were 6.40, 3.91 and 2.20 cd/m^2. The luminance of the background was 0.05 cd/m^2 and 0.06 cd/m^2 on the left and right monitors respectively. Subjects self initiated the experiment by pressing the mouse. All other methodological details are as in the previous experiment.

Orientation difference thresholds

Figure 7.4. shows the 75% orientation difference thresholds for each Luminance by Task for each subject. Only subject VB shows possible evidence of poorer performance in the different luminance conditions.

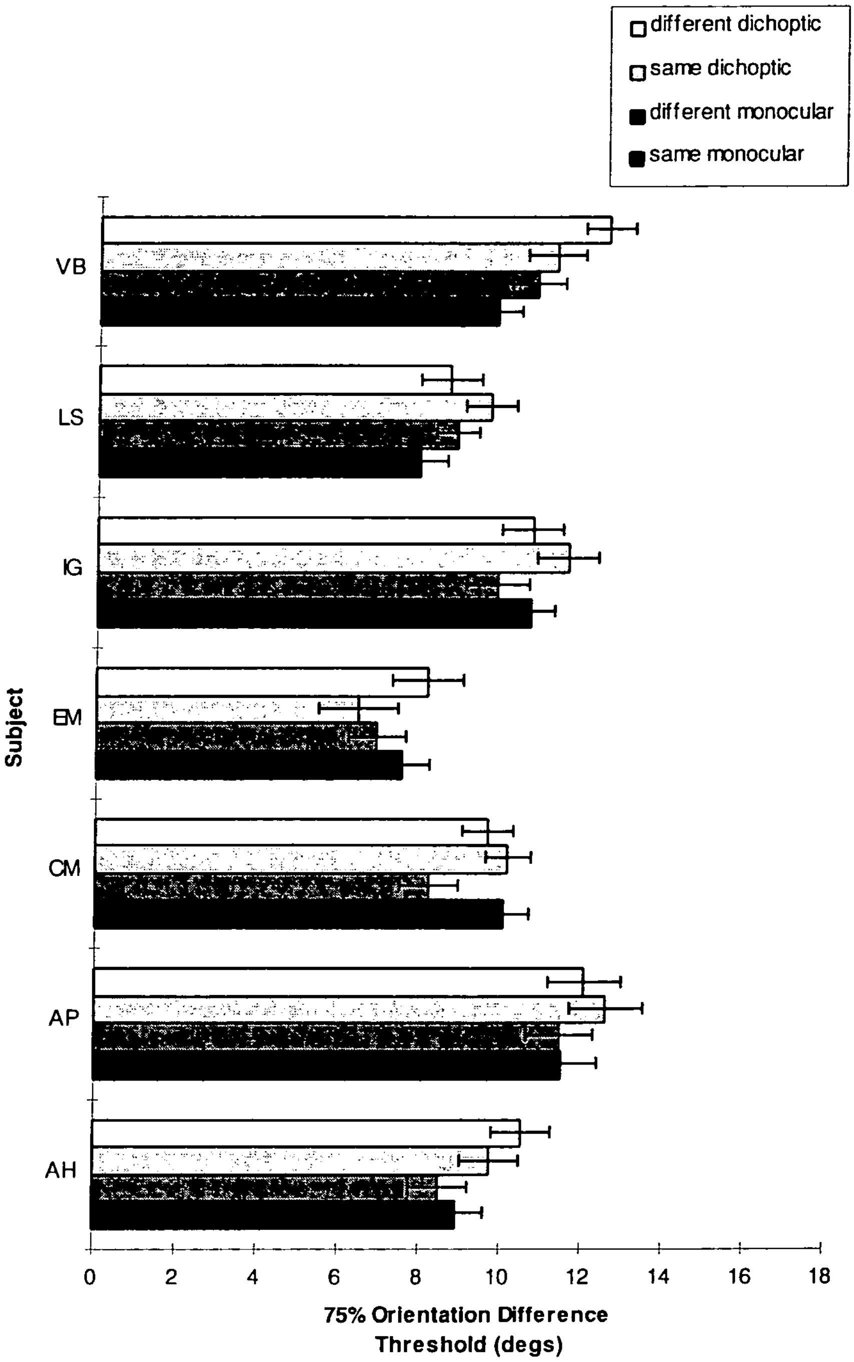


Figure 7.4. 75% orientation difference thresholds obtained for 7 subjects for each Luminance by Task. Error bars represent +/- one S.E. whose estimates were also obtained from probit.

The threshold estimates formed the raw data for a two way repeated measures ANOVA using Task and Luminance as Factors. A summary of the main effects in the data is shown in Figure 7.5. There was no significant main effect of Luminance on performance (F = 0.04, df = 6,1, P > 0.05) nor was there any interaction between Task and Luminance (F = 0.51, df = 6,1, P > 0.05). However there was a significant effect of Task (F = 23.91, df = 6,1, P < 0.05) with threshold estimates being higher in the dichoptic condition (mean = 10.27, S.E. = 0.47) compared to the monocular condition (mean = 9.35, S.E. = 0.39). This represents a difference in thresholds of 0.92°, just over half the size of the effect observed in the previous experiment.

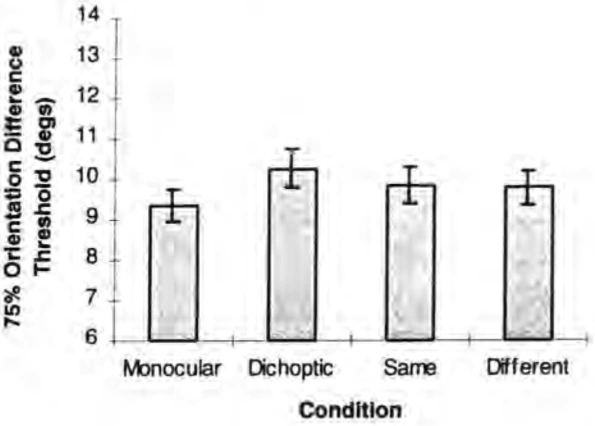


Figure 7.5. Summary of the means and S.E.s of the main effects for N=7 subjects. S.E.s reflect the S.D. of threshold estimates across subjects.

Reaction times

This experiment failed to replicate the previous finding of slower RTs in the dichoptic condition. To remove outliers in the data, RTs longer than 2000 ms were removed. This resulted in a loss of less than 2% of each subject's data. Next mean and median RTs were calculated for each subject in each combination of task and luminance. These values were used as the raw data in a two way repeated measures ANOVA using Luminance and Task as Factors. There were no significant main effects or interactions when either the medians or the means were used. The results of this analysis for the means is shown in Table 7.3.

Effect	Condition	Mean	S.E.	F	d.f.	P
Task	Monocular	554.77	27.48	1.92	6,1	N.S.
	Dichoptic	562.88	27.39			
Luminance	Same	557.68	27.03	0.24	6,1	N.S.
	Different	559.97	27.88			
Task x Luminance	Monocular, Same	553.21	39.11	0.04	6,1	N.S.
	Monocular, Different	556.33	41.75			
	Dichoptic, Same	562.14	40.36			
	Dichoptic, Different	563.62	40.28			

Table 7.3. Summary of means, S.E.s and the results of a two way repeated measures ANOVA using individual means as the raw data.

GENERAL DISCUSSION

Summary of results

Overall, the results reported in this chapter suggest that orientation difference sensitivity is poorer for dichoptic compared to monocular stimuli. In the first experiment, thresholds were higher in the dichoptic condition by 1.7° while in the second experiment, a somewhat smaller difference of 0.9° was observed. Although reaction times were slower in the dichoptic condition in the first experiment, this difference was not observed in the second experiment. Randomising the luminance of the central line had no effect on thresholds suggesting that a subtle difference in image quality between the two eyes is not responsible for the effect. This discussion will consider two possible peripheral explanations for the result; the disinclination of the vertical meridians and torsional instability between the two eyes. Finally, a 'central' explanation will be offered. A qualitative model will be presented which accounts for the higher dichoptic thresholds in terms of differential physiological inhibition.

Shear of the vertical meridians

One factor which is known to differentially affect the apparent orientation of stimuli in the two eyes and, which could conceivably make the task of orientation difference discrimination harder in the dichoptic condition, is the retinal shear of the vertical meridians. The locus of points seen in the same (corresponding) direction by the left and right eye, is represented by a single line (vertical horopter) which is tilted in the median plane away from the observer by about 45° (Nakayama et al., 1977). In 1910, Helmholtz (cited in Cogan, 1978), on the basis of his and Volkmann's independent experiments, suggested that the tilt of the horopter was due to a disinclination of the vertical meridians of the two eyes relative to retinal horizontal. Thus if the two retinas were superimposed with their fovea coincident, the two vertical meridians would form a cross at approximately 2.5° with the meridian of the right eye rotated clockwise and that of the left eye rotated anticlockwise.

The shear of the vertical meridians might mean that orientation matching across each eye is less accurate for vertical compared to horizontally oriented stimuli. In Volkman's (1863-4) experiment (cited in Krekling & Blika, 1983), subjects were presented with two lines dichoptically, displaced slightly to either side of a fixation point. The orientation of one line (reference) was set by the experimenter and the observer adjusted the orientation of the other until both lines appeared parallel. The orientation difference between lines matched for apparent orientation was about two degrees for the vertical reference line and tended towards zero as the orientation of the reference line approached horizontal.

Could the shear of the vertical meridians account for the higher orientation difference thresholds obtained dichoptically? The shear of the meridians means that when the lines in the display are near vertical and their presentation is dichoptic, the two flanking lines in one eye and the central line in the other, may appear to be tilted away from each other by equal and opposite amounts. This distortion may make the distractor a more likely candidate for the target since with regard to orientation, it appears less similar to the central line than it would if presented monocularly. If this has affected the results, it should be possible to demonstrate a relationship between the actual orientation of the central line and performance, with performance being worst for vertically oriented stimuli. Figure 7.6 shows the proportion correct for subjects AH and VB according to the orientation of the central line (unfortunately this information is not available for the other subjects). This shows that neither subject performed conspicuously worse for vertical (90°) compared with horizontal stimuli. Thus there is no evidence to suggest that at least in these two subjects, the disinclination of the vertical meridians is responsible for the poorer performance in the dichoptic condition.

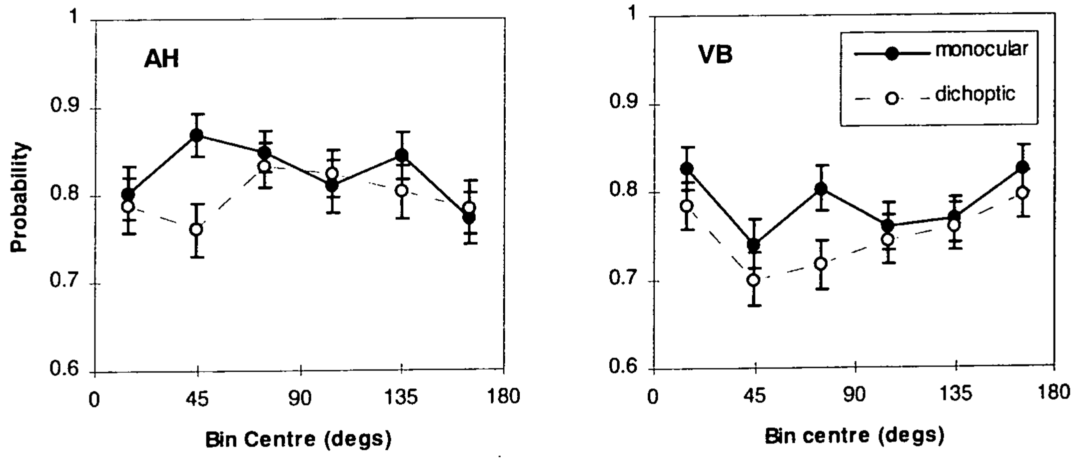


Figure 7.6. Probability of a correct response against absolute orientation of the central stimulus for two subjects. Since data was available for all integer orientations (0-180°), the data were binned and plotted against the proportion correct for that bin. The bin width was 30°. Vertical is 90°, horizontal is 0° and 180°.

Torsional instability between the two eyes

Any torsional instability might produce a difference in the apparent orientation of lines presented to each eye and hence might make the orientation difference task more difficult in the dichoptic condition. The stability of torsional fixation measured monocularly in the absence of any visual background has been found to have a mean SD of 16.2 mins within periods of fixation (Ferman et al., 1987). A smaller value of 10.8 mins was found by Ott et al., (1992). However, what is of interest to this discussion is the degree of binocular torsional stability. Binocular torsion can be quantified in terms of the degree of cycloversion and cyclovergence. Cycloversion refers to conjugate rotations of the eyes, whereas cyclovergence refers to co-ordinated movements of the eyes in opposite directions. Clearly only random fluctuations of cyclovergence are likely to lead to spurious orientation differences between the two eyes and therefore it is the stability of cyclovergence that is most crucial to this study.

Cyclovergence variability was initially studied by Enright (1990) who examined both binocular and monocular torsion (with a large cross present in the background to aid cyclofusion). He found that within periods of fixation, the variability of cyclovergence (SD = 4 mins) was much smaller than the variability of monocular torsion (SD = 17 mins). Recently, Van Rijn et al. (1994), using scleral induction coils also found that cyclovergence was more stable (SD = 5.04 mins) than cycloversion (SD = 11.22 mins) in the absence of any visual background. Moreover, the stability of cyclovergence was improved by the presence of a square background pattern comprised of binocular random squares while having no effect on the stability of cycloversion. The SD of cyclovergence with this background was just 2.64 mins. These studies lead to the conclusion that the inherent noise in cyclovergence during fixation, even in the absence of any stabilising background, is too small to account for the magnitude of the effect observed here.

A model of orientation difference coding

This section presents a model that accounts for the higher orientation difference thresholds observed dichoptically in terms of differential orientation dependent inhibition. First the assumptions and predictions of the model will be described and then their plausibility in the light of current evidence will be assessed.

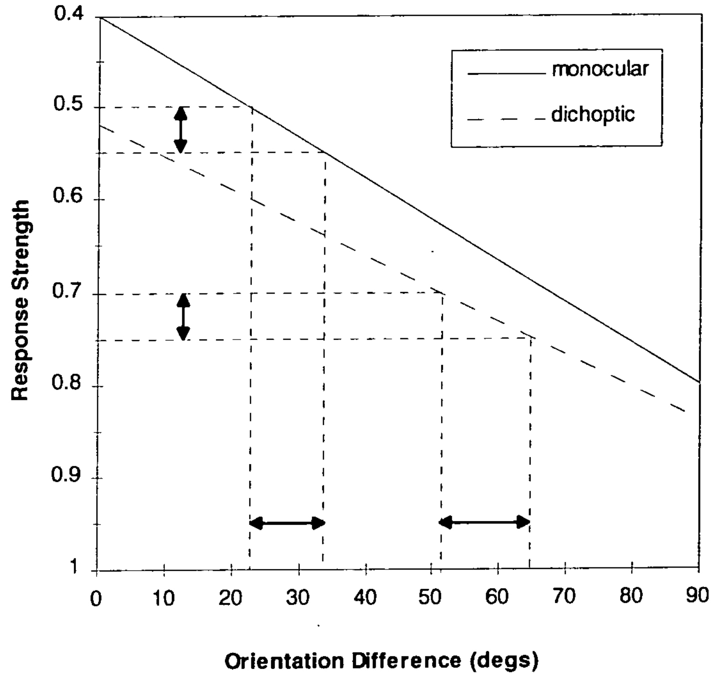


Figure 7.7 Qualitative model which predicts that the minimum resolvable orientation difference will be smaller when oriented lines are presented dichoptically compared with monocular presentation. The numbers for the monocular line are based on figures from Knierim & Van Essen (1992). See text for further details.

The model is based on Kneirim & Van Essen's (1992) finding of orientation contrast cells. The response of such a cell to a stimulus within its classical receptive field is more suppressed by a parallel surround than an orthogonal surround. About a third of the population of cells studied showed orientation contrast effects. For these cells, if the mean response in the absence of a textured surround was normalised to 1.0, then the mean response to an orthogonal texture was 0.8 and the mean response to a parallel texture was 0.4. These figures are shown in Figure 7.7 and represent the relationship between response strength (mean normalised response for orientation difference cells) and orientation difference for monocularly presented stimuli. It is assumed that response strength is linearly dependent on orientation difference.

For dichoptically presented stimuli, it is assumed that the degree of suppression is smaller by a constant fraction (0.8 in the model). Therefore the response strength, for dichoptically presented stimuli is

$$d = 1 - ((1 - m)c) \tag{7.1}$$

where m is the response strength for monocularly presented stimuli and c is a constant. The model depends on c acting in a multiplicative way and as a result, for dichoptically presented stimuli there is a narrower range of values across which orientation differences can be coded. Since change in response strength can only be measured with finite accuracy, the minimum resolvable orientation difference must be larger in the dichoptic case. As Figure 7.7 shows, if a 0.05 change in response strength were the smallest resolvable step size, then the smallest discriminable difference in orientation would be larger in the dichoptic case by about 2°.

Physiological justification of the model assumptions

In monkey V1, a number of studies have examined the responsivity of a cell to an oriented stimulus within its receptive field as a function of the orientation of a surround stimulus (see Chapter 4). These studies have shown there is both a general suppression and an orientation dependent inhibition with an orthogonal surround being less inhibitory than a parallel surround (Born & Tootell, 1991; Knierim & Van Essen, 1992; Grinvald et al, 1994). It remains to be established whether the degree of inhibition scales linearly with orientation difference. Evidence supporting the proposition that it scales at least monotonically is provided by Born & Tootell (1991) who found that inhibition was maximal when the orientation of the surround grating was parallel to the centre grating, diminished or absent when the surround was orthogonal and moderate at intermediate orientations.

It is also unknown whether inhibition is weaker when the surround is presented to the contralateral eye. It seems plausible to assume that it would be given that the strength of lateral inhibition is likely to reflect the degree of input to the receptive fields stimulated by the surround. Cells tuned to the contralateral eye respond less strongly to the surround and therefore inhibit the central stimulus to a lesser extent. This implies that lateral connections underlying inhibition are eye specific. Malach et al (1993) used optical imaging and *in vivo* targeted biocytin injections to show that in the monkey, this is indeed the case. Monocular regions of cortex are selectively connected to other monocular regions with the same eye preference while binocular regions are selectively connected to other binocular regions. In addition, since excitatory orientation dependent lateral connections are more likely to be found between cells sharing the same eye preference, it seems likely that inhibitory connections will be similarly organised (T'so et al, 1986; T'so & Gilbert, 1988).

The physiological evidence explains orientation difference coding in terms of interactions that occur outside the classical receptive field. A further problem with interpretation is that it is not clear that the results represent interactions between filters because the line stimuli used in the experiments have a broad-band spatial frequency spectrum and may activate many overlapping filters of different sizes. It has been suggested that a limited set of filters can be activated using gabor patches (Sagi, 1990; Polat & Sagi, 1993; Polat & Sagi, 1994) and it would be interesting to use such stimuli to examine the number of cycles over which the effect operates. If the result is due to a central mechanism such as that suggested by the model then it might also be possible to demonstrate radially shaped interaction zones like those identified by Toet & Levi (1992).

It has been suggested that orientation dependent surround effects may be generated by the extensive network of long-range horizontal connections in V1 which may extend for several mm (4 mm according to Blasdel et al, 1985). However, at the fovea, 4 mm only corresponds to approximately 0.2° (Hubel & Wiesel, 1977) whereas this experiment implies that surround effects operate up to a distance of 1.5°. Contour interaction at the fovea extends from 0.04°-0.08° (Toet & Levi, 1992) while the tilt illusion, also held to reflect lateral interactions, operates at an interstimulus distance of less than 1° (see Howard, 1986). It remains to be seen whether the physiological evidence can show context dependent effects at the fovea across the range suggested by this experiment.

Why was there a reduction in the size of the effect?

The mean effect size diminished from 1.7° to 0.98°. This may be due to a practice effect because 5/8 subjects who participated in the first experiment also participated in the second experiment. Looking at the mean size of the effect for these subjects reveals that it diminished from 2.05° (first experiment) to 0.80° (second experiment). This difference is significant for a one tailed repeated measures 't' test ($t = 2.42$, $df = 4$, $p < 0.05$). This suggests that dichoptic orientation difference discrimination is modifiable with experience. Perhaps the connections that subserve dichoptic orientation difference coding are actually strengthened through dichoptic visual experience. In terms of the model this would correspond to a greater range of inhibition over which to code orientation differences.

Conclusion

The model predicts that large orientation differences will be discriminated equally well regardless of whether the stimuli are presented monocularly or dichoptically hence it is consistent with the results of chapter 5 which found no difference between monocular and dichoptically presented targets that were orthogonal to the distracters. Pop-out for oriented lines should be worse in the dichoptic case when the orientation difference is close to threshold. Perhaps this would have been found if it had been possible to eradicate all other cues to the target in Experiment B of Chapter 6.

8

Conclusion

Summary of experimental findings

The aim of this thesis was to study binocular interactions in human vision. This was accomplished in two ways. Firstly, a region devoid of normal binocular interactions, the region corresponding the blind spot, was studied and secondly, stimuli were presented dichoptically to binocularly represented areas of the visual field.

The first experimental study showed that the region corresponding to the blind spot has a contrast sensitivity which is effectively binocular. This conclusion was based on the observation that this region has a higher monocular contrast sensitivity than a control location also tested monocularly. In addition, the contrast sensitivity of the region corresponding to the blind spot was not significantly different from that obtained binocularly in the control region. Lastly, a model of normal sensitivity (based on the logarithmic scaling function observed by Pointer & Hess 1989, 1990) was able to account fairly well for sensitivity in the control region but not in the region corresponding to the blind spot. This provided additional evidence that the region corresponding to the blind spot is hypersensitive.

The increase in monocular contrast sensitivity in the region corresponding to the blind spot was interpreted as arising from both probability summation and release from interocular suppression. If these explanations are correct, they imply two things about the limits of normal contrast sensitivity. Firstly, sensitivity must be limited by cortical noise and not simply by the physical noise inherent in the stimulus and secondly, normal monocular contrast sensitivity must be limited by suppression emanating from the other eye. The probability summation hypothesis is based on the observation that the number of cells devoted to processing information from the region corresponding to the blind spot is what would be expected if both eyes projected to it (LeVay cited in Westheimer, 1982). This preserves the cortical magnification factor with respect to the rest of the cortex and presumably accounts for why size distortions across the blind spot are absent (Tripathy et al., 1995).

As outlined in Chapter 2, the probability summation hypothesis and release from interocular suppression hypothesis both depend on an intact striate cortex for their mediation. To establish whether these explanations were sufficient to explain the effect in normal observers, a patient with damage restricted to the left striate cortex was studied. If an increase in monocular contrast sensitivity in the region corresponding to the blind spot could be shown in the blind hemifield, it would suggest that the effect did not depend exclusively on striate cortex. An additional explanation such as the Sprague effect (which explains the effect in terms of a pathway connecting prestriate cortex via a subcortical pathway) would be required.

However in contrast to the results of Pöppel & Richards (1974), no evidence of an increase in monocular contrast sensitivity in the region corresponding to the blind spot was found in the blind hemifield. Furthermore the study failed to observe an increase in monocular contrast sensitivity in the region corresponding to the blind spot in the sighted hemifield. A further puzzle was that the contrast sensitivity of GY's sighted hemifield was at the high end of the range of scores obtained from normal observers. This conflicts with the results of Hess & Pointer (1989) who found that the contrast sensitivity of GY's sighted hemifield was actually lower than normal. The reason for the discrepancies between these results and the aforementioned studies is unclear. Although this study did not help to explain the neurological basis of the effect observed in Chapter 2, it suggests that the response properties of supposedly intact areas of the visual field in patients with field defects warrants further study.

The pilot experiment reported in Chapter 5 found that pop-out in the region corresponding to the blind spot was similar to that of adjacent regions of the visual field at the same eccentricity suggesting that the monocularity of the blind spot has no effect on pop-out. In addition, presenting targets either monocularly or dichoptically with respect to the distracters had no effect on the degree of pop-out obtained further suggesting an absence of interocular interactions in visual search. However this experiment was considered to be an insensitive test of dichoptic interactions since it did not maximise the potential for lateral interactions between the target and distracters. This is because the identity of the target was prespecified and the targets and distracters were widely spaced.

For this reason, the issue was pursued further in Chapter 6 which examined orientation pop-out in central vision using a dense display and with targets defined by sensory pop-out. Varying degrees of orientation difference between the targets and distracters were employed. This experiment found no difference between dichoptic and monocular targets over a range of orientation differences (7.5-21°). However the percentage of targets correctly localised at the lowest orientation difference (3.5°) was higher in the dichoptic condition while performance in the monocular condition was close to chance. This suggested the possibility that subjects could identify targets based solely on their eye of origin. However, further investigation revealed that subjects were able to perform the task by identifying a luminance difference between the target and distracters since randomising the luminance of the elements in the display reduced the proportion of subjects who could localise the target at a level greater than chance. Together, the experimental results of Chapters 5 and 6 lead to the conclusion that dichoptic interactions in visual search are absent. This is consistent with Wolfe's suggestion that visual search is mediated beyond V1.

The fast detection of a target which occurs irrespective of the number of distracters is commonly referred to as preattentive, implying that attentional resources are not required. From this view, the identification of processes in V1 with preattentive vision seems consistent with the observation that activity in V1 is not modulated by attention. However, Joseph (1997) recently demonstrated that orientation pop-out is impaired by performing a concurrent task which requires attention. This suggests that even so-called preattentive vision demands attention and provides additional evidence that processing in V1 is not sufficient to mediate orientation pop-out.

The final experimental chapter sought to measure orientation difference sensitivity more directly than the search experiments. By simplifying the task it was hoped that the effects of earlier processing mechanisms would be revealed. This chapter reports that dichoptic orientation difference thresholds are higher than monocular thresholds and that this result cannot be attributed to the presence of a luminance artefact. Other spurious artefacts such as the disinclination of the vertical meridians and torsional instability between the two eyes can also be ruled out as explanations for the finding. The result can be accounted for by a model of orientation difference coding which assumes that orientation differences are coded in terms of the strength of inhibition occurring between two oriented stimuli. This inhibition is maximal for parallel stimuli and reduced for orthogonal stimuli. For dichoptically presented stimuli, the range of inhibition occurring between stimuli is smaller leading to a greater minimum resolvable orientation difference.

This model makes some suggestions for future work. Kneirim & Van Essen (1992) showed that the response of a cell to a stimulus within its classical receptive field is suppressed more by a parallel surround than an orthogonal surround. The model predicts that this inhibition should be smaller when the surround is presented to the contralateral eye.

If the model is correct, many orientation dependent surround effects that have been documented should be reduced with dichoptic presentation of the target and surround. Such effects include the reduction in apparent contrast in the presence of a surround (Cannon & Fullencamp, 1991) and the suppression and facilitation of threshold contrast by lateral masking (Polat & Sagi 1993).

Finally, it would also be interesting to establish whether the effect really does represent the result of interactions between different filters by using gabor patches to examine the number of cycles over which the effect operates.

Final conclusion

To what extent is the binocularity of V1 apparent in the psychophysical experiments reported in this thesis? The most negative result is the failure to find evidence for utrocular discrimination. Eye of origin is represented in V1 and yet this thesis and many other researchers have failed to find positive evidence of this ability. This casts doubt on the idea that the results of behavioural experiments can be used to make inferences about the processing of information in striate cortex or that it is possible to make predictions from the physiology about behaviour.

Yet other results presented in this thesis suggest this may be possible. The finding of binocular interactions in orientation difference sensitivity suggest that the lateral interactions in striate cortex which mediate this function are eye specific. The finding of increased monocular contrast sensitivity in the region corresponding to the blind spot is consistent with the physiological evidence concerning the number of cells in the cortical representation of this region and their lack of interocular inhibition. Here the behavioural results are in agreement with what would be predicted from the physiology.

The failure to find evidence of binocular interactions in visual search suggests that pop-out may be mediated at a higher level where the cells are binocularly balanced. This interpretation relies on the assumption that ocular dominance has effects which can be detected behaviourally. This assumption would be justifiable if the failure to find evidence of utrocular discrimination could be explained. Utrocular discrimination differs from the other visual functions investigated in this thesis in that it is an ability that depends exclusively on ocular dominance. Perhaps the effect of binocularity can only be detected indirectly through its effect on other visual functions like orientation difference sensitivity and contrast sensitivity. To conclude this thesis demonstrates that the binocular mechanisms in V1 have effects that go beyond their putative role in processing binocular stimuli, they also impose constraints on the limits of vision in other functional domains.

9

References

Arditi, A (1986) Binocular Vision. In: Boff, K.R., Kaufman, L. & Thomas J.P.(Eds.) Handbook of Perception & Human Performance Vol I: Sensory Processes & Perception. New York: Wiley 23.01-23.41

Badcock, D.R. & Schor, C.M. (1985) Depth-increment detection function for individual spatial channels. Journal of the Optical Society of America A, 2. 1211-1215.

Barbeito, R., Levi, D., Klein, S., Loshin, D., & Ono, H. (1985). Stereo-deficients and stereoblinds cannot make utrocular discriminations. Vision Research, 25, 1345-1348.

Barbur, J. L., Harlow, A. J., & Wieskrantz, L. (1994). Spatial and temporal response properties of residual vision in a case of hemianopia. Philosophical Transactions of the Royal Society. London. Series B, 343, 157-166.

Barbur, J. L., Ruddock, K. H., & Waterfield, V. A. (1980). Human visual responses in the absence of the geniculo-calcerine projection. Brain, 103, 905-928.

Barlow, H. B., Blakemore, C. & Pettigrew, JD. (1967). The neural mechanism of binocular depth discrimination. Journal of Physiology. 193. 327-42.

Battersby, W. S. (1951). The regional gradient of critical flicker frequency after frontal or occipital lobe injury. Journal of Experimental Psychology, 42, 59-68.

Benevento, L. A., & Standage, G. P. (1983). The organisation of projections of the retinorecipient and nonretinorecipient nuclei of the pretectal complex and layers of the superior colliculus to the lateral pulvinar and medial pulvinar in the macaque monkey. Journal of Comparative Neurology, 271, 307-336.

Bergen, J. R., & Adelson, E. H. (1988, May 26). Early vision and texture perception. Nature, 333, 363-364.

Bisti, S., & Trimarchi, C. (1993). Visual performance in cats after prenatal enucleation. Proceedings of the National Academy of Science. USA, 90, 11142-11146.

Bisti, S., Trimarchi, C., & Turlejski, K. (1995). Prenatal monocular enucleation induces a selective loss of low-spatial-frequency cortical responses to the remaining eye. Proceedings of the National Academy of Sciences of the U.S.A., 92, 3908-3912.

Blake, R. Fox, R. & McIntyre C (1971) Stochastic properties of stabililized-image binocular rivalry alternations. J Exp Psychol. 88, 327-32.

Blake, R., & Fox, R. (1973). The psychophysical inquiry into binocular summation. Perception and Psychophysics, 14, 161-185.

Blake, R. & Fox, R. (1974) Adaptation to invisible gratings and the site of binocular rivalry suppression. Nature. 249. 488-90.

Blake, R., & Cormack, R. H. (1979a). On utrocular discrimination. Perception and Psychophysics, 26, 53-68.

Blake, R., & Cormack, R. H. (1979b). Psychophysical evidence for a monocular visual cortex in stereoblind humans. Science, 203, 274-275.

Blake, R., Sloane, M., & Fox, R. (1981). Further developments in binocular summation. Perception and Psychophysics, 30, 266-276.

Blasdel, G., G, Lund, J., S, & Fitzpatrick, D. (1985). Intrinsic connections of macaque striate cortex: axonal projections of cells outside lamina 4C. Journal of Neuroscience, 5, 3350-3369.

Born, R. T., & Tootell, B. H. (1991). Single-unit and 2-deoxyglucose studies of side inhibition in macaque striate cortex. Proceedings of the National Academy of Science. USA, 88, 7071-7075.

Bravo, M., & Blake, R. (1990). Preattentive vision and perceptual groups. Perception, 19, 515-522.

Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual-search tasks. Perception and Psychophysics, 51, 465-472.

Campbell, F. W., & Green, D. G. (1965). Monocular versus binocular acuity. Nature, 208, 191-192.

Cannon, M., W, & Fullencamp, S., C. (1991). Spatial interactions in apparent contrast: Inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. Vision Research, 31, 1985-1998.

Cavanagh, P., Arguin, M., & Treisman, A. (1990). Effect of surface medium on visual search for orientation and size features. Journal of Experimental Psychology: Human Perception and Performance, 16, 479-492.

Chalupa, L. M., & Williams, R. W. (1984). Organisation of the cat's lateral geniculate nucleus following interruption of prenatal binocular interactions. Human Neurobiology, 3, 103-107.

Chalupa, L. M., Williams, R. W., & Henderson, Z. (1984). Binocular interaction in the fetal cat regulates the size of the ganglion cell population. Journal of Neuroscience, 12, 1139-1146.

Cogan, A. (1979). The relationship between the apparent vertical and the vertical horopter. Vision Research, 19, 655-665.

Coren, S., & Porac, C. (1979). Eye signature: Phenomenal difference as a function of sighting dominance. Presented at. Meetings of the Psychonomics Society, Phoenix, Arizona, November.

Cowey, A., & Steorig, P. (1991). The Neurobiology of Blindsight. Trends in Neurosciences, 14, 140-145.

Curcio, C. A., Sloan, K. R., Packer, O., Hendrickson, A. E., & Kalina, R. E. (1987). Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. Science, 236, 579-582.

Denny, N., Frumkes, T. E., Barris, M. C., & Eysteinsson, T. (1991). Tonic interocular suppression and binocular summation in human vision. Journal of Physiology, 437, 449-460.

Derrington, A. (1996). Filling-in and pop out. Current Biology, 6, 141-143.

DeValois, R. L. & DeValois, K. K. (1990). Spatial Vision. New York, N.Y. Oxford University Press.

DeWeerd, P., Gattass, R., Desimone, R., & Ungerleider, L. G. (1995, October 26). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. Nature, 377, 731-734.

De Yoe E. A. & Van Essen, D.C. (1985) Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. Nature. 317. 58-61.

DeYoe, E., Knierim, J., Sagi, D., Julesz, B., & Van Essen, D. (1986). Single unit responses to static and dynamic texture patterns in macaque V2 and V1 cortex (Abstract). Investigative Opthalmology & Visual Science, 27.

Dobbins, A. C., & Kolb, C. (1995, March 15). MT-suppressing stimulus unmasks eye of origin. Investigative Opthalmology & Visual Science, 36(No. 4), S57.

Drasdo, N. (1991). Neural substrates and threshold gradients of peripheral vision. In J. J. Kulikowski, V. Walsh, & I. J. Murray (Eds.), Vision and Visual Dysfunction: limits of vision (Vol. V, pp. 251-264). Basingstoke: Macmillan.

Duncan, J. (1995). Co-operating brain systems in selective perception and action. In T. Inui & J. McClelland L (Eds.), Attention and Performance XVI. Cambridge MA: MIT.

Durgin, F. H., Tripathy, S. P., & Levi, D. M. (1995). On the filling in of the visual blind spot: some rules of thumb. Perception, 24, 827-840.

Efron, R., & Yund, E., W. (1996). Spatial nonuniformities in visual search. Brain and Cognition, 31, 331-368.

Enoch, J., Goldman, H., & Sunga, R. (1969). The ability to distinguish which eye was stimulated by light. Investigative Opthalmology & Visual Science, 8, 317-331.

Enright, J. T. (1990). Stereopsis, cyclotorsional "noise" and the apparent vertical. Vision Research, 30, 1487-1497.

Estevez, O., & Cavonius, C. R. (1976). Low-frequency attenuation in the detection of gratings: sorting out the artifacts. Vision Research, 16, 497-500.

Eysteinsson, T., Barris, M. C., Denny, N., & Frumkes, T. E. (1993, July). Tonic interocular suppression, binocular summation, and the visual evoked potential. Investigative Opthalmology & Visual Science, 34(8), 2443-2448.

Ferman, L., Collewijn, H., Jansen, T., C, & Van Den Berg, A. V. (1987). Human gaze stability in the horizontal, vertical and torsional direction during voluntary head movements, evaluated with a three-dimensional scleral induction coil technique. Vision Research, 27, 811-828.

Ferster, D. (1981). A comparison of binocular depth mechanisms in area 17 and 18 of the cat visual cortex. Journal of Physiology, 311, 623-655.

Findlay, J. (1969). A spatial integration effect in visual acuity. Vision Research, 9, 157-166.

Findlay, J. M. (1997). Saccade target selection during visual search. Vision Research, 37, 617-631.

Finlay, B. C., Schiller, P. H., & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex. IV. Corticotectal cells. Journal of Neurophysiology, 39, 1352-1361.

Fish, S. E., & Rhoades, R. W. (1981). Hamsters intercollicular pathway: Electrophysiological experiments. Investigative Opthalmology & Visual Science, 20, 185.

Foley, J. M., & Legge, G. E. (1981). Contrast detection and near threshold discrimination in human vision. Vision Research, 21, 1041-1053.

Fox, R. (1985) Interaction of image characteristics of stereoscopic forms during depth perception (Tech. Report N14-0001-85C-0001). Arlington, VA: Office of Naval Research, Engineering Psychology Programs.

Freeman, R. D., Abramson, B. P., & Nordmann, J. P. (1989). Contrast sensitivity in human subjects with one eye. Investigative Opthalmology & Visual Science, 30 (abstract), 376.

Freeman, R. D., & Bradley, A. (1980). Monocularly deprived humans: non deprived eye has supernormal vernier acuity. Journal of Neurophysiology, 43, 1645-1653.

Fry, G. A. & Hill, W.W. (1962) The centre of rotation of the eye. American Journal of Optometry.

Gardner, J. C., & Raiten, E. J. (1986). Ocular dominance and disparity-sensitivity: why there are cells in the cortex driven unequally by the two eyes. Experimental Brain Research, 64, 505-514.

Gilbert, C., D, & Wiesel, T., N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. Vision Research, 11, 1689-1701.

Girard, P., & Bullier, J. (1989). Visual activity in visual area-V2 during reversible inactivation of area-17 in the macaque monkey. Journal of Neurophysiology, 62, 1287-1302.

Goldberg, M. E., & Wurtz, R. H. (1972). Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons. Journal of Neurophysiology, 35, 542-559.

Goldman, P. S., Lodge, A., & Hammer, L. R. (1968). Critical flicker frequency after unilateral temporal lobectomy in Man. Neuropsychologia, 6, 355-363.

Gonzalez, E. G., Steinbach, M. J., Ono, H., & Rush-Smith, N. (1992). Vernier acuity in monocular and binocular children. Clinical Vision Sciences, 7, 257-261.

Goodale, M., A. (1973). Cortico-tectal and intertectal modulation of visual responses in the rat's superior colliculus. Experimental Brain Research, 17, 75-86.

Graham, C. H. (1965) Visual space perception. In Graham, C. H. (Ed.), Vision & Visual Perception (pp. 504-547). New York: Wiley.

Grinvald, A., Lieke, E., E, Frostig, R., D, & Hildesheim, R. (1994). Cortical point-spread function and long-range lateral interactions revealed by real-time optical imaging of macaque monkey primary visual cortex. Journal of Neuroscience, 14, 2545-2568.

Gurnsey, R., Humphrey, G. K., & Kapitan, P. (1992). Parallel discrimination of subjective contours defined by offset gratings. Perception and Psychophysics, 55, 261-268.

Hegdé, J., & Felleman, D., J. (1996, February 15). Neurons in area V1 respond similarly to pop-out and non pop-out stimuli. Investigative Opthalmology & Visual Science, 37(3), S484.

Hess, R. F., Field, D. J., & Watt, R. J. (1991). The puzzle of amblyopia. In C. Blakemore (Ed.), Vision: coding and efficiency (1st ed., pp. 267-280). Cambridge: Cambridge University Press.

Hess, R. F., & Pointer, J. S. (1985). Differences in the neural basis of human amblyopia: the distribution of the anomaly across the visual field. Vision Research, 25, 1577-1594.

Hess, R. F., & Pointer, J. S. (1989). Spatial and Temporal Contrast Sensitivity in Hemianopia. Brain, 112, 871-894.

Heywood, C. A., Silveira, L. C. L., & Cowey, A. (1988). Contrast sensitivity in rats with increased or decreased numbers of retinal ganglion cells. Experimental Brain Research, 70, 513-526.

Hollander, H. (1974). Projections from the striate cortex to the diencephalon in the squirrel monkey (Saimiri sciureus): a light microscopic radioautographic study following intracortical injection of H3 leucine. Journal of Comparative Neurology, 155, 425-440.

Holtzman, J. D. (1984). Interactions between cortical and subcortical visual areas: Evidence from human comissurotomy patients. Vision Research, 24, 801-813.

Horton, J. C. (1984). Cytochrome oxidase patches: a new cytoarchitectonic feature of monkey visual cortex. Philosophical Transactions of the Royal Society. London. Series B, 304, 199-253.

Horton, J. C., & Hedley-Whyte, E. T. (1984). Mapping of cytochrome-oxidase patches and ocular domninance columns in human visual cortex. Philosophical Transactions of the Royal Society. London. Series B, 304, 255-272.

Horton, J. C., & Stryker, M. P. (1993). Amblyopia induced by anisometropia without shrinkage of ocular dominance columns in human striate cortex. Proceedings of the National Academy of Sciences of the U.S.A., 90, 5494-5498.

Horton, J., C, & Hocking, D., R. (1996). Pattern of ocular dominance columns in human striate cortex in strabismic amblyopia. Visual Neuroscience, 13, 787-795.

Howard, I., P. (1986). The perception of posture, self motion and the visual vertical. In R. Boff K, L. Kaufman, & J. Thomas P (Eds.), Handbook of Perception and Human Performance (Vol. 1). New York: Wiley.

Howard, I. P. & Rogers, B.J. (1995) Binocular Vision and Stereopsis. Oxford University Press, New York. pp736.

Howell, D. C. (1992). Statistical methods for Psychologists (3rd ed.). California: Duxbury.

Howell, E. R., & Hess, R. F. (1978). The functional area for summation to threshold for sinusoidal gratings. Vision Research, 18, 369-374.

Hubel, D. H. & Weisel, T. N. (1962) Receptive fields, binocular interaction and functional architecture in the cats visual cortex. Journal of Physiology. 160. 106-54

Hubel, D., H, & Wiesel, T., N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. Journal of Neurophysiology, 28, 229-289.

Hubel, D., H, & Wiesel, T., N. (1968). Receptive fields and functional architecture of monkey striate cortex. Journal of Physiology, 195, 215-243.

Hubel, D. H. & Weisel, T. N. (1970) Stereoscopic vision in the macaque monkey. Nature. 225. 41-42.

Hubel, D. H., & Wiesel, T. N. (1972). Laminar and columnar distribution of geniculo-cortical fibres in the macaque monkey. Journal of Comparative Neurology, 146, 421-450.

Hubel, D. H., & Wiesel, T. N. (1977). Functional architecture of the macaque monkey visual cortex. Proceedings of the Royal Society of London. Series B, 198, 1-59.

Hubel, D. H., Wiesel, T. N., & LeVay, S. (1977). Plasticity of ocular dominance columns in monkey striate cortex. Philosophical Transactions of the Royal Society. London. Series B, 278, 377-409.

Ikeda, H., & Wright, M. J. (1976). Properties of LGN cells in kittens reared with convergent squint: a neurophysiological demonstration of amblyopia. Experimental Brain Research, 25, 63-77.

Johnson, C. A., Post, R. B., Chalupa, L. M., & Lee, T. J. (1982). Monocular deprivation in humans: a study of identical twins. Investigative Opthalmology & Visual Science, 23, 135-138.

Jones, R. K. & Lee, D. N. (1981) Why two eyes are better than one: The two views of binocular vision. Journal of Experimental Psychology: Human Perception and Performance. 7. 30-40

Joseph, J. S., Chun, M. M., & Nakayama, K. (1997). Attentional requirements in a "preattentive" feature search task. Nature, 387, 805-807.

Julesz, B. (1960) Binocular depth perception of computer generated patterns. Bell System Technical Journal. 30. 1125-1162.

Julesz, B. (1971) Foundations of cyclopean perception. Chicago: University of Chicago Press.

Julesz, B. (1984, February). A brief outline of the texton theory of human vision. Trends in Neurosciences, 7, 41-45.

Kaas, J. H., Guillary, R. W., & Allman, J. M. (1973). Discontinuities in the dorsal lateral geniculate nucleus corresponding to the optic disc: a comparative study. Journal of Comparative Neurology, 147, 163-180.

Kastner, S., Nothdurft, H.-C., & Pigarev, I., N. (1997). Neuronal correlates of pop-out in cat striate cortex. Vision Research, 37, 371-376.

Kennedy, C., Rosiers, M. H., & Jehle, J. W. (1975). Mapping of functional neural pathways by autoradiographic survey of local metabolic rate with (14C) deoxyglucose. Science, 187, 850-852.

Kennedy, C., Rosiers, M., H, Sakurada, O., Shinohara, M., Reivich, M., Jehle, W., & Sokoloff, L. (1976). Metabolic mapping of the primary visual system of the monkey by means of the autoradiographic (14C) deoxyglucose technique. Proceedings of the National Academy of Sciences of the U.S.A., 73, 4230-4234.

Kirby, M. A., & Chalupa, L. M. (1986). Retinal crowding alters the morphology of alpha ganglion cells. Journal of Comparative Neurology, 251, 532-541.

Knierim, J., J, & Van Essen, D., C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. Journal of Neurophysiology, 67, 961-980.

Koerner, F., & Teuber, H.-L. (1973). Visual field defects after missile injuries to the geniculo-striate pathway in man. Experimental Brain Research, 18, 88-113.

Kolb, F. C., & Braun, J. (1995, September 28). Blindsight in normal observers. Nature, 377, 336-338.

Kovacs, I. (1996). Gestalten of today: early processing of visual contours and surfaces. Behavioural Brain Research, 82, 1-11.

Krekling, S., & Blika, S. (1983). Meridional anisotropia in cyclofusion. Perception and Psychophysics, 34, 299-300.

Krüger, J. (1977). The shift-effect in the lateral geniculate body of the rhesus monkey. Experimental Brain Research, 29: 387-392.

Krüger, J., Fischer, B., & Barth, R. The shift-effect in retinal ganglion cells of the rhesus monkey. Experimental Brain Research, 23: 443-446.

Legge, G. E. (1984). Binocular contrast summation - I. Detection and Discrimination. Vision Research, 24, 373-383.

LeGrand, Y. (1967). Entopic phenomena. In Space and Form Vision (pp. 147-157). Bloomington: Indiana University Press.

Lehmkuhle, S. & Fox, R. (1975). The effect of binocular rivalry suppression on the motion after-effect. Vision Research. 15. 855-60.

Lema, S. A., & Blake, R. (1977). Binocular summation in normal and stereoblind observers. Vision Research, 17, 69.

Leopold, D. A., & Logothetis, N. K. (1995). Cell activity reflects monkeys perception during binocular rivalry. Investigative Opthalmology & Visual Science, 36, 813.

LeVay, S., & Nelson, S. B. (1991). Columnar organisation of the visual cortex. In J. Cronly-Dillon (Ed.), Vision and Visual Dysfunction (Vol. IV). London: Macmillan.

Levi, D. M., Harweth, R. S., & Manny, R. E. (1979). Suprathreshold spatial frequency detection and binocular interaction in strabismic and anisometropic amblyopia. Investigative Opthalmology & Visual Science, 1979(18), 716-725.

Livingstone, M.S. & Hubel, T.N. (1988) Segregation of form, colour, movement and depth: Anatomy, physiology and perception. Science. 240. 740-749.

Livingstone, M. A., Nori, S., Freeman, D. C., & Hubel, D. H. (1995). Stereopsis and binocularity in the squirrel monkey. Vision Research, 35, 345-354.

Livingstone, M. S. (1996). Ocular dominance columns in new world monkeys. Journal of Neuroscience, 15, 2086-2096.

Logothetis, N. K., Schiller, P.H., Charles, E.R.& Hurlbert, A.C., (1990) Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. Science. 247. 214-217.

Lund, J., S, Lund, R., D, Hendrickson, A., E, Bunt, A., H, & Fuchs, A., F. (1975). The origin of efferent pathways from the primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. Journal of Comparative Neurology, 164, 287-304.

Maeda, M., Shibazake, T., & Yoshida, K. (1979). Monosynaptic inhibition evoked in superior colliculus neurons following contralateral collicular stimulation. In M. Ito (Ed.), Integrative Control Functions of the Brain (pp. 68-71). Amsterdam: Elsevier/North Holland Biomedical Press.

Malach, R., Amir, Y., Harel, M., & Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. Proceedings of the National Academy of Sciences of the U.S.A., 90, 10469-10473.

Martens, W., Blake, R., Sloane, M., & Cormack, R. H. (1981). What masks utrocular discrimination. Perception and Psychophysics, 30, 521-532.

Maunsell, J. H. R. & Van Essen, D. C. (1983) Functional properties of neurons in middle temporal visual area of macaque monkey: II Binocular interaction and sensitivity to disparity. Journal of Neurophysiology, 49, 1148

Maunsell, J. H. R., & Van Essen, D. C. (1983). The connections of the middle temporal visual area MT and their relationship to a cortical hierarchy in the macaque monkey. Journal of Neuroscience, 3, 2563-2586.

McIlwain, J. T. (1964). Receptive fields of optic tract axons and lateral geniculate cells: peripheral extent and barbituate sensitivity. Journal of Neurophysiology, 27, 1154-1173.

McColl, S. L., & Mitchel, D. E. (1997). Stereoanomalous observers show complete interocular transfer of the motion coherence adaptation aftereffect. Investigative Opthalmology & Visual Science, 38, 4592.

McGuire, B. A., Gilbert, C. D., Rivlan, P. K., & Wiesel, T. N. (1991). Targets of horizontal connections in macaque primary visual cortex. Journal of Comparative Neurology, 305, 370-392.

McKee, S.P.& Mitchison, G.J.(1988) The role of retinal correspondence in stereosopic matching. Vision Research. 28. 1001-1012.

Meigen, T., Lagreze, W.-D., & Bach, M. (1994). Asymmetries in preattentive line detection. Vision Research, 34, 3103-3109.

Mohn, G., & van Hof-van Duin, J. (1983). On the relation of stereoacuity to interocular transfer of the motion and the tilt affereffects. Vision Research, 23, 1087-1096.

Morgan, M. J., Mason, A. J. S., & Soloman, J. A. (1997, January) Blindsight in normal subjects. Nature, 385, 401-402.

Marrocco, R. T., McClurkin, J.W. & Young, R. A. (1982) Spatial summation and conduction latency classification of cells of the lateral geniculate nucleus of macaques. J. Neuroscience, 2, 1275-1291.

Moschovakis, A. K., & Karabelas, A. B. (1982). Tecto-tectal interactions in the cat. Proceedings of the Society of Neuroscience, 8, 293.

Mulligan, J. B. (1986). Optimizing stereo separation in color television anaglyphs. Perception, 15, 27-36.

Nakayama, K., Tyler, C. W., & Appelman, J. (1977, April). A new angle on the vertical horopter. Proceedings of the Association for Research in Vision and Opthalmology, Sarasota, Florida, p82.

Nelson, J. I., & Frost, B. J. (1985). Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex. Experimental Brain Research, 61, 54-61.

Nicholas, J. J., Heywood, C. A., & Cowey, A. (1996). Contrast sensitivity in one-eyed subjects. Vision Research, 36, 175-180.

Nothdurft, H., C. (1985). Sensitivity for structure gradient in texture discrimination tasks. Vision Research, 25, 1957-1968.

Nothdurft, H., C. (1990). Texton segregation by associated differences in global and local luminance distribution. Proceedings of the Royal Society of London. Series B, 239, 295-320.

Nothdurft, H., C. (1991a). Different effects from spatial frequency masking in texture segregation and texton detection tasks. Vision Research, 31, 299-320.

Nothdurft, H., C. (1991b). Texture segmentation and pop-out from orientation contrast. Vision Research, 31, 1073-1078.

Nothdurft, H., C. (1992). Feature analysis and the role of similarity in preattentive vision. Perception and Psychophysics, 52, 355-375.

Nothdurft, H., C. (1993). The role of features in preattentive vision: comparison of orientation, motion and colour cues. Vision Research, 33, 1937-1958.

Ogle, K. N. (1950). Researches in Binocular Vision. Philadelphia: Saunders.

Ogle, K. N. (1964). Binocular Vision. New York: Hafner.

Ono, H., & Barbeito, R. (1985). Utrocular discrimination is not sufficient for utrocular identification. Vision Research, 25, 289-299.

Orban, G., A, Kato, H., & Bishop, P., O. (1979). Dimensions and properties of end-zone inhibitory areas in receptive fields of hypercomplex cells in cat striate cortex. Journal of Neurophysiology, 42, 833-849.

Ott, D., Seidman, S. H., & Leigh, J. R. (1992). The stability of human eye orientation during visual fixation. Neuroscience Letters, 142, 183-186.

Patterson, R. & Martin, W. L. (1992) Human Stereopsis. Human Factors. 34(6), 669-692.

Poggio, G. F., & Fisher, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. Journal of Neurophysiology, 40, 1392-1404.

Poggio, G. F. & Talbot, W. H. (1981) Mechanisms of static and dynamic stereopsis in foveal cortex of the rhesus monkey. Journal of Physiology, 315, 469-492.

Poggio, G. F. & Poggio, T. (1984) The analysis of stereopsis. Annual Review of Neuroscience. 7. 379-412.

Poggio, G. F., Motter, B.C., Squatrito, S. & Trotter, Y. (1985). Responses of neurons in visual cortex (V1 and V2) of the alert macaque to dynamic random-dot stereograms. Vision Research, 25, 397-406.

Pointer, J. S., & Hess, R. F. (1989). The contrast sensitivity across the human visual field: with emphasis on the low spatial frequency range. Vision Research, 29, 1133-1151.

Pointer, J. S., & Hess, R. F. (1990). The contrast sensitivity gradient across the major oblique meridians of the human visual field. Vision Research, 30, 497-501.

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vision Research, 33, 993-999.

Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. Vision Research, 34, 73-78.

Pöppel, E., & Richards, W. (1974). Light sensitivity in cortical scotomata contralateral to small islands of blindness. Experimental Brain Research, 21, 125-130.

Porac, C., & Coren, S. (1984). Monocular asymmetries in vision: a phenomenal basis for eye signature. Canadian Journal of Psychology, 38, 610-624.

Porac, C., & Coren, S. (1986). Sighting dominance and utrocular discrimination. Perception and Psychophysics, 39, 449-451.

Press, W., H, Flannery, B. P., Teukolsky, S. A., & Vetterling, W., T (Eds.). (1992). Numerical Recipes in C: The Art of Scientific Computing (2nd ed.). Cambridge: Cambridge University Press.

Provis, J. M., VanDriel, D., Billson, F. A., & Russel, P. (1985). Human fetal optic nerve: Overproduction and elimination of retinal axons during development. Journal of Comparative Neurology, 238, 92-100.

Rafal, R. D., Calabresi, P. A., Brennan, C. W., & Sciolto, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. Journal of Experimental Psychology: Human perception and performance, 15, 673-685.

Rafal, R. D., Smith, J., Krantz, J., Cohen, A., & Brennan, C. (1990) Extrageniculate vision in hemianopic humans: saccade inhibition by signals in the blind field. Science, 250, 118-120.

Rafal, R. D., Henik, A., & Smith, J. (1991) Extragniculate contributions to reflex visual orienting in normal humans: A temporal hemifield advantage. Journal of cognitive neuroscience, 3, 322-328.

Rakic, P. (1981). Development of visual centres in the primate brain depends on binocular competition before birth. Science, 214, 928-931.

Rakic, P., & Riley, K. P. (1983). Overproduction and elimination of retinal axons in the fetal rhesus monkey. Science, 219, 1441-1444.

Ramachandran, V. S. (1992, May). Blind spots. Scientific American, 266, 86-91.

Ramachandran, V. S., & Gregory, R. L. (1991, April 25). Perceptual filling-in of artificially induced scotomas in human vision. Nature, 350, 699-702.

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. Psychological Bulletin, 114, 510-523.

Reed, M. J., Steeves, J. K. E., & Steinbach, M. J. (1997). A comparison of contrast letter thresholds in unilateral eye enucleated subjects and binocular and monocular control subjects. Vision Research, 37, 2465-2469.

Richards, W. (1971) Anomalous Stereoscopic depth perception. Journal of the Optical Society of America. 61. 410-414.

Richards, W. & Kaye, M. G. (1974) Local versus global stereopsis: Two mechanisms? Vision Research. 14. 1345-1347.

Rijsdijk, J. P., Kroon, J. N., & Van Der Wildt, G. J. (1980). Contrast sensitivity as a function of position on the retina. Vision Research, 20, 235-241.

Rizzo, M., & Robin, D. A. (1996). Bilateral effects of unilateral visual cortex lesions in humans. Brain, 119, 951-963.

Robinson, S. R., & Dreher, B. (1990). The visual pathways of etherian mammals and marsupials develop according to a common timetable. Brain Behaviour and Evolution, 36, 177-195.

Robson, J. G., & Graham, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. Vision Research, 21, 409-418.

Rocha-Miranda, C. E., Bender, D. B., Gross, C. G., & Mishkin, M. (1975). Visual activation of neurons in inferotemporal cortex depends on striate cortex and forebrain commissures. Journal of Neurophysiology, 38, 475-491.

Rodman, H. R., Gross, C. G., & Albright, T. D. (1989). Afferent basis of visual response properties in area MT of the macaque. I. Effects of striate cortex removal. Journal of Neuroscience, 9, 2033-2050.

Rosa, M. G. P., Gattass, R., Fiorani, M., & Soares, J. G. M. (1992). Laminar, columnar and topographic aspects of ocular dominance in the primary visual cortex of Cebus monkeys. Experimental Brain Research, 88, 249-264.

Rovamo, J. (1978, January 5). Cortical magnification factor predicts the photopic contrast sensitivity of peripheral vision. Nature, 271, 54-56.

Rovamo, J., Virsu, V., Laureinen, P., & Hyvarinen, L. (1982). Resolution of gratings oriented along and across meridians in peripheral vision. Investigative Opthalmology & Visual Science, 23, 666-670.

Rubin, G. S. (1983). Suppression and Summation in Binocular Pattern Vision. Unpublished Ph.D. Thesis, Univ of Minnesota.

Ruddock, K., H, Waterfield, V., A, & Wigley, E. (1979). The response characteristics of an inhibitory binocular interaction in human vision. Journal of Physiology, 290, 37-49.

Sagi, D. (1990). Detection of an orientation singularity in gabor textures: effect of signal density and spatial-frequency. Vision Research, 9, 1377-1388.

Sagi, D., & Julesz, B. (1987). Short range limitations on detection of feature differences. Spatial Vision, 2, 39-49.

Schiller, P. H., Stryker, M. P., Cynader, M., & Berman, N. (1974). Response characteristics of single cells in the monkey superior colliculus following ablation or cooling of visual cortex. Journal of Neurophysiology, 37, 181-194.

Schmielau, F., & Marzi, C. A. (1983, March). Mirror-symmetric facilitation contralateral to the blind spot in normal subjects. ARVO abstracts, Supplement to Investigative Opthalmology and Visual Science, 24, pp. 186

Schofield, A. J., & Foster, D. H. (1995). Artificial neural networks simulating visual texture segmentation and target detection in line-element images. Philosophical Transactions of the Royal Society. London. Series B, 350, 401-412.

Shatz, C. J., & Stryker, M. P. (1978). Ocular dominance in layer IV of cat's visual cortex and the effects of monocular deprivation. Journal of Physiology, 281, 267-283.

Sheedy, J. E., Bailey, I. L., Buri, M., & Bass, E. (1986) Binocular versus monocular performance. American Journal of Optometry and Physiological Optics. 63. 839-46.

Sherman, S. M. (1974). Visual fields of cats with cortical and tectal lesions. Science, 26, 355-357.

Sherman, S. M. (1977). The effect of superior colliculus lesions upon the visual fields of cats with cortical ablations. Journal of Comparative Neurology, 172, 211-230.

Shook, B. L., Maffei, L., & Chalupa, L. M. (1985). Functional organization of the cat's visual cortex after prenatal interruption of binocular interactions. Proceedings of the National Academy of Sciences of the U.S.A., 82, 3901-3905.

Sillito, A. M., Kemp, J. A., & Patel, H. (1980). Inhibitory interactions contributing to the ocular dominance of monocularly dominated cells in the normal cat striate cortex. Experimental Brain Research, 41, 1-10.

Smith, S. (1945). Utrocular or 'which eye' discrimination. Journal of Experimental Psychology: Human Perception and Performance, 35, 1-14.

Sprague, J. M. (1966). Interaction of superior colliculus in mediation of visually guided behaviour in the cat. Science, 153, 1544-1547.

Standage, G. P., & Benevento, L. A. (1983). The organisation of connections between the pulvinar and visual area MT in the macaque monkey. Brain Research, 262, 288-294.

Stemmler, M., Usher, M., & Niebur, E. (1995). Lateral interactions in primary visual cortex: A model bridging physiology and psychophysics. Science, 269, 1877-1880.

Sur, M. (1988). Development and plasticity of retinal X-axon and Y-axon terminations in the cats lateral geniculate-nucleus. Brain Behaviour and Evolution, 31, 243-251.

Templeton, W. B., & Green, F. A. (1968). Chance results with utrocular discrimination. Quarterly journal of Experimental Psychology, 20, 200-203.

Teuber, H.-L., Battersby, W. S., & Bender, M. B. (Eds.). (1960). Visual field defects after penetrating missile wounds of the brain. Cambridge, MA: Harvard University Press.

Teuber, H.-L., & Bender, M. B. (1949). Alterations in pattern vision following trauma of the occipital lobes in man. The Journal of General Psychology, 40, 37-57.

Timney, B., Pearson, P., & Macuda, T. (1997, March 15). Is utrocular discrimination based on labelled lines? Investigative Opthalmology & Visual Science, 38(No. 4), S908.

Toet, A., & Levi, D., M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. Vision Research, 32, 1349-1357.

Treisman, A. (1985). Preattentive processing in vision. Computer Vision, Graphics and Image Processing, 31, 156-177.

Treisman, A. (1986). Features and objects in visual processing. Scientific American, 255/11, 106-115.

Treisman, A., M, & Gelade, G. (1980). A feature integration theory of attention. Cognitive Psychology, 12, 97-136.

Treisman, A., M, & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. Psychological Review, 95, 15-48.

Tripathy, S. P., & Levi, D. M. (1994). Long-range dichoptic interactions in the human visual cortex in the region corresponding to the blind spot. Vision Research, 34, 1127-1138.

Tripathy, S. P., Levi, D. M., Ogmen, H., & Harden, C. (1995). Perceived length across the physiological blind spot. Visual Neuroscience, 12, 385-402.

Ts'o, D., Y, & Gilbert, C., D. (1988). The organisation of chromatic and spatial interactions in the primate striate cortex. Journal of Neuroscience, 8, 1712-1727.

Ts'o, D., Y, Gilbert, C., D, & Wiesel, T., N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. Journal of Neuroscience, 6, 1160-1170.

Tyler, C.W & Scott A.B. (1979) Binocular Vision. In: Records R. (Ed.) Physiology of the Human Eye and Visual System. Hagerstown, Md.: Harper & Row. 643-71.

Tyler, C.W. (1983) Sensory Processing of Binocular Disparity. In: Vergence Eye Movements: Basic & Clinical Aspects. Schor C.M. & Ciuffreda, K.J. (Eds.). Butterworths. Woburn, MA.

Van Essen, D. C., DeYoe, E. A., Olavarria, J. F., Knierim, J. J., Fox, J. M., Sagi, D., & Julesz, B. (1989). Neural responses to static and moving texture patterns in visual cortex of the macaque monkey. In D. M. K. Lam & C. Gilbert (Eds.), Neural Mechanisms of Visual Perception (pp. 137-154). Woodlands, Texas: Portfolio.

Van Rijn, J., Van Der Steen, J., & Collewijn, H. (1994). Instability of ocular torsion during fixation: cyclovergence is more stable than cycloversion. Vision Research, 34, 1077-1087.

Wallace, S. F., & Rosenquist, A. C. (1986). The role of the substantia nigra (pars reticulata) in the mediation of the Sprague effect. Proceedings of the Society of Neuroscience, 12, 1032.

Watson, A. B., Barlow, H. B., & Robson, J. G. (1983). What does the eye see best? Nature, 302, 419-422.

Weiskrantz, L., Harlow, A., & Barbur, J. L. (1991). Factors affecting visual sensitivity in a hemianopic subject. Brain, 114, 2269-2282.

Westendorf, D. H., Langston, A., Chambers, D., & Allegretti, C. (1978). Binocular detection by normal and stereoblind observers. Perception and Psychophysics, 24, 209-214.

Westheimer, G. (1982). Do ocular dominance columns set spatial limits for hyperacuity processing? Vision Research, 22, 1349-1352.

Westheimer, G. (1990). Simultaneous orientation contrast for lines in the human fovea. Vision Research, 30, 1913-1921.

White, C. A., & Chalupa, L. M. (1991). Development of mammalian retinofugal pathways. In J. Cronly-Dillon (Ed.), Vision and Visual Dysfunction: neuroanatomy of the visual pathways and their development (Vol. III, pp. 129-149). London: Macmillan.

White, C. A., Chalupa, L. M., Maffei, M. A., Kirby, M. A., & Lia, B. (1989). Response properties in the dorsal lateral geniculate nucleus of the adult cat after interruption of prenatal binocular interactions. Journal of Neurophysiology, 62, 1039-1051.

Wiesel, T. N., & Hubel, D. H. (1963). single-cell responses in striate cortex of kittens deprived of vision in one eye. Journal of Neurophysiology, 26, 1003-1017.

Wiesel, T. N., & Hubel, D. H. (1965). Comparison of the effects of unilateral and bilateral eye closure or cortical unit responses in kittens. Journal of Neurophysiology, 28, 1029-1040.

Wiesel, T. N., Hubel, D. H., & Lam, D. M. K. (1974). Autoradiographic demonstration of ocular-dominance columns in the monkey striate cortex by means of transneuronal transport. Brain Research, 79, 273-279.

Williams, L. G. (1967). The effects of target specification on objects fixated during visual search. In A. F. Sanders (Ed.), Attention and Performance (Vol. I, pp. 355-360). Amsterdam: North Holland.

Williams, C., Azzopardi, P., Cowey, A. (1995). Nasal and temporal retinal ganglion-cells projecting to the midbrain – implications for blindsight. Neuroscience, 65, 577-586.

Wilson, H. R. (1983). Psychophysical evidence for spatial channels. In O. J. Braddick & A. C. Sleigh (Eds.), Physical and biological processing of images. Berlin: Springer.

Wolf, E., & Gardiner, F. S. (1963). Sensitivity of the retinal area in one eye corresponding to the blind spot in the other eye. Journal of the Optical Society of America, 53, 1437-1439.

Wolf, E., & Zigler, M., J. (1959). Uniocular and binocular scotopic responsiveness of the peripheral retina. Journal of the Optical Society of America, 49, 394-398.

Wolfe, J. M. (1996). Visual search. In H. Pashler (Ed.), Attention. London: University College London Press.

Wolfe, J. M., Friedman-Hill, S. R., Stewart, M. I., & O'Connell, K. M. (1992). The role of categorization in visual search for orientation. Journal of Experimental Psychology: Human Perception and Performance, 18, 34-49.

Wolfe, J., M, & Franzel, S., L. (1988). Binocularity and visual search. Perception and Psychophysics, 44, 81-93.

Zeki, S. M. (1974). Functional organisation of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. Journal of Physiology, 236, 549-573.

Zeki, S. M. (1979). Functional specialisation and binocular interaction in the visual areas of rhesus monkey prestriate cortex. Proceedings of the Royal Society of London. Series B, 204, 379-397.

Zeki, S. M. (Ed.). (1993). A Vision of the Brain (1st ed.). London: Blackwell.

Zihl, J., & Von Cramon, D. (1979a). Collicular function in human vision. Experimental Brain Research, 35, 419-424.

Zihl, J., & Von Cramon, D. (1979b). The Contribution of the "second" visual system to directed visual attention in man. Brain, 102, 835-856.

Zihl, J., Von Cramon, D., Poppel, E., & Singer, W. (1979). Interhemispheric modulation of light difference threshold in the periphery of the visual field. In J. S. Russell, M. W. Van Hof, & S. G. Berlucchi (Eds.), Structure and Function of the Cerebral Commisures (pp. 421-427). : McMillan Press Ltd.