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SOME ASPECTS OF THE PUPIL RESPONSE IN RELATION TO STIMULUS MOVEMENT AND COLOUR

by

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DECLARATION

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ABSTRACT

Recent investigations have shown that the activity of the visual system in the processing of some stimulus attributes such as spatial structure and stimulus colour are reflected in the pupil response in the form of a small transient constriction at the stimulus onset. The response amplitude appears to be proportional to the level of activity generated and varies systematically with the properties of the visual stimulus.

In this report, it has been shown that the processing of coherent motion information can also produce pupillary changes in the form of pupil motion responses (PMRs). The results show that PMRs are present for both foveal and peripheral stimulus presentations and are not affected significantly by degradation of retinal image quality. It has been demonstrated that PMRs are also elicited to sudden changes in stimulus speed and direction, and that the response amplitudes vary systematically with the percentage change involved.
There are extensive psychophysical data showing that blindsight subjects are sensitive to movement information when the stimulus is presented in their blind field. In this study, pupillometric parallels for the psychophysical findings have been demonstrated.

Data which reveal the existence of residual chromatic discrimination in the absence of V1 have also been obtained in two blindsight subjects. It has been shown that their psychophysical performance improves with the level of chromatic saturation of the stimulus.

The pupil colour responses have been investigated under similar conditions. Results show that the pupil responses to coloured stimuli can also be elicited in the blind field and that these responses parallel the psychophysical findings.
The results obtained have been discussed in relation to the properties of the neuronal structures and visual pathways which are likely to mediate the observed pupillometric and psychophysical findings.

Justification of the Proposed Investigation

The present knowledge of physiological data on human brain is far from complete. Studies carried out on cats and primates have provided information on the neuronal processing in these species. Although there is no direct evidence on the similarity of the perception of a stimulus in primates and in man, the large degree of similarity in the underlying neural connectivity between the different species indicates that it might be reasonable to assume some equivalent functional processing in man. Indeed some pathological disorders can cause alike deficits in man and monkey. The lesion studies in man and monkey as well as the results of PET studies have shown parallels between the functional specialisation of the primate visual cortex explained in chapter I, and the comparable cortical processing in man.

The human psychophysical data provide information on the parameters affecting the perception of stimuli. The questions asked in these measurements may have to be modified when obtaining parallel primate data. In the absence of human physiological data, it may then be possible to compare the human psychophysics with the primate physiological findings.

The neuronal substrates and functional hierarchy of movement processing and the results of pupillometric study of movement processing in both normal subjects and a subject with damaged central visual pathways are outlined in chapters III and IV. The results of a similar approach to processing of colour information is described in chapter V.

CHAPTER I
Introduction

1.0 Summary

In this chapter, a review of the physiology of the visual pathways is given. Movement pathways have been discussed in greater depth with emphasis on the psychophysical and physiological data on orientation, direction and speed tuning. Emphasis has been placed upon the data obtained for cat and monkey.
Since this study concerns the visual processing in both normal subjects and in subjects with damaged central visual pathways, the extrageniculate as well as the retinogeniculostriate projections have been discussed. In describing the connectivity of the structures involved, the afferents of one structure are the efferents of many others. The repetition of some neuronal connections is however inevitable. Nevertheless efforts have been made to minimise them.
A resumé of blindsight literature has been outlined and an introduction to the pupil pathways and pupillary responses has been presented.

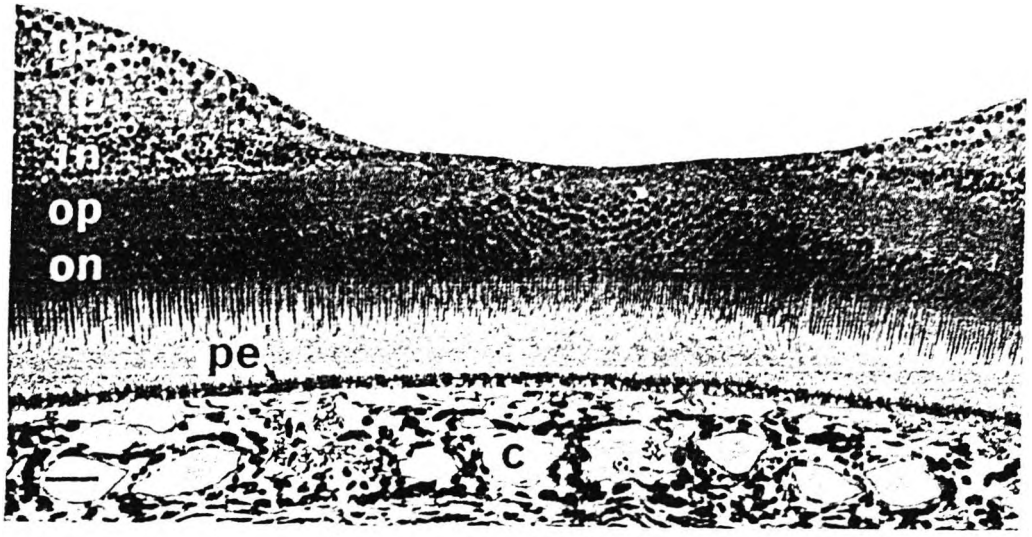


Figure 1.1: the fovea of a rhesus monkey. The fovea is reduced to a thickened outer nuclear layer (on), part of the outer plexiform layer (op) and the internal limiting membrane at the centre of the foveal pit. The inner nuclear layer (in) consists of a few nuclei close to the centre, but thickens rapidly at the edges of the figure where the inner plexiform layer (ip) and ganglion cell (gc) layers appear (from Ruskell, 1988 reprinted with permission).

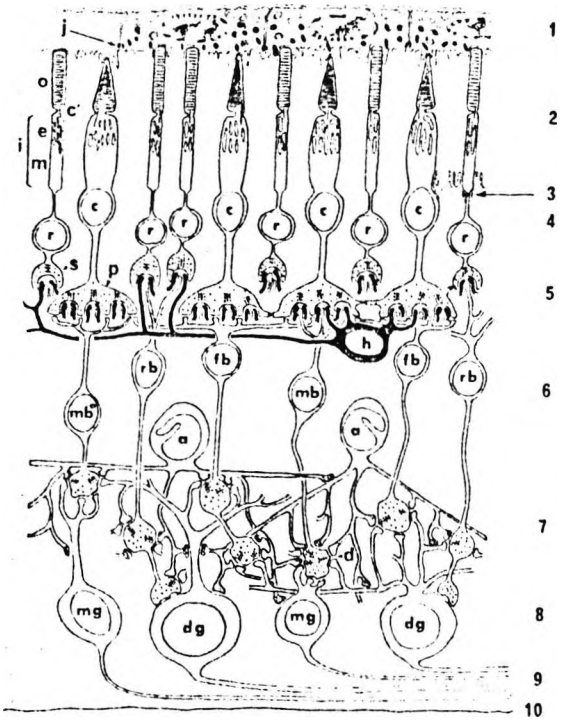


Figure 1.2: the ten layers and neurones of the retina (see text); j, junctional complexes near the apices of pigment epithelial cell interfaces; h, horizontal cells; a, amacrine cells; c, cone nucleus; c', connecting stalk; d, dyad synapse; dg, diffuse ganglion or alpha cell; e, ellipsoid; fb, flat bipolar; i, inner segment; mb, invaginating midget bipolar; mb°, flat midget ganglion or beta cell; p, cone pedicle; r, rod nucleus; rb, rod bipolar; s, rod sphrule (from Ruskell, 1988 reprinted with permission).

1.1 Physiology of the visual pathway

The information contained in the retinal image formed by the optics of the eye is encoded by over one hundred million receptors. After some retinal processing, the visual information traverses from each eye to the brain via some one million fibres of the optic nerve. In primates, the majority of the optic nerve fibres project to the striate cortex via the dorsal lateral geniculate nucleus. In addition to this pathway, approximately 150,000 neurones project to various visual areas via nine parallel projections. An in-depth anatomical description of the structures involved is not included in this thesis and can be found in many standard textbooks and only a summary of some important anatomical and physiological properties, relevant to this report is described below.

Retina

The retina is thin and transparent and is situated between the vitreous and choroid. The inner or neural retina has a weak attachment to the pigment epithelium which is in turn attached firmly to the choroid. The retina is thinnest at the foveola, a small area providing the greatest visual resolution at the centre of the retina (0.1mm), and thickest at the parafovea (0.23mm) and at the optic disc margin where retinal nerve fibres emerge from the eye to form the optic nerve (Ruskell, 1988).

The visual process is initiated in the retina which houses the light receptive cells: rods and cones. The information from these receptors is transmitted to the brain after extensive interneuronal processing within the retina.

A feature of the stained cross-section of the retina is its sharply defined layered structure (see figure 1.1).

Figure 1.2 represents a schematic diagram of the retinal interneuronal connections. The layers and membranes are numbered conventionally from the outermost layer as follows: 1, retinal pigment epithelium; 2, rod and cone layer; 3, outer limiting membrane; 4, outer nuclear layer; 5, outer plexiform layer; 6, inner nuclear layer; 7, inner plexiform layer; 8, ganglion cell layer; 9, nerve fibre layer and 10, inner limiting membrane.

The pigment epithelium is composed of a single layer of cells packed tightly together, whose principle function is the absorption of light that has failed to bleach receptors, thus preventing its back scattering and hence the degradation of the retinal image.

The second layer of the retina consists of the rod and cone receptors. Their inner

processes traverse the outer limiting membrane, the outer nuclear layer where their nuclei are located, finally terminating in the outer plexiform layer. The rod inner segment is cylindrical and maintains the same width throughout its length from the external limiting membrane to the connecting stalk. The outer segment is also cylindrical, about 1.4 μm wide and just noticeably thinner than the inner segment. The cone inner segment departs slightly from the shape of a cylinder because its width increases from the outer limiting membrane to a maximum of 5 or 6 μm near its centre and then tapers as it approaches the connecting stalk. At the stalk the inner and outer segment have the same width but the outer segment continues to taper to give the cone its characteristic shape (Ruskell, 1988). cones display some variations in shape and in man they assume the appearance of rods at the foveal region with a maximum width of 2.5μm.

Osterberg (1935) estimated the total number of rods and cones in the human retina to be between 110 and 125 million and 6 and 8 million, respectively.

Receptor outer segments consist of a dense stack of 700 to 1200 disc-shaped double membranes enclosed by the cell membrane. The neural process of vision begins with the bleaching of receptor photopigments by light. The highly specialised structure of the receptor outer segment provides an efficient photon catching device because the regular disposition of photopigment molecules on each disc reduces the chance of photons traversing the receptor without being absorbed.

There are three types of cone photoreceptors in mammals. These absorb light maximally at three different wavelengths, and contain one of three pigments. They are thus referred to as red, green or blue cones. In baboon, 33% of cones are red, 54% green and 13% blue, with the proportion of blue cones reducing to 3% in the central retina. A similar distribution of cone types exists in man (Ruskell, 1993).

Receptors are known to display a marked directional sensitivity, ie., only axial or nearly axial rays are accepted and funnelled to the outer segments (Stiles-Crawford effect). Laties et al. (1968) studied the receptor alignment and observed an increasing inclination from the normal to the retinal surface with distance from the fovea so that all receptors were directed towards the front of the eye in the vicinity of the exit pupil. After certain pathological disorders, the disturbed receptor orientation is corrected during recovery suggesting the presence of an orientation mechanism.

The difference in sensitivity of rods and cones is several orders of magnitude which gives rise to scotopic and photopic response of visual performance. The sensitivity difference is attributed to the summation permitted by the substantial convergence of rods to bipolar and ganglion cells which constitutes a wide quantum catching

system. In contrast, cones display minimal summation because they lack neural convergence and so are at a disadvantage when the quantity of impinging light quanta is low.

Rod and cone receptors synapse in the outer plexiform layer. Cones synapse with midget, flat midget and flat bipolar cells. Midget bipolar cells possess a tight cluster of dendrites in contact with a single cone. Flat midget bipolar cells also contact cones on one-to-one basis. Rod bipolar cells constitute a single class and they have the broadest spread of up to 45 dendrites and are in contact with a similar number of rod receptors. Hence, at the first synapse, convergence of rod input is evident whereas convergence is lacking in the cone/midget bipolar pathway.

Horizontal cells also synapse in the outer plexiform layer with each cell contacting 6 to 12 cones centrally and 30 to 50 cones peripherally. They have extremely fine cell axons and are up to 1mm long, and may contact 80 to 150 rods.

Bipolar, ganglion and amacrine cells synapse in a complex manner and at several levels within the inner plexiform layer (Dowling and Boycott, 1966). Some amacrine cells, as well as having dendritic communications with other amacrine cells, have an axon which passes back to the outer plexiform layer where they synapse by bipolar dendrites with horizontal cells.

Retinal Ganglion Cells

Retinal neurones which have an axon that joins the optic nerve are called retinal ganglion cells. There are approximately 1.2 million ganglion cells in the human retina (Oppel, 1967). Their greatest density is at the macular region and the density falls to a minimum in the periphery. A great variety of ganglion cells have been described. In cat, they can be divided anatomically into three main categories of alpha, beta and gamma cells as shown in figure 1.3. In primates, small ganglion cells are far more common than large ones and few or no large cells are present in the central retina. The small or beta cells are the midget ganglion cells, and they have small dendritic fields which increase in size with increasing eccentricity. Large or alpha cells have large dendritic fields, which increase greatly with eccentricity (from $\approx 35\mu$m at 3° to 170μm at 18°). On the basis of neuroanatomical studies, ganglion cells cannot be designated as rod or cone types in cats, and mixed rod and cone inputs may be demonstrated by appropriate manipulation of stimuli (Rodieck and Rushton, 1976; Kolb, 1979).

In monkey, alpha cells project to magnocellular laminae, beta cells to parvocellular laminae and gamma cells to interlaminar of LGN. In addition, alpha and gamma cells project to midbrain structures (Perry and Cowey, 1984).

Anatomical classification	*Cell type*		
	Alpha	*Beta*	*Gamma*
Cell diameter (μm)	24–28	12–25*	5–15
Dendritic spread (μm)	300–600	25–250*	Wide
Proportions (%)	4	55	41
Projections	LGN, SC	LGN	LGN, SC
Physiological classification	Y	X	W or Q
Response characteristics	Brisk Transient	Brisk Sustained	Sluggish Sustained
Receptive field size	Large	Small	Large
On-centre, off-centre	Both	Both	Both
Spatial summation	Non-linear	Linear	Linear
Conduction velocity	Relatively fast	Slower	Slowest
Possible function	Movement detection	Visual resolution	Uncertain

*Diameter and dendritic spread increase with eccentricity.
Derived from the data of Enroth-Cugell and Robson (1966, 1984), Stone and Hoffman (1972), Boycott and Wässle (1974), Cleland and Levick (1974a, b), Rowe and Stone (1976) and Wässle, Boycott and Illing, 1981.
LGN = lateral geniculate nucleus; SC = superior colliculus.

Figure 1.3: ganglion cell types and their properties in cats (from Ruskell, 1988 reprinted with permission).

Classification of retinal ganglion cells

It is possible to classify ganglion cells by a number of physiological criteria. Ganglion cells fire "*all-or-none*" spike discharges. In primate retina, some ganglion cell have a low, sustained firing rate in the absence of light. The firing rate may be either increased when a spot of light is placed in the cell's receptive field in which case the cell is termed an "*on*" cell; or reduced in which case the cell is termed an "*off*" cell. An "*on centre*" cell may also be viewed as a cell which has an increased firing rate in response to centre illumination, above that of the surround, whereas "*off centre*" cell responds with a depression of the firing rate to a reduction in centre illumination below that of the surround.

Another classification of the ganglion cells is based on whether the cell response is continued over the period of the stimulus presentation for light or dark stimuli, ie., the firing rate is elevated after the onset or offset of the stimulus. There are two classes of neurones termed "*tonic* or *sustained*" or "*transient* or *phasic*" cells. This classification may prove difficult for some cells (Cohen, 1987).

An experimental classification with fewer ambiguities is that of "*X*" and "*Y*" cells (Enroth-Cugell and Robson, 1966). These correspond roughly to the sustained and phasic types, respectively. When a grating or a chequerboard pattern is passed over the centre of a Y cell receptive field, it responds to each rearrangement of the dark and light elements, whereas an X cell maintains a steady firing rate while the elements are moved in the centre of its receptive field providing that the net illumination is unchanged (Enroth-Cugell and Robson, 1966).

A ganglion cell type named "W" cell has been described (Fukuda and Stone, 1974; Stone and Fukuda, 1974). These cells are quite numerous (see figure 1.3), can have small receptive fields and have the slowest conduction rate.

Finally, the "*briskness*" or "*sluggishness*" of a response is another independent dichotomy that has been found useful in classifying the response of ganglion cells.

In species with colour vision the responses of many ganglion cells are influenced by the wavelengths of light in their receptive fields. The ganglion cells in macaque are either broad-band, where they respond to light or dark stimuli, or are colour opponent cells (Schiller and Malpeli, 1978). The broad-band cells receive input from two types of cones, both of which are excited in the centre and inhibited in the surround. The broad-band cells respond phasically to maintained stimuli. Two types of colour opponent cells are known (Cohen, 1987). In cell types which show centre field colour opponency only, one wavelength on the centre excites and another on the centre inhibits the cell response, usually red versus green or blue versus yellow. In the second class of cells, centre surround, colour opponency exists

between a particular colour on the cell centre and another colour on the surround, but the colour affecting the centre does not have an opposite effect when on the surround. These cells tend to respond tonically, have smaller axons, and have slower conduction velocities than the phasic types. Response of a double opponent colour cell, is one where one colour excites in the centre and also inhibits in the surround, and a second colour inhibits in the centre but excites in the surround. In primates these cells seem to be exclusive to the higher visual areas and are not present at retinal level.

Optic Nerve, Tract and Chiasm

Axons of ganglion cells turn into the plane of the retina and pass towards the optic disc to form the optic nerve. The optic nerve then conducts nerve fibres from the retina to the chiasm. The chiasm is a midline structure of the hypothalamus of the brain and is formed by the junction of the two optic nerves. At the optic chiasm semi-decussation of nerve fibres takes place, ie., the nasal fibres which make up about 53% of the total in monkey cross to the contralateral hemisphere (Kupfer et al., 1967), and form the optic tract.

The first branching of nerve fibres from the optic tract form the retinohypothalamic pathway. The majority of optic tract fibres terminate on the lateral geniculate body. Some however, leave the tract in the superior brachium which lies immediately anterior to the lateral geniculate body and project to the pregeniculate nucleus, pretectal nuclei, superior colliculus, pulvinar and the accessory optic nuclei. These visual centres are discussed below.

Lateral Geniculate Nucleus (LGN)

The lateral geniculate body houses a nucleus consisting of six roughly dome-shaped layers of neurones stacked above each other concentrically. The nucleus is based on a hilum, which is a shallow sagittal sulcus. Numbered from the hilum, two magnocellular layers lie closest and four parvocellular (small cell) layers farthest away (see figure 1.4). The nasal fibres terminate in layers 1, 4 and 6 and temporal fibres in layers 2,3, and 5. Within each layer there is a topographical map of the contralateral visual hemifield (Hubel, 1988). The morphological and physiological characteristics of retinal neurones are duplicated in the LGN with alpha or Y neurones confined to the magnocellular and beta or X neurones to the parvocellular layers (Ruskell, 1988). Schiller and Malpeli (1978) found that in the macaque, "on" colour-opponent ganglion cells projected to layers 5 and 6 whereas "off" colour-opponent cells projected to layers 3 and 4. The transient broad-band

Figure 1.4: frontal section through the LGN of a rhesus monkey; h, hilum. Marker = 0.5mm (from Ruskell, 1988 reprinted with permission).

Figure 1.5: some physiological properties of the magno and parvo geniculate division (from Livingstone and Hubel, 1987)

Property	Magnocellular cells	Parvocelluar cells
Colour	broadband	colour-opponent
Contrast threshold	high (threshold < 2%)	low (threshold > 10%)
Temporal response	fast transient responses high conduction velocity	slow sustained responses low conduction velocity
Spatial resolution	low	high by 2-3 fold

ganglion cells project to layers 1 and 2.
A summary of the physiological properties of cells in the magnocellular and parvocellular layers are listed in figure 1.5. Although the precise functions of the nucleus are not known, it does not seem to be a simple relay station since substantial integrative activity occurs within each layer by a large number of small interneurones (Wong-Riley, 1972).
The activity of LGN is modulated by a variety of inputs from visual and non-visual areas. These include the occipital cortex (Lund et al., 1979), reticular formation, pons and pretectum (Wilson et al., 1973). Control of eye movement during selective attention and state of arousal are suggested as possible functions of these modulations (Holden, 1976). This suggests that signals of retinal origin are subject to a variety of influences preceding conduction to the optic radiations and striate cortex.

Optic Radiations

The nerve fibres leaving LGN dorsolaterally are termed optic radiations and form a thin vertically oriented band lying close to the wall of the posterior horn of the lateral ventricle and directed towards the occipital lobe. The band is twisted with the inferior fibres directed forward into the lateral lobe of the brain, skirting the inferior horn of the lateral ventricle, before turning back sharply. Some geniculate fibres in monkey terminate in prestriate cortex equivalent to area 18 and 19 in man (Yukie and Iwai, 1981; Yoshida and Benvento, 1981; Bullier and Kennedy, 1983).

Primary Visual Cortex (V1)

With the exception of a small number of neurones, the optic radiations terminate on the primary visual area V1 equivalent to the Brodmann's area 17 (Brodmann 1909), it is distinguished from other cortical areas in possessing a thin band of medullated nerve fibres running parallel to the cortical surface. This appearance gives rise to the name striate area or striate cortex.
V1 in humans is located on both sides of the calcarine fissure on the medial aspect of the occipital lobe, extending for a short distance onto the occipital pole (Pearlman, 1987) (see figure 1.6). It is bordered anteriorly by an approximately 1cm wide rim of cortex, called parastriate cortex or area 18 of Brodmann, which lacks the stria of area 17 and is considerably thinner. Practically all of the remainder of the occipital lobe is occupied by the area 19. The cytoarchitectonic differences between areas 18 and 19 are not easily recognised. These areas are concerned exclusively with vision and may be described collectively as the prestriate

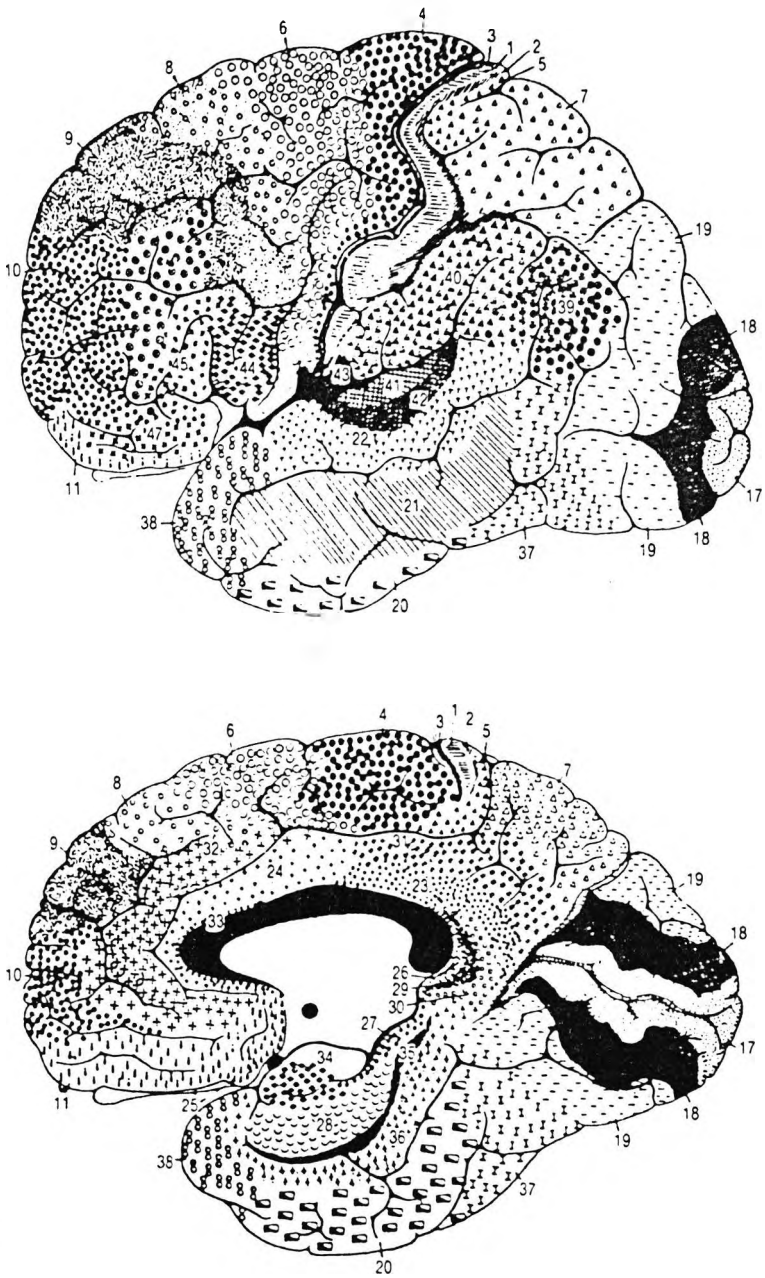


Figure 1.6: classification of human cortex (from Brodmann, 1909).

visual areas (Ruskell, 1993).

The stria of area 17 is common to most mammals but the surface area it occupies varies considerably. For example, the lateral aspect of the occipital lobe may be taken up mainly by the striate cortex as it is in monkeys (see figure 1.7). The relationship between visual field loss and the site of the responsible cerebral lesion has provided details of retinotopic projections to the cortex (Cowey and Weiskrantz, 1963). The most dependable human data are obtained from field losses following gunshot wounds caused during the first and second world wars. This kind of observation suggested that the lower and upper retina project to the lower and upper striate cortex respectively and the horizontal meridian is represented in the floor of the calcarine sulcus. The central retinal projections lie most posteriorly at the pole of the occipital lobe advancing in sequential order to the anterior part of the striate cortex with increasing eccentricity from the fixation point (Ruskell, 1993). The spatial analysis of visual stimuli is far greater for central vision than peripheral vision. The extra demands of central vision are achieved by greater thickness of the ganglion cell layer at retinal level. The geniculate nucleus copes differently by allocating a larger area for central projections. At the cerebral level one part of the cortex at V1 is cytologically indistinguishable from another, showing no variation in its thickness or cell density. The cortical analysis of the central visual field is far more detailed than for the periphery and the extra demands of the central vision are met by a greater cortical area receiving central retinal projections for unit angle of field, reducing gradually with eccentricity (see figure 1.8).

Cortical Lamination and Ascending and Descending Projections

Variations in staining the visual cortex indicate distinct lamination due to distribution of different cell bodies, synapses and dendritic interconnections. There are six laminae numbered from the surface inward (see figure 1.9). Further subdivision of lamina 4 into sublaminae A, B and C was proposed by Brodmann and remains appropriate with 4B representing a broad, largely horizontally oriented nerve fibre zone sandwiched by a wide 4C and narrow 4A cell rich sublaminae (Ruskell, 1993). Layer 1 contains few nerve cells but has abundant axons, dendrites and synapses. In the striate cortex., laminae 2, 3 and 4A contain a continuously high density of cells and the borders of 3 cannot be identified with any confidence in any routinely produced histological section. There are fibre concentrations in laminae 1, 5 and 4B with the fibre orientation in each case being predominantly horizontal, in the plane of cortex.

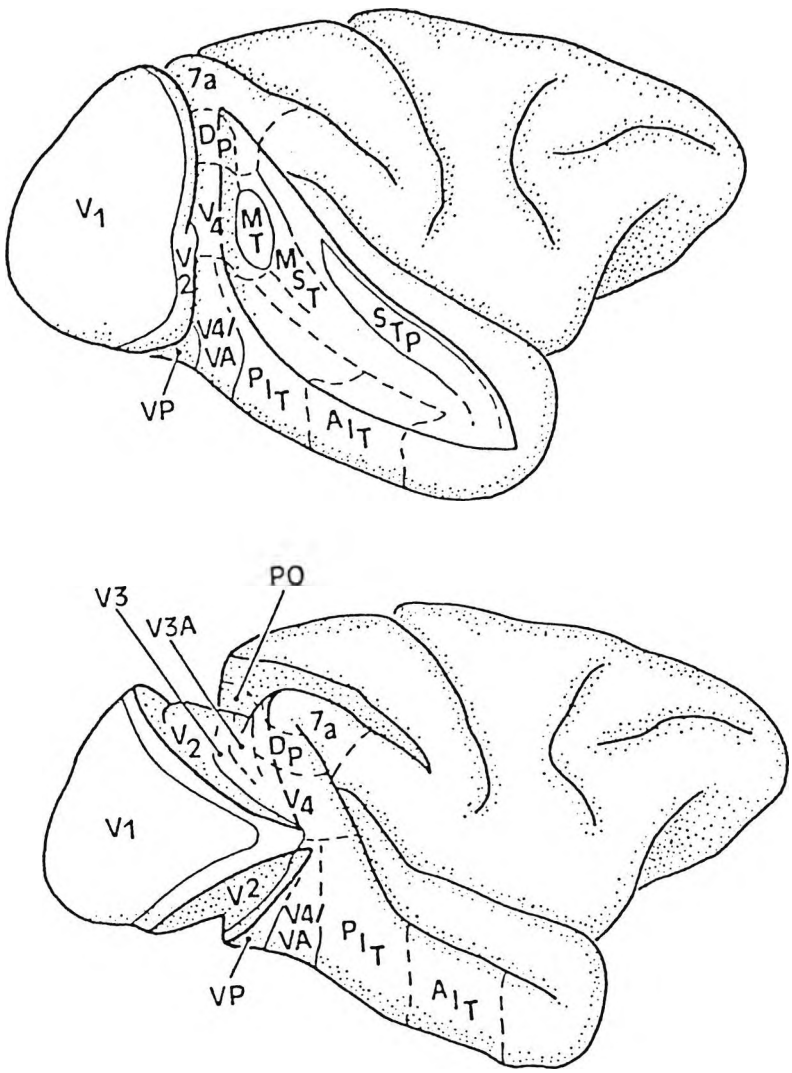


Figure 1.7: the location of visual areas buried within sulci in macaque monkey. The upper half of the figure is a lateral view in which the superior temporal sulcus has been opened to show the positions of visual areas within it. Areas of the superior temporal sulcus that are not visible in the intact view are the middle temporal area (MT), the medial superior temporal area (MST), and the superior temporal polysensory area (STP). The lower half of the figure is a view in which the lunate intraparietal, parieto-occipital, and inferior occipital sulci have been opened, exposing parts of V3, V3A, and ventral posterior area (VP) (from Maunsell and Newsome, 1987).

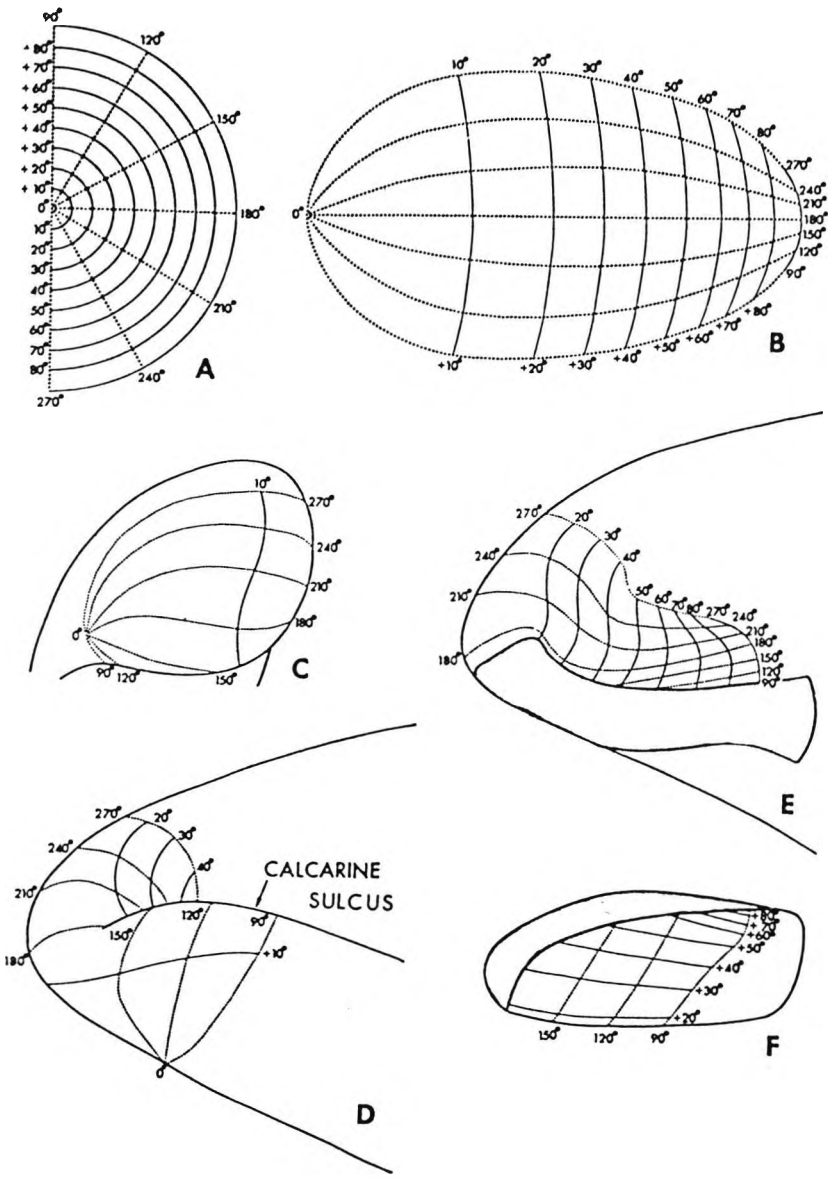


Figure 1.8: the representation of the visual field in the striate cortex of the owl monkey. A, planar representation of the contralateral hemifield. B, planar representation of the unfolded striate cortex. The organisation and location of the striate cortex is shown in four views; C, posterior view; D, ventromedial view; E, ventromedial view with the lower bank of the calcarine fissure removed to show the upper bank; F, the removed lower bank of the calcarine fissure is viewed dorsally (from Holden,1976).

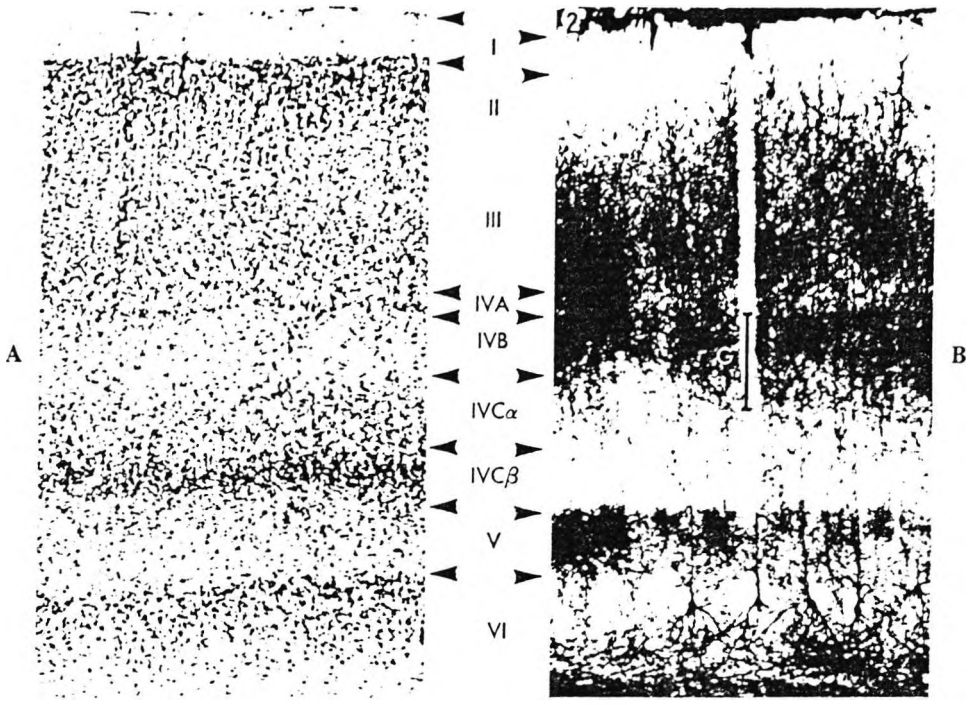
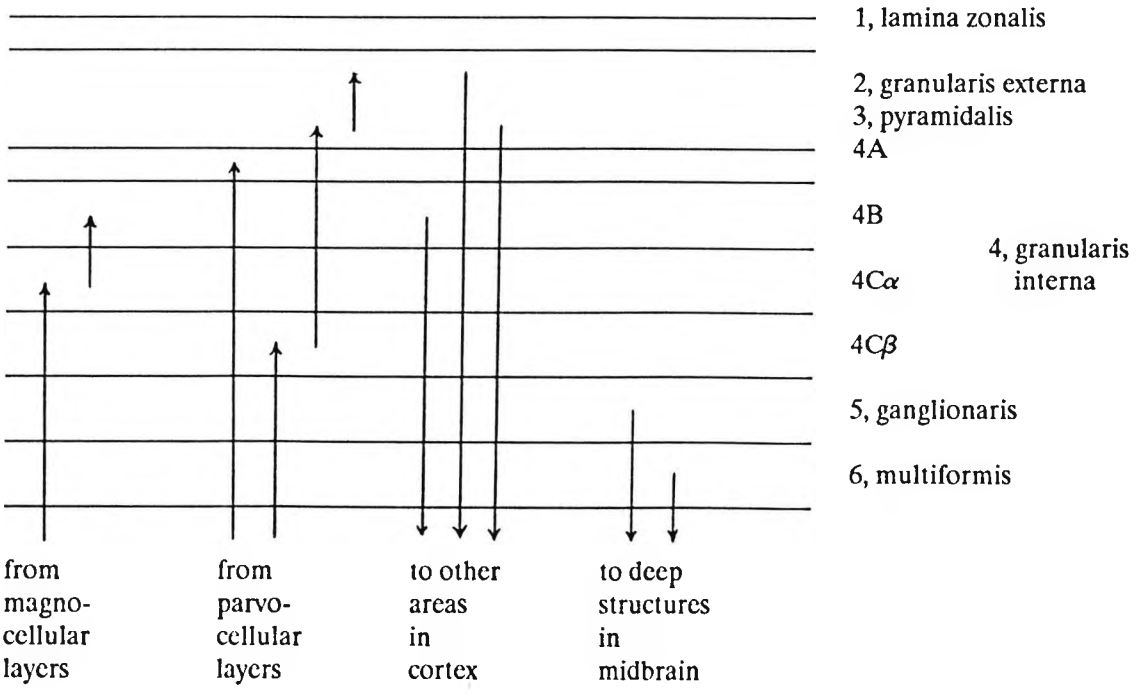


Figure 1.9: A,Nissl-stained section of area 17 of monkey.This method predominantly stains nuclei of cortical cells. B, Section prepared by the Golgi rapid method which stains cell bodies and many processes of cortical neurones (from Pearlman, 1987).

Figure 1.10: the main connections made from lateral geniculate body to the striate cortex and from the striate cortex to other brain region (from Hubel, 1988).



Layers 4C and 6 are the densest and the darkest; layers 1, 4B and 5 are loosely packed. The two major classes of cortical cells are the pyramidal cells, which occur in all layers except 1 and 4, and the stellate cells, which are found in all layers (Hubel, 1988). Fibres from the magnocellular layers of LGN, terminate in the upper half of 4C called 4Cα and those from the parvocellular layers terminate in the lower half of 4C (4Cβ). Figure 1.10 shows a schematic representation of some further projections from these layers.

Most pyramidal cells in layers 2, 3, 5 and 6 send axons out of the cortex. Collaterals of the same descending axons connect locally and help to distribute information through the full cortical thickness.

Ascending and descending projections can be distinguished from each other by determination of the cortical layers in which they originate and terminate. Ascending projections, which transmit information away from primary sensory areas, arise primarily in the superficial layers of cortex and terminate primarily in layer 4 and the lower part of layer 3. Descending projections, which carry signals back towards primary sensory areas, originate largely from neurones in the deep layers and end primarily in the superficial and deep layers. Most connections among the extrastriate cortical areas have one of these patterns and can be assigned as forward (ascending) feedback (descending) by these anatomical criteria alone (Maunsell and Newsome, 1987). If area A sends a forward projection to area B, which in turn sends a forward projection to area C, then a projection from A to C must have the forward pattern of laminar termination. All adequately studied connections among visual cortical areas in the macaque conform to this scheme. In the striate cortex, upper layers 2 and 3 and layer 4B project mainly to other cortical regions (see chapter III), whereas the deep layers project down to subcortical structures. Layer 5 projects to the superior colliculus and layer 6 projects back to lateral geniculate body (Zeki, 1993).

Columnar Organisation

Studies of ocular dominance of the cortical cells have revealed a discrete physiological organisation of cells which have differing binocular responses (Hubel and Wiesel, 1977). The process of convergence of information from the two eyes occurs first in the striate cortex but it is delayed beyond the first level of synapses at least, for cells in lamina 4 which are largely monocular. At levels above and below lamina 4 many of the neurones respond to a stimulus exposed to both eyes and excitation is greater than when one or the other eye is occluded. Such cells are binocular cells. All cells along a locus perpendicular to the cortical surface display ocular dominance of a varying degree from monocular, to partial dominance, to

binocular. Cells with these characteristics occupy a column about 0.4mm in width neighboured on each side by dominance columns of the same width but for the opposite eye (Hubel and Wiesel, 1977; Hubel, 1988; Ruskell, 1988, 1993). In fact the columns extend through the cortex for considerable distance constituting slabs rather than columns (see figure 1.11).

Repeated electrode penetrations of adjacent regions of the striate cortex have demonstrated that cells with receptive fields of a particular orientation are grouped together (Hubel and Wiesel, 1977; Hubel et al., 1978). An electrode penetration perpendicular to the cortical surface will encounter cells with receptive fields of only one orientation as it travels through the layers thus forming orientation columns as shown schematically in figure 1.12. Adjacent orientation columns differ slightly in their orientation selectivity in a systematic way such that an electrode moved almost parallel to the cortical laminae encounters cells with receptive fields of the first one orientation and then with an orientation selectivity that differs by about 10° in a clockwise or anticlockwise direction (Pearlman, 1987).

The ocular dominance and orientation columns do seem to be independent of each other.

Classification of Cortical Cells

Concentric cells. The receptive fields of many cells in layer 4 of the striate cortex are similar to LGN cells. They have a concentric centre-surround arrangement and are monocular. Their similarity to geniculate cells indicates that very little transformation of the geniculate input has occurred. Their presence in layer 4 where most geniculate afferents terminate, together with their geniculate-like receptive fields suggests that they receive direct geniculate input (Hubel and Wiesel, 1968; Dow, 1974).

Simple cells. The striate simple cells have receptive fields that can be mapped with small spots of light, and shown to be divided into on and off areas. These on and off regions are mutually antagonistic and arranged in parallel bands, rather than in the concentric centre-surround form of the geniculate cells. Receptive fields of simple cells often have a central band that is either an on, or an off region, with parallel flanking regions on two sides that are opposite. The flanking regions are not always equal in size and sometimes there is only one.

In monkey the majority of simple cells are found in layer 4, but they are also present in the more superficial and deeper layers. Layer 4 simple cells are often monocular and have smaller receptive fields than those in other layers (Hubel and Wiesel,

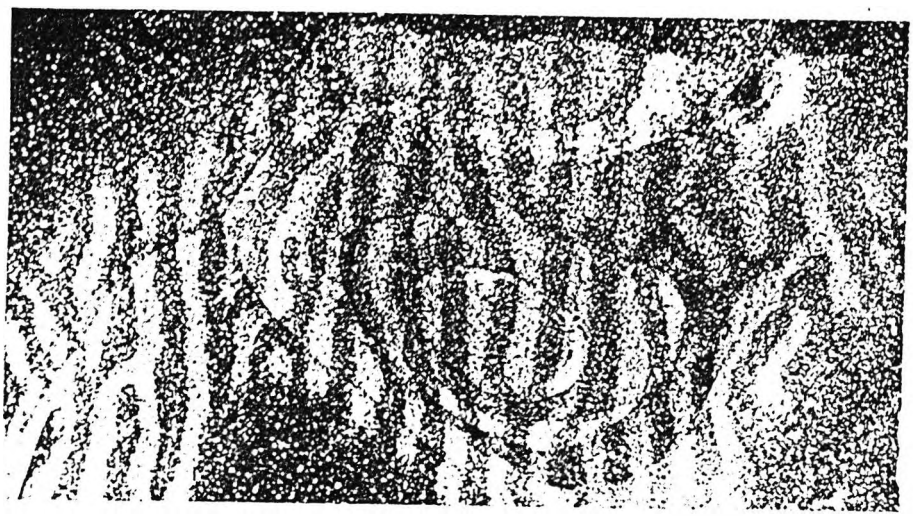
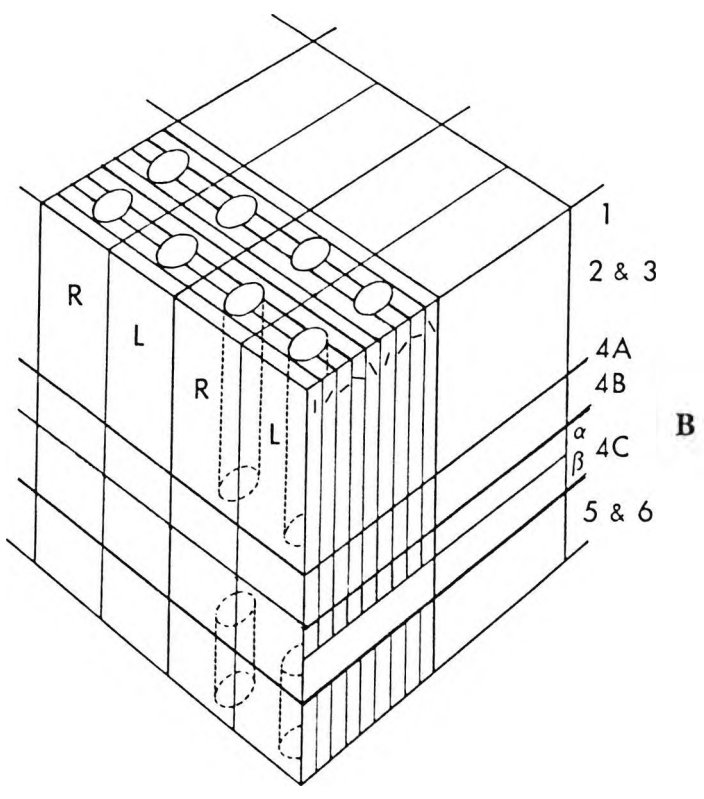


Figure 1.11: a composite autoradiograph visualising the pattern of ocular dominance columns over an area some 10mm wide. Above was obtained by cutting out and pasting together the regions representing layer 4 in a number of parallel sections (from Hubel, 1988).

Figure 1.12: a model of the modular organisation of primate striate cortex. Ocular dominance columns are labelled as right (R) or left (L) dominant. Orientation columns are indicated as slabs running perpendicular to ocular dominance columns, marked by lines of differing orientations. Perpendicular arrangement of ocular dominance and orientation columns is for diagrammatic convenience only. Cytochrome oxidase blobs are shown as vertical cylinders. Cortical layers are labelled by numbers on the right (from Livingstone and Hubel, 1984b)



1968; Dow, 1974; Pearlman, 1987).

Complex cells are distinguished from simple cells by the fact that it is not possible to map out distinct antagonistic on and off regions in their receptive fields. They respond to light or dark bars of a specific orientation anywhere in their receptive field. Complex cells produce the greatest response to moving stimuli and often are directionally selective. They are binocular and found in cortical layers above and below layer 4 of the striate, but only rarely in layer 4 itself (Hubel and Wiesel, 1962, 1968).

End-stopped cells. Length summation is observed in simple and complex cells. The longer the stimulus line, the greater the cell response, until the line is as long as the receptive field. Further increases in the line length has no additional effect. Thus for an end-stopped cell lengthening the line stimulus improves the response up to a limit, but exceeding that limit in one or both directions results in a weaker response. A complex end-stopped cell does not respond to a long line. End-stopped cells are therefore sensitive to corners, curvatures and/or sudden breaks in lines.

Colour-coded cells. Some cells in monkey striate cortex, especially in the part of the cortex representing fovea, are highly specific for colour. These colour-coded cells have the same types of spatial organisation as non-colour-coded concentric, simple, complex and end-stopped cells, but they respond preferentially to particular colours and not to white light. For example, the central region of a receptive field of a colour-coded simple cell might be excited by green and the flanking bands by red. Thus the best response would be to a specifically oriented green bar that fills the centre band while the adjacent bands are illuminated by red. Colour-coded concentric and simple cells are found primarily in layer 4, while colour-coded complex and end-stopped cells are prevalent in layers 2, 3, 5 and 6 (Dow, 1974; Hubel and Wiesel, 1968; Pearlman, 1987). A special class of concentric colour-coded cells called double opponent cells explained earlier is present in layer 2 and 3.

Prestriate Visual Areas

Brodmann's area 18, a rim of cortex about 1cm wide adjacent to the striate cortex and area 19 adjacent and anterior to area 18 are considered to be the areas where further analysis of visual information occurs. This idea was based on clinical evidence of perceptual deficits associated with lesions of these areas. Deductions of

this kind are approximate and subject to different interpretations due to the difficulty of assessing symptoms and the imprecise localisation of the lesions that commonly also involved white matter (Ruskell, 1988, 1993).
Animal studies have shown that the visual field is not confined to a single representation located in the striate cortex. Anatomical and functional studies of the visual cortex of monkeys and other mammals have shown that it is made up of a multiplicity of distinct areas, most containing a full topographical representation of the contralateral visual hemifield. Several maps may occur within a single Brodmann area with the exception of the striate cortex. Consequently, the Brodmann areas do not express a satisfactory representation of functional territories and the visual areas have been divided according to their field maps. Zeki (1971b) has used V1 to V5 designation for the maps in rhesus monkey and Allmann, Kass (1971) and their colleagues employed descriptive terms based on anatomical locations in owl monkey. Areas 17 and 18 of the owl monkey are each filled by a single representation of the visual field but in rhesus monkey there are at least four maps in area 18; V2, V3, V3A and V4 each with similar cytoarchitecture. A visual field representation occupying a short length of the posterior bank of the superior temporal sulcus is visual area V5 identified in area 19 of the rhesus monkey (Zeki, 1969) and is equivalent to MT (middle temporal area) of owl monkey. Altogether in macaque some twenty areas are candidates for being largely or exclusively visual in function; 11 of these are demonstrably visual and have been identified with a reasonable degree of confidence (van Essen, 1985). A brief description of some of these cortical visual areas are given below.

V2 has a long common border with V1 and a visual representation which is a mirror image of that in V1. The representation of the vertical meridian is at the border between these two regions and the horizontal meridian is represented at its border with V3. V2 receives patchy input from V1 (see section 1.6) and subcortical structures.

V3 and ventral posterior area (*VP*). V3 was first identified by Zeki (1969) on the basis of the pattern of degeneration found after making discrete lesions in various parts of V1. Evidence suggested that V3 was a narrow strip adjoining both dorsal (lower field) and ventral (upper field) subdivisions of V2. Van Essen and colleagues however argued that the ventral posterior area is a separate visual area, joining ventral V2, on the basis that they found major differences between the two areas with regard to colour and direction selectivity and receptive field sizes (see

review by van Essen, 1985).

V3A was mainly identified on the basis of the pattern of callosal inputs to cortex in the lunate and parieto-occipital sulci. The region adjacent to V3 consists of a central callosal-free zone surrounded by a horseshoe-shaped ring of callosal recipient cortex. Within this region there are upper and lower field representations that are distinct from both V3 medially and V4 laterally (van Essen and Zeki, 1978)

V4. Lying lateral to V3A in the lunate sulcus, and extending on to the prelunate gyrus, and then the lateral part of the posterior bank of the superior temporal sulcus (STS) is a zone of cortex which can be subdivided into a posterior and an anterior area, each having its own distinctive anatomical and callosal connections (Zeki, 1971b). The visual fields are separately mapped in each area with the same part of the field being multiply represented. They are grouped together as a visual area V4 (Zeki, 1978a).

V5/MT was originally identified in the macaque as a V1 recipient zone on the posterior bank of the STS (Zeki, 1969). However later studies showed that identification based on characteristic pattern of heavy myelination coincides with the borders of V1 recipient cortex to within 1mm (van Essen et al., 1981). MT is termed a motion area due to the prevalence of directionally selective neurones (see section 1.6).

MST (medial superior temporal area) and *VIP* (ventral intraparietal area) have been identified chiefly on the grounds that they are restricted regions receiving major inputs from MT (Maunsell and van Essen, 1983c). MST occupies a narrow strip of cortex immediately medial to MT, along the fundus of the STS. Receptive fields in MST are often large and MT lacks obvious topographic organisation. The situation with VIP is similar. MT projects to a strip of cortex along the fundus of the intraparietal sulcus (Maunsell and van Essen, 1983c).
There are two visual areas within the inferotemporal cortex. These are posterior inferotemporal (*PIT*) and anterior inferotemporal (*AIT*) areas. An additional four partially delineated areas are strongly visual but are also involved in visuomotor, polysensory and/or other functions. These are lateral intraparietal area (*LIP*), the superior temporal polysensory area (*STP*), and areas *7a* and *8*. There are areas which are likely to be at least partially visual in function but for which physiological information is sparse. These include the temporal frontal area (*TF*) and the

prostriate area (*PS*).
The positions of these visual areas in macaque brain are shown in figure 1.7, and a schematic representation of their hierarchical interconnectivity is represented in figures 1.14 & 3.1.

Retinal Projections to Midbrain Structures

At the level of the superior brachium, some optic tract fibres separate and terminate on other midbrain structures rather than on LGN. These structures are discussed here under the following headings:

1. accessory optic system
2. pretectal nuclei
3. superior colliculus
4. hypothalamus and thalamus
5. pulvinar.

Accessory Optic Nucleus

The accessory optic system (AOS) is a visuosensory pathway with a direct retinal input to the midbrain. Three nuclei have been identified in primates' AOS namely, dorsal, lateral, and medial terminal nuclei. In primates the medial nucleus has migrated to a more dorsal location (Cooper and Mangin, 1986). Predominantly crossed retinal fibres pass to the lateral terminal nucleus, but uncrossed fibres are also well presented in rhesus monkey (Ruskell, 1993). The AOS is similar in several species of monkey and contrasts with the non-primate systems in which there are usually two outlets from the tract (Simpson, 1984). The presence of this system has not been clearly demonstrated in man but the paralemniscal nucleus of the human midbrain may be the equivalent of the accessory optic nuclei of other primates. Afferent terminals in the nucleus are not exclusively derived from the retina because many of the cells survive subsequent to eye enucleation. There are also suggestions that the AOS receives afferents from other structures such as pretectum, cortex and superior colliculus (Pasik et al., 1973).
The efferents of AOS include projections from medial terminal nuclei to the vestibular nuclei (Cooper and Mangin, 1986) and to the pretectum and flocculus (Pasik et al., 1973). The dorsal terminal nuclei projects to the inferior olivery pretectal nucleus (Hoffmann et al., 1988).
The role of AOS in normal visual behaviour is not known. It has been suggested that some cells respond to large textured moving stimuli similar to that obtained due to self motion. This, together with connections with the vestibular nuclei, may

indicate that the AOS is involved in visuomotor tasks such as stabilisation of the eyes, head and pursuit eye movements (Simpson, 1984).
After cortical ablation, it has been shown that monkeys can still perform flux discrimination tasks provided that AOS is intact. Destruction of other midbrain structures such as pulvinar, superior colliculus and pretectum in destriated monkeys or the destruction of AOS with intact striate however, does not abolish the flux discrimination ability, thus emphasising the role of AOS in mediating this behaviour in the absence of the striate (Pasik and Pasik, 1973).

Pretectal Nuclei

The pretectal region lies in the uppermost part of the midbrain, immediately rostral to the superior colliculus at the level of the posterior commissure. The anatomical descriptions of the region are inconsistent among different species. In monkey, five pretectal nuclei have been identified. These include the anterior, medial and posterior pretectal nuclei, the nucleus of the optic tract and the olivery pretectal nucleus (Hutchings and Weber, 1985; Ruskell, 1993). The afferent fibres pass directly from the retina through the superior brachium to terminate in the olivery and sublentiform nuclei and the nucleus of the optic tract (Benvento and Standage, 1983; Hutchings and Weber, 1985). These nuclei also receive afferents from the superficial layers of the superior colliculus as well as from visual cortex (Benvento and Davis, 1977). The lateral pretectum also receives input from the dorsal terminal accessory optic nucleus (Hoffmann et al., 1988).
The pretectal nuclei project to the ventral lateral geniculate nucleus, the peripeduncular nucleus and the superior colliculus. Benvento et al. (1977) suggested that this triad may be involved in eye movements associated with visual attention and in the modulation of cortical activity via effects on the zona incerta and reticular formation. In addition, the visual and association cortices may receive input from the pretectum via its projections to the pulvinar (Benvento and Standage, 1983).
The pretectal nuclei form part of the pupillary light reflex pathway through the connections with the oculomotor complex (Benvento et al., 1977). The portions of the pretectum which receive cortical and tectal input project to the Edinger-Westphal nuclei and form the parasympathetic control of the constrictor pupillae as well as being involved in control of lens and eye movement (see section 1.5).

Superior Colliculus

The tectum (roof) or quadrageminal plate of the midbrain consists of the structures dorsal to the cerebral aqueduct and is composed substantially of the superior and inferior colliculi. In submammalian vertebrates the optic tectum, a structure homologous with the mammalian superior colliculus, has a complex laminated structure and is of primary importance in vision. In mammals, the geniculostriate system has assumed the major role in vision and in man the superior colliculi are reduced in size and are thought to serve mainly as mediators of head and eye position in response to visual, auditory and somatic sensory stimuli (Ruskell, 1993). Each superior colliculus displays a laminated structure of white and grey matter which is conventionally divided into superficial and deep layers (Stein, 1984). From the surface inwards the layers are:

1. stratum zonale (thin and mainly fibrous)
2. stratum griseum superficiale (a substantial grey layer with the greatest density of cells)
3. stratum opticum (mainly fibrous)
4. stratum griseum intermediale
5. stratum album medium
6. stratum griseum profundum
7. stratum album profundum.

The visual system provides a substantial part of the input to the superior colliculus. The crossed and uncrossed fibres separate from the optic tract at the superior brachium and terminate in superficial grey matter (Perry and Cowey, 1984). The contralateral hemifield of vision is represented topographically in each colliculus with the macula projections occupying a disproportionately large territory (Ruskell, 1993). Each superior colliculus also receives an input from the ipsilateral visual cortex mainly in the stratum opticum with terminations in the superficial and intermediate grey layers (Graham et al., 1979). Other corticotectal fibres arise from parietal, temporal and frontal lobes including the visual association areas (Sparks, 1986). Some forty subcortical structures have been found to project to the superior colliculus and probably as many structures receive collicular fibres. Auditory inputs from the cortex, inferior colliculi and other auditory central structures, are present as well as from the substantia nigra, brainstem and spinal somato sensory sources. These fibres terminate in the deeper layers of the superior colliculus with some or all of the connections being reciprocal (Ruskell, 1993). Most collicular efferent fibres issue from the larger cells of the ventral layers and include tectothalamic, tectoreticular, tectopontine and tectospinal fibres. Targets

of tectothalamic fibres include the LGN, pregeniculate nucleus, suprageniculate nucleus, nucleus lateralis posterior and pulvinar, and others pass to lateral pretectal nuclei (Huerta and Harting, 1984). Tectoreticular fibres pass to the parabigeminal nucleus, accessory optic nucleus and pontine reticular structures. The latter, together with some tectopontine projections are important in visuomotor mechanisms.

Collicular cells are nearly all binocular, driven from the contralateral hemifield. Their properties however, are dependent on the lamina they occupy. The superficial grey layer and the dorsal stratum opticum contains cells exclusively responsive to visual stimuli. They have receptive fields and respond to static and moving stimuli independent of the sign of the contrast (Goldberg and Wurtz, 1972; Schiller, 1972; Schiller and Stryker, 1972). In monkey the majority of cells show no directional selectivity, although a few cells do display sensitivity to a broad range of movement directions (Goldberg and Wurtz, 1972). In cat, directional selectivity is a common property of the collicular cells. The ventral stratum opticum, intermediate grey and deeper layers contain cells that respond vigorously prior to saccades and have visual receptive fields, and are specific for size and direction of rapid eye movement independent of eye position in the orbit (Schiller and Stryker, 1972; Schiller and Koerner, 1971).

In monkey some eye movement related cells with visual receptive fields near the centre of the fovea, discharge both prior to small saccades and during smooth pursuit movements. These units appear to participate in the correction of retinal-target errors during tracking (Schiller and Koerner, 1971). This view was emphasised in the primate studies of Wurtz and Goldberg (1972), and Albano and Wurtz (1982) where they showed that following lesions of superior colliculus, the size, number and latency of the correcting saccades were elevated. In the case of a more extensive lesion, to include the pretectal region, the initial saccade is also impaired and the tracking of a target is no longer possible.

The collicular motor map in the deeper layers overlaps with the somatosensory map in the same layers and has extensive interconnectivity with other visual and motor areas. This may indicate that the superior colliculus plays a role of sensor-motor integrator (Robinson, 1972). Indeed, some neurones in dorsal layers in cat respond to extraocular muscle stretch and others, responsive to visual stimulation, are inhibited by stretch; thus convergence of sensory information on single collicular cells occurs. This type of interaction between eye movements and visual information may be used in distinguishing between retinal image displacement due to movement of objects and that due to eye movement.

Lesions of the superior colliculus can also give rise to deficits in pattern discrimination tasks, possibly by affecting the vergence eye movements (Lawler and Cowey, 1986).

Collectively, it seems likely that areas such as the pretectum are involved in the generation of eye movements, whereas the superior colliculus provides the error signal between the retinal image and the eye position necessary for correcting motor activity. In fact, some collicular cells have been identified such that they fire vigorously prior to saccade initiation but their discharge rate decreases during the saccade and stops at its termination (Waitzman et al., 1988).

To summarise, the superior colliculus is involved in the coding of visual stimuli and the control of the eye movements. It provides a convergence stage for sensory and motor information and its complex pattern of connectivity with a large number of nuclei in brain and the spinal cord suggests that it may be involved in other sensory and motor functions.

Hypothalamus and Thalamic Nuclei

Only a very limited retinal projection to other thalamic nuclei occurs besides that to the lateral geniculate body. Moore and Lenn (1972) and Hendrickson et al. (1972) (cited by Holden, 1976) established a retinal projection to the suprachiasmatic nucleus (SCN). SCN is a group of small neurones in the basal part of the anterior hypothalamus and is involved in the transmission of seasonally changing information from the outside world to the pineal gland (Cassone, 1990). The retinal projection may provide the photopic information required for synchronisation of circadian clock (Hofmann and Swaab, 1992).

Pulvinar is another thalamic nuclei receiving retinal input and is described below.

Pulvinar

The pulvinar is one of a pair of large nuclei of the posterior thalamus and it is several times the size of the lateral geniculate body. It is subdivided into inferior and superior nuclei with the smaller posterior nucleus often included in the pulvinar complex. The superior nucleus is further divided into lateral and medial subnuclei. The medial subnucleus occupies the dorsomedial two-thirds of the pulvinar, while the inferior nucleus is adjacent to the lateral geniculate body (Petersen et al., 1985; Ruskell, 1993).

In primates, the response characteristics of pulvinar neurones to visual stimulation have been studied, and reveal a topographical representation of the contralateral hemifield in the inferior pulvinar. The arrangement is such that the more rostral

portion represents the upper visual field with the lower part represented in the more medial portion of the nucleus (Bender, 1981; Ungerleider et al., 1983; Nakagawa and Tanaka, 1984). Most or all of the units respond to moving stimuli, and are monocular in squirrel monkey and binocular in owl monkey. In addition many pulvinar cells receive input from colour-opponent retinal beta cells. Unlike the superior colliculus which has become diminished in size in higher mammals, the pulvinar has undergone a phylogenetic enlargement, which parallels that of the neocortex (Petersen et al., 1985).

In the absence of physiological data on human pulvinar pathways and function, it may be assumed that similarity with other primates is likely (Ruskell, 1993). Retinal input to the pulvinar was established by Campos-Ortega et al. (1970, cited by Weiskrantz et al., 1977). The pulvinar also receives afferents from other midbrain and cortical structures. Projections from the superior colliculus issue largely from dorsal layers and terminate mainly in the inferior nucleus of the pulvinar. Projections are also received from various cortical regions including striate and extrastriate areas (Benvento and Fallon, 1975; Benvento and Davis, 1977; Graham et al., 1979; Ungerleider et al., 1983). Pulvinar projections to the cortical areas associated with vision issue from the inferior and lateral subnuclei and perhaps from the medial part of the superior nucleus. They terminate mainly in area 18 although less substantial projections to area 19, MT, parietal cortex, temporal and frontal lobe (areas 5, 7, 20 & 21) have also been reported (Benvento and Rezak, 1976; Benvento and Standage, 1983).

Lesion studies have shown that following the destruction of the superior colliculus, the cellular properties of inferior pulvinar are not affected. Striate lesions however, give rise to a large proportion of pulvinar cells (85%) becoming unresponsive to visual stimuli (Bender, 1983). The remaining cells could be activated and consisted of transient on-off responses with relatively short latencies. These cells were not directionally or orientationally selective immediately after the lesions, but three weeks after the event such selective cells could be found in inferior pulvinar. Studies of Petersen et al. (1985) suggest that some pulvinar cells are involved in selective attention and eye movement. Indeed a patient with pulvinar lesions described by Zihl and von Cramon (1979) suffered from 'neglect' which was markedly different from visuospatial disorientation. Similar results may be demonstrated in primate lesion studies. For example, following an inferior pulvinar lesion a monkey's learning ability for a pattern discrimination task consisting of briefly presented stimuli was impaired (Chalupa et al., 1976). This deficit was not attributed to any deficit in visual acuity, pursuit eye movement, visuomotor

co-ordination or orientation ability.

In summary, as with the superior colliculus, the pulvinar has extensive connections to many cortical and midbrain structures, many of them being reciprocal. This suggests a role in convergence and integration of sensory and motor inputs. The role of pulvinar in selective attention has also been demonstrated and it is possible that such a role may be achieved by modulation of cortical and visuomotor activity through its reciprocal connections (Petersen et al., 1985).

1.2 Other Subcortical Projections to Visual Cortex

The activity of many cortical visual areas is influenced through a variety of other sensory stimuli, including vestibular, acoustic and somatosensory (Morrell 1972). This arises due to the convergence of sensory information either via intracortical connections or by subcortical projections. The influence of subcortical structures has been investigated using histochemical techniques such as the retrograde transport of horseradish peroxidase (HRP). This has been used in particular to investigate LGN projections to the striate and extrastriate areas. It has been shown that following injections of HRP into the prestriate region, labelled cells are found in both laminae and interlaminar layers of LGN (Yukie and Iwai, 1981; Benvento and Yoshida, 1981; Fries, 1981; Hendrickson and Dineen, 1982).
Bullier and Kennedy (1983) used a different labelling agent (fast blue and diamidino yellow) and found evidence for geniculate projections to prestriate area V2.
Using another technique histofluorescence; it was found that in addition to LGN and Pulvinar, two other structures: raphe nuclei and locus coeruleus, project to the primary visual cortex (review by Ungerstedt, 1971). The characteristics of these projections differ radically from those of the lateral geniculate nucleus and pulvinar complex. The inputs provided by these subcortical projections contribute to the complexity of intracortical processing of visual information (Tigges and Tigges, 1985). These findings stimulated investigations into the possibility of the presence of further subcortical sources for projection to the cortical areas. Neuroanatomical tracing methods involving anterograde and retrograde axonal transport of detectable substances have been applied in order to identify further subcortical afferents and more than twenty subcortical structures and nuclei have been identified as projecting to the mammalian occipital lobe (Tigges and Tigges, 1985; see figure 1.13). Some of these are multiareal, ie., project to a number of other cortical areas. There are sparse data on the laminar termination of these subcortical projections. Subcortical regions such as the locus coeruleus and nucleus dorsalis raphae terminate diffusely into all cortical laminae and may influence every neurone in the cortex. In contrast, others such as the pontine reticular formation project mainly to layer 4C of area 17 in similarity to the geniculate input and are in position to modulate the early processing of visual information. If a projection terminates in the supragranular or infragranular layers, however, they may influence large blocks of output neurones. Although the exact way in which these subcortical projections influence the perception of a visual stimulus is not known, they occur in a wide range of mammalian species with divergent habits and different external and internal needs. This fact emphasises the

	S-210	S-313	S-317	R-302	R-309	K-321	K-322
	Age at time of injection						
	9 mo	1 day	7 days	23 yr	>20 yr	6 mo	6 mo
	Injected areas						
	17, 18, 19	17	17	17	17	17, 18, 19	17, 18, 19
LC	+	+	+	+	+	+	+
DR	+	+	+	+	+	+	+
NA	+	+	+	+	+	0	+
NCS	+	+	+	+	+	+	+
pRF	+	+	+	+	+	+	+
mRF	+	+	+	+	+	0	0
NL	+	+	+	0	0	+	+
LH	+	+	+	+	+	+	+
NBM	+	+	+	+	+	+	+
NDB	+	+	+	+	+	+	+
C	+	+	+	+	+	+	+
BLA	+	+	+	+	+	0	0
LGN	+	+	+	+	+	+	+
MIN	NA	NA	NA	NA	NA	+	+
P	+	+	+	+	+	+	+
LP	0	0	0	0	0	+	+
Li	+	+	+	+	+	0	0
Cel	0	0	0	0	0	+	+
CeM	+	+	+	+	+	+	+
Pc	+	+	+	+	+	+	+
VAm	+	+	+	+	+	+	+

* Three squirrel monkeys (S-210, S-313, S-317), two rhesus monkeys (R-302, R-309), and two cats (K-321, K-322) received HRP injections in their visual areas. NA, not applicable; +, labeled cells present; 0, no labeled cells present.

Figure 1.13: the subcortical sites that contain retrogradely labelled neurones following a transport time of 3 days in squirrel monkey, rhesus monkey and cat. BLA, nucleus basalis lateralis amygdalae; C, claustrum; CeM nucleus centralis medialis; DR, nucleus dorsalis raphae; LC, locus coeruleus; LH, lateral hypothalamus; Li, nucleus limitans; LP, nucleus lateralis posterior; mRF, mesencephalic reticular formation; NA, nucleus annularis; NBM, nucleus basalis of Meynert; NCS nucleus centralis superior; NDB nucleus of diagonal band of Broca; P, pulvinar; Pc, nucleus paracentralis; pRF, Pontine reticular formation; VAm, nucleus ventralis anterior, pars magnocellularis (from Tigges and Tigges, 1985).

phylogenetic stability of these projections and suggests that they may perform generalised functions (Tigges and Tigges, 1985).

1.3 Functional Specialisation of Visual Cortical Areas

Broca (1961) and Fritsch and Hitzig (1970) (Cited by Zeki, 1991) were the first to state that the integrity of the separate cortical areas was required for the successful functioning of speech and limbal motor systems. Subsequently more cortical areas were associated with the performance of specific tasks. By the 1930s the functional specialisation of cortical areas was accepted such that Lashly wrote "...in the field of neurophysiology no fact is more firmly established than the functional differentiation of various parts of the cerebral cortex...No one today can seriously believe that the different parts of the cerebral cortex all have the same functions or can entertain for a moment the proposition of Hermann that because the mind is a unit the brain must also act as a unit" (Lashly 1931, cited by Zeki, 1991). Today many clinical syndromes such as prosopagnosia and achromatopsia are associated with certain cortical lesions.
The concept of functional specialisation in the visual cortex is more recent. Evidence that different submodalities of vision are processed in different cortical regions was established from studies of visual cortex of rhesus monkey by Zeki (Zeki, 1969, 1978a). The primary visual area contains cells which respond to a wide range of submodalities. There is however, a segregation which exists between the processing of movement and that of colour in cytochrome oxidase rich blobs and interblobs (see section 1.6). Although the mixture of submodalities is still present in V2, this segregation is kept in the form of thin, thick and interstripes (see section 1.6). From this region the visual information is passed to other prestriate areas: V3, V4 and V5 (Zeki, 1975).
Various visual areas are interconnected (see figure 1.14), but the main processes of V4 and V5 are associated with the analysis of colour and motion respectively.
The indirect evidence for such segregation and allocation of visual submodalities to cortical areas in man, comes from clinical cases of cerebral achromatopsia and akinetopsia following naturally occurring cortical lesions in stroke patients. In these patients, lesions in the lingual and fusiform gyri cause disturbances or complete lack of perception of colour, while the striate cortex is intact. Zihl et al. (1983) described a patient who became defective in her ability to see moving objects following a bilateral cerebral vascular lesion in cortex outside the striate area. A review of literature concerning the cerebral achromatopsic and akinetopsic cases has been given by Zeki 1990 and 1991, respectively.
Psychophysical evidence for the possible segregation of colour and movement

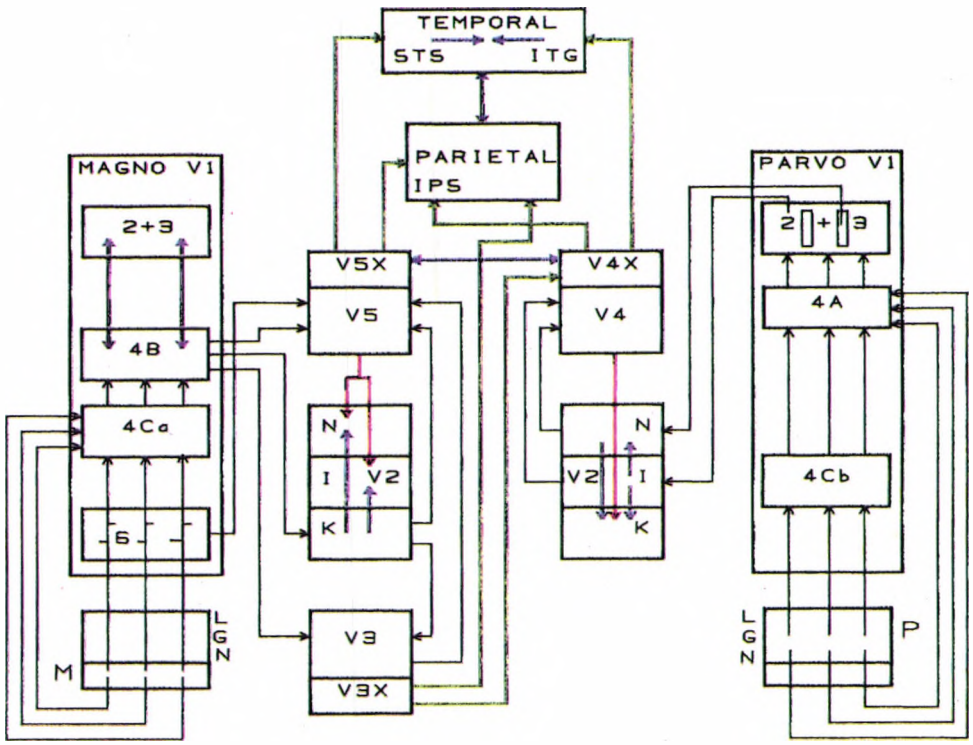


Figure 1.14: diagrammatic representation of the projections from P and M layers of LGN to cortical areas (black arrows) and the interconnections between them (coloured arrows). Green lines represent forward connections, but similar to those shown in black, they are also reciprocated. Connections in red are backward and those in blue are lateral or intrinsic. V1 subdivided into layers 6, 4Cb, 4Ca, 4B, 4A, 3 & 2. V2 subdivided into cytochrome oxidase thick (K), thin (N) and inter (I) stripes; areas V3X, V4X & V5X represent the whole visual complexes. IPS, intraparietal sulcus; ITG, inferotemporal gyrus; STS, superior temporal sulcus (from Zeki and Shipp, 1988, reprinted with permission).

processing is based on the fact that the perception of at least some moving stimuli is impaired when the motion discrimination is based on colour information alone (Ramachandran and Gregory, 1978; Ramachandran, 1987; see section 1.7 for review). Only recently the direct evidence for functional specialisation of cortical areas in man has been demonstrated by measuring the regional cerebral blood flow using positron emission tomography (PET) technique (Zeki et al., 1991). When a subject views either a coloured pattern such as a Land colour Mondrian, or a moving random-square pattern, the blood flow to areas V1 and V2 is increased. In addition, viewing of the colour pattern gives rise to increased activity in a unique area located in the lingual and fusiform gyri corresponding to V4. For motion, regional cerebral blood flow maps identified a unique area located in the region of the temporo-parietal-occipital junction (V5) (see figure 1.15). Therefore, just as in macaque, different areas of the human prestriate visual cortex are specialised for processing different visual attributes.

The combined effects of cortical and subcortical interconnectivity and cerebral functional specialisation may be responsible for the visual mechanisms in blindsight described in the next section.

1.4 Visual Mechanisms in Subjects with Cortical Lesions

In addition to the retino-geniculo-striate pathway, a short description of nine other parallel pathways in non-human primates has also been given. In a destriated monkey, other structures involved in processing of visual information are intact, therefore, at least some visual capacities may be expected to survive. The extent of these capacities and the recovery of function have been subjects of vigorous debate during the last hundred years (see reviews by Weiskrantz, 1986, 1990).

Early in the present century, it was established that a destriated monkey responds to the presence of light (Marquis and Hilgard, 1937). The light response was further investigated by Klüver (1942) and he concluded that a destriated monkey responds to total luminous flux and is unable to discriminate the shape and size of the visual stimuli.

Later, it was found that the performance of destriated monkeys in a variety of visual tasks was not as limited as that reported by Klüver. They could retain the ability to respond to contour information (Weiskrantz, 1963), were sensitive to small objects and could locate accurately randomly positioned stimuli (Humphrey and Weiskrantz, 1967; Humphrey, 1970, 1974; Weiskrantz et al., 1977). The spatial localisation ability was significant even when the stimulus duration was too brief to allow cues due to

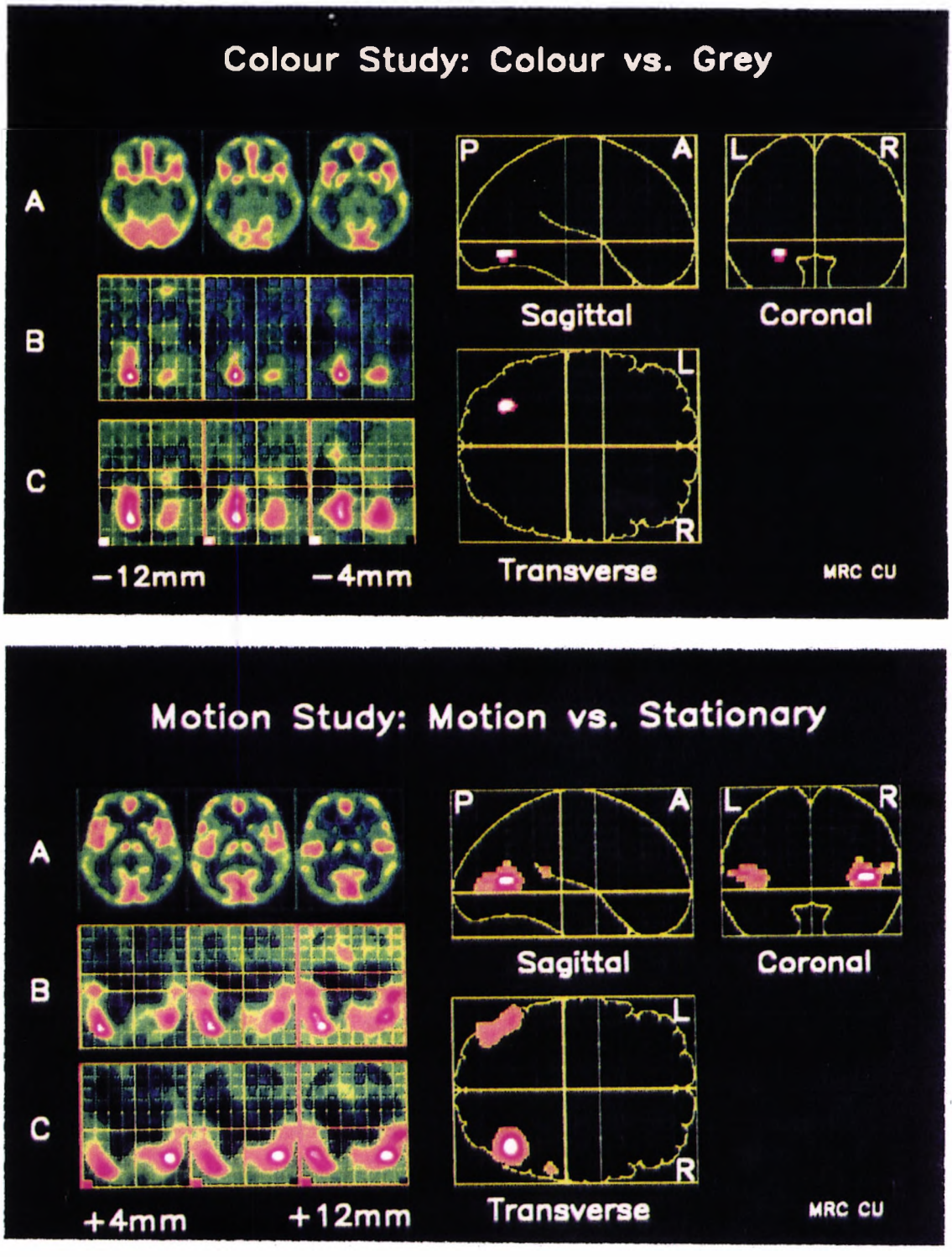


Figure 1.15: the PET scans results averaged for six normal subjects. The white and red end of the colour scale shows areas of maximally significant regional cerebral blood flow change, and the blue and green end shows the threshold. Subjects viewed either a Land colour Mondrian (top) or a moving random dot display (bottom). On the left are transverse images of the brain at planes -12, -8, and -4 mm relative to the ACPC line. A, anatomical features averaged from the subjects into Talairach space. B, the arithmetical difference between adjusted mean blood flows for colour and grey (top) and moving and stationary random dots (bottom) stimuli. C, the statistical parametric maps derived from a formal comparison of the adjusted mean blood flows and variances for each of the two conditions. On the right are the orthogonal projections of the statistical comparison at a threshold of $p<0.05$. On the top picture, the areas showing increased flow, subserving the perception of colour are located inferiorly and medially in the occipital cortex (V4). In the bottom picture, areas subserving the motion perception (V5) are located on the convexity of the prestriate cortex at the junction of areas 19 and 37 of Brodmann (from Zeki et al., 1991, reprinted with permission).

saccadic eye movements to occur (Weiskrantz et al., 1977). Pattern and brightness discrimination abilities (Pasik and Pasik, 1971; Schilder et al., 1972) and visual acuity of 11 cycles/° were also reported (Miller et al., 1980). Furthermore, an orientation difference as small as 8° could also be discriminated (Pasik and Pasik, 1980).
Regarding wavelength discrimination ability following striate ablation there have been claims (Schilder et al., 1972; Cowey, 1992, 1993) and counter-claims (Malmo, 1966; Humphrey, 1970; Leporé et al., 1975) of the presence of some residual colour discrimination.
The discrepancy between the findings of Klüver and more recent results are related to the size of the brain lesion. It has been shown that in Klüver's destriated monkeys, parts of the cortex anterior to the striate and extending into the temporal lobe had also been removed, resulting in a more limited visual capacity. In the case where lesions were less extensive, but including the entire striate cortex, performances similar to those outlined above could be demonstrated (Weiskrantz, 1986).
In humans, as in other primates, following striate lesions or damaged optic radiation, scotomata in the contralateral visual field are observed, the extent of which is similar to that expected from the classical topographical representation of the visual field (Holmes, 1918; Cowey and Weiskrantz, 1963). Normal visual experiences are absent within the scotoma. Some residual visual capacities however are demonstrable and indeed, a completely blind scotoma does not seem to exist (Poppelreuter, 1917; Riddoch, 1917). An account of these functions has been given in this section.
Despite the close resemblance of neuroanatomy, functional hierarchy and performance characteristics of human and non-human primate visual systems, there are two important problems that have to be taken into account when comparing performance deficits in lesion studies (from Weiskrantz, 1989).
One is a geometrical problem and concerns the site and extent of the lesion and the age of the subject at its onset. As mentioned above, the extent of lesion in the prestriate area affects the pattern of deficits. This is of particular importance when the lesion includes areas involved in specialised functions (see section 1.3) which are positioned anatomically very close to the striate cortex. The human striate cortex is mainly buried in the medial surface in the calcarine fissure (Weiskrantz, 1986) and it is rare for any lesion to occur without damage to underlying white matter and the extrastriate areas. In monkey however, the striate cortex covers the lateral surface mainly and precise lesions can be induced as experimental objectives require. Therefore, comparison of lesions and their effect are not necessarily a reliable procedure.
The second problem encountered when comparing human and non-human primate

data is a methodological one. In primate studies, residual visual performance is measured behaviourally for a range of stimulus parameters. Monkeys are made to make a choice between alternative responses. Often, a large number of practice trials are needed to achieve a good performance level for a certain discrimination task. In human studies, however, a faster route is taken by relying on the subject's verbal response. A verbal response is a conscious response associated with the perception of a stimulus. Subjects with cortical lesions cannot "see" an object when positioned within their blind field. If, on the other hand, a forced-choice paradigm is adapted, and the subject is instructed to "*guess*" a stimulus attribute or choose amongst the alternatives, some surprising results are obtained. Subjects may achieve a well above chance performance level in some discrimination tasks in their blind field in the absence of any visual experience, when other artefacts such as light scatter and audio cues have been eliminated.

This visual discrimination in the absence of acknowledged awareness is termed "*blindsight*" (Sanders et al., 1974; Weiskrantz et al., 1974). Many experimenters have examined the spatial localisation, orientation and form discrimination, movement and spectral sensitivity, bilateral interactions and spatio-temporal properties in blindsight subjects. These properties, now firmly established, were initially attributed to visual artefacts such as unstable or eccentric fixations and light scatter by some experimenters (Campion et al., 1983). An extensive evaluation of residual capacities has been carried out on a blindsight subject DB by Weiskrantz and colleagues (Weiskrantz, 1986, 1987) and on subject GY by Barbur and colleagues (Barbur et al., 1980, 1987a, 1988, 1990, In press; Weiskrantz et al., 1991).

A summary of these residual capacities in the absence of acknowledged awareness is given below.

Spatial Localisation

The ability of blindsight subjects to detect the spatial location of a visual target can be tested in different ways. Subjects may be asked to saccade to a position in their blind field where they "guess" the visual stimulus had been presented (saccadic localisation) or alternatively may be asked to point or touch the supposed location on a perimeter screen (manual localisation) or report its coordinates verbally. The former technique was first implemented by Pöppel et al. (1973) where they reported that for four cortically damaged patients tested, the amplitude of saccadic eye movements was proportional to stimulus eccentricity. In all the cases, the stimulus was not "seen" and its duration was brief (100ms), therefore the target disappeared before saccade initiation so as to eliminate possible experimental artefacts. Similar results were

obtained in primate studies of Mohler and Wurtz (1977) and Pasik and Pasik (1971, 1973).

Subsequently many experimenters have investigated both the saccadic and manual localisation in subjects with damaged striate cortex (Weiskrantz et al., 1974; Weiskrantz, 1986; Perenin and Jeannerod, 1978; Zihl, 1980; Barbur et al., 1980, 1988; Blythe et al., 1987; Stoerig and Cowey, 1989b; Rafal et al., 1990).

In some subjects, a good correlation between stimulus location and its "guessed" position is observed as far in periphery as 30°. Successful localisation following training was also present in hemidecorticated subjects (Zihl, 1980, 1981).

Detection of stationary targets, independent of their spatial location has also been studied using a forced-choice technique (Barbur et al., 1980; Stoerig and Pöppel, 1986; Weiskrantz, 1986; Stoerig and Cowey, 1989b; Ptito et al., 1991). Target detection performance in cortically blind subjects is dependent on stimulus size (Barbur et al., 1980; Stoerig and Cowey, 1989b) and can also be demonstrated in hemispherectomised subjects (Perenin and Jeannerod, 1978).

Pattern Discrimination

Discrimination of orientation with bar stimuli has been reported in blindsight subjects (Weiskrantz et al., 1974; Weiskrantz, 1986). Weiskrantz's subject DB could discriminate between patterns accurately in the absence of any awareness of stimulus presentation when orientation was the only cue. For example, DB's discrimination between 'X' vs. 'O' and square vs. diamond were well above chance when they were presented successively in his blind field. Pattern discrimination ability was lost when the orientation cues were small or minimal for example in the discrimination task of straight vs. curved triangle and 'X' vs. triangle (Weiskrantz, 1986). In addition the subject was unable to make a "same-different" comparison when both patterns presented simultaneously in his blind field (Weiskrantz, 1987).

The ability to discriminate large simple patterns were also reported in two out of six hemidecorticated subjects studied by Perenin (1978). She attributed their ability to spatial distribution of luminance flux rather than orientation content of the pattern.

Object discrimination (3-dimensional pattern) was performed above chance level in all four hemispherectomised subjects of Ptito et al. (1987) when they were unable to perform 2-dimensional pattern discriminations. It does not seem clear whether the object discrimination ability was also based on the stimulus orientation since all the four subjects could not distinguish between two dimensional patterns.

Movement Detection

In general, a moving stimulus is more salient than a stationary one when presented in a normal or scotomatous field. Studies of brain damaged subjects have shown that the sensitivity to movement is disturbed when the lesion includes the movement sensitive area V5 (Zihl et al., 1983; see also sections 1.3, 1.8, 1.9 & 3.1). Lesions of the striate cortex however, result in a different type of deficit. The ability to detect a moving stimulus in a perimetrically blind field was described by Riddoch (1917) and Poppelreuter (1917) in their classical studies.

Weiskrantz and colleagues have shown that blindsight subjects are able to point at the direction of motion when it was confined to their blind field (Weiskrantz et al., 1974; Weiskrantz, 1986, 1989, 1990), or can track a moving object in the absence of any visual sensation (ter Braak et al., 1971).

Barbur et al. (1980) investigated movement sensitivity in the blind field of subject GY They found that GY could discriminate the direction of apparent motion caused by two successively flashed line targets. Speed discrimination in the blind field was effectively normal, in the high speed range, despite the subject's inability to "see" the stimulus. Under optimum conditions (ie., high contrast, high speed), the subject reported the perception of a "shadowy" movement in the blind field. By performing a large number of experiments using coloured moving targets they concluded that GY's responses were driven dominantly by rod inputs. Although the ability to detect fast moving target persists in GY's blind field, the critical flicker fusion frequency measurement was found to be 8Hz. Rod saturation may have been involved because of the high light levels employed since under low light levels the rod receptors continue to respond up to 18Hz (Brindley et al., 1966).

The intact capacity to discriminate the direction of apparent motion generated by two spatially separated targets flashed in sequence was studied further in GY as well as in a second subject with striate lesion by Blythe et al. (1986).

In a larger study, Blythe et al. (1987) showed that the discrimination of target displacement as well as manual and saccadic localisation is not impaired in blindsight subjects. This study also confirmed earlier findings of low flicker fusion frequency and higher sensitivity to faster speeds in the blind field.

Ptito et al. (1991) investigated movement sensitivity in hemispherectomised subjects and found that all three subjects tested could detect the moving stimuli and carry out speed discrimination tasks. Their ability to discriminate the relative directions of moving gratings was however at chance level. This observation suggests that motion perception in the absence of V1 is markedly different to that experienced in normal vision.

The pupillometric study of movement processing in a blindsight subject is described in chapter III.

Spectral Sensitivity

Unlike movement detection, wavelength discrimination in blindsight subjects and non-human primates has yielded diverse results. Primate experiments of Klüver (1942), Weiskrantz (1963), Humphrey (1974), Malmo (1966) and Leporé et al. (1975) indicated that visual responses demonstrated after partial or complete removal of the striate cortex are based largely on rod responses. On the other hand, experiments of Schilder et al. (1972), Keating (1979) and Cowey (1993) have indicated some residual colour discrimination capability.

In cortically blind subjects Barbur et al. (1980) and Perenin et al. (1980) found no evidence of cone response with the stimulus located in the far periphery of the visual field.

Stoerig (1987) found that six out of ten cortically damaged subjects tested could discriminate between red and green in a "guessing" paradigm. She also found that some subjects were able to discriminate between coloured test patterns and not an achromatic pattern presented at the same eccentricity suggesting that colour and luminance are processed differentially.

In a series of experiments, Stoerig and Cowey have shown that the blind field spectral sensitivity is 1 log unit less than the sighted field across the visible range and is essentially normal for both photopic and scotopic conditions with stimuli located in the near periphery. They found a shift in spectral sensitivity from medium to shorter wavelengths in adaptation to dark (the Purkinje shift). Together with discontinuities in the light adapted curve they showed that blindsight involved both rod and cone contributions. Some colour-opponency was preserved (Stoerig and Cowey, 1989a, 1991; Cowey and Stoerig, 1991a,b). It must be emphasised that the spectral sensitivity was obtained while subjects had no conscious experience of "colour" throughout experiments. They attributed the colour processing capacity to the extrastriate cortical visual pathways.

The colour response in blindsight and the related pupillometric studies is discussed further in chapter V.

Bilateral Interactions

Evidence for visual processing in the blind hemifield can also be obtained by comparing responses to stimulus presentation in the sighted field alone and in both the sighted and the blind field together. The subject may then be asked to either draw or

choose amongst a set of drawings, the shape of the visual stimuli. Using essentially similar tasks, interactions between sighted and blind fields have been observed by many experimenters (Poppelreuter, 1917; Warrington, 1962; Torjussen, 1976, 1978). For example, when a full circle was presented as a brief stimulus to a hemianopic subject such that one half of the circle fell in subject's blind field when fixated at the centre, he reported "seeing" a complete circle. If only half a circle was presented in the blind field, nothing was reported. The subject reported half a circle if it was shown in the sighted field only. This phenomena is known as completion and has been observed by other experimenters (Perenin et al., 1986), including in a hemispherectomised subject (see review by Weiskrantz, 1990) which indicates that this type of processing must be mediated either by midbrain pathways or by ipsilateral input to the intact hemisphere.

Two out of four hemispherectomised subjects of Ptito et al. (1987) could carry out "same-different" comparison of three dimensional stimuli shown simultaneously in both fields, emphasising further the visual processing in these subjects.

Other evidence for bilateral interactions comes from the studies of Ruddock et al. (cited by Weiskrantz, 1990). They employed "imaginary" contours produced by Kanizsa triangles (Gregory, 1972) and found that if one corner of the triangle was placed within the blind field, then the subject (GY) could detect the presence of the triangle only when the appropriately aligned stimulus was in the blind field. Similar results have been confirmed in other subjects by Marcel and Weiskrantz (unpublished results, cited by Weiskrantz, 1986, 1989, 1990).

One interesting property of the completion effect is its mirror symmetry. If the images presented in both hemifields are not symmetrical, then the effect is minimal or abolished entirely (Weiskrantz, 1986).

Singer et al. (1977) have noted that the detection threshold of a peripherally located target is elevated following repeated stimulation. Sensitivity can be "reset" if a mirror symmetric region of the other hemifield is adapted in turn. In hemianopic subjects, they showed that resetting in the good hemifield occurred when the stimulus was directed to the blind hemifield. They attributed this reciprocal interaction to midbrain mechanisms since it was absent in a subject with a retino-tectal lesion.

Marzi et al. (1986) applied the measurement of reaction time to the study of bilateral interactions. They exploited the fact that a faster reaction time is performed in response to a pair of stimuli than in response to a single stimulus. This applies both for pairs of stimuli presented within the same hemifield and for pairs of stimuli in which one of the two flashes are presented in each hemifield. In four out of twenty subjects studied, they found evidence of this kind of summation. They speculated that

a larger proportion of subjects might have responded positively if further modification of stimulus parameters had been undertaken.

The inhibition of saccadic eye movements to a target presented in sighted hemifield due to presentation of distractor targets in blind hemifield was reported by Rafal et al. (1990). Marcel (1983a,b) applied the "guessing" paradigm to higher semantic levels and showed that in GY as well as in a second blindsight subject the meaning of an "unseen" word flashed in the blind hemifield could influence the selection of another flashed in the sighted hemifield.

Spatio-temporal Properties of Blindsight

Evidence has been cited in support of the ability of blindsight subjects to localise a stationary flickering stimulus or follow the path of a moving target when presented in their blind field. Sensitivity of blindsight subjects to moving stimuli has been studied by many experimenters (see section under Movement Detection). Since the sensitivity to movement information is high in these subjects it would be of interest to investigate the spatial and temporal properties of visual mechanisms involved in blindsight.

Hess and Pointer (1989) investigated the temporal sensitivity in the sighted and blind hemifield of four hemianopic subjects using Gaussian modulated stimuli. The Gaussian modulation had been performed in both spatial and temporal domains. Its effect was to make the stimulus onset and offset gradual and to smooth out the spatial edges. It was then possible to isolate the effect due to the spatial edge from the temporal transients. They found that the sensitivity was reduced in the sighted hemifield of all subjects. In the blind hemifield, using a two alternative forced-choice procedure, none of the subjects could perform above chance in detecting the stimuli. This was somewhat surprising in view of ample evidence on sensitivity to transient stimuli in blindsight (Barbur et al., 1980, 1988; Blythe et al., 1986, 1987). Hence, they concluded "... the contrast sensitivity associated with the subcortical projection in man cannot be measured by the standard psychophysical means used...".

Weiskrantz et al. (1991) extended the range of spatio-temporal parameters of Gaussian-weighted stimuli and performed the same experiment on one of the subjects (GY) used in the study of Hess and Pointer. Some of the results obtained are outlined below and explain the earlier negative findings.

Weiskrantz et al. found that the size and temporal properties of the stimuli had a powerful effect on its detection when presented within the subject's blind field. A blob of spatial standard deviation (SD) of 2.1°, similar to that of Hess and Pointer was not detected and GY's response was at chance level. For a larger stimulus (SD of 3.3°) with a short temporal Gaussian SD (200ms), however, he reached a 90% correct

response level . A 98% correct response was achieved with a SD of 3.3° and 50% with SD of 1° when squarewave grating stimuli were used at a square-pulsed temporal presentation. GY's response was at chance level for a temporal SD of 250ms (used by Hess and Pointer) or more, but reaching a performance score of 90% correct for SD of 200ms or shorter. The effect of temporal SD controlling stimulus onset and offset was also found to be independent of stimulus duration. Performance scores of 90-100% were achieved when favourable size and temporal characteristics were combined both for blobs and structures. Although only one subject was tested, it is likely that the negative findings in other subjects reflect the less than optimum stimulus parameters employed.

Barbur et al. (in press) in the continuation of their systematic study of spatiotemporal parameters in blindsight, used the above criteria for selecting stimuli for the evaluation of both spatial and temporal characteristics. Stimuli with temporal Gaussian parameters outside the range of effective transient envelopes, and large sizes with Gaussian spatial borders were used. The effect of sinusoidal temporal modulation frequency on stimulus detection for both grating and uniform blobs was investigated. The effect of grating spatial frequency was also studied at a fixed temporal modulation frequency. They concluded that there were two distinct channels mediating blindsight in GY. A spatially tuned channel with bandpass spatial frequency response characteristics and a light flux discrimination channel with extensive spatial summation.

They speculated that the spatially tuned channel found was the same as that found in normal vision by Holliday and Ruddock (1983, cited by Barbur et al., in press) reflecting the activity of subcortical pathways. The second channel is ideal for the discrimination of overall light flux changes and may also reflect subcortical processes involved in the light reflex response. They emphasise however, that in view of spectral sensitivity results discussed previously, these channels may not be the only mechanisms involved in blindsight. Moreover, these two channels may not be present in all subjects with damaged central visual pathways.

Recovery of Visual Functions in Subjects with Cerebral Lesions

Loss of visual functions within the scotomatous field caused by partial removal of striate cortex in primates is not severe with recovery of visual ability within a short period post-operatively (Cowey and Weiskrantz, 1963; Weiskrantz, 1972). After unilateral and even bilateral ablation of striate cortex, sensitivity is significantly regained following specific training (Cowey, 1967; Humphrey, 1974; Mohler and Wurtz, 1977). Stimulation of the scotomatous field by a visual scene alone does not

seem to produce an improvement in performance. Shrinkage of the scotoma is only achieved when the monkey was made to respond to the stimulus presentation. Similar training tasks have also been carried out in human subjects and the recovery of sensitivity in their blind fields monitored (Zihl and von Cramon, 1979, 1985; Zihl, 1980, 1981; Bridgeman and Staggs, 1982).

Zihl (1980) studied saccadic localisation in 3 subjects with damaged geniculostriate pathways and found their ability to detect and localise light stimuli had improved markedly after the systematic training of visually evoked saccadic eye movements. In a later study of fourteen subjects, he found that saccadic localisation led to an increase in visual field size only in the region subjected to the practice (Zihl, 1981). The degree of recovery was related to the sharpness of the visual field border. In subjects with a shallow gradient of light sensitivity in the area between the intact visual field and scotoma, recovery was greater than in cases were the gradient was steep. In addition, visual acuity and colour identification was found to have improved in the restored region. He suggested that the recovery had taken place at the level of the striate cortex and was mediated by the retinotectal pathway.

Bridgeman and Staggs (1982) reported improvement of spatial detection, orientation and manual localisation in a subject with a large cortical scotoma, following training to locate an oscillating target. There was no improvement in visual field which had been stable for four years prior to the experiment. They suggested that the improvement of blindsight was mediated by plasticity in subcortical pathways. They pointed out that the success of training may depend on the subject's age at the onset of the lesion as well as its nature and extent.

Zihl and von Cramon (1985) reviewed 55 cases of subjects with homonymous field defects caused by vascular or traumatic postgeniculate damage. They showed that, following saccadic localisation training, similar to that carried out by Zihl (1980, 1981), scotomatous fields shrank by 1.5° to 38° of visual angle. Similarly, form and colour identification had improved. They concluded that recovery of visual field sensitivity was possible, provided the field defect did not result from completely irreversible brain damage. In such cases, the functional efficiency diminished by reversible damage, could be improved by systematic treatment. Visual information could then be transferred to higher visual areas by recovered striate neurones resulting in an improvement in the perception of form and colour.

Collectively, there seems to be a fundamental difference in visual functions within scotomata in humans and non-human primates following postgeniculate lesions. Monkeys can recover faster and function normally, avoid obstacles and perform fine object detection even after bilateral decortication. In humans, some shrinkage of field

defect is possible, and given an appropriate testing paradigm, subjects are still able to perform target detection, localisation, movement detection and wavelength discrimination tasks within their perimetrically blind and stable field despite the lack of any conscious awareness. The possible underlying neuronal connectivity responsible for structural implementation of the above functions in blindsight is given below.

Neurobiology of Blindsight

Some functional characteristics of blindsight have been described above, many of which are present not only in subjects with cortical lesions, but also in those who have undergone hemispherectomy. The pathways involved in the structural implementation of the above functions include midbrain structures which receive direct or indirect retinal projections from regions such as the pulvinar, superior colliculus and accessory optic system. Extrastriate cortical regions if intact, receive retinal input via LGN and from midbrain structures and may be involved in mediating blindsight. In cases where striate lesions are incomplete, the remaining regions may also contribute to information processing (see section 1.1). The role of the superior colliculus in visual attention was established by Mohler and Wurtz (1977) where they showed saccadic eye movements to a light stimuli presented within a cortical scotoma recovers following training. If however, the corresponding region of superior colliculus was subsequently lesioned the recovered ability was lost and was not regained. Lesions of the superior colliculus alone, did not abolish the visual attention. Pasik and Pasik (1971,1973) had also reported the greater impairment of the ability to detect visual stimuli after lesions of the accessory optic system than of superior colliculus in monkeys with striate lesions.

Zihl and von Cramon (1979) reported attention deficit and "neglect" in a subject with a pulvinar lesion indicating the role of tectopulvinar extrastriate visual pathways in the control of visual attention.

The two distinct channels in blindsight found by Barbur et al. (in press) have properties which are consistent with the properties of neurones in superior colliculus, pretectal nuclei and the accessory optic system.

Collectively, these findings indicate that visual functions may be explained in terms of a "two visual system" proposal put forward by Trevarthen (1968) and Schneider (1969) whereby the first system is concerned with identification of objects and perception of complex patterns and is mediated by retino-geniculo-striate pathways. The second system concerns the detection of events, their location in space and the control of orientating responses to them for subsequent identification by the first system. This is mediated by midbrain structures.

Cowey and colleagues, demonstrated that, despite the retrograde degeneration of the majority of retinal ganglion cells following striate lesions, a small proportion of beta ganglion cells survive (Cowey et al., 1989). Within the parvocellular layers of LGN topographically representing the lesioned striate, a small number of projection neurones also survived. Using retrograde HRP labelling techniques it was demonstrated that these surviving neurones projected to extrastriate areas. The anterograde labelled surviving retinal cells were found to connect with surviving LGN neurones via inhibitory interneurones, allowing retinal information to be transmitted to extrastriate cortex (Stoerig and Cowey, 1991; Cowey, 1993). This pathway may be involved in mediating the observed spectral sensitivity in blindsight. Nevertheless, this may not be the only pathway involved since colour-opponent, beta ganglion cells also project to pulvinar (Felsten et al., 1983).

In this section, various approaches to the study of blindsight have been discussed. It was stated that methods involving saccadic eye movements and forced-choice guessing techniques proved useful in the study of visual processing in the absence of any conscious awareness of the stimulus.
In the next section, an introduction to the pupil pathways and its reflex responses is given. Evidence is presented to show that the activity of some central visual mechanisms are reflected in the pupil response. Pupillary responses in normal subjects and their possible use in blindsight studies are also discussed.

1.5 Physiology of the Pupillary Pathways and Pupil responses

The iris diaphragm, (ie., the pupil) forms the entrance aperture of the eye. The pupil size has three principal effects on image formation in the eye:

1. It regulates the amount of light entering the eye. The pupil ranges from 2mm at full miosis to 9 mm at full mydriasis. It can therefore regulate the amount of light flux entering the eye by a factor of 20. This span however, has a limited effect since the visual system can function over a luminance range of over 7 log units.
2. It affects the depth of focus of the eye by controlling the entrance aperture of the optical system. When the eye is focused on a distant point, any relatively near point is imaged as a blur circle. The size of the blur circle is directly proportional to the diameter of the pupil. When the pupil contracts to half its diameter, then the image can be twice as far from the retina but still result in the same size of blur circle.
3. It determines the quality of the retinal image by controlling the aberrations in the dioptrics of the eye by reducing the entrance aperture.

Measurement of the effect of pupil size on contrast sensitivity has shown that the optimum pupil (ie., highest resolution) under various illumination levels is close to the size of the natural pupil (Campbell and Gregory, 1960; Woodhouse, 1974).

Structure of the Iris

The iris is a vascular structure and forms a diaphragm with a central opening, and together with ciliary body and choroid is a part of the uveal tract. Posteriorly, it is covered by the pigment epithelium which contributes to the quality of retinal image by preventing the entry of non-axial rays. Its absence may therefore, contribute to the poorer visual acuity of albinos (Spalton, 1984). The central anterior portion is pushed forward by the crystalline lens. The outer section of the iris is attached by comb-like insertion bundles at the ciliary edge to the trabeculae and is hidden behind the corneo-scleral margin. The inner section formed by the pupil lies slightly nasal to the centre of the iris by $\approx$1 mm (Spalton, 1984).

When viewed in a sagittal cut, the iris varies in thickness, being thinner at the iris root. The muscle system of the iris is composed of the radial dilator pupillae and the circular sphincter pupillae. The pupil size is determined by the sympathetic and parasympathetic innervations of the iris muscles (Lowenstein and Loewenfeld, 1969).

The sphincter pupillae is 0.5 - 1.0 mm wide and 40 - 80 μm thick (Alexandridis, 1985). It consists of bundles of smooth muscle fibres that encircle the pupil in the

posterior stroma of the iris, and anterior to the pigment epithelium (Spalton, 1984). The fibres encircle the pupil near the pupillary margin and are primarily innervated by parasympathetic fibres. Connecting tissue fibres attach the iris firmly to its surrounding structures, thus preserving constriction of the iris even when the muscle is perforated. The circumferential arrangement of fibres results in the reduction of the aperture upon contraction.

The dilator pupillae is a clear myoepithelial layer, approximately 2mm thick and extends radially between the ciliary margin and the sphincter pupillae and it is anterior to pigment epithelium (Alexandridis, 1985).

Since the sphincter and dilator muscles are connected by arcade-like connecting fibres (see figure 1.16), each muscle is able to act directly upon the other thus forming an antagonistic mechanism: the sphincter stretches the dilator while the dilator unfolds the sphincter. Both muscles have dual autonomic innervation but the dilator pupillae is predominantly driven by the sympathetic fibres (Apter, 1956).

The Afferent Pupillary Pathways

The sensitivity of the iris to light in some vertebrates has been reported (Duke-Elder, 1970). In mammals however, the iris is insensitive to light and detection takes place at the retinal level (Lowenstein and Loewenfeld, 1969).

The afferent pupillary light reflex commences with the absorption of light in the visible region by rod and cone photoreceptors. Information containing retinal illuminance is relayed to the retinal ganglion cells via bipolar cells. The axons of the retinal ganglion cells which carry the pupillomotor information follow a pathway similar to that for visual information, ie., they run within the optic nerve. The pupillary fibres from the nasal retina decussate at the optic chiasm and run with the temporal uncrossed fibres within the ipsilateral optic tract. They leave the optic tract at its posterior third and pass to the pretectal area via the brachium of the superior colliculus. They synapse at the pretectal nuclei which are located near the posterior commissure (see figure 1.17). The axons of the pretectal nerve cells carry the pupillary information to the ipsilateral Edinger-Westphal nuclei or decussate in the posterior commissure of the midbrain and synapse with the contralateral Edinger-Westphal nucleus, located within the mesencephalon. A small number of them also terminate on the contralateral pretectal nuclei. The presence of consensual responses of the pupils to the visual stimuli is therefore not surprising in the view of number of decussations involved within the afferent pathways.

Afferent sympathetic nerve fibres (retinohypothalmic projections) have been demonstrated in animals. They run within the optic nerve and exit in the posterior

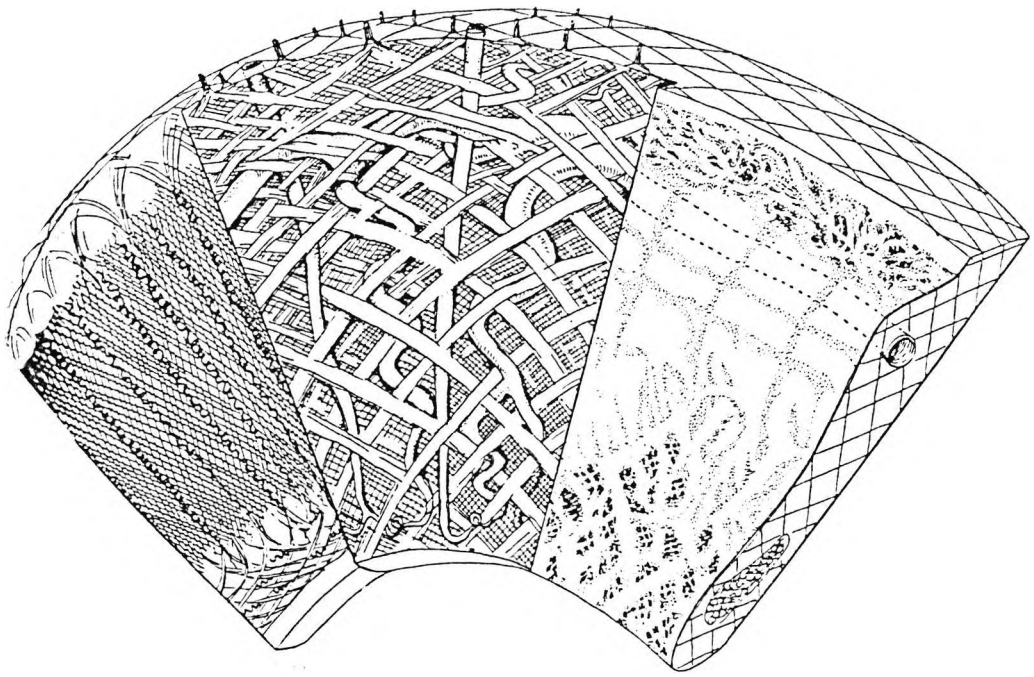


Figure 1.16: the structure of the iris. The vascular arrangement, intertwined with the connective tissue structure. The arcade-like connecting fibres connect the sphincter and dilator muscles (from Rohen, 1951).

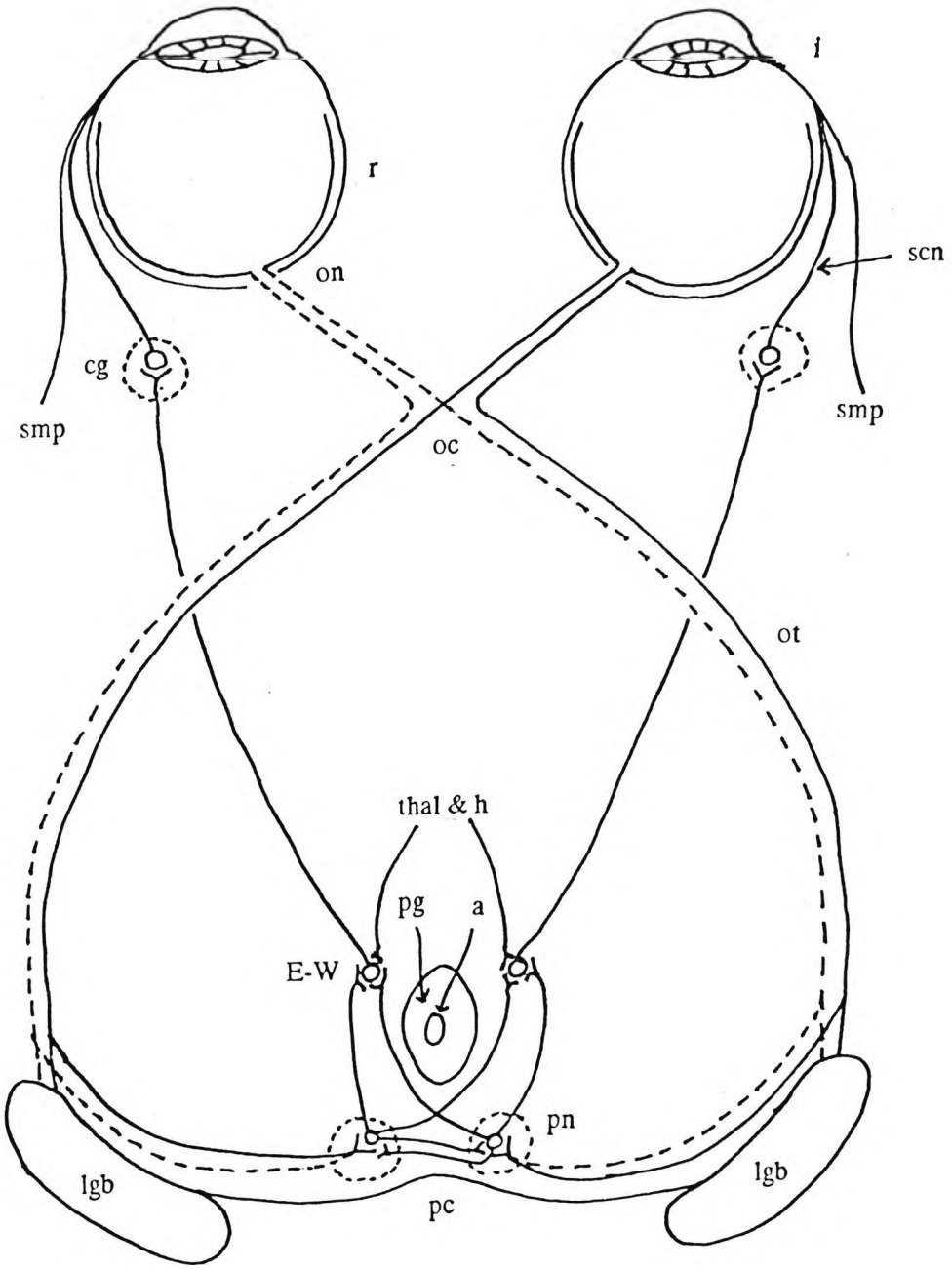


Figure 1.17: schematic representation of the human pupillomtor pathways,
a = aqueduct of sylvius; cg = ciliary ganglion; E-W = Edinger-westphal nucleus;
i = iris; lgb = lateral geniculate body; oc = optic chiasma; on = optic nerve;
ot = optic tract; pc = posterior commissure; pg = preiaqeduct grey;
pn = pretectal nucleus; r = retina; scn = short ciliary nerve; smp = sympathetic innervation of dilator muscle; thal & h = thalamus and hypothalamus (based on refereces cited in the text).

portion of the optic chiasm on their way to hypothalamus (Zinn, 1972).

Parasympathetic Efferent Supply to the Sphincter Muscle

There are numerous excitatory and inhibitory neuroanatomical pathways that affect the activity of the Edinger-Westphal nucleus. Therefore, many factors can influence its functioning. At a particular moment the summation of these various modalities upon the inherent constrictor tonus of the Edinger-Westphal nucleus determines the amount of parasympathetic outflow to the sphincter pupillae (Zinn, 1972).

Preganglionic fibres exit from the Edinger-Westphal nucleus, situated dorso-rostrally to the main mass of the oculomotor nuclear complex in mesencephalic brain stem, and give rise to pupillary constriction. They continue along the oculomotor fibres which supply the extraocular muscles (Lowenstein and Loewenfeld, 1969).

The distribution of the efferent pupillary fibres varies with respect to other nerve fibres along the path of the IIIrd cranial nerve, but once the nerve enters the superior orbital fissure, they follow the inferior division of the oculomotor nerve which goes to the inferior oblique muscle. The fibres leave that division to form the motor root of the ciliary ganglion. The postganglionic fibres leave via the short ciliary nerves to innervate the iris and ciliary body, the majority terminating on the sphincter pupillae although a few go to the dilator.

Studies of ciliary ganglion suggest that only 3% of the fibres emerging and travelling in the short ciliary nerves are concerned with pupillomotor functions (Alpern, 1969).

Sympathetic Efferent Supply to the Dilator Muscle

The sympathetic innervation of the dilator pupillae is a three neurone system. The fibres of the first neurone arise from the hypothalamus and pass to the ciliospinal centre located in the lateral part of the anterior horns of the spinal cord (Lowenstein and Loewenfeld, 1969; see figure 1.18).

The second neurone leaves the ciliospinal centre of Budge via the ventral root to pass to the paravertebral sympathetic chain. These fibres continue, without synapse through the stellate ganglion. The majority of the fibres travel in the anterior loop to the ansa subclavia only to return to the main trunk of the sympathetic chain and subsequently ascend through the inferior and middle cervical ganglia. These fibres terminate in the superior cervical ganglion.

The third neurone travels upward through the carotid plexus to the first division of

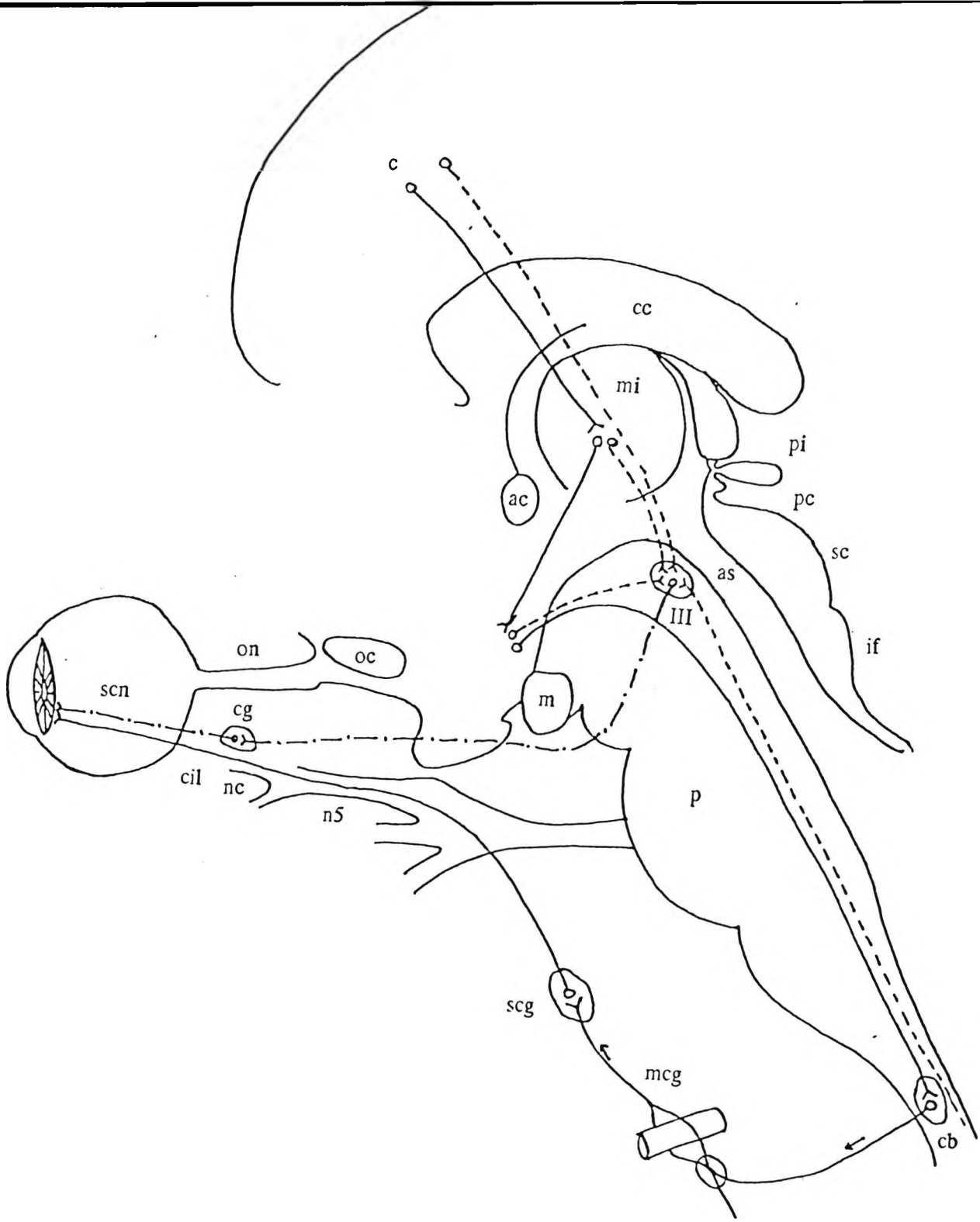


Figure 1.18: schematic representation of human brain;
Solid lines: efferent sympathetic path from cortex, thalamus and hyperthalamus via the cervical cord and peripheral sympathetic chain to the dilator pupillae.
Dotted lines: Inhibitory paths to the occulomotor nucleus; direct afferent connections in the brainstem reticular formation and descending connections from cortex, thalamus and hyperthalamus.
ac = anterior commissure; as = aqeduct of sylvius; c = cortex; cb = ciliospinal "centre" of budge; cc = corpus callosum; cg = ciliary ganglion; scn = short ciliary nerves; cil = long ciliary nerves; if = inferior colliculus; m = mammillary body; mcg = middle cervical ganglion; mi = massa intermedia; nc = nasociliary branch of the ophthalminc 5th nerve; n5 = ophth. division of 5th nerve; p = pons; pc = posterior commissure; pi = pineal body; sc = superior colliculus; scg = superior cervical ganglion; III = oculomotor nucleus (Lowenstein and Loewenfeld, 1969).

the trigeminal nerve and goes on to run in the nasociliary branch and finally enters the globe via the long ciliary nerves. Once these fibres are within the globe, they run in the suprachoroidal space towards the ciliary body and then turn axially to innervate the dilator pupillae muscle (Zinn, 1972).

Cortico-Pretectal Connections

As early as the turn of the century investigators have demonstrated that the electrical stimulation of some parts of the cortex can result in a pupillary change alone or a pupil response together with accommodation and convergence changes in animals (Piltz, 1899, Cited by Lowenstein and Loewenfeld,1969 ; Wang et al., 1931; Barris, 1936).

Barris (1936) observed that following the destruction of the posterior lateral gyrus in cat, degenerated corticifugal fibres were traced to the pretectal area, the stratum opticum of the superior colliculus and the pontine nuclei. Following lesions of the pretectal area he also traced the degenerated fibres to the white substance underlying the posterior lateral gyrus. In addition, the presence of cortico-pretectal connections have been demonstrated by the existence of a systematic pupillary response as a result of the presentation of some visual attributes (see below).

Pupillary responses

Pupil Light Reflexes

In normal subjects, when a light stimulus is presented to one eye only, the pupil of the non-stimulated eye also responds. The response phase and amplitude are equal in both eyes. This phenomenon is called the consensual pupillary light reflex. For a sustained stimulus the response is a tonic light reflex whereas for a brief flash of light the response is termed the phasic light reflex. The amplitude of the response depends on the background adaptation state of the retina, the region of the retina stimulated (the retina is more sensitive in the fovea and macular regions than in the periphery and in regions adjacent to the optic nerve head), the direction of the incoming quanta of light (Stiles and Crawford effect), and the level of subject's consciousness (Lowenstein and Loewenfeld, 1969).

Mathematical models for determining the amplitude and latency of the pupillary response from any given retina locus were described by Varju (1964) and Knopp et al. (1969).

The base pupil diameter following adaptation at a given background luminance is variable between subjects (Crawford, 1963; de Groot and Gebhard, 1952). Similar inter-subject variability is reported for the shape of the pupil light reflex (Webster

et al., 1968). Increasing the target luminance causes an increase in the response amplitude, but the response latency decreases. Latency reductions as large as 120ms are reported to a 6 log unit increase in stimulus intensity (Webster et al., 1968; Lee et al., 1969). For a flashed stimulus, the response amplitude is proportional to the product of the stimulus duration and intensity at short stimulus durations (<10 ms) (Baker, 1963).

Classically, mechanisms for the tonic and phasic reflexes are explained in relation to the efferent and afferent pathways described earlier. Lesions along the optic tract are therefore expected to produce possible scotomas and disturbances of pupillary light reflexes.

Wernicke (1883) suggested that pupillary hemiakinesia, ie., the lack of a pupillary reaction in the blind part of a visual field while being maintained in the seeing portion, would only occur when lesions were situated anterior to the lateral geniculate body since the pupillary fibres leave the optic tract at this level.

A relative afferent pupillary defect (RAPD) is an objective sign of an asymmetrical lesion of the afferent visual system (Cox et al., 1982). An RAPD is seen with major retinal lesions or neurological lesions of the afferent visual pathway. Stimulation of one eye by a bright light produces an equal constricting response in both eyes due to the direct and consensual light reflexes and if the afferent visual system is normal, transfer of the light to the fellow eye will maintain the same constriction and tone on this pupil. If there is an asymmetrical lesion in the afferent visual pathway on one side , however, transfer of light from the good eye to the bad eye will result in a comparative dilation of both pupils (Spalton, 1984). Cox et al. (1981) showed that RAPD is a sensitive indicator of optic neuritis.

Thompson et al. (1982) suggested that in patients with anterior ischemic neuropathy, disciform maculopathy and trauma to one optic nerve, the amplitude of the afferent pupillary defect is closely related to the visual field loss.

Another method for measuring the disturbance of the pupillary light reflex is the measurement of pupil cycle time suggested by Miller and Thompson (1978) which utilises disorders in the response latency. In this examination technique, a horizontal slit beam of light of low to moderate intensity, ½ mm thick, is directed perpendicular to the plane of the iris at the inferior limbus. The beam is slowly elevated until it overlaps the margin of the pupil, which then constricts vigorously. The beam is held in this position so that the constricted iris blocks the light. The retinal will now be in darkness and the pupil will dilate to overlap the edge of the light beam again, producing another pupil constriction, thus setting up a persistent oscillation. The prolonged latency of the pupil light reflex in diseases of optic nerve

are due to the sensory defect (Lowenstein, 1954) and reduced speed of the transmission ability (Alexandridis et al., 1981) and is of clinical interest when monitoring the extent of the disease (Bell, 1978). Ukai et al. (1980) and Cox et al. (1982) found that the pupil cycle time is abnormal during acute optic neuritis and optic nerve compression but becomes normal as the acute episode resolves and suggested that this property of the pupil light reflex may be used in detecting subtle changes in efferent pupil pathways.

Wernicke's theory of pupillary hemiakinesia seemed very conclusive as far as the infrageniculate lesions were concerned.

Brindly et al. (1969) reported an impaired pupil light response to the global light changes in cortically blind subjects. Objective infrared pupillometry carried out by Cibis et al. (1975) on subjects with suprageniculate lesions also showed an impaired pupillomotor response in the subject's blind hemifield and postulated the existence of an inhibitory influence of higher lesions on the mesencephalon or damage to efferent fibres due to retrograde degeneration across the geniculate synapse or into the pretectal area from the neocortical visual system.

Hamann et al. (1979, 1981) categorised the pupillary responses in hemianopic subjects into three groups; 'hemiakinetic' (no pupil response from the blind half retina), 'hemihypokinetic' (impaired response from the blind half-retina), and 'eukinetic' (normal response from the blind half-retina). In normal subjects, retinal stimulation at increasing distances from fovea decreases the amplitude of the pupillary response and increases the latency.

Hamann et al. (1981) measured the responses from corresponding retinal loci in the blind field and the seeing retinal half in subjects with damaged optic radiations. The blind hemiretina was often found to produce responses with a prolonged latency and complete pupillary eukinesia were not encountered in blind hemifield. Pupillometric and visually evoked potential (VEP) studies in subjects with congenital and acquired lesions of optic radiations and lesions of LGN also suggest that hemianopic pupillary hypokinesia are expressive of suprageniculate lesions, in which the promptness of pupillomotor response is closely linked to the side of the lesion, unveiling the problem whether the lesion is extrinsic or intrinsic in nature (Hamann et al., 1979; Wilhelm and Wolfgang, 1991).

Pupillary Responses to Structure

When temporally modulated, uniform fields are presented to the eye, the pupil responds with a contraction (Varju, 1964). A band-pass frequency response is measured depending on the temporal modulation frequency of the stimulus with

maximal net contraction between 1 and 3 c/sec.

Troelstra (1968) investigated the pupillary responses to a temporally modulated uniform field and noted a good correlation with observed brightness, similar to earlier findings of Clynes (1962) and Varju (1964). He suggested that the findings may be explained in terms of linear and non-linear operators acting prior to pretectal regions.

Many experimenters have used sinusoidal gratings to investigate the spatial characteristics of the visual system. These techniques were primarily designed to study image reproduction in optical systems (Duffieux and Lansraux, 1945) and have formed the basis for many studies in visual psychophysics. Since many of the cells at various stages of the visual system respond to a stationary grating pattern (see section 1.11), the use of gratings in the clinical assessment of deficiency of visual function is to be expected. Disc targets moving over stationary gratings have also been used to study the spatial characteristics of motion detection mechanisms (Barbur et al., 1981).

The most common use of the stationary grating patterns involves the measurement of minimum contrast required to perceive a grating as a function of spatial frequency (Campbell, 1974). The reciprocal of such measurements defines the contrast sensitivity function.

Slooter and van Norren (1980) measured pupillary responses to chequerboard patterns, when the pattern alternated with a blank field of equal average luminance. It was shown that a measure of visual acuity could be derived from pupil responses since the magnitude of the response varied as a function of check size, which showed a high correlation with subjective measurements of acuity using the same checkerboard stimuli. They stated that the phenomena observed in their study did not fit the classical descriptions of pupil responses since the average retinal luminance was kept constant between the pattern and the uniform field. They hypothesised that "the response of local retinal elements, modified by a differentiation mechanism" played a role in eliciting such responses. In later studies (Slooter, 1985) similar responses could not be elicited in the blind field of patients with cortical lesions and it was concluded that " the pupillary light-reflex with a checkerboard as stimulus involved the visual cortex".

In 1985, Ukai measured similar responses to checkerboard patterns and hypothesised that either "pupillary afferent fibres have features that make them responsive to the [*spatial*] pattern" or "the responses reflect the activity of the central mechanism involved in pattern perception". They also concluded that accommodation changes might have been involved despite the experimental

techniques implemented to minimise them and the clear argument put forward in discarding such possibilities.

Barbur and Forsyth (1986) investigated the pupillary response to sinusoidal grating patterns and to counter-phase temporal modulation of a grating field. Experiments were carried out both in normal subjects and with a hemianope with clear bilateral field loss due to accidental cranial damage and subsequent unilateral degeneration of his primary visual cortex. They found that the size of pupillary constrictions varied with modulation frequency and stimulus modulation depth, both in the spatial and the temporal domain in the absence of accommodation and convergence changes. These pupillary changes were either absent or much reduced when the stimuli were presented in the blind hemifield of hemianopic subjects (see also Keenleyside et al., 1988; Keenleyside, 1989). They concluded that "the dependence of pupillary responses on the spatial and temporal modulation frequency of the stimulus reflect the activity of central mechanisms since such responses are either diminished or eliminated in the absence of the geniculo-striate projection".

Further investigations showed a systematic relationship between the amplitude of the responses and the grating spatial frequency (Barbur and Thomson, 1987; Barbur et al., 1987a,b). Contrast sensitivity measurements have been employed extensively in visual psychophysics and they may reflect the activity of central mechanisms (Blakemore and Campbell, 1969). The pupil grating response curves were found to resemble the contrast sensitivity functions under identical experimental conditions, both for foveal targets and when the target was presented in the subjects peripheral visual field (see figure 1.19). It is important to note that pupil grating response curves also follow the contrast sensitivity curves for various dioptric defocus (see figure 1.20). Their results also suggested the pupillary responses may be used as an objective method of measuring contrast thresholds for detection of spatially structured stimuli.

Pupil grating responses (PGR) have latencies between 260 to 340ms. Measurements of achromatic PGRs at various spatial frequencies indicate the presence of a small response to the stimulus offset, indicating the presence of a transient channel (Barbur, 1991). Pupillary constrictions elicited in response to gratings of lower luminance than the background despite a net reduction in retinal light flux level, and in the absence of accommodation and/or convergence changes triggered by the presentation of the stimulus support the hypothesis concerning the involvement of central visual pathways in such responses (Barbur, 1991; Barbur et al., 1992a).

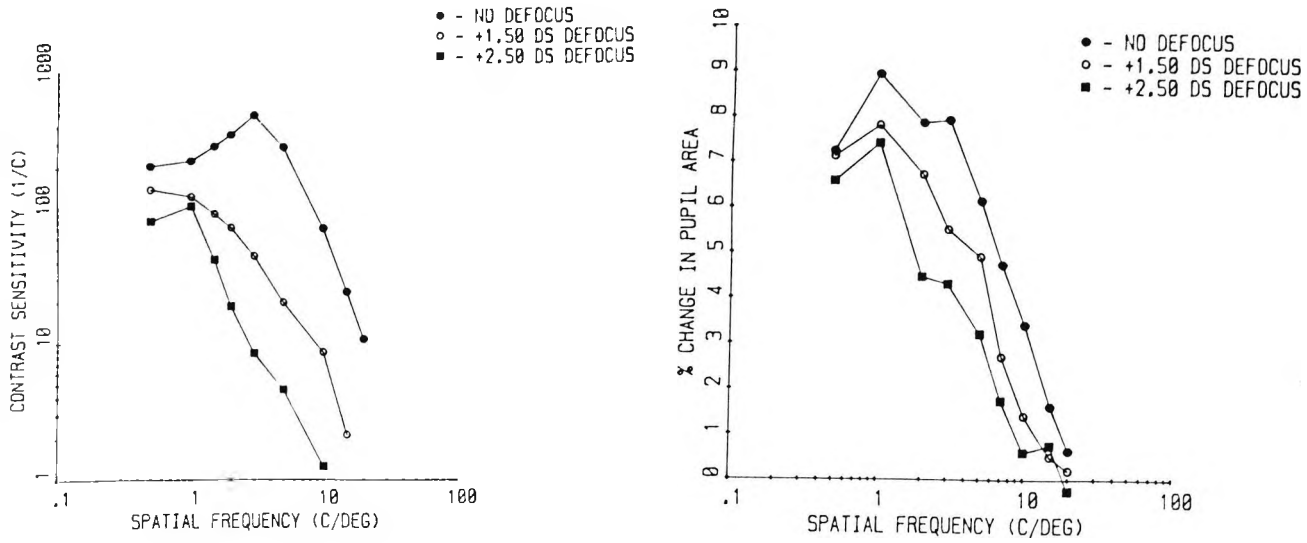


Figure 1.19: the pupil grating response curves are of the same characteristics as that of the contrast sensitivity when measured under similar experimental condition, both for foveal target as well as the peripheral presentations. Results given above are for a grating stimulus of 4.8° diameter and luminance background field of 12.7 cd/m², when presented in the foveal region and at an eccentricity of 8° (from Barbur and Thompson, 1987 reprinted with permission).

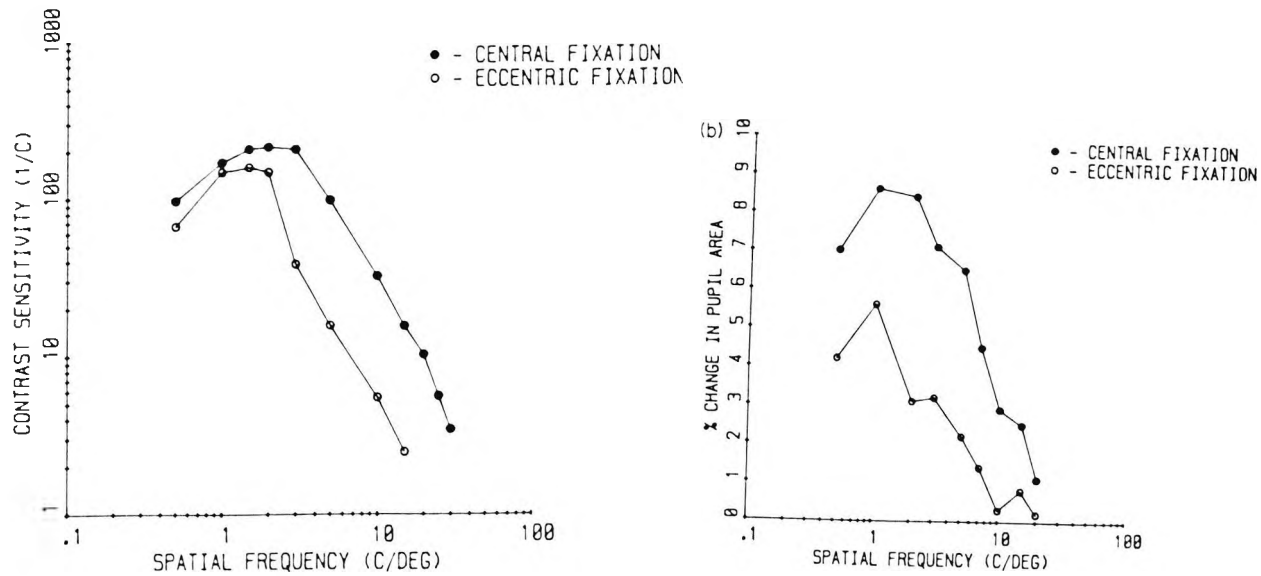


Figure 1.20: the effect of stimulus defocus on the contrast sensitivity and the pupil grating response curves (from Barbur and Thompson, 1987 reprinted with permission).

Pupillary Responses to Colour

Early investigations of the spectral responsivity of the pupil indicated that the observed brightness of light stimuli of different wavelengths and the level of pupillary response elicited were in good agreement. The Purkinje shift has been demonstrated to be identical for psychophysically measured scotopic and photopic vision and the pupil (Laurens, 1923; Alpern and Campbell, 1962).

This shows that both rod and cone signals contribute to pupillary constriction in response to light. In 1969, Kohn and Clynes showed that when two scotopically balanced fields at different wavelengths are alternated, the pupil shows a constriction response at each transition, giving an indication of the influence of chromatic mechanisms on the control of the pupil. Using this technique, Saini and Cohen (1979) proposed a four chromatic channel model based on the pupil response to changes in stimulus spectral distribution.

Young and Alpern (1980) carried out similar experiments and by placing the foveal stimulus inside a large rod saturating annulus, obviated the response evoked by rod signals. As expected, the exchange of standard light (580nm) to either shorter or longer wavelength lights produced a transient constriction of the pupil; the greater the wavelength difference the larger the constriction. They showed that responses were not a consequence of chromatic aberration or chromatic differences in magnification. They also observed that exchanges of equal luminance lights matched by heterochromatic flicker photometry evoked a response with a larger latency (50ms longer on average) than the same amplitude constriction evoked by a step increase in luminance of homochromatic light which lead them to hypothesise "[*it is possible*] that photopupil responses evoked by equiluminant heterochromatic exchanges may be produced by signals that are not a part of the ordinary pupillary light reflex, but on the contrary, must first travel to visual cortex before descending to the pupillomotor nuclei of the midbrain".

Krastel et at. (1985) obtained photopic increment threshold curves with narrow spaced monochromatic stimuli on a white background. The peaks and troughs of the sensitivity curve were observed which were not in accordance with the V-lambda curve, but were due to the activity of opponency mechanisms arising between the cone outputs. The pupil responses were found to closely parallel the peaks and troughs of the increment spectral responsivity curve as ascribed to opponency. They attributed their findings to a colour-opponent retinal input to the pretectum.

Barbur et al. (1987a) measured the pupil responses when the centre of a uniform white background field was altered in chromaticity and/or luminance. The results

showed that the constriction of the pupil to the onset of a test stimulus of lower luminance than the background field is increased significantly when the chromatic content of the stimulus is different to that of the background field. Pupil Colour Response (PCR) defined as a transient constriction of the pupil, triggered by chromatic changes in the visual field (Barbur, 1991), was investigated further in subsequent studies. PCRs to red/green isoluminant gratings were found to vary systematically with both spatial frequency and contrast in normal subjects (Barbur, 1989). PCRs in comparison with PGRs, for equal response amplitudes, were some 80 - 100 ms longer in latency (see figure 1.21) (Keenleyside et al., 1987).
From psychophysical studies of contrast sensitivity (Mullen, 1985) and VEPs measured for isoluminant gratings (Murray et al., 1987), it is believed that the spatial resolution of mechanisms involved in detection of chromatic, isoluminant gratings is poorer than for achromatic gratings, the peak response being shifted to much lower spatial frequencies.
Pupil colour responses, like PGRs, are absent when the stimulus is restricted to an area of the blind hemifield in a hemianopic subject (Keenleyside, 1989). Similarly, when using a random luminance modulation technique such that the detection of a stimulus pattern is only performed based on its chromatic content and any luminance cues are eliminated, then the lack of perception of the pattern in the cases of achromatopsic or colour deficient subjects parallels the absence of corresponding pupillary responses indicating the role of cortical processing in generation of these colour responses(Birch et al., 1992; Barbur et al., 1993). The absence of a pupil response when the chromatic modulations are restricted to the colour confusion lines of dichromats also rules out any rod mediated responses.
In order to explain the existence of the responses outlined above and to establish a working theory for future investigations, Barbur et al. (1987b) hypothesised that " When a change in the neural activity has taken place due to a stimulus attribute being presented to the eye, the steady state supranuclear inhibitory input to the pupillomotor nucleus is weakened transiently resulting in a pupillary constriction. The constriction amplitude appears to be proportional to the level of activity generated".
If the above hypothesis is correct, then similar responses could be elicited in response to changes in neuronal activity when viewing moving stimuli. Investigations of such responses are outlined in this thesis and the possible mechanisms involved are discussed.

Other Pupillary Reflexes

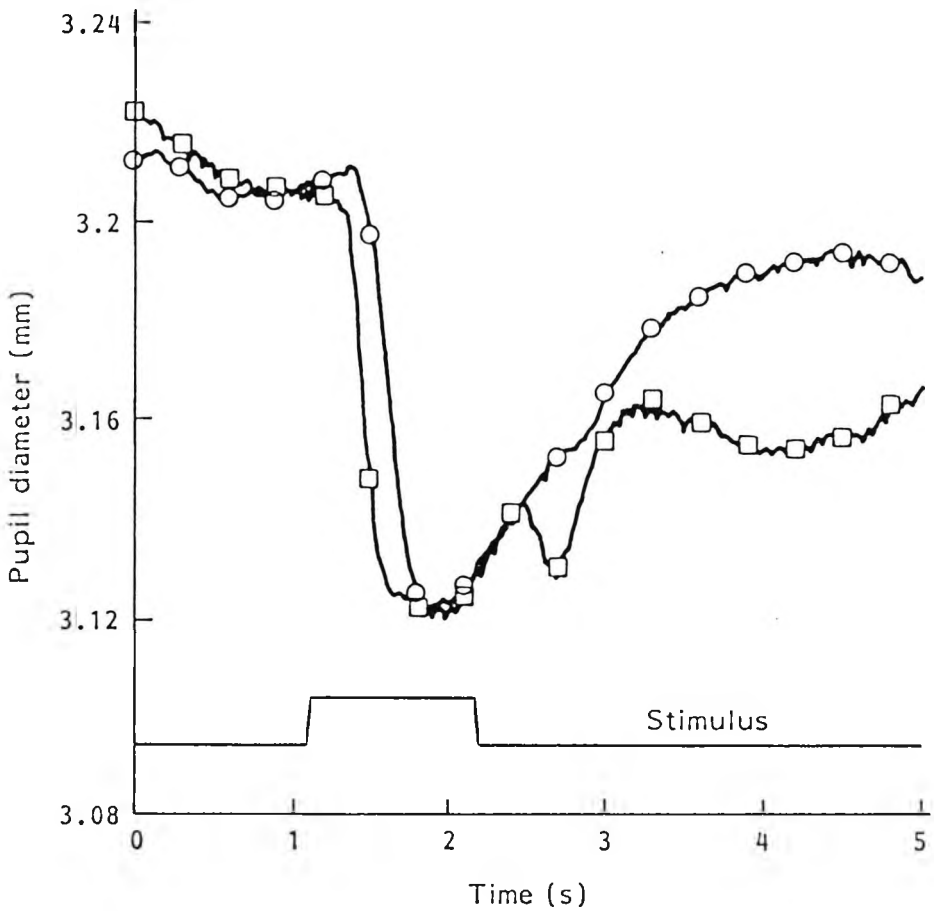


Figure 1.21: comparison of pupil responses to an achromatic grating of 1.21 c/deg and space-averaged luminance equal to that of a uniform background field and to an isoluminant, red/green chromatic grating of the same spatial frequency. The chromatic grating (circles) generates a response latency of about 360 ms which is about 80 ms longer than the latency associated with the achromatic grating (squares) response (from Barbur et al., 1992a, reprinted with permission).

Pupillary Near Reflex

There are three components of the near vision reaction, namely accommodation, convergence and pupillary constriction. They have separate centres within the third cranial nerve nucleus and separate efferent fibres (Lowenstein and Loewenfeld, 1969). When a subject views an approaching target, the following triad of events occurs:

1. The eyes converge so that the image of the approaching object is kept on each fovea in both eyes.
2. The curvature of the lens increases due to accommodation to bring the close object into focus.
3. The sphincter pupillae muscle is activated causing miosis of the pupil.

Pupillary constriction seems to be related to the amount of convergence (Schor and Ciuffreda, 1983).

Accommodation, convergence and miosis can be elicited by electrical stimulation of areas 19 and 22 of the cat cortex (Barris, 1934). Light impulses reach the parasympathetic oculomotor nucleus via the pretectal nuclei, whereas cortical impulses for accommodation are carried to the oculomotor nerve outside the pretectal area. The non-involvement of the pretectal nuclei in accommodation accounts for the clinical signs observed in Argyll Robertson syndrome (Alexandridis, 1985). In this syndrome the pupillary response to light is abolished while the pupil still constricts in association with the near response triad.

Dark Reflex

Reduction in the luminance of the environment results in pupillary dilation. Comparison of pupil responses to withdrawal of light in a normal pupil and a sympathectomised pupil, shows that the dark-redilation is reduced on the side of the lesion, but it is not abolished. The anisocoria due to the lesion consequently increases during the dark-dilation, and then decreases again after the light has been re-admitted (Lowenstein and Loewenfeld, 1969). The redilation is therefore due to 1) relaxation of the pupillary sphincter 2) active contraction of dilator pupillae via the cervical sympathetic pathway.

Orbicularis Reflex (lid closure)

On closing of the eyelids, miosis occurs. This can be demonstrated by asking a subject to close their eyes while the lids are held open. In addition, the globe rotates upward as part of the lid-closure reaction. This reflex has been used as evidence of direct connections between the facial (VIIIth) cranial nerve nucleus

and the oculomotor nuclear complex. In cases where the pupil fails to react to light and accommodative effort, the orbicularis reflex is helpful in establishing the integrity of the efferent pupillary pathway (Zinn, 1972)

Vestibular Reflex

On stimulation of the vestibular nerve there is a pupillary dilation due to the fact that some of the sympathetic nerves that serve the iris transverse the middle ear (Alexandridis, 1985). This reflex is demonstrated if a person rotates around their body axis. Their eyes do a counter rotation to the body of about 30° then flip back and begin to repeat the counter rotation. This is known as vestibular or flick nystagmus. The pupils dilate as the eyes move in the counter rotation and then constrict when they flip back. It is thought that the pupils dilate to increase the amount of light available to the eye to facilitate vision.

Trigeminal Reflex

Any persistent irritation of the cornea, conjunctiva or eyelids results in constriction of the pupil. Painful stimuli lasting a brief time will result in mydriasis. If the pain continues, there will be a resultant miosis, which is bilateral, with the pupil on the affected side being more miotic (Alexandridis, 1985). This is a true reflex because the Vth nerve is being stimulated and this is linked to both the Vth nerve nucleus and the oculomotor nucleus.

Axon Reflex

This is a second mechanism or pathway for miosis secondary to painful stimuli. Following painful irritation of skin, stimulus is sent to the Dorsa Root ganglion. An antidomic impulse results in a release of neuropeptide substance which in turn releases histamine causing blanching, hyperaemia and oedeama of the skin. As there is a dilation of the iris capillaries, the increased blood volume causes miosis.

Psycho-Sensory Stimuli

Pupillary responses to audio stimuli have previously been demonstrated and their mathematical analysis were outlined by Clynes (1962). There appears to be a pupillary dilation response to a load noise, but a change in audio frequency produces a pupillary constriction.

In general, it is assumed that constriction is a characteristic pupillary response to many aversive psycho-sensory stimuli and dilation is an indication of interest.

In an attempt to provide an objective assessment of subjects views in clinical

psychology applications, this generalisation was investigated by Hess (1965) using a variety of tasks, both in male and female subjects. A series of photographs which were equated for luminance were shown to the subjects. Photographs were divided into two of "Shock" and "pleasant" categories. A "shock" picture typically produced dilation, but with repeated presentations, constriction took place and persisted for any further presentation of the same picture. Hess suggested that the initial dilation is a representative of stress and anxiety and the following constriction is as a result of the negative attitude.

Pupillary responses as a measure of self-esteem have also been investigated. Results show that for females a relationship exists between self-esteem and pupillometric response (Zeitner and Weight, 1979).

It seems however, that the pupillometric studies offer a very limited possibilities as an objective measure of attitudes and interests.

1.6 Distinct Cortical Pathways

The primate LGN neurones fall into six distinct cellular layers. Neurones in the four most dorsal layers, ie., the parvocellular laminae (P), are very sensitive to chromatic differences and have low sensitivity to luminance modulation. The remaining neurones: those located in the magnocellular layers (M) of the LGN, receive a broad band chromatic input without colour opponency and have a high contrast sensitivity (Kaplan and Shapley, 1982).

The magnocellular cells have a low spatial resolution, some 2-3 fold lower than the parvocellular cells for a given eccentricity. Parvocellular layer neurones have low conduction velocities and their responses are sustained, in contrast to the fast and transient responses of the magnocellular cells (Livingstone and Hubel, 1987). It is possible that the segregation of the X and Y pathways (explained in section 1.1) may continue beyond the geniculate but, there is conclusive evidence to support the segregation of P and M pathways (reviewed by Kulikowski and Vidyasagar, 1990). The cortical input from the P and M pathways and its further distribution may be categorised as follows (see figure 1.22):

1. The magno pathway (M layers of LGN → 4Cα → 4B → Thick stripes → MT)
2. The parvo pathway (P layers of LGN → 4Cβ → interblob → interstripes → V3/V4).
3. The blob pathway (blobs → thin stripes → V4).

Prior to describing the role of these distinct pathways, the properties of their individual components are discussed:

4Cα of striate receives magnocellular input (Hubel and Wiesel, 1972). Cells in this layer of striate cortex display orientation selectivity (Dubner and Zeki, 1971; Dow, 1974) and, as with the M cells of LGN, have broad band receptive fields (Motter and Mountcastle, 1981; Livingstone and Hubel, 1984a). Their receptive field centres have diameters two or more times as great as those of 4A or 4Cβ. The cells have a higher contrast sensitivity than those of 4Cβ layer (Blasdel and Fitzpatrick, 1984; Hawken and Parker, 1984).

4B of striate cells display orientation selectivity (Dow, 1974; Poggio and Fischer, 1977; Maunsell and Van Essen, 1983a). Many cells prefer moving stimuli and are direction selective (Dow, 1974; Livingstone and Hubel, 1984a; Movshon and Newsome, 1984), they are also binocularly driven (Hawken and Parker, 1984), and

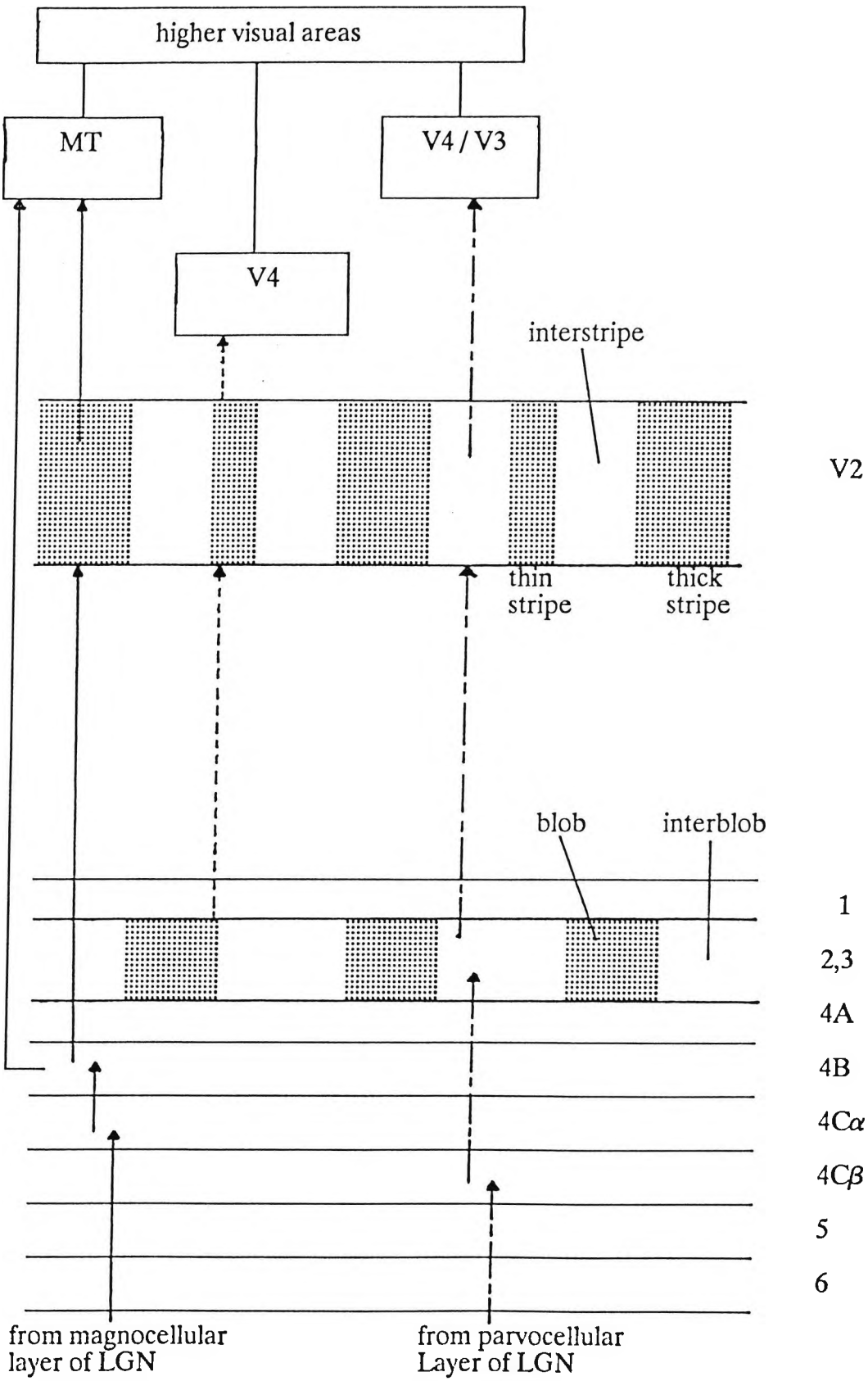


Figure 1.22: schematic diagram of three cortical pathways (based on Hubel and Livingstone, 1987; Hubel, 1988; Zeki, 1993).

give rise to most of direct projections from V1 to MT.

4Cβ of striate cells receive parvocellular input (Hubel and Wiesel, 1972) and are similar to the parvocellular geniculate cells in that they have small circular symmetrical receptive fields with centre-surround antagonism. However, they differ in that their colour opponency may be less prominent or explicit (Bullier and Henry, 1980; Blasdel and Fitzpatrick, 1984).

Interblob cells are precisely tuned for stimulus orientation, mostly complex and unselective for stimulus colour. Orientation selectivity is far more common in the interblob region than the blob region (Livingstone and Hubel, 1984b). The receptive fields of interblob cells are consistent with a fine grained parvocellular input, because their optimum stimulus size is also small. Interblob cells strongly prefer moving stimuli and do not respond to flashed stationary stimuli, however, many are not direction selective. In general colour opponency is rare, occurring in only 10% of the orientation specific cells which is surprising since they receive inputs from 4Cβ where the cells are mostly colour opponent (Hubel and Wiesel, 1968). Nevertheless seem to carry some kind of colour information since Gouras and Krüger (1979) showed that many cells, even though they responded to white light and showed no demonstrable opponency, they responded to a colour contrast boarder at all relative settings of intensities of the two colours. This suggested that colour coded inputs are somehow pooled in such a way that information about the sign of the colour opponency and also the sign of black-white contrast is lost, but the responsiveness to colour contrast and to luminance contrast is retained.

Blobs are an array of dot-like patches of cytochrome oxidase rich tissue (Horton and Hubel, 1980). The cells receive both M and P inputs, are not selective for stimulus orientation and, in the main, have centre-surround receptive fields with a minority having a centre only without antagonistic surround. They do not seem to be concerned with movement, responding well to stationary stimuli, giving sustained responses to appropriately coloured spots and showing no direction selectivity. In macaque monkey, roughly half of the blob cells are colour coded with colour opponent centres and antagonistic colour opponent surrounds. The remainder are broadband centre-surround, possibly analysing colour, with the broadband cells conveying information on brightness (Livingstone and Hubel, 1984a). The colour opponent blob cells must derive their colour properties from colour selective geniculate inputs, possibly parvocellular neurones (Hubel and Livingstone, 1987),

but they have response properties similar to some magnocellular cells (Wiesel and Hubel, 1966; Livingstone and Hubel, 1984a). These colour properties of blob cells would be compatible with input from both M and P system. Receptive fields have coarse resolution with the field centre diameter at least twice as large as the optimum line widths for interblob cells at the same eccentricity (Livingstone and Hubel, 1984a).

Thin stripes of V2 consist of stripes of cytochrome oxidase rich tissue. The corresponding cells are similar to those found in blobs in that they lack orientation selectivity and show a high incidence of colour opponency. Many are complex in the sense that they respond to a stimulus over a larger region of the visual field without an increase in optimum stimulus size (Hubel and Livingstone, 1985). They receive inputs from V1 cytochrome oxidase rich blobs (Livingstone and Hubel, 1984a) and project to the extrastriate area V4 (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985).

Thick stripes of V2 cells are orientation selective (Zeki, 1980; Livingstone and Hubel, 1984a; Poggio et al., 1985), and are involved in stereoscopic depth, such that two thirds of them are tuned for binocular disparity. Cells with similar disparities are clustered together (Zeki, 1974; Livingstone and Hubel, 1987). Many respond only to moving stimuli and a high proportion of them display direction selectivity (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985).

Interstripes contain cells which resemble the properties of cells in the interblobs of the striate, except that a high proportion are in addition end-stopped, ie., they respond to short but not long bars. These end-stopped cells are very sensitive to movement.

MT / V5 is regarded as a "movement area", due to its high prevalence of directional selectivity (80%) with cells of similar directionality clustered together (Dubner and Zeki, 1971; Albright, 1984). Many cells are selective not only for the direction of stimulus motion but also for speed and binocular disparity (Zeki, 1974, 1980; Maunsell and Van Essen, 1983b), thus suggesting that MT is well suited to the analysis of visual motion in three dimensional space and is concerned with textures and figure-ground relationships (Allman et al., 1985b). The major outputs of MT appear to be relayed to the parietal cortex via intermediate areas, including MST (Jones and Powell, 1970). MT receives additional inputs from striate cortex via

indirect routes through V2 and V3 (Maunsell and Van Essen, 1983c). These projections may also play a significant role in motion processing since 40% of the neurones in V3 are directionally selective (Felleman and Van Essen, 1987).

Having outlined the physiological properties of different cortical laminae and some of their interconnections, the following functions may be attributed to the three anatomical subdivisions stated earlier.

The magno pathway (M layers of LGN → 4Cα → 4B → Thick stripes → MT)
Since the cells in this pathway strongly prefer moving stimuli, are binocular and display orientation and directional selectivity, the magno pathway is largely involved in the detection of motion. In addition, it is involved in extracting movement in depth information from the binocular disparity. The magno pathway has high contrast sensitivity and temporal resolution, and relatively low spatial resolution. Moreover many cells in layer 4B of the striate project directly to MT.
From the physiological data it is not possible to conclude whether magno pathway is involved in the analysis of shape (Livingstone and Hubel, 1987).

The parvo pathway (P layers of LGN → 4Cβ → interblob → interstripes → V3/V4)
The cells are not colour opponent, but they do carry some form of colour information which may be used in detection of colour contrast borders. The parvo pathway includes end-stopped cells, and has a high spatial resolution as well as being orientation selective. Therefore, it may be involved in high resolution form perception.

The blob pathway (blobs → thin stripes → V4)
This is concerned with colour only. Its resolution is low and its lack of orientation tuning suggests that it is not involved in form perception (Livingstone and Hubel, 1987).

1.7 Is the Movement Pathway Independent of Colour Contrast and Form Information

If the perception of motion were entirely dependent on the magno system, then the colour information would not affect the perception of movement except under conditions of isoluminance. Several experimenters have investigated the contribution of colour contrast to movement perception:

Campbell and Maffei (1981) and Thompson (1982) found that by altering the contrast of a moving grating, the perceived speed of the movement is affected, indicating the contribution of luminance contrast to the motion pathway.
Livingstone and Hubel (1987), using red/green horizontal gratings with 180° phase difference between its colour components, found that movement was not seen when the luminance of the gratings was set to within 5% of that required for isoluminance.
Ramachandran and Gregory (1978) reported that the apparent movement disappeared at isoluminance for random dot kinematograms, but not for simple line stimuli at short interstimulus intervals. Livingstone and Hubel (1987) repeated the experiments and found that the perception of movement was absent for certain red/green luminance ratios and showed that the effect of eccentricity on isoluminance also had to be taken into account and concluded "for apparent movement, our results give no indication of any contribution from colour contrast information". This result agreed with the previous findings (Kolers and Pomerantz, 1971; Campbell and Maffei, 1981) which showed that for movement perception, luminance differences are much more important than colour differences.
Even though the apparent motion studies of targets at isoluminance have shown the segregation of the movement and colour processing, the existence of movement dependent colour aftereffects such as MacKay illusions (Hepler, 1968) and colour dependent movement aftereffects (Livingstone and Hubel, 1987) indicate the convergence of colour and movement pathways. Since the aftereffects require long exposure durations, the convergence may occur at more central stages of processing.
Segregation of movement and form pathways is not as evident as the separation of the movement and colour pathways. Many findings however, indicate that some components of form and movement are analysed independently by the visual system. Both magno and parvo pathways carry information about edge orientation and both are sensitive to the stimulus movement. Movement seems to be important in the parvo pathways for overcoming adaptation since the stabilisation of the retinal image increases the form detection threshold (Riggs et al, 1953).
Threshold studies also indicate that the threshold required for detecting the flicker or movement of a grating is different from that for resolving the grating and the thresholds vary independently with spatial frequency (Kulikowski and Tolhurst, 1973). Tolhurst (1973) found that the sensitivity for detecting a moving or stationary grating is affected by preadaptation with a moving grating, but preadaptation with a stationary grating affected sensitivity for a stationary grating

but not a moving one, which suggests the existence of a form channel that is sensitive to motion, as well as a movement channel that is independent of the form channel.
Kolers and Pomerantz (1971) investigated the effect of form on apparent movement and found that the form or shape of an alternating stimuli had little effect. They also found that line orientation had no effect on the preferred direction of movement. Livingstone and Hubel (1987) showed that form, or at least the fine detail of shape, had little influence on the early stages of the movement detection system, however, some effect of orientation on the perception of apparent movement has been demonstrated (Green, 1986).

1.8 Lesion Studies of the Motion Areas

Selective lesions of areas involved in processing of movement information in primates, trained on appropriate psychophysical tasks, has provided a valuable insight into the contributions of different visual areas to visual perception.
In related motion experiments, the effect of destruction of an area on the psychophysical threshold for motion related and non-motion related tasks can be determined. If lesions elevate motion thresholds relative to non-motion thresholds, it is possible to infer the presence of a link between the neural activity of that area and motion perception.
It is thought that a velocity signal is required to perform smooth pursuit eye movements. If MT is involved in determination of the velocity, then any damage to MT may affect the pursuit eye movements. Using small chemical lesions in MT, Newsome et al. (1985) demonstrated a specific oculomotor deficit in the matching of smooth pursuit eye velocity to the target velocity. Eye movements to stationary targets were not affected. This impairment was different to that which may be obtained from the lesions restricted to V1 area which affect the eye movements to both the stationary and moving targets.
Newsome and Wurtz (1988) showed that following lesions in the peripheral representation of MT, the psychophysical thresholds for determination of the direction of motion were elevated, but the contrast sensitivity was unaffected. The eye movement recording showed that following small MT lesions, the pursuit initiation is impaired only for target motion in a small region of the visual field that corresponded topographically to the location of the lesion. Pursuit initiation was normal at all other locations. In addition to this pursuit deficit, the monkeys were also impaired in their ability to adjust the amplitude of their saccades to

compensate for target motion. For lesions of the foveal representation in MT, deficits were present for any pursuit eye movement towards the damaged hemisphere regardless of the point of origin.
Dürsteler et al. (1986) demonstrated that following the MT lesions, the pursuit eye movements for stabilised retinal images were not impaired and only the responses to moving targets being affected.
Lesion studies carried out by Newsome and Parè (1988) also showed that the small lesions of MT resulted in elevated psychophysical threshold for motion sensitivity tasks, while thresholds for contrast sensitivity were affected little or not at all.
Salzman et al. (1990) trained rhesus monkeys to report to the direction of motion in a visual display whilst, with the use of electrical microstimulation, the firing rate of clusters of direction selective neurones in the middle temporal visual area were modified. It was demonstrated that the microstimulation biased the animals judgements towards the direction of motion encoded by stimulated neurones.

Collectively, the above findings indicate that MT plays a role in a broad range of perceptual and behavioural functions and can be viewed as a general purpose motion processor with its outputs feeding into a number of higher processors. In almost all lesion studies, upto a certain extent, a recovery of impaired functions take place, starting almost immediately after the damage has taken place. This may be due to plastic changes in topography or receptive field size within MT or other visual area operating in parallel with MT, which may assume the functions of the lost MT cells. It is also possible that the small lesions may not eliminate the entire stimulus aperture representation in MT. However, the fact that recovery exists does not compromise the role of a visual area. The impairment caused indicates the selectivity of the lesion and the recovery of functions demonstrates the ability of a hemisphere to generate alternative strategies.
The effect of lesions on the perception of movement in man is discussed in section 1.4.
A detailed analysis of orientation, speed and direction selectivity is outlined in sections 1.11-13.

1.9 Psychophysics and Physiology of Apparent Motion

In 1912, Wertheimer found that when two spatially separate stationary stimuli were flashed sequentially, a perception of motion can occur although real motion was absent. Later experimenters found that the perception of motion for bar stimuli

could occur for displacements over large visual angles (Neuhaus, 1930; Zeeman and Roelfs, 1953) and even when the stimuli presentation occurred to the temporal margin of each eye (Smith, 1948). The maximum displacement of two sequential presentation which could still elicit a movement perception (Dmax), appeared to depend on the viewing conditions, inter-stimulus interval and number of target displacements. The classical method for studying the parameters that control apparent motion involved observers judging whether a sequence of simple stimuli appeared simultaneously, in motion or successively. These perceptual categories, however were not very stable or well defined.

Shortly after the introduction of random dot kinematograms by Julesz (1971) Braddick (1973, 1974) investigated the processing of movement information using two random dot patterns which were presented alternately at an appropriate rate. An identical region of dots appeared in both patterns, except that one region was uniformly displaced with respect to the other. This region appeared to oscillate and became visible, being segregated from its surround by clear boundaries. The boundaries were purely motion defined and no such region was visible on either pattern when solely presented. Dmax was defined as the maximum displacement which gave rise to the perception of an oscillatory region.

Braddick's experiments (1974) proved one important fact, ie., the segregation effect was only perceived over a small spatial and temporal range, (Dmax=15 min arc) and for inter-stimulus intervals (isi) of less than 80ms. In addition, the segregation was abolished when the patterns were presented dichoptically, or when a bright field was presented shortly after each random dot pattern (Braddick, 1973). These observations lead to a prediction of the existence of an early motion processing stage and the hypothesis that "a low-level motion detecting process, with a very limited spatial range [*the short-range process*], may underlie the occurrence of perceptual segregation in random dot array".

Perception of the classical "apparent" motion is attributed to the higher level of motion detecting process but its output cannot be used to segregate an area of the field. The characteristics of the short-range process and the classical apparent motion are summarised below (Braddick, 1974).

Barbur et al. (1980) showed that there is no perceptual difference between real and apparent motion stimuli in the short range condition.

Criterion of segregation in random dot display	*Criterion of smooth apparent motion for isolated elements*
Dmax < 15' isi < 80ms segregation masked by bright uniform field in isi.	Dmax may be many degrees isi measured upto 300ms. no masking.
successive stimuli must be delivered to the same eye or to both eyes together as must the masking field.	successive stimuli may be delivered to the same or different eyes.
pattern defined by chromatic but not luminance contrast is inadequate	stimuli may be defined by chromatic contrast alone

The criteria for the two movement categories given above are different. One category depends on segregation and is a result of an early processing stage, since it has restricted spatial and temporal ranges, can be masked and is not dichoptic. The other has the characteristics of the more interpretive or the higher level processes, ie., it operates dichoptically and with more freedom.

A Dmax similar to the value given for the short range process has also been measured for a line stimulus when presented in several successive equidistant positions, whereas, for only two sequential presentations, apparent motion can be perceived with separations as large as 7.5° (Kolers, 1972).

Furthermore, similar spatial limits have been measured for square-wave gratings (Dmax=24'), where the light and dark bars were alternated to give rise to the apparent motion (Kulikowski, 1975).

Braddick (1973) indicated that the short range process had a fixed Dmax, and the number of dots in the patch was not a confounding variable.

Lappin and Bell (1976), in contradiction, presented evidence that the limiting Dmax was determined by the size of the displacement expressed as a number of array positions (pixels).

Baker and Braddick (1982), in later experiments demonstrated that the displacement limit for perception of motion from random dot stimuli was expressed more consistently as the retinal angle of that displacement. In addition, they showed that Dmax varied with receptor field size, being much smaller for small field sizes and larger for larger field sizes. Their observations were also confirmed by Petersik et al. (1983).

The effect of luminance and contrast degradation on foveal and peripheral detection of motion in moving random dots patterns (low-level system) was

investigated by van der Grind et al. (1987) and Koenderink et al. (1987). They found that the short-range system, responsible for detection of coherent movement, is highly robust for luminance degradation and reasonably robust for contrast degradation.

Physiology of Apparent Motion

As explained earlier (see sections 1.3-4, 1.8, also see 3.1), both lesion studies as well as single cell recordings showed that specific cortical areas are involved in the processing of movement information. It would appear that the processing of visual motion is organised in an hierarchical order with an increase in specialisation of cells in their response specificity as the hierarchy proceeds.

Mikami et al. (1986b) studied the responses of V1 and MT neurones to flashed bar stimuli. A comparison of the psychophysical data with the recorded neurone responses indicated that the spatio-temporal limits for perception were similar to the limits for direction selectivity in MT neurones but contrasted markedly with those for V1 neurones, suggesting a correspondence between neuronal responses in MT and the short-range processes of apparent motion.

Newsome et al. (1986), using the same stimuli reported that for high apparent speeds, physiological data from MT, but not V1, corresponded closely to the psychophysical data. This was not the case for V1 at low apparent speeds, however, physiological data from MT and V1 were similar to each other and to the psychophysical data, hence, they concluded that "neurones in either V1 or MT could mediate the perceptual effect at low speeds whereas MT is a stronger candidate for this role at high speeds". They suggested that according to the spatio-temporal content of the stimulus, the processing may be carried out at different cortical areas.

Subsequent studies compared the Dmax values obtained psychophysically with the physiological data obtained from neurones in area MT, for both the slit and random dot stimuli (Mikami 90). It was found that the Dmax for the alternating random dots was smaller than the Dmax for the alternating slits, and it was suggested that the slit stimuli could stimulate both the short-range and the long-range processes whereas the random dots could stimulate only the short-range system. Thus, it would appear that the MT neurones were involved in both short and long range processes.

1.10 The use of the Random Dot Patterns to Study Direction and Speed Discrimination

The analysis of random dot patterns is based on movement sensitive mechanisms without the confounding interference of position sensing mechanisms (Nakayama and Tyler, 1981).

At the single cell level a bar stimulus can be an appropriate stimulus to study motion analysis. When evaluating the visual system as as a whole, a random dot pattern is a better stimulus in the study of the contributions of local motion measurements. While motion of a bar can be detected by the long range process, the analysis of random dot pattern is based on the short range process (Braddick, 1974).

The use of random dot patterns isolate the short range motion mechanism and facilitate the comparison with physiological results since the direction selective and speed tuned cortical cells are considered to be the neuronal hardware underlying the short range mechanism.

Speed tuned and directionally selective cells have been reported in areas 17 and 18 of cat (Orban et al., 1981a,b) and area V5 of monkey (Zeki, 1978a; Maunsell and van Essen, 1983a) and they respond maximally at intermediate speeds (Orban et al., 1981a,b; Maunsell and van Essen, 1983a).

The velocity discrimination thresholds measured using random dot patterns are also optimal at intermediate speeds (4 to 64b °/s) and are comparable with data on the short range process of human motion perception (De Bruyn and Orban, 1988).

The speed and direction discrimination curves obtained with random dot patterns are similar to those obtained with light bars, with Weber fractions for speed discrimination approximately 7% and 1.8° for direction discrimination when moving at optimum speeds. The U-shaped relation between the velocity Weber fractions and the stimulus velocity is a fundamental relationship (De Bruyn and Orban,1988). It does not depend on changes in luminance, contrast and length of the bar stimulus, it is similar for bar stimuli and random dot patterns and it persists for a range of stimulus sizes and durations. Both discrimination thresholds show very similar dependence on stimulus speed (De Bruyn and Orban, 1988). While cortical cells which are bandpass filters for speed are selective for direction, the converse is not necessarily true (Orban et al., 1981a,b, 1986). The range of velocities over which the cortical cells are direction selective is wider than the range of velocities over which the cortical cells are speed selective. Hence, one might expect the function for the direction discrimination to be broader than for the speed

discrimination. However the results do not support this. It is therefore, possible that the same initial set of detectors is used both for direction and speed discrimination and only those cortical cells which are direction as well as speed selective are involved in the local analysis of a moving random dot pattern (De Bruyn and Orban, 1988).

Van Doorn and Koenderink (1982a,b, 1983) have shown that motion detectors tuned to a given velocity can use a range of spans (dx) and delays (dt), hence the optimal velocity of the detector equals dx / dt. Thus for each velocity, it can be assumed that for each retinal locus there is a pool of detectors tuned to a single velocity but covering a range of spans. Data obtained by van der Grind et al., (1986) shows that the elementary motion detectors are bilocal detectors, ie., their characteristics are modelled as correlation devices, and their delays and spans are scattered around a mean value. Hence, manipulation of the size of a moving stimulus involves both recruitment from the local pools and spatial summation across the local pools. Increasing the duration of the stimulus involves both the recruitment of more detectors from the pool at a given locus as well as the temporal integration within the local pool due to activation of the elements of the pool for a longer time.

De Bruyn and Orban (1988) observed that velocity discrimination is equally efficient when tested with a light bar and random dot patterns, indicating that the spatial extent of the pattern itself has little effect. That is, the optimal number of motion detectors pooled in order to make a fine speed discrimination is reached for both the bar and the random dot pattern. The motion signal does not improve as detectors from several local pools are recruited. They concluded that " spatial summation in speed and direction discrimination relies entirely on recruitment from local pools, while temporal summation relies on recruitment from local pools for direction discrimination, but on recruitment and on temporal integration of signals from single detectors".

In parallel to the velocity discrimination threshold measurements, van der Grind et al. (1987) defined a threshold signal to noise ratio for the detection of coherent motion in a random dot pattern, and showed that the discrimination of the pattern was independent of the contrast of the pattern dots for contrast levels higher than 30% for both foveal and peripheral presentations. At low contrast levels however, the fovea is the least, and the far periphery the most resistant to contrast degradation. These qualitative results are also in good agreement with the predictions based on the bilocal velocity tuned model for movement detection.

Using random dot patterns, Levinson and Sekuler (1976) estimated the tuning of

direction specific mechanisms by determining the perceived direction shift for the test motion as a function of the adapting direction. They found that even with as much as 60° difference between the directions of the adapting and test dots, pre-exposure to the moving adaptating dots could substantially alter the direction in which the test dots appeared to move. Similar broad tuning properties were reported by Ball and Sekuler (1979) and Sekuler et al. (1990), also using random dot patterns.

Segregation by motion was investigated by van Doorn and Koenderink (1983). The Weber fractions for segregating an area of a random dot pattern based on variation in the speed and direction of the motion were measured to be 100% and 30%, respectively. These values were considerably higher than those obtained at local velocity and direction resolution levels. The rise in threshold has been attributed to the hypothesis that there are two pathways for the processing of the outputs of cortical cells tuned to a given stimulus parameter such as orientation, speed or direction. In one pathway the local to global differences are computed and these signals are used for segregation. The second pathway processes the continuous values of the same domain (De Bruyn and Orban, 1988). In this scheme, the discrimination thresholds for the direction and speed rely on the processing in the "continuous" pathway while the segregation by speed or direction would rely on the "discontinuity" pathway.

1.11 Orientation Tuning

1.11.1 Psychophysical Studies

In order to examine the response of visual mechanisms to a visual stimulus, and to investigate the possible interactions between channels which may be involved in the processing of certain stimulus attributes, various psychophysical techniques have been developed. One method applied in the case of orientation selectivity, involves the use of suprathreshold summations techniques. The minimum contrast required for the detection of a stimulus corresponds to one threshold unit. To investigate the interactions between two mechanisms involved in the detection of a stimulus, one of the stimuli (ie., the background) may be presented at threshold or at suprathreshold level. The threshold required to make the second (ie., the target) stimulus detectable is then measured (see figure 1.23).

There are three possible outcomes:

1. The threshold for the target stimulus is lower than unity. This means that the channels for the detection of both stimuli interact such that their interaction results in partial summation.
2. The threshold for target detection is unaffected. The two channels are therefore independent of each other.
3. The presence of the background stimulus results in the elevation of threshold for the detection of the target. This means that the channel responsible for detection of the background inhibits the response of the channel involved in detecting the target.

Campbell and Kulikowski (1966) investigated the effect of orientation of the test pattern on the background. They superimposed optically a test grating on a suprathreshold background grating of the same spatial frequency, and determined the threshold for detection of the test grating in the presence of the background. When the gratings were presented with the same orientation, the increment threshold of the test grating was found to be proportional to the suprathreshold contrast of the masking grating. As the angle between the test and masking gratings was increased, the masking effect fell, reaching half its maximum value for an orientation difference of 12°. They concluded that this effect was psychophysical evidence for a narrow orientationally tuned channel with a half amplitude bandwidth of 24°.

There are two possible explanations for the difference between the bandwidth measured psychophysically and the one obtained from the physiological data (see

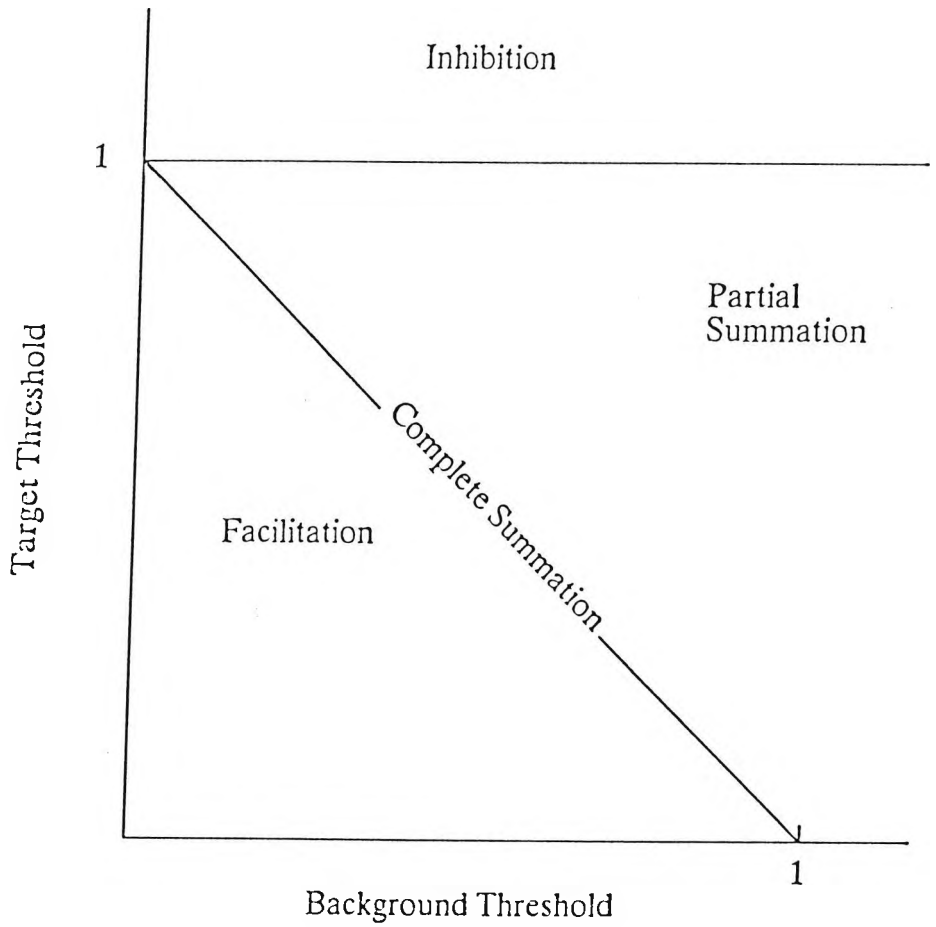


Figure 1.23: Possible interactions between two channels responsible for detection of target and background stimuli (see text).

section 1.11.2).

1. the narrower orientation tuning measured psychophysically may reflect a species difference, ie., this selectivity is simply finer in humans than in monkeys.
2. the performance of a subject may reflect the activity of finely tuned orientationally selective neurones rather than corresponding to the mean selectivity of the cells.

Using a preadaptation technique, Blakemore and Campbell (1969) found that the adaptation to a high contrast grating resulted in a temporary fivefold rise in contrast threshold of a test grating with the same spatial frequency and orientation. By determining the rise of the threshold over a range of spatial frequencies for a number of adapting frequencies, it was found that the threshold elevation was limited to a spectrum of frequencies with a bandwidth of just over an octave at half amplitude, centred on the adapting frequency. This effect was orientation specific, ie., a horizontal adapting grating did not influence the threshold of a vertical test grating. In later studies (Blakemore et al., 1970; Blakemore and Nachmias, 1971), it was also found that the high contrast adaptation resulted in an apparent shift in the spatial frequency of the test grating, away from that of the adapting grating. Both aftereffects were orientation selective and their magnitude was decreased by the introduction of an orientation difference between the test and adapting gratings.

The threshold elevation phenomenon is an indication of the presence of spatially tuned mechanisms. The spatial frequency shift suggests that the adaptation to a grating depresses the sensitivity of a limited group of tuned frequency-selective neurones amongst the whole population of such cells, each optimally sensitive to a different range of spatial frequencies. Also the adaptation of one of these mechanisms disturbs the distribution of activity in the population of such mechanisms activated by a nearby spatial frequency (Blakemore and Nachmias, 1971).

In addition to the above techniques, visually evoked potentials have been utilised in the study of orientation selectivity and spatial tuning, using temporally modulated stimuli (Campbell and Maffei, 1970; Fiorentini et al., 1983). The bandwidth of orientation tuning, estimated from these experiments, was approximately 30°, which was in close agreement.

The Oblique Effect

Human observers are more sensitive to horizontal and vertical gratings than to

oblique gratings at high spatial frequencies. This phenomenon has been attributed to the asymmetric orientational distribution in eye movements, refractive errors, astigmatisms induced in accommodation, and the presence of embryological lens sutures (reviewed by Campbell et al., 1966). Further studies, however, showed that the optical factors cannot significantly account for these preferred directions of resolution. Experiments were carried out by Campbell and Kulikowski (1966) to establish whether some channels in the visual system were sensitive to the angle of orientation of contours. They found that the angular selectivity for the 45° presentation was 25% worse than that for the vertical orientation (bandwidth at half amplitude of 30° at 45° orientation compared to 25° for vertical and horizontal gratings.

The physiological data show a wide range of tuning properties of cortical cells. Some studies have found no significant difference in distribution of cells tuned to the vertical and horizontal orientations as compared with cells responding to the oblique orientations (Rose and Blakemore, 1974; Poggio et al., 1977), whereas some have found a very small, but statistically significant difference in their distributions in the fovea, but not in the peripheral region in monkeys (Mansfield, 1974; De Valois et al., 1982a).

De Valois et al. (1982a) also found that cells tuned to high spatial frequencies were slightly more often tuned to the vertical or horizontal orientations. In spite of the sparse and not very convincing physiological data on the oblique effect, it must be emphasised that the psychophysical data also indicate a very small effect.

1.11.2 Physiological Studies

Hubel and Wiesel (1959, 1962, 1968) discovered that many cortical cells are selective for orientation. They found that a large number of cells in the striate cortex of the cat and monkey responded to a line target of a certain orientation, and that the optimum orientation varied from one cell to another.

Subsequent studies have confirmed the presence of orientationally selective cells, both in the striate and extrastriate areas of many species (Campbell et al., 1968, 1969; Henry et al., 1973; Rose and Blakemore, 1974; Mansfield, 1974; Finlay et al., 1976; Schiller et al., 1976; Poggio et al., 1977; Zeki, 1971, 1980; De Valois et al. 1982a,b; Albright, 1984).

The anatomical and physiological basis for the formation of a directionally selective cell is uncertain (De Valois et al., 1982a). Nevertheless, it may be hypothesised that they are formed due to the convergence and summation of the geniculate cells

with different receptive fields onto a simple cortical cell (Hubel and Wiesel, 1962). This organisation should give rise to the minimum response at 90° to the optimum orientation of a single cell. On the other hand, recordings show that for some narrowly tuned cells the minimum response may occur at orientations, only 30° from the optimum orientation. In addition, for some of the cells, at the minimum response, the discharge rate is less than the base discharge rate. To explain such findings, alternative explanations have been put forward which involve the inhibitory interactions amongst cortical neurones (Benvento et al., 1972; Albright, 1984).

Many investigators have carried out quantitative studies of the distribution, bandwidth, and variation in the functional characteristics of these cells.

Hubel and Wiesel (1968) reported that the orientation could be specified to within 5 - 10° in monkey cortical cells compared to 10 - 15° in cat, and concluded that the orientation selectivity was more prominent in monkey than in cat. Comparison of more recent observations, however, suggests that the striate cortical cells in cat exhibit a narrower orientation tuning than those in monkey (Rose and Blakemore, 1974; Schiller et al., 1976; De Valois, 1982a).

The bandwidth of an orientation selective cell is determined by the angular rotation of a test target between positions on either side of the maximum response where the response amplitude falls to half of that obtained at the optimum orientation. Poggio et al. (1977) measured an average bandwidth of 50° for the orientation specific cortical cells in monkey. Data obtained by Mansfield (1974) indicate a median bandwidth of 66° and 97° for simple and complex cells respectively.

De Valois et al. (1982a), using line and grating targets obtained quantitative data on the orientation tuning of cells in macaque monkey striate cortex. They found a wide range of orientation bandwidths among cells in a given cortical region. These ranged from 8° for the most narrowly tuned cells up to more than 100° for the most broadly tuned. The median bandwidths for simple and complex cells were estimated to be 40° and 44° respectively.

Most investigators have found that simple cells are more narrowly tuned for orientation than complex cells.

The followings may be considered as the possible contributing factors to the large variability in all bandwidth measurements:

1. Random variability with no significance to be attached to cells of differing selectivity.
2. Cells with different orientation selectivity indicate various stages of production of narrowly tuned cells.

3. More broadly tuned cells provide the inhibitory input necessary to produce the fine tuning of other cells.

4. The range of orientation bandwidths reflects the differing functional roles of cells in different cortical layers, ie., some cells may provide feedback to other parts of the visual pathways such as LGN and colliculus.

The random variability is not an attractive possibility since it undermines the efficiency in the pathways. As far as the multiple stages of the formation of fine tuned cells are concerned, the convergence theory postulates the existence of a single synapse. The remaining contributing factors remain as possible sources of the variability.

The orientation selectivity in V5 neurones of the owl monkey was reported by Zeki (1980). Albright (1984) investigated the effect of orientation of stationary flashed stimuli on the cells in MT and V1 of macaque monkey. He found that many MT neurones were orientation selective and that the mean orientation tuning bandwidth in V1 was significantly narrower than that in MT, but the responses were of a similar magnitude.

1.12 Direction tuning

1.12.1 Psychophysical Studies

The orientational selectivity described above plays an important role in the detection of form and structure in static images. For moving images, however, a single motion detector suffers from limitations when extracting the movement information. One limitation concerning the ambiguity of the direction of motion is termed the aperture problem, and is described below.

The Aperture Problem

If a localised receptive field detecting the movement of a contour in a pattern, or alternatively, a one dimensional pattern such as an extended grating passing over the receptive field of a neurone is considered, in both cases, the velocity of the contour may be defined as the velocity vector orthogonal to the orientation of the contour (V_L). This local velocity vector is insufficient to specify the true direction of the moving contour, since an infinite number of velocities , along directions $\pm 90°$ with respect to the orthogonal to the contour, may give rise to V_L (see figure 1.24a).

The velocity space is the representation of velocities in polar co-ordinates, starting

at the origin. The length of the vector corresponds to the speed of motion and the angle to direction. Therefore, the locus of motion of the one dimensional stimulus maps to a line in velocity space. This line is perpendicular to the primary vector and represents the motion normal to the one dimensional pattern (Adelson and Movshon, 1982). Although an ambiguous direction of motion is obtained from the response of a single motion detector, it has the advantage of restricting the solution of the motion to a single line in the velocity space (figure 1.24b).

The aperture problem for a moving two dimensional pattern may then be solved by evaluating the velocity domain locus of individual one dimensional components, as long as the components are not in parallel. An example of this method is shown in figure 1.25. As the diamond pattern is moved to the right, the upper motion detector detects a movement upwards and towards the right whereas the lower motion detector detects a movement downwards and towards the right. In the velocity space, the two edges set up two lines of possible motion. Only one single point in the velocity space is consistent with both motions, (their intersection) which in this case corresponds to a pure rightward motion. This method is termed the "*intersection of constraints*" and was described by Adelson and Movshon (1982). It provides a solution to the problem of ambiguous direction of motion for a complex pattern, having two orientations, using a pair of orientation selective speed detectors and resulting in the reconstruction of the real direction and speed.

The combination of two sinusoidal gratings, having non-parallel orientation, results in the formation of a simple two dimensional pattern called a plaid.

When the gratings are moved in a direction perpendicular to their orientation, the perceived direction of movement of the pattern as a whole is different than the direction of the individual one dimensional components. Psychophysical measurements have shown that the perceived direction of motion for plaids are in quantitative accordance with the results obtained using the intersection of constraints method (Adelson and Movshon, 1982). See figure 1.26 for an illustration.

The same principle can be applied to the movement of dots in a random dot pattern as shown in figure 1.27. The locus of motion in a random dot pattern with dots moving at a constant speed but in a random direction, lies on a circle (figure 1.27a). Alternatively, for a random dot pattern with restricted movement direction the overall velocity and direction can also be calculated using the intersection of constraints method (figure 1.27b).

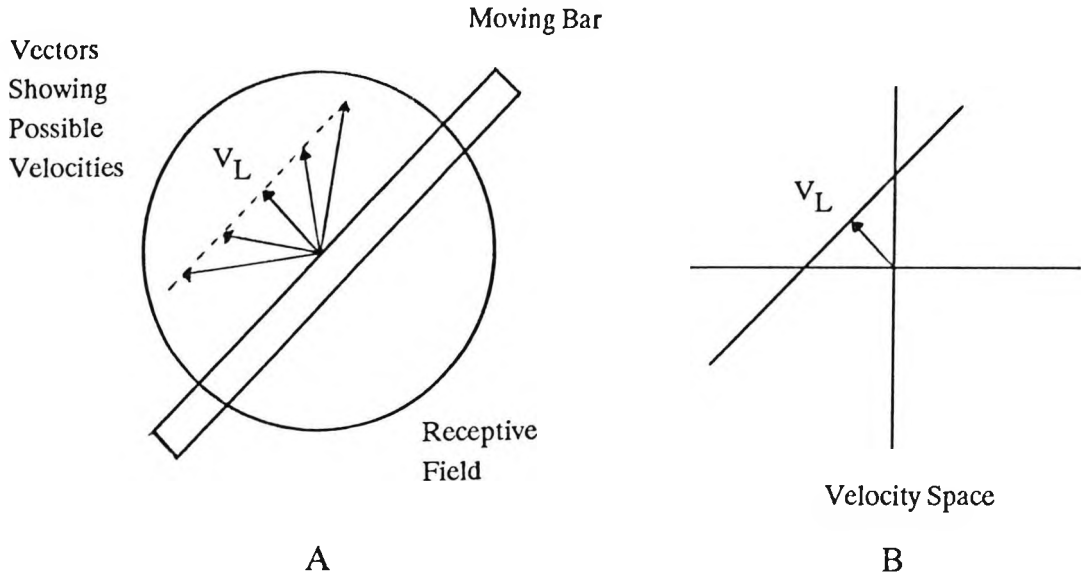


Figure 1.24 : A, a range of velocities along the directions ±90° to the orthogonal could be detected as having a velocity V_L; B, movement of a one dimensional spatial component (bar) represented in polar velocity space (see text).

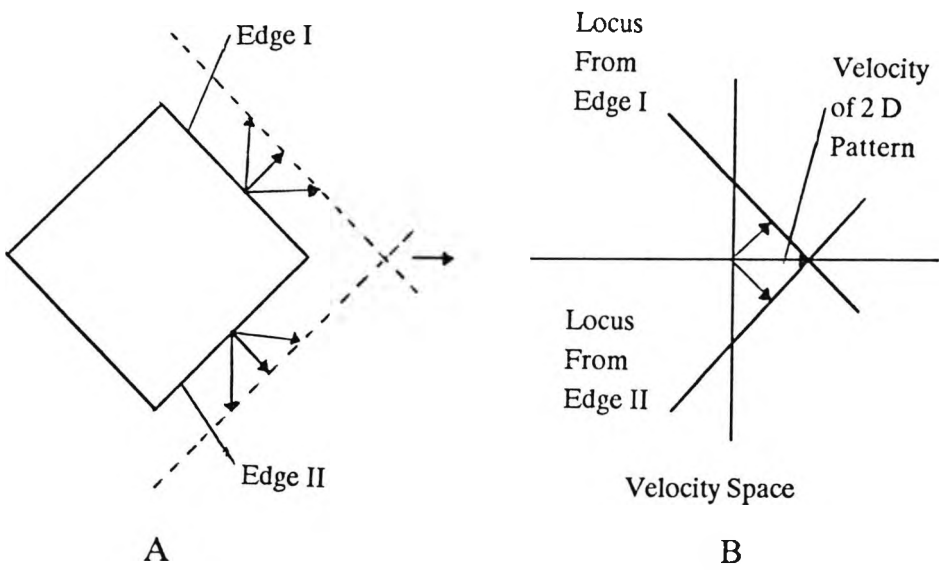


Figure 1.25 : A, movement of edges detected by velocity detector units; B, locus of the individual components and the motion of the pattern in velocity space.

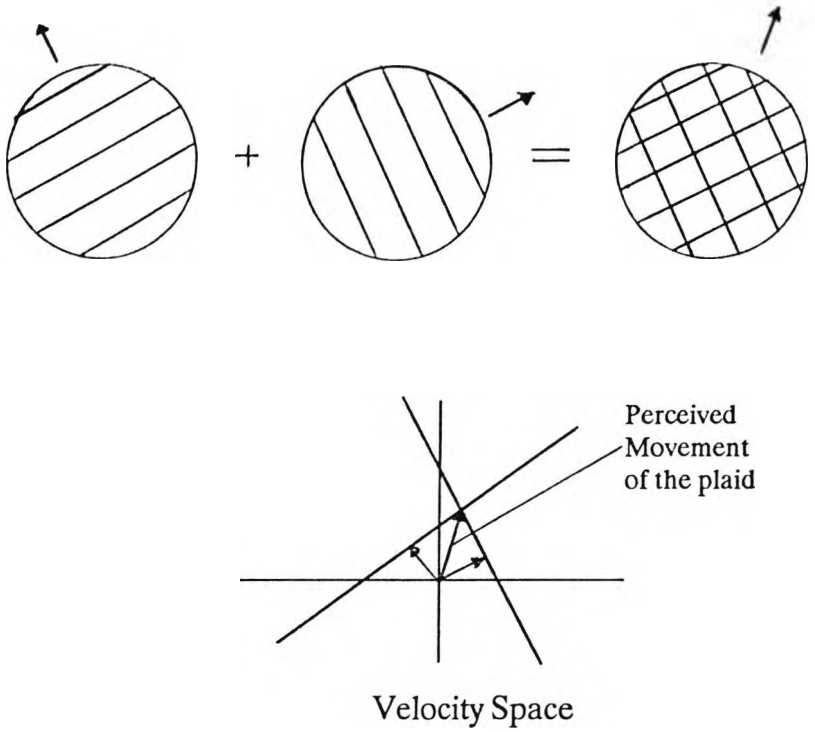


Figure 1.26 : The perceived direction of a plaid can be calculated from the motion of its components in the velocity space

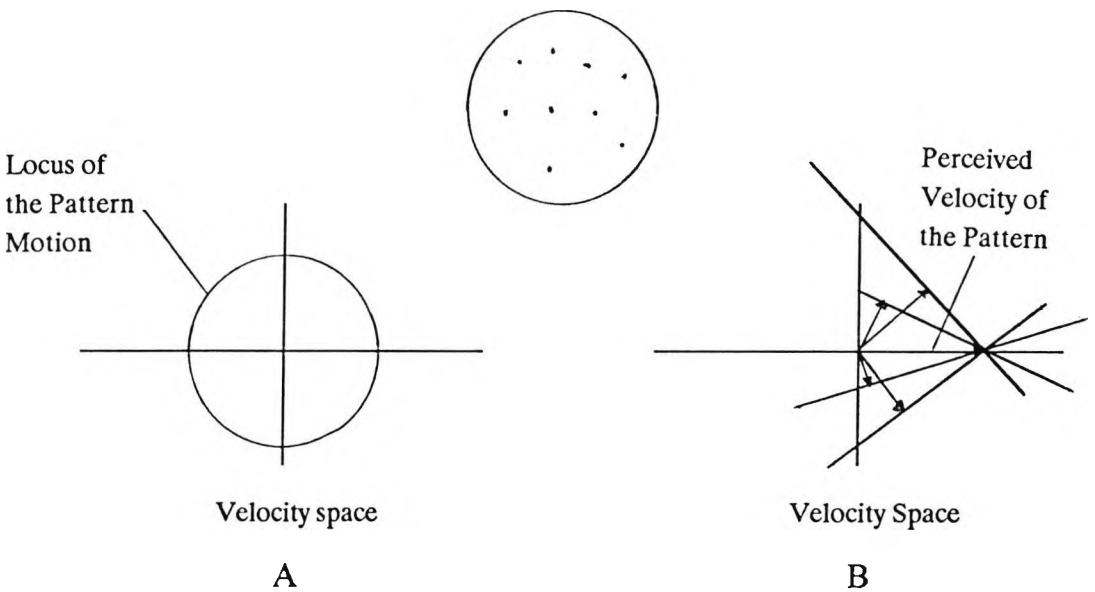


Figure 1.27 : A, for a random dot pattern, when dots move with the same speed but in a random direction, the locus lies on a circle; B, for a random dot with no leftward motion component of the dots, the overall motion lies on the right in the velocity space.

Parameters Affecting the Motion of a Simple Two Dimensional Pattern

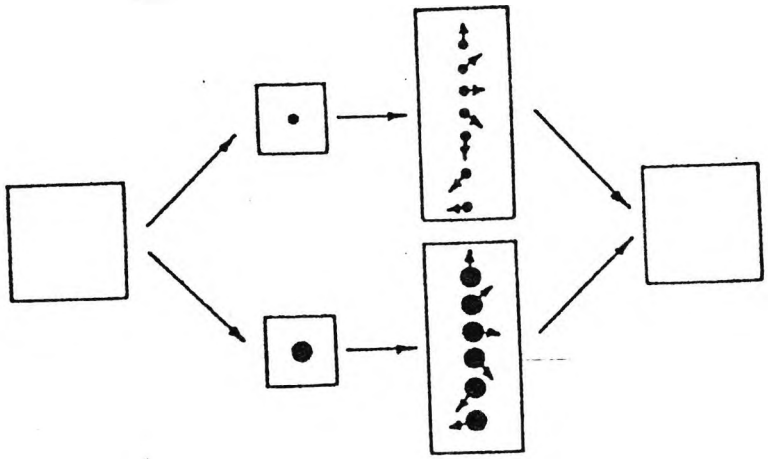
When two suprathreshold moving gratings are superimposed at an angle, the coherent movement of a two dimensional pattern is perceived rather than the perception of two gratings passing over one another. Conditions for the perception of the coherent movements of a plaid for various stimulus parameters were investigated by Adelson and Movshon (1982) and Movshon et al. (1985). Some of their experimental results have been discussed below, since they seem to reveal some important spatial aspects of the visual system.

In the presence of a suprathreshold grating of 1.5 c/deg at 0.3 contrast, moving with a speed of 3 deg/s, a second grating of 2.0 c/deg was superimposed at an angle of 120° moving with similar speed. The probability of detection of the second grating as well as the coherence of the plaid were evaluated at various contrast levels. It was found that for a range of contrast levels both gratings were visible but failed to cohere. The coherence threshold was then defined as 50% probability of coherence, and was measured for a range of spatial frequencies at various orientations and directions. The results showed that the coherence threshold rises as the angle between the gratings is made larger and as their speed and spatial frequency increases. Under ideal conditions, (e.g., identical spatial frequencies, low speed and modest angle), the coherence threshold approaches detection threshold. Based upon the above observation, models can be constructed for the coherence phenomena (Movshon et al., 1985).

Models for the Perception of Coherence

The fact that the optimum coherence is achieved when the gratings are of similar spatial frequencies suggests that bandpass filtering is being performed on the visual information before extracting the coherence perception. The bandpass filtering can be achieved by two possible methods, either using circularly symmetric bandpass filters resembling the function of some retinal ganglion cells, or by a set of spatially tuned, orientationally selective filters with properties similar to those of some simple cortical cells. To implement these two possible methods, two distinct models have been put forward, as shown schematically in figure 1.28 (Movshon et al., 1985).

Model 1



Model 2

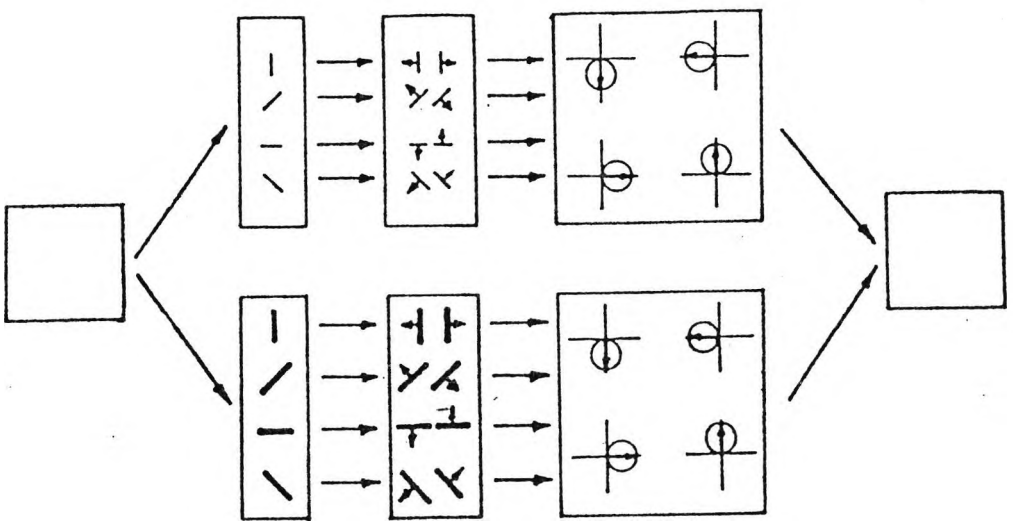


Figure 1.28: two models of mechanisms underlying perceptual coherence. Model 1, the concentric symmetric spatial filters with differing bandpass is shown. Dots with arrows represent the direction of motion designators using either cross-correlation or tracking. This analysis proceeds in parallel in several spatial frequency bands, two of which are shown in the above schematic diagram; Model 2, the first stage of the image analyser contains a series of orientational filters tuned to a constant spatial frequency and differing in orientation. Bars with arrows are the first stage of the motion analyser providing information on motion normal to their orientation. The output of these one directional analysers are combined in the second stage, that is, the 2D motion analyser, in a manner possibly the same as the intersection of constraint method to give the perception of pattern motion. The analysis described in the second model is carried out at a large number of spatial frequencies, two of which are shown above (from Movshon et al., 1985).

Model 1: The visual information is passed through a set of bandpass non-orientational spatial filters, tuned at various spatial frequencies. The output of each filter is then passed to a motion analysing system, which assigns a motion direction by tracking the local peaks or by cross-correlating a series of temporally delayed filter outputs. The output from the direction analysers, tuned to various spatial frequencies, is then compared to give the coherence percept.
In the case of a plaid consisting of similar spatial frequencies, where the bars move over each other, strong peaks are formed at the output of the spatial frequency filter, giving rise to unambiguous detection of the direction of motion by the feature tracker or cross-correlators. For a plaid consisting of different spatial frequencies, each spatial frequency filter detects a single grating, resulting in perception of two gratings moving over each other at a direction perpendicular to their orientation.

Model 2: The visual information is passed through a set of orientationally selective spatial filters. At each spatial frequency the output of an orientational filter is passed to a motion analyser which provides information on the motion at the direction perpendicular to the filter orientation. Then the motion direction of the two dimensional pattern can be obtained from the velocities of its orientational components by applying the intersection of constraints as explained earlier, using the combination of signals from several appropriately distributed one directional detectors. In a similar way to the previous model, the analysis is carried out in several spatial frequency bands.
The major difference between the two models is the fact that the first assumes that the visual system tracks the peaks of a spatially analysed visual information, whereas the second starts by extracting the motion at various orientations. The psychophysical and physiological data, some of which are outlined in the next section, seem to support the orientationally selective model.

Effect of One Dimensional Noise on Coherence
One dimensional noise, consisting of parallel stripes of various widths, can be superimposed on a plaid and will mask the component gratings of the pattern. By measuring the coherence threshold for a wide range of orientations of one dimensional patterns, the effect of masking can be investigated. If the coherence involves non-orientated filtering, then the coherence threshold should not be affected. However, if the coherence depends on the output of oriented analysers, then the masking should elevate the coherence threshold when the orientation of the one dimensional noise is parallel to one of the component gratings of the plaid.

Movshon et al., (1985) demonstrated an orientation dependence on masking, such that, when the one dimensional noise was oriented within 20° of the orientation of any component gratings, the coherence threshold was elevated. Outside this 20° range, no effect on coherence was observed. They thus concluded that the mechanisms responsible for the phenomenal coherence of a two dimensional pattern belong to a pathway which pass through a stage containing an orientation selective spatial analyser, as described by the second model.

Direction Specific Mechanisms

The first stage of the motion analyser in the second model for detection of coherence described above, provides information on the velocity of the one dimensional components of a complex pattern. It has been shown that many cells in the mammalian visual brain provide information about a target's direction of movement (Hubel and Wiesel, 1962; Wurtz, 1969). The directionally selective units have an important role in extracting motion information at early stages of processing (Marr and Ullman, 1981). These direction specific cells fire strongly when a properly orientated stimulus drifts in one direction and fires less strongly or not at all, when the same stimulus moves through the field in the opposite direction. Selective adaptation is a basic method for analysing the response of a visual mechanism. The response characteristics of a mechanism sensitive to an adapting target can be investigated by comparing sensitivity across some stimulus dimension, before and after the adaptation. This method can also be applied to movement processors to investigate the properties of the direction specific mechanisms, since, should our perception of moving objects depend upon the action of directionally sensitive processes, prolonged exposure to motion in one direction would diminish the responsivity of whatever processes were sensitive to that direction of motion (Sekuler et al., 1968).

Sekuler and Ganz (1963) applied the selective adaptation method by presenting adapting gratings of vertical bars moving either to the left or right through the visual field. The luminance thresholds for similar gratings were then measured. They found that, when the test and the adapting gratings moved in the same direction, thresholds were about twice as high as when they moved in the opposite directions, indicating that the adapting grating had a strong direction specific effect on the threshold. This adaptation is also orientation specific such that an oblique drifting grating has little or no effect on the threshold of vertical gratings (Sharpe and Tolhurst, 1973).

A special case of a plaid is a counterphase grating and is formed when two vertical

gratings of similar spatial frequencies are superimposed and moved in opposite directions with similar speeds. A counterphase grating is perceived as a stationary pattern in the absence of eye movement saccades. Using the subthreshold summation procedure explained earlier, it has been shown that at threshold, the directional movements of the component gratings are detected *independently* and that there is no interaction between the direction specific mechanisms at threshold (Levinson and Sekuler, 1974). Adaptation to a suprathreshold counterphase gratings on the other hand, elevates the detection threshold for both right and left moving gratings, but this elevation effect is far less than that which would have been obtained had the adapting grating been a single grating moving in the same direction as the test grating. This suggests that at suprathreshold levels, the direction specific mechanisms interact with each other, and this interaction is in the form of inhibition (Sekuler et al., 1968; Sekuler and Levinson, 1974). The effect of interactions between various mechanisms at suprathreshold is discussed later (see section 4.1).

Effect of Contrast on Direction Specific Mechanisms

Pantle and Sekuler (1969) measured direction specific adaptation as a function of the contrast of the adapting grating, and estimated the contrast responses of motion and orientation sensitive mechanisms. They found that the direction specific mechanisms saturate at relatively low contrast levels whereas the orientation sensitive mechanisms respond linearly to a much larger range of contrast adaptation.

If it is assumed that the stages for orientation analysis and for direction analysis are arranged in series, as assumed in the second model for extracting the motion of a two dimensional complex pattern. Then these observations strengthen the view that the orientational analysis must precede the directional analysis.

Effect of Adaptation on the Perception of Coherence

The perceived direction of motion of a plaid is different to the direction of movement of its component gratings, as it has been illustrated earlier. In the model described above, the detection of pattern motion takes place in two distinct stages. The first stage deals with the movement of one dimensional components and has been explored by the effect of adaptation on gratings. The second stage is a two dimensional pattern movement analyser which gives rise to the perceptual coherence of a two dimensional pattern. If these two stages are distinct then it may be possible to affect these stages differentially in direction specific adaptation

experiments, e.g., component motion, rather than pattern motion, is the factor which affects the coherence phenomena (Adelson and Movshon, 1982).
The results of direction specific adaptation experiments have showed that, as far as the detectability of one and two dimensional patterns is concerned, the detection threshold for a plaid or grating pattern was strongly elevated in a directionally selective manner following adaptation to a similar pattern, but was only slightly changed after adaptation to a different pattern.
Adaptation could also alter the perception of coherent motion. Similar experiments show that the coherence threshold of a plaid is elevated following adaptation to motion in the same direction as the movement of the plaid, whereas the coherence threshold for plaids moving in the opposite direction is not elevated (Movshon et al., 1985).
These directional adaptation experiments suggest the existence of two distinct stages where the adapting effect of a moving pattern may be expressed.

Comments on the Model for Extracting Motion of Two Dimensional Patterns
The model outlined earlier, to encode the motion of a complex, two dimensional pattern, consisted of orientationally tuned filters and a two stage motion analyser. This model appears to be consistent with the results obtained from the direction specific adaptation experiments, coherence threshold measurement and the effect of the contrast of the adapting stimuli. Inherent in this model is the dependence of the final perception of the movement on the output of a two dimensional motion analyser. A moving grating is a strong stimulus input for both a one and two dimensional motion analyser, however, the perception of coherence of a plaid and the motion of its components are mutually exclusive. Consequently, in some parts of the second stage of the motion analyser, suppression of the component motion takes place. At the same time, when the visual stimulus is a single grating, its motion is always detected by the direction specific mechanism when the contrast is higher than its detection threshold. Thus, the model explained is relatively simplified since it does not show the suppression and inhibitory interactions between motion channels. Nevertheless, its overall configuration is in close agreement with many experimental observations.

1.12.2 Physiological studies

Hubel and Wiesel (1962) first reported that some cortical cells respond equally well to stimuli at a given orientation moving in either direction whereas others respond

only to stimuli moving in one particular direction.

Barlow and Hill (1963) suggested that a truly directionally selective cell is essentially invariant over a wide range of contrasts and most critically, their selectivity remained the same for stimuli having reversed contrast. This definition is not, however, complete since the discharge rate of many directionally selective cells in the mammalian striate cortex can be influenced by contrast, temporal and spatial frequencies as well as velocity.

Barlow and Levick (1965) defined the term "*directionally selective unit*" as a unit which gives a vigorous discharge of impulses when a stimulus object is moved through its receptive field in one direction (called the preferred direction), whereas motion in the reverse direction (called the null direction) evokes little or no response. They showed that many ganglion cells in the rabbit's retina were directionally selective and they attributed this property to a subset of bipolar cells that responded to the corresponding sequence of excitation of two neighbouring retinal regions with which they connect. They also suggested that this sequence discrimination was brought about by a laterally connecting inhibitory element from one of these regions, possibly mediated by horizontal cells.

Single cell recordings have been carried out in a large number of studies in order to investigate the directional selectivity of cortical cells in cats and primates (Zeki, 1971; Henry et al., 1974; Hammond and MacKay, 1975; De Valois et al., 1982a; Albright, 1984; Newsome et al., 1986; Mikami, 1991). A wide range of stimuli have been used including spots, edges, bars, gratings and random dots. Spots have proved less effective as a stimulus in eliciting directional tuning in many simple and complex cortical cells (Henry et al., 1974; Hammond, 1978).

Albright (1984) observed that the tuning for a moving spot was, on the average, significantly broader than that for either a moving bar or a random dot field. Furthermore, he found very little correlation between tuning for the moving spot and that for either of the stimulus types.

Hammond and MacKay's (1975) recordings from the simple and complex cells of area 17 in cat showed that directional selectivity was a common feature of cortical cells, for both luminance-defined (gratings) and kinetically defined (random dot) stimuli. Further investigations, using line targets moving in a direction perpendicular to their orientation and random textures, showed that the tuning functions were dependent on the type of the stimuli used in many cells. In general, isotropic random dots had a broader directional tuning function than lines.

De Valois et al. (1982a,b) studied the distribution of direction selective cells in macaque cortex. Having recorded the responses of a large number of V1 cells (222

cells), they found that 29% were directionally tuned. In addition from this sample of cells the breakdown of the population in to simple / complex and foveal / parafoveal categories revealed no differences in directionality as a function of those classifications. They also concluded that directionally selective cells tend to be more narrowly tuned for orientation compared to non-directional units.

In the previous section the psychophysical approach to movement of a complex two dimensional pattern in terms of motion of its components was discussed. The underlying neuronal representation of the coherence may also be investigated in relation to the directional tuning of cortical cells (Maunsell and van Essen, 1983a; Movshon et al., 1985; Maunsell and Newsome, 1987).

If motion sensitive neurones in V1 respond only to the oriented components of a plaid stimulus, their discharges will encode the motion of the component gratings rather than the motion of the complex pattern. The motion of the pattern, however, may be extracted at higher levels of processing.

Movshon et al. (1985) recorded the responses of direction selective neurones in cat and monkey cortex to a plaid consisting of two drifting sinusoidal gratings. They found that while neurones in V1 encode the motion of the oriented components, a population of neurones in MT encode the unitary motion of the entire pattern. The responses of each type of neurone are illustrated in figure 1.29. Figure 1.29a is a polar plot of a direction tuning curve obtained from a V1 neurone responding to a narrow range of directions down and to the right. Figure 1.29b illustrates the responses of the same neurone to the plaid pattern as it drifted through the receptive field in various directions. If the neurones were responsive to the unitary motion of the whole pattern, the tuning curve would have been similar to that of figure 1.29a. If however, the neurone responded only to the individual motions of the components, the neurone should yield a bimodal tuning curve, responding first when the motion of the plaid is such that one component grating traverses the receptive field in the preferred direction and responding again when the motion of the other component grating is in the preferred direction. The responses illustrated in figure 1.29b show that the neurone responded to the motion of the components and yielded no response when the unitary motion of the plaid was in the preferred direction.

Their recordings show that about 20% of the neurones in MT area responded to the unitary motion of the plaid as shown in figure 1.29c. Figure 1.29d the dotted bimodal response curve indicates the predicted response pattern for a component direction selective neurone, but the data they obtained (solid curve) shows that this neurone responded optimally when the unitary motion of the plaid was in the

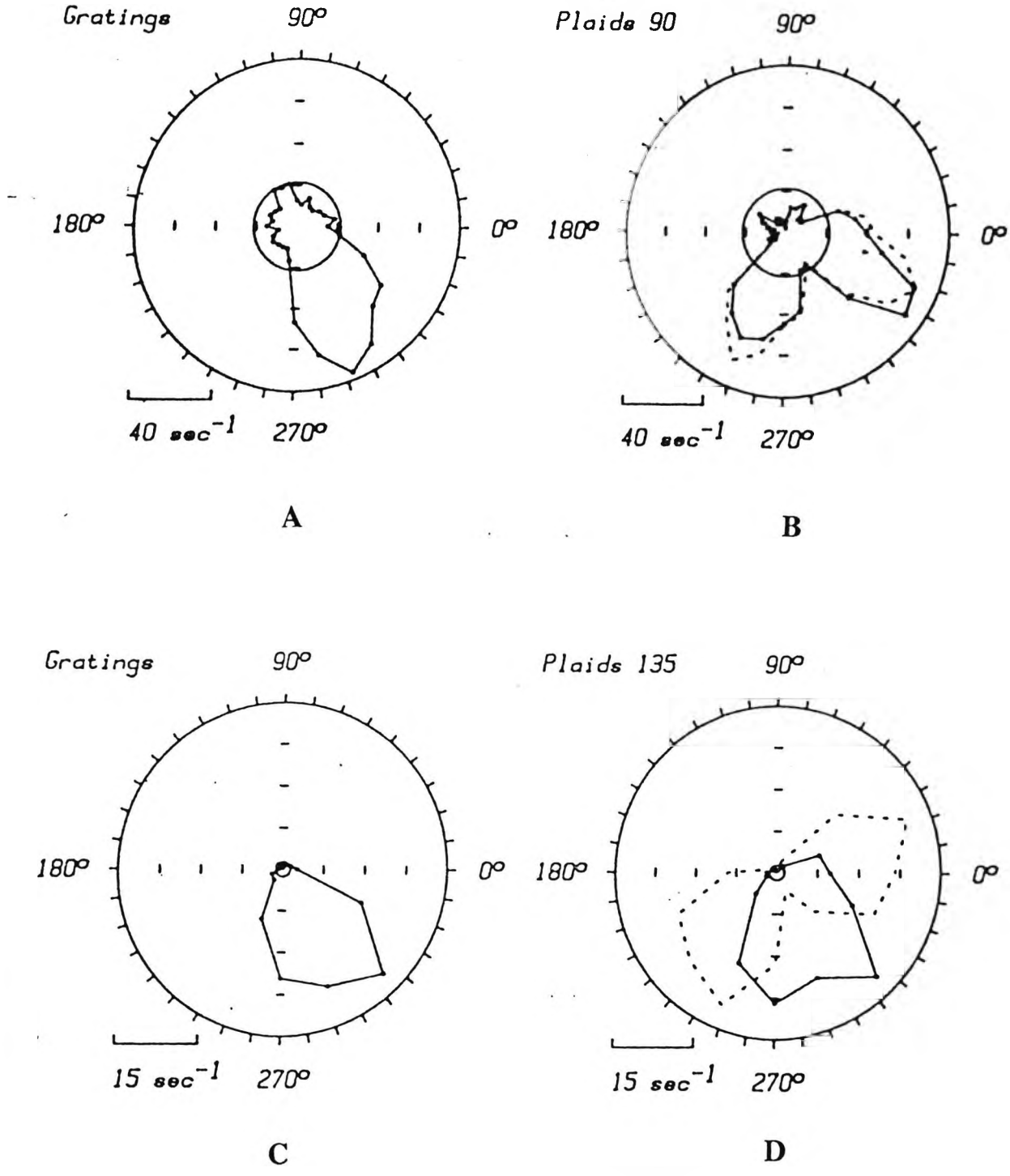


Figure 1.29: Direction tuning curves for a component direction selective neurone in cat striate cortex in response to a single sinusoidal grating (A) and a sinusoidal plaid (B). This neurone responded to the motion of the components of the plaid rather than to the unitary motion of the plaid itself. This response pattern is typical of V1 neurones in cat and monkey. Direction tuning curves for a pattern direction selective neurone in macaque MT in response to a single grating and a plaid are shown in C and D respectively. This neurone responded to the unitary motion of the plaid pattern. The dashed lines in B and D indicate predicted tuning curves for a component direction selective response, assuming that the neurones respond to each component of the plaid in the same way that they respond to the single grating (A & B) (from Maunsell and Newsome, 1987).

neurone's preferred direction. Thus pattern direction selective neurones in MT encode information about the motion of complex patterns that is not signalled by single neurones in V1.
Several experimenters have reported the existence of MT neurones whose preferred orientation for stationary bars is parallel to the preferred direction of motion. It might therefore be possible to explain their behaviour in terms of the pattern direction selectivity (Baker et al., 1981; Maunsell and van Essen, 1983a; Albright, 1984).

1.13 Speed Tuning

1.13.1 Psychophysical Studies

Motion mechanisms can discriminate both direction and speed changes when viewing moving visual stimuli. The selective response to a narrow range of motion direction, was discussed earlier (see section 1.12.1). Direction specific mechanisms may discriminate the speed of a stimulus in two distinct manners. Either all of the mechanisms sensitive to motion along a specific direction respond to a range of speeds, ie., they have essentially the same function relating their response rate to velocity; or they differ in their responses to velocity with subsets differentially tuned to stimulus speed (Sekuler, 1975). In the former hypothesis, speed is coded by the integrated response within one direction analyser, whereas in the latter, the coding is carried out by distinguishing the maximally responsive subset of the mechanisms. Pantle and Sekuler (1968) and Tolhurst (1973) used direction specific adaptation to study the above hypothesis. They adapted subjects to gratings moving at various velocities (0.5 to 4 °/s), and measured the direction specific adaptation at three distinct speeds (2, 5 and 9 °/s). They found three distinct speed profiles about each of the three test speeds. These results suggest that there are several channels responsive to somewhat different but overlapping ranges of speeds, since, if there were only one general mechanism for motion detection the adaptation functions measured with any test velocity would have the same shape and peak response. In addition, when a test and adaptation pattern had similar velocities, direction specific adaptation increased linearly as a function of adaptation spatial frequency. Therefore, the direction specific adaptation varied as a function of both the temporal and spatial frequencies since the two parameters covary.
The variations in direction specific adaptation has also been measured for a range of adapting velocities while the spatial content of the adapting field was altered to

achieve a constant temporal frequency (Pantle and Sekuler, 1968, 1969). It has been established that the stimulus velocity itself has some control over direction specific adaptation and the adapting effects of a moving grating may be decomposed into an effect due to its velocity and an effect due to its temporal frequency. The contrast threshold measurements on moving gratings show that the sensitivity is best for a constant temporal frequency of approximately 10Hz (Breitmeyer, 1973; Burr and Ross, 1982). To achieve the constant temporal frequency, the velocity and spatial frequency must be inversely varied. The reciprocity between spatial frequency and velocity implies that the velocity tuning and the preferred spatial frequency of motion mechanisms are related. This view is further strengthened by experiments which show that the visibility of fast moving test gratings are degraded by adaptation to stationary gratings of low spatial frequencies and the visibility of slowly moving test gratings are maximally degraded by adaptation to a stationary grating of high spatial frequency (Pantle, 1970). Conversely, adaptation to a high velocity target increased the threshold to the highest level for low spatial frequency stationary test gratings and the adaptation to low velocity targets increased the threshold to the highest level for high spatial frequency stationary test gratings (Breitmeyer, 1973).

Several computational theories of motion perception have given detailed and explicit account of direction discrimination (Marr and Ullman, 1981; Santen and Sperling, 1984), but have not attempted to provide a comprehensive theory of the velocity coding. Adelson and Bergen (1985) proposed a system whereby the velocity is derived from a comparison of activity in sensors responding to the opposite directions. A two stage model of velocity sensor was proposed by Watson and Ahumada (1985), in which, the output of a set of scalar motion sensors is passed through temporal frequency meters. The stimulus velocity is then derived from the frequency output of the direction sensor whose frequency output is the highest. The computational models for the determination of velocity are constrained largely by the growing psychophysical data on the detection of moving images, and perceptual interactions and differences between moving stimuli. The discriminability of moving stimuli has proved valuable in the study of velocity selective mechanisms. An introduction to the discrimination thresholds and the properties of underlying circuitry is given below.

Discrimination Threshold and Velocity Tuning

Quantitative analysis of the velocity discrimination is typically carried out by measurement of the Weber fraction (dv/V), which gives the proportional change in velocity that can be detected at some threshold criterion.

McKee (1981) introduced a paradigm to measure the precision of velocity discrimination for successively presented moving line targets. The observer was given a large block of trials containing a small range of speeds and was required to decide whether a given stimulus was faster or slower than the mean for that block of trials. The Weber fractions for the speed range (3 to 70 °/s) were essentially constant and were about 5%. The same results were obtained in periphery, but the range over which the low velocities had a Weber fraction of greater than 5% increased in accordance with that expected from increases in the spatial grain of the periphery as estimated from visual acuity measurements (McKee and Nakayama, 1984).

Consistent and similar Weber fractions were also reported in studies of Nakayama (1981), van Doorn and Koendrink (1983) and Orban et al. (1984).

The Weber fraction for discrimination of velocity direction has been found to be approximately 1° (Levinson and Sekuler, 1976). Theoretically it is possible to resolve the velocity of an image into its horizontal and vertical components in a velocity space diagram. Given the Weber fractions for the velocity direction and magnitude, it is then possible to generate a set of hypothetical points representing the discrimination boundaries at any given velocity. These points form discrimination ellipses in cartesian velocity space as shown in figure 1.30.

Is Velocity a Primary Dimension of Sensory Coding?

Do observers respond to the target velocity or to the target temporal frequency and contrast? If the velocity discrimination were not affected by changes in a stimulus dimension, then, either that stimulus dimension is not a critical component of the velocity code, or its perturbing effects can be eliminated by neural operations within the velocity network.

It is known that the velocity discrimination thresholds are not affected by random changes of the stimulus contrast (McKee et al., 1986). Swift and Panish (1983) found that the perceived velocity is very slightly affected with changes in spatial frequency. In the studies of McKee et al. (1986), a subject was asked to detect small changes in target velocity while changes in spatial frequency of the target were introduced. It was found that velocity discrimination was not affected.

If an observer can make a precise judgement of velocity despite the randomisation

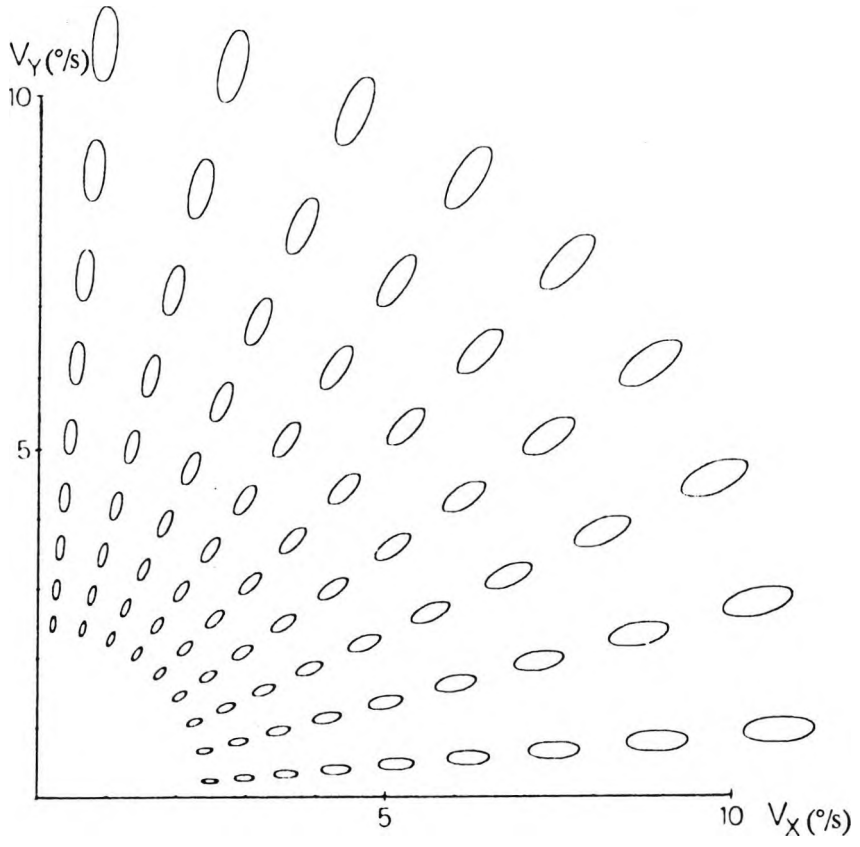


Figure 1.30: estimated discriminability ellipses for motion. One quadrant of a hypothetical four quadrant "velocity space" is presented where Vx and Vy designate horizontal and vertical velocities, respectively (from Nakayama, 1985).

of temporal frequency, then it is likely that the human visual system responds to the velocity and not to the temporal frequency. The Weber fraction for a random mixture of spatial frequencies presented for a relatively longer duration is slightly worse than those for shorter stimulus durations in naive subjects. The duration effect on velocity discrimination is attributed to the effect of temporal frequency on velocity and is diminished with feedback and practice (McKee et al., 1986).
Models put forward to account for velocity discrimination are based on multiple mechanisms each tuned to a different, but overlapping velocity range (Thompson, 1983, 1984; Adelson and Bergen, 1985). In these models the contrast effects can be eliminated by an "*opponent*" stage which uses the ratio of the signals emerging from the separate tuned mechanisms to estimate the velocity. The velocity tuning is given by the ratio of the optimal temporal frequency to the optimal spatial frequency. However, there are an infinite number of spatial and temporal frequency combinations that could give rise to the same velocity. In addition, if the perceived velocity depends on the ratio of the integrated stimulus energy detected by two or more overlapping mechanisms, then this ratio is unchanged when there is an alteration in the spatial and temporal properties to give a different velocity or if the velocity remains unchanged but a new combination of the spatial and temporal frequencies is used. Human observers are never confused by these two events at short stimulus durations. The discrimination between these two events may be attributed to a stationary spatial frequency detector whose response declines monotonically with increasing temporal frequency (Thompson, 1984; Adelson and Bergen, 1985). If such detectors existed, then one would expect the temporal discrimination to match the speed discrimination, since equally precise information regarding the temporal frequency can be obtained. The temporal discrimination, however, is found to be worse than the speed discrimination (McKee et al., 1986).
An alternative model is where each velocity mechanism is served by multiple overlapping subunits with different spatial and temporal frequency tunings but the same velocity tuning. All signals from one velocity group are pooled and compared to the signals emerging from other adjacent velocity groups. The velocity discrimination would then depend on the ratio of the pooled signals. The information about the temporal frequency is sensed indirectly via the underlying velocity mechanisms, and so, the temporal frequency discrimination would be more difficult than judging the changes in velocity (McKee et al., 1986).
In summary, the experimental results outlined above indicate that velocity is a primary dimension of sensory coding and is unaffected by variations in contrast, temporal and spatial frequencies.

1.13.2 Physiological Studies

Movshon (1975) investigated the velocity tuning in simple and complex cells in cat striate cortex and found that the simple cells preferred lower velocities (mean 2.2°/s) than the complex cells (mean 18.8°/s).
Orban et al. (1981) studied the velocity sensitivity of cells in cortical area 17 and 18 of cat for a range of eccentricities. They measured the maximum firing rate of a cell as function of velocity to obtain a velocity response curve. The response curves could be divided into four separate cell-type categories: velocity low-pass, velocity high-pass, velocity tuned and velocity broadband cells, examples of which are shown in figure 1.31. Their major findings were as follows:

1. The largest proportion of velocity tuned cells occurred in the subregion of area 18 which subserves central vision. The equivalent part of LGN, area 17 and other parts of area 18 have a smaller proportion of velocity tuned cells.
2. The velocity tuned cells as a group contain the largest proportion of direction selective cells.
3. Although the overall number of velocity tuned cells decreases as a function of eccentricity, the number of velocity tuned cells in the slow, medium and fast classes decrease at different rates. In those cortical regions subserving the more peripheral vision (>15° eccentricity), velocity tuned cells which respond optimally to low velocities are absent. More specifically velocity tuned cells with an optimum speed below 8°/s represent 41% of the velocity tuned cells whose receptive fields fall within 5° from the fixation.

The small proportion of velocity tuned curves observed at the lateral geniculate level suggests that the velocity tuning is mainly a cortical property (Orban, 1985).

The velocity tuned cells in macaque monkey were reported by Maunsell and van Essen (1983), Orban et al. (1986) and Mikami et al. (1986a).
Maunsell and van Essen (1983) measured the velocity tuning curves for MT cells and found that their distribution with respect to eccentricity was similar to that found in area 17 and 18 of cat. As in the cat, the tuned cells with slow optima were absent from the eccentricity class 15°-25°. Velocity tuned cells with slow optima (<8°/s) decreased from 48% at 0°-5° eccentricity to 0% at 15°-25° eccentricity. Conversely, velocity tuned cells with fast optima (>32°/s) increased with eccentricity from 5 to 28%.
Similar trends were observed in velocity tuning curves obtained from cells in V1 and

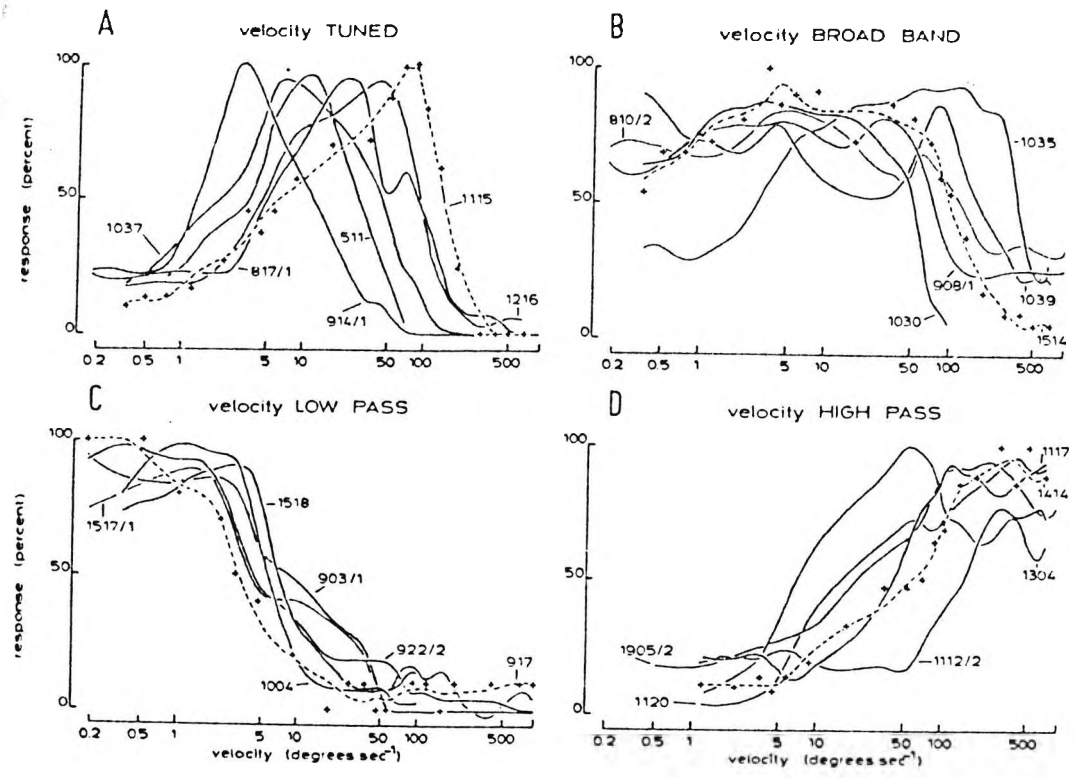


Figure 1.31: representative examples of velocity response curves for the four different classes of velocity sensitive neurones. A: velocity tuned cells; B: velocity broadband cells; C: velocity low-pass cells; D: velocity high-pass. Response is plotted as a percentage of maximum response (from Orban et al., 1981).

V2 of macaque monkey (Orban et al., 1986). The velocity sensitivity of V1 neurones shifts to faster velocities with increasing eccentricity and V1 and V2 neurones subserving central vision have a similar preference for slow movements. Orban et al. (1986) also observed that most cells in parts of V1 and V2 subserving central vision were velocity low-pass. As eccentricity increases in V1, these give way to velocity broadband cells.

1.14 Mechanisms Underlying Colour Vision

Theoretical models developed to explain colour vision can be classified into the two groups proposed by Young and Helmholtz and later Hering. The Young-Helmholtz theory is based on three colour fundamentals namely red, green and blue. The trichromatic theory is based upon the colour matching technique, whereby any visible hue may be matched with a mixture, in correct proportions, of three light stimuli. All colour sensations, arise therefore, as an effect of excitation within three sensory systems, with white arising from equal excitation of all three (Young, 1802).

The Hering theory is similar to Young-Helmholtz theory in that it postulates three independent variables as a basis for colour vision. Each variable however, consists of a pair of opponent processors (Hering, 1887). These paired and opponent visual qualities are yellow-blue, red-green and white-black. Some of the ideas developed based on the Young-Helmholtz theory, its limitations, and possible solutions given by opponent theory are outlined below.

The Two-Colour Increment Threshold Procedure and the π-Mechanisms

In a series of papers, Stiles described the measurement of the fundamental colour mechanisms using increment thresholds (Stiles, 1939, 1946, 1949, 1959). Some of his findings are given below and are excerpts from Stiles (1978). In Stiles' measurements, the stimuli used can be regarded as comprising of a conditioning stimulus (wavelength μ) and a test stimulus (wavelength L) presented foveally. The eye is exposed to the conditioning or background stimulus for a period that is sufficiently long to allow full adaptation before application of the test stimulus. The increment threshold for detection of the test stimulus may then be obtained for a range of L at a given μ. The test sensitivity is defined as the reciprocal increment threshold luminance. Alternatively, for a range of monochromatic background wavelengths the intensity of the conditioning field may be altered such that it elevates the increment threshold of a test stimulus of fixed characteristics to a specified multiple of its value on a zero field. The reciprocal of the field intensity, is then defined as the field sensitivity. Stiles proposed that the spectral sensitivity curves obtained from the detection threshold for a range of stimulus wavelengths on a uniform background is determined by the properties of several component mechanisms operating in the retinal area to which the test stimulus is applied. Corresponding curves of the individual components may only be obtained if they are the only mechanisms contributing to the detection of the stimulus under given

experimental conditions. Symbols $\pi 0$, $\pi 1$, $\pi 2$, etc. were then used to denote the component mechanisms inferred in applications of the two-colour increment threshold technique, when the field and test colours were varied independently. For a particular mechanism πi, the test and field sensitivities were defined respectively as, the reciprocal of the absolute threshold and the reciprocal of the monochromatic field required to raise the increment threshold from the absolute threshold to ten times that value. Stiles,using the Young-Helmholtz theory as a basis, postulated that the three peaks of spectral sensitivity curve represent the activity of three colour mechanisms and the overall shape of the spectral sensitivity may be regarded as the resultant of three component sensitivities or four when the scotopic mechanism played a part.

Using the two-colour increment threshold technique, he found that the "blue-cone" system comprises a group of three response mechanisms (named $\pi 1$, $\pi 2$ & $\pi 3$) which are maximally sensitive in blue, but have different sensitivities at longer wavelength. The two medium and long wavelength mechanisms corresponding respectively to "green-cone" and "red-cone" systems exist in two modifications depending on different conditioning stimuli, with small differences in spectral sensitivity. They were named $\pi 4$ and $\pi'4$ for the medium wavelength mechanism "green-cone", and $\pi 5$ and $\pi'5$ for long wavelength mechanism "red-cone". Figure 1.32 shows the field sensitivities for the five π-mechanisms and a summary description of their characteristics is given in figure 1.33.

Alpern et al. (1970) showed that if a foveal increment threshold curve was derived with a flash rather than a steady background, the threshold intensity increased very rapidly as the background intensity was increased above a certain level. Presumably the visual system saturates or overloads at these high intensities. If saturation occurs independently in short, medium and long wavelength mechanisms, then it may be possible to isolate one colour mechanism by using a test flash which causes complete saturation in the other two mechanisms.

King-Smith and Webb (1974) and Shevell (1977) measured the fundamental colour mechanisms using this saturation technique and found a close agreement between their data and Stiles π-mechanisms.

Interactions Between Colour Vision Mechanisms

Since stimulus colour may activate a number of colour mechanisms, a response may arise through an apparent summation of their effects. This summation is termed probability summation and is consistent with the independence of component mechanisms (Mollen, 1982). If the thresholds of the independent component

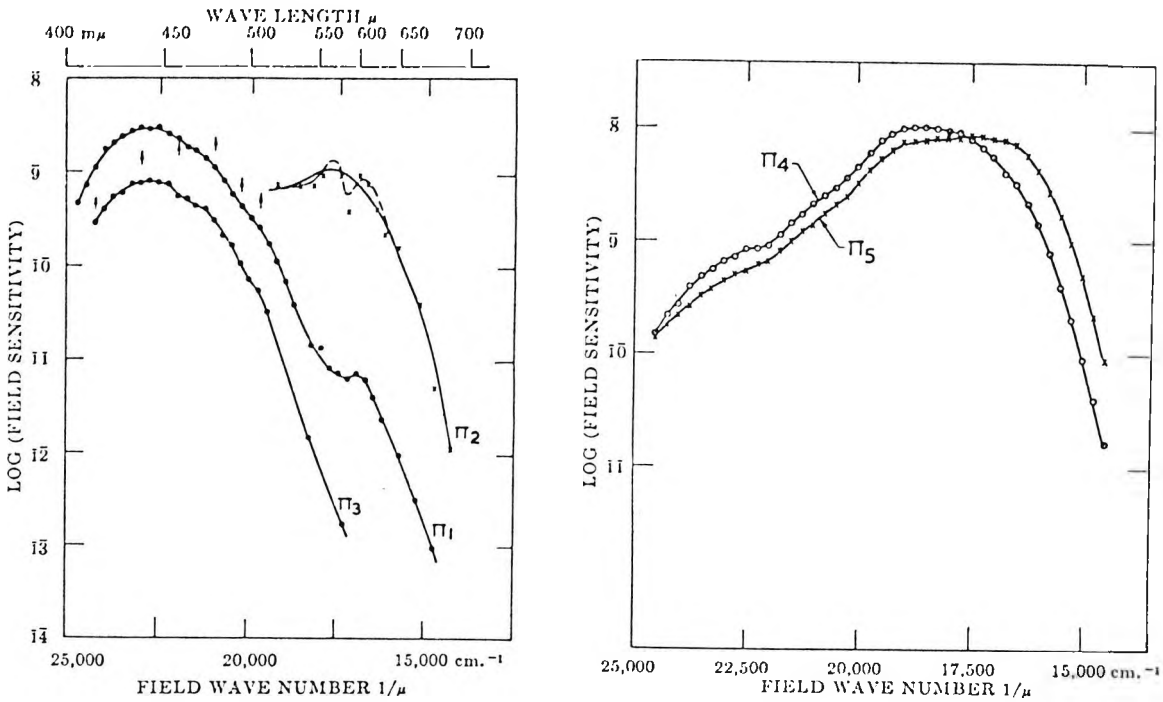


Figure 1.32: field spectral sensitivities of foveal cone mechanisms. For L< 510nm the arrow points on the left plot indicate values below which the undetermined part of $\pi 2$ curve cannot fall (from Stiles, 1959).

Figure 1.33: some properties of π-mechanisms (from Stiles, 1959).

Mechanism	Symbol	Remarks	Wavelength of max. sensitivity	% Weber-Fechner fraction (1°,200ms)
Rod	$\pi 0$	absent at fovea	503	30
		blue/yellow sen. at		
	$\pi 1$	440/590nm ≈ 2.6log	440	8.7
Blue-cone	$\pi 2$	1 log	440-480	8.7?
	$\pi 3$	4 log	440	8.7
Green-cone	$\pi 4$		540	1.9
	$\pi' 4$	high intensity	540	
Red-cone	$\pi 5$		575	1.8
	$\pi' 5$	high intensity	587	

mechanisms, when acting alone have infinitely sharp value as a function of stimulus wavelength, then there is no probability summation and the observed threshold is the lower of the component thresholds. If however, a threshold is simply the value of the stimulus required to yield a certain probability of detection, the lowering of the resultant threshold will be determined by the steepness of the probability-of-detection curves given by the component mechanisms, acting alone. In a case where the observed threshold cannot be identified as the resultant of the thresholds of independent component mechanisms the summation is described as physiological summation and acts as evidence of some interaction in the threshold responses of the mechanisms (Stiles, 1978). Stiles π-mechanisms description of colour vision assumes that the component mechanisms are independent so that only probability summation operates or that any physiological summation is small enough to be ignored.

To study the amount of summation between the π-mechanisms, Stiles(1958) carried out experiments in which in the presence of a suitably chosen background field, the threshold for detection of a test stimulus consisting of a mixture of two wavelengths was measured. By varying the proportions in the mixture, the way in which the responses from the two mechanisms were summating could be determined. Results in some cases showed physiological inhibition rather than summation (Stiles, 1967). Similar inhibition or non-linear summations have also been reported by other experimenters (Ikeda, 1963; Boynton et al., 1964).

Studies of Wald (1965) on normal and colour blind subjects showed that measurements of spectral sensitivity on zero background field may be interpreted by three cone sensitivity curves. At higher luminance white background levels, interpretation of spectral sensitivity curves based simply upon the upper threshold sensitivity of fundamental mechanisms, is not satisfactory. The spectral sensitivity curves generally lie below the sensitivity predicted from the most sensitive fundamental mechanisms and the peak sensitivity at medium and long wavelengths are also shifted with respect to the maximally sensitive wavelengths measured for cone pigments. To account for this Sperling and Harwerth (1971) proposed a general inhibitory interaction between the outputs of the long and middle wave cones. If linear subtraction of long-wave output from the middle-wave output and vice versa was assumed, then the spectral sensitivity curve would fit the cone response data.

Stromeyer et al. (1978a) showed that the detectability of a red flash on a bright yellow field is reduced if it is accompanied by a similar green flash. Red flashes similarly reduced the detectability of green targets. These inhibitory interactions

and subtractive processes between colour vision mechanisms are believed to be related to opponency phenomena (See review by Mollen, 1982).
Some characteristics of the opponent mechanisms are outlined below.

Opponent Processes in Colour Vision

The cone receptors and rods have pigments with quantum capture characteristics that peak at 419nm, 531nm, 559nm and 496nm, respectively (Knowles and Dartnall, 1977). The spectral sensitivity curve obtained for long duration stimuli on a white background field however, has peaks at 440nm, 530nm and 610nm with characteristic troughs at 480nm and 580nm. The peak at 440nm is attributed to the short-wave mechanism. The displaced peak at long wavelength and the troughs however may be explained by the activity of chromatic opponent mechanisms (Hering 1978, Hurvich and Jameson, 1957, Guth and Lodge, 1973).
To a good approximation, detection sensitivity corresponds to opponent colour sensitivity or luminance sensitivity, whichever is the greater (King-Smith, 1975; King-Smith and Carden, 1976).
King-Smith and Carden (1976) predicted that if chromatic opponent channels are used for the detection of a test flash, then the colour of the test flash should be apparent at detection threshold. They found that when a large test target (1°) of long duration (200ms) was presented on a uniform white background, then the curves for detection and colour discrimination coincided largely (see figure 1.34).
Regan and Tyler (1971) investigated temporal summation and its effect on detection thresholds and found that chromatic mechanisms have integration times between 150-300ms depending on the stimulus wavelength, which are much longer compared to the integration time in the luminance channel (60ms). Colour opponent mechanisms also have a much larger spatial summation than the broadband luminance channel (Horst et al., 1967; Hiltz and Cavonius, 1970). It has been suggested that this may be due to the relationship between the retinal receptor population and the target surface area (Mollen, 1982). In other words, the number of colour opponent cells available for detection should be proportional to πr^2, since any such cell can compare local differences between signals from different types of cone; but the number of non opponent cells available for detection may increase only as $2\pi r$, since such cells are more sensitive to spatial transients than to homogeneous illuminations. Therefore, a combination of a large stimulus and long presentation interval promotes detection by colour opponent mechanisms and a small stimulus size and short presentation time favours detection by the luminance channel (King-Smith and Carden, 1976, see also figure 1.35).

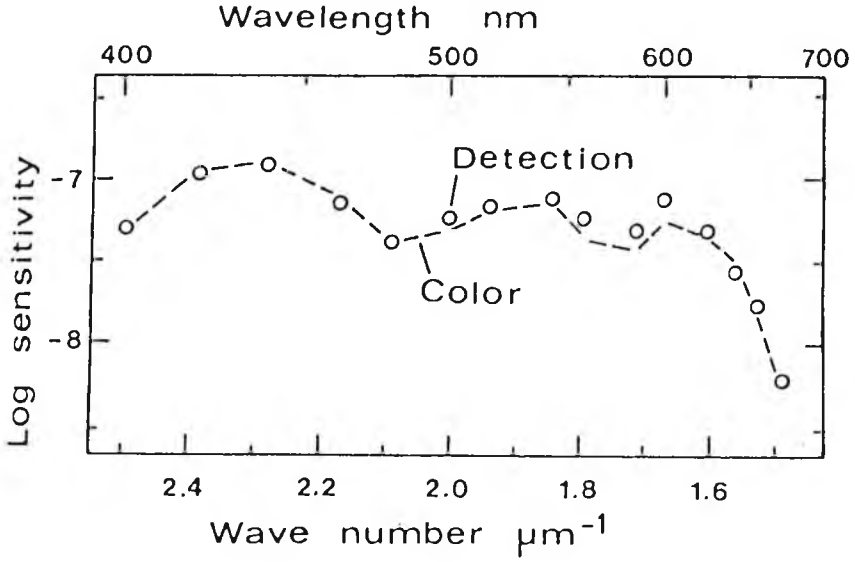


Figure 1.34: comparison between the detection sensitivity (circles) and colour discrimination (dashed line). Sensitivities have been averaged for two observers and are for 1°, 200ms test flashes on a 1000 td white background (from King-Smith and Carden, 1976).

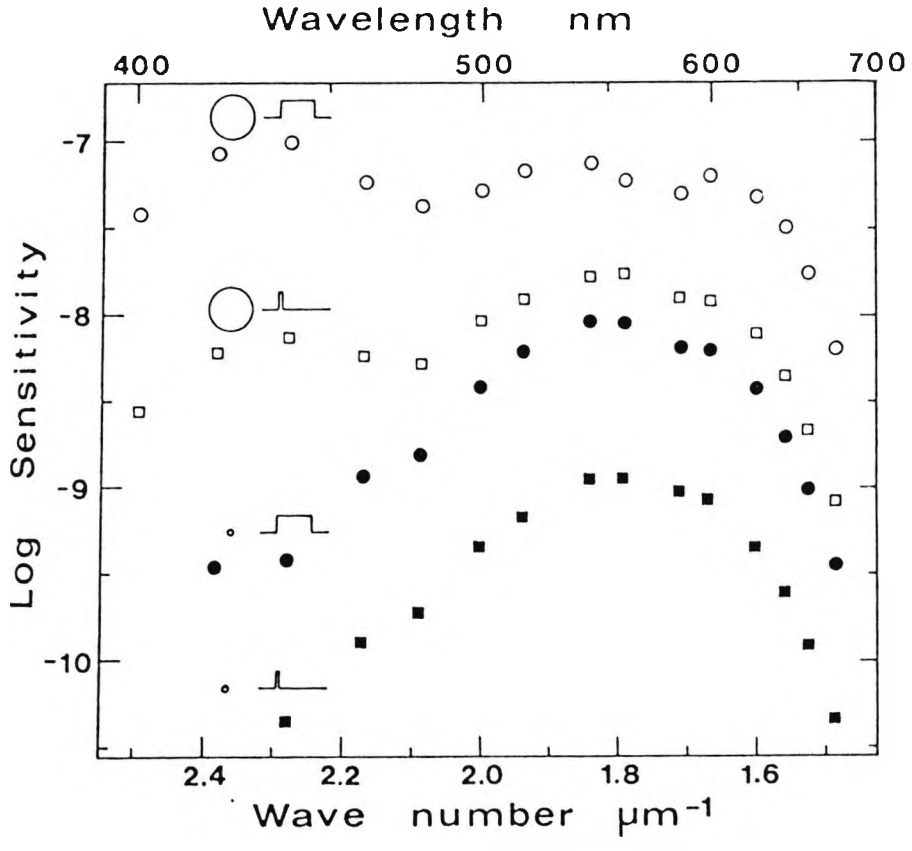


Figure 1.35: spectral sensitivity curves for detecting large and small, short and long test flashes on a 1000 td white background. ○ ,1°, 200ms; □ , 1°,10ms; ● ,0.05°, 200ms; ■ ,0.05°, 10ms (from King-Smith and Carden, 1976).

The assumption that the presence of a white conditioning field depresses the sensitivity of the luminance channel as a result of achromatic adaptation was first made by King-Smith and Kranda (1981). This assumption was tested further by Foster and colleagues when they measured the spectral sensitivity with emphasis on the trough at 580nm and the peak at 610nm, for a range of white background luminances and showed that for sufficiently high background luminances (3log td or greater) there was little or no difference between simple detection and colour discrimination thresholds implying that these conditions produced complete isolation of opponent colour system at increment threshold (Foster, 1981; Foster and Snelgar, 1983; Foster et al., 1986; Snelgar et al., 1987). The isolation of chromatic opponent and luminance mechanisms are also enhanced by introduction of a small white auxiliary field positioned such that it spatially coincided with the test target (Foster and Snelgar, 1983; Snelgar et al., 1987).

The colour opponent mechanisms operate not only in the fovea but also in the peripheral retina. Their existence has been demonstrated by the characteristic peaks and troughs in the spectral sensitivity curve at eccentricities 1.5° (Harwerth and Levi, 1977), 5° (Stiles and Crawford, 1933), 6° (Wooten et al., 1975; Verriest and Uvjls, 1977 sighted by Snelgar et al., 1987), 33° (Krastel et al., 1983) and 45° (Kuyk, 1982). At large eccentricities the peaks and troughs are only significant if larger test targets (5.5° and 16° test target at 33° and 45° eccentricity respectively) are used.

The spatio-temporal properties of the colour opponent and luminance mechanisms have been investigated by measuring contrast sensitivity using monochromatic and blue/yellow and red/green gratings (Stromeyer et al., 1978; Mullen, 1985, 1987; Lee and Stromeyer, 1989). Results suggest that the colour opponent mechanisms which determine detection below 1 c/°, have low pass spatial characteristics. This contrasts to the band pass characteristics which are obtained for achromatic luminance gratings and suggests that, as spatial frequency is reduced, luminance sensitivity falls increasingly below colour sensitivity.

There is ample neuroanatomical evidence for colour opponency in the primate visual system (see review by Livingstone and Hubel, 1984 & Mollen, 1982; also Schiller and Logothetis, 1990; Cowey and Stoerig, 1991b). The evoked potentials elicited to chromatic stimuli on a white background may also be interpreted in terms of opponent colour interactions (Gouras and Padmos, 1974; Padmos and Norren, 1975). Colour opponent retinal ganglion cells project predominantly to the parvocellular layers of the LGN (see section 1.1 for more details). Cells in layer

4Cβ of V1, like the parvocellular cells, are either broadband or colour opponent centre-surround eg. red-on-centre green-off-surround. Red/green and blue double-opponent cells have been recorded in blobs of V1, thin stripes of V2 and V4 (Livingstone and Hubel, 1984; Hubel and Livingstone, 1985; De Yoe and van Essen, 1985). See sections 1.1 and 1.6 for more details on the colour pathways.

CHAPTER II
Equipment and Experimental Conditions.

2. Equipment

In order to investigate the possible systematic fluctuation in the pupil size with the presentation of moving stimuli, an accurate pupillometer was used to provide measurements of pupil size and eye fixation. Use of a P_SCAN 100 system (see below) was available throughout this study with a range of software designed for averaging and the analysis of response amplitude and latency.

Equipment Used for Generating Movement Stimuli

The software developed and executed on a 25MHz Vectra RS/25C Hewlett Packard Personal Computer (model D2020A) which included a mathematics coprocessor (Intel 80287), two video graphics cards driving one VGA monochrome monitor (HP D1181A) and one VGA colour monitor (HP D1182B), and one pupillometer board (see below).

The graphics card used to drive the colour VGA monitor was set to the standard graphics mode D, providing eight graphics pages, each having a resolution of 320 x 200 pixels. Multiple graphics pages were required in order to produce a random noise effect and could be accessed and manipulated within the frame rate. The frame rate of the monitors was 70Hz, hence the maximum time available for calculation and writing of pixel parameters and switching between the graphics pages was 14.29ms.

The option of generating the graphics pages in the dynamic memory to obtain more than eight graphics pages was investigated in the development stages of this study. The access and writing time for a new graphics page was found to be approximately 36ms which was too slow to produce some of the stimuli used.

The relative low resolution of 320 x 200 pixels was a compromise between the graphics memory available, number of graphics pages and calculation and update time requirements. The dimensions of each pixel was 0.763 x 0.906 mm subtending a visual angle of 3' 16" x 3' 54" of visual angle at a viewing distance of 800 mm. The dimensions of the screen were 244 x 181 mm subtending 16.8° x 12.3° of visual angle at the same viewing distance.

The graphics card, in the standard mode used, provided access to a palette of 16 colours on the screen from a total of 64 which was sufficient for the purpose of this study.

The VGA monochrome monitor was used to provide information on the progress of the experiment and on the parameters selected.
The software for the experiments were written in ANSI C programming language and compiled using a Lattice C Compiler for DOS and OS/2 (Version 6.02, Lattice Inc.).

Experimental Conditions for Motion Experiments

The experimental room was artificially lit by a diffused light emitted by a 40 Watts desk lamp and reflected from a diffusing white surface. The minimum luminance measured on the colour monitor screen, was 0.27 cd/m^2. The subject's eyes and the pupillometer cameras were shielded from possible glare from the room lighting a matt black, horizontal shade, and the monitor was shielded by black curtains from the top, below and both sides. Prior to the experiments, the monitor was switched on and a stationary pattern was presented for warm-up period of 30 minutes. Before the experiment commenced, the subject was made as comfortable as it was possible by adjusting the height of the chair so that subject's eyes and the fixation points were in the same horizontal plane. He/she was then asked to observe a stationary test pattern for a period of 3 to 4 minutes. The subject was encouraged to move their eyes about the screen so that afterimages were avoided, but adaptation to the ambient illumination occurred. They were also instructed to avoid blinking and to fixate on the fixation target during the stimulus presentation. The end of each presentation was indicated by an auditory bleep. Subjects were then allowed to blink but were asked not to close their eyes for long periods.
When more than one stimulus condition was studied, the different stimuli presented randomly. Each stimulus was presented after an interval of random duration when the GO button on the response buttons (see below) was pressed. Short breaks were taken frequently during measurements, and none of the experiments exceeded a period of 30 minutes.
Fixation stability was monitored through out and fixation drifts were found to be less than 40' arc.

Equipment Used for Generating Colour Stimuli

The Personal Computer with coprocessor were the same as those used in motion experiments. The progress of experiments was monitored using a HP D1182B monitor driven by a super VGA card. The coloured stimuli were presented on a high resolution, non-interlaced, 19", 60Hz, HP 1187A monitor. The resolution of the monitor was 1280 x 1024 pixels and this provided a field size of 28° x 22° at a

viewing distance of 700mm. The high resolution monitor was driven by a HP IGC-20 graphics card providing 256 grey levels per gun. The luminance of each gun was calibrated prior to the experiments. All luminances measured in this study were made with a LMT (L1003) photometer. Figure 2.1 shows the spectral characteristics of the three screen phosphors, measured using a telespectroradiometer (Gamma Scientific Model 2009) which was calibrated against a Clark-Berry lamp. The lamp was in turn calibrated for absolute irradiance measurements by the NPL.

Experimental Conditions for Colour Experiments

The experimental room for colour measurements was different than that for the motion experiments. The room was lit entirely by artificial lighting, generated by 4 spot lamps which were angled to illuminate an extended white Lambertian surface positioned on the ceiling above the display monitor. This arrangement provided diffuse illumination, but contributed little to the luminance of the display. To minimise the amount of scattered light, the monitor borders and the pupillometer base unit were covered with black velvet and the walls of the room were painted matt black. The subject's eyes and the pupillometer cameras were shielded from possible glare from room lighting by matt black horizontal shade. The subject was separated from the experimenter and the control pads by a curtain partitioning the room into two parts. With the exception of the points mentioned above, the experimental conditions were the same as those for motion experiments.

The Pupillometer

A schematic diagram of P_SCAN 100 system used in experiments described in chapter V , is shown in figure 2.2. Experiment described in chapters III and IV however, were carried out using a monocular version of the pupillometer. The detailed descriptions and algorithms employed in this system have previously been published (Barbur et al., 1987a, Barbur, 1992). The main features, however, are given below.

The P_SCAN 100 system was designed for simultaneous measurement of pupil size and two-dimensional eye movements. The system is based on the analysis of pupil images from reduced video frames and results in high measurement accuracy. PC AT compatible adapter boards were designed for the processing of the video signals and the extraction of the co-ordinates of intersection between the edge of the pupil and a series of equidistant scan lines. The image of the iris and the superimposed scan lines were also shown on a separate video monitor within the experiment.

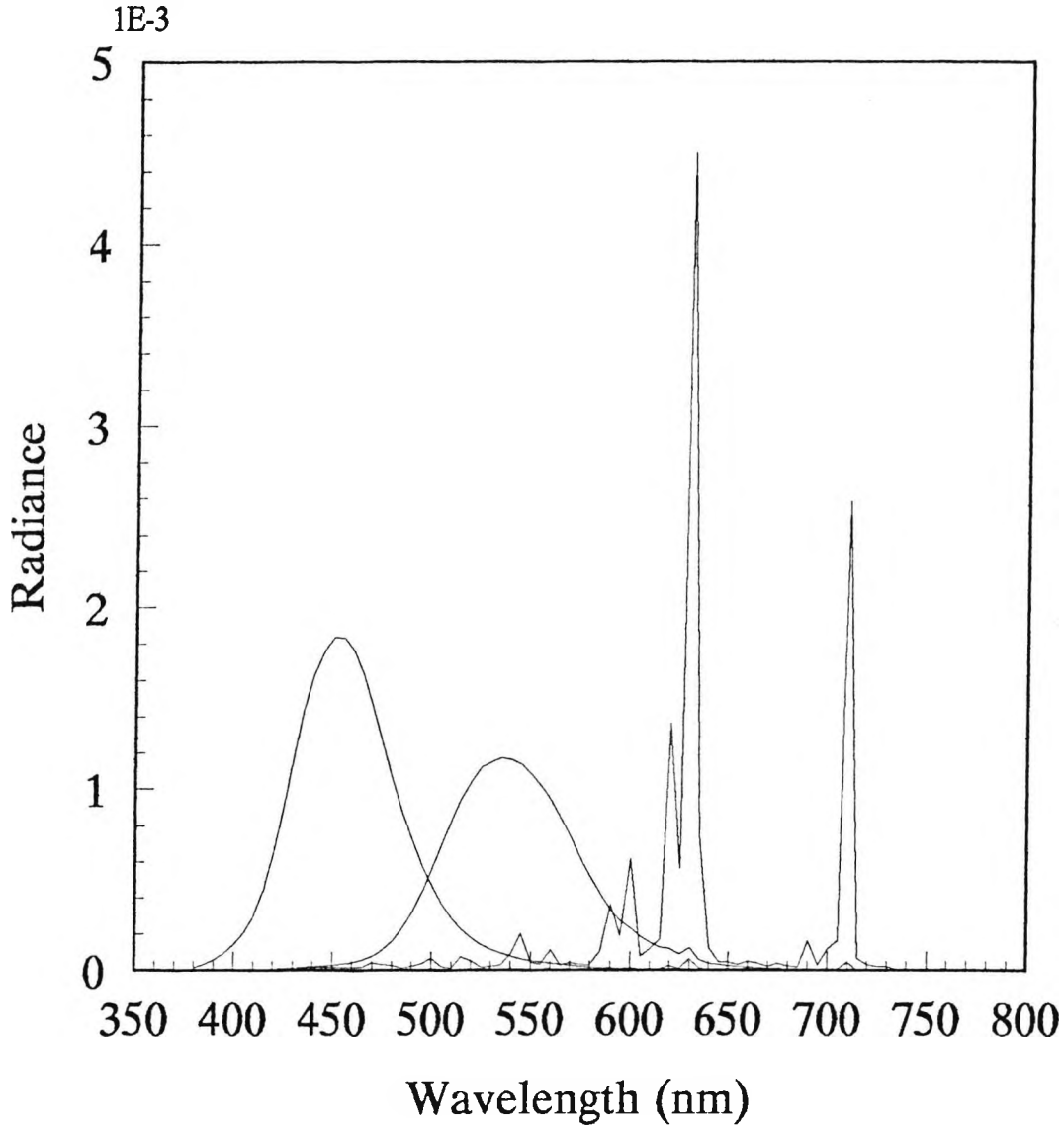


Figure 2.1: spectral radiance (mW/m²/nm/sr) of the three screen phosphors.

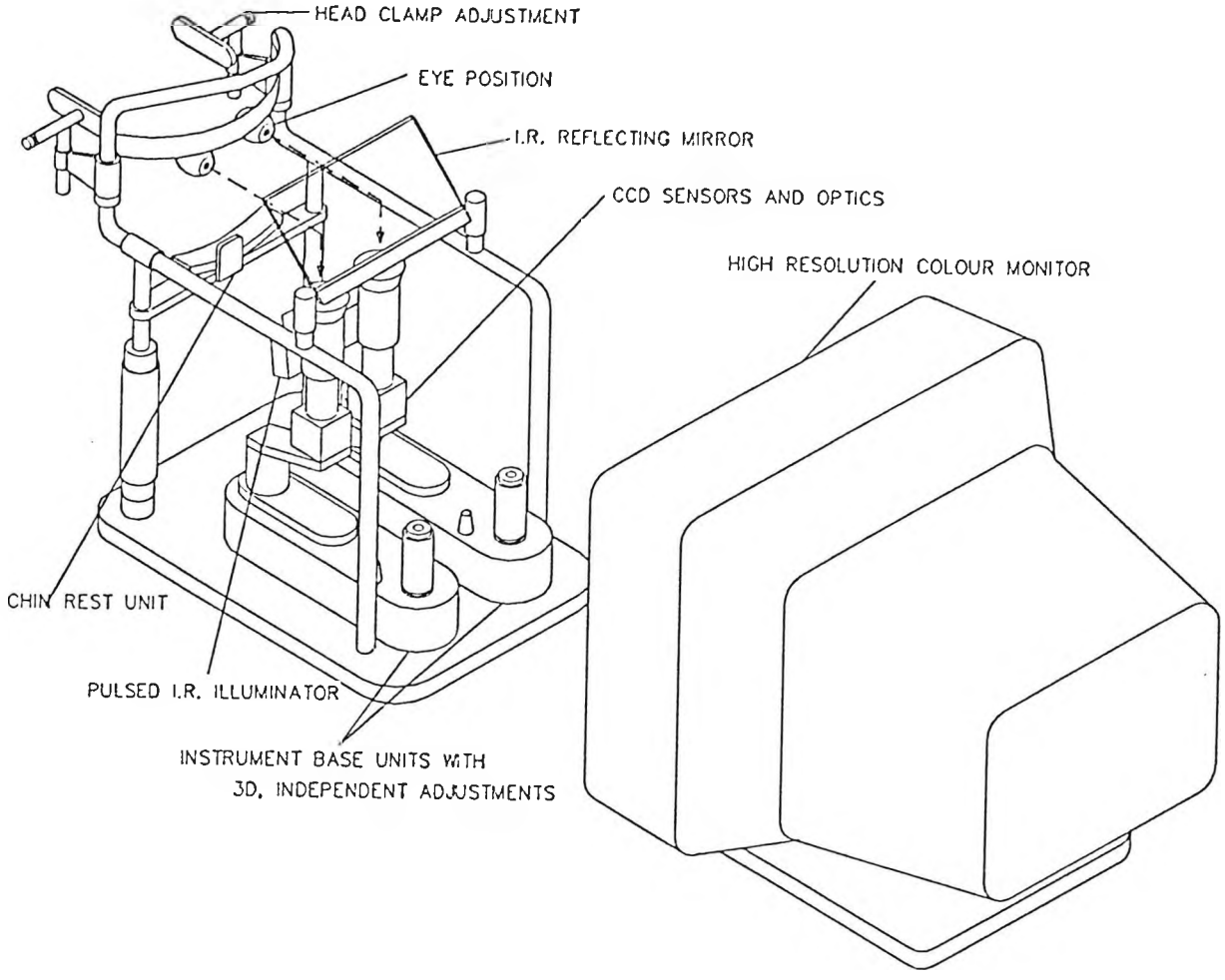


Figure 2.2: schematic drawing of the P_SCAN 100 system for the simultaneous measurement of pupil size and eye movements. The diagram shows the instrument base unit which allows easy adjustment of the CCD sensors as required for positioning and focusing of the images of the eye (from Barbur, 1992).

During the recordings, each stimulus is initiated after the GO button on the response button is pressed. The threshold for the intersection of the scan lines and the image of the pupil is set prior to the experiment. However, the response button also provides the facility for allowing minor adjustments of the threshold setting as well as recalibration of the fixation point and recording of the yes/no verbal response of the subject when appropriate. The results of sampling analysis (Barbur, 1989) show that the sampling rates associated with video systems can produce all the information contained in pupillary response. Measurement of response latency do however require synchronisation of stimulus onset with the first measured data point in each trace.

The algorithms which are used to extract the parameters of interest yield accurate measurements with typical resolutions of 5 minutes of arc for eye movements and better than 0.01 mm for the measurement of pupil diameter. The calibration procedures are easy to implement and do not require frequent recalibration. The apparatus is mounted on a modified Zeiss instrument base unit which allows easy alignment of the optics and CCD sensors (photon EEV 883357).

A simple and effective arrangement is provided for minimising the movements of the subjects' head. The subject then views a high resolution monitor through a large, infra red reflecting mirror.

To avoid image smear caused by eye movements, pulsed 10ms infra red illumination of the iris is employed using of a 2 x 6 matrix of LED's with peak spectral transmission of 850nm through an infra red transmitting filter (Hoya, IR76). Graphical methods have been developed for averaging multiple traces and for extraction of the response amplitudes and latencies in the measurement of pupil response. Corresponding eye movement traces can also be examined by means of interactive graphical methods. Data files are then generated to contain results of the analysis carried out. The files also store the parameters of the experiment and subject's details. When the pupillary responses to a stimulus attribute are small, a large number of traces must be recorded and averaged to obtain a high signal to noise ratio . During a typical experiment, several traces are recorded and averaged and the parameters of interest such as response amplitude and latency extracted from the average trace. Figure 2.3 shows a typical averaged trace of the pupil diameter against time. The response amplitude, latency, stimulus onset and offset where mentioned in later chapters, refer to the parameters indicated in this figure. The pupil noise standard deviation associated with the average of traces shown in each graph were calculated and the mean value for each graph are stated in captions.

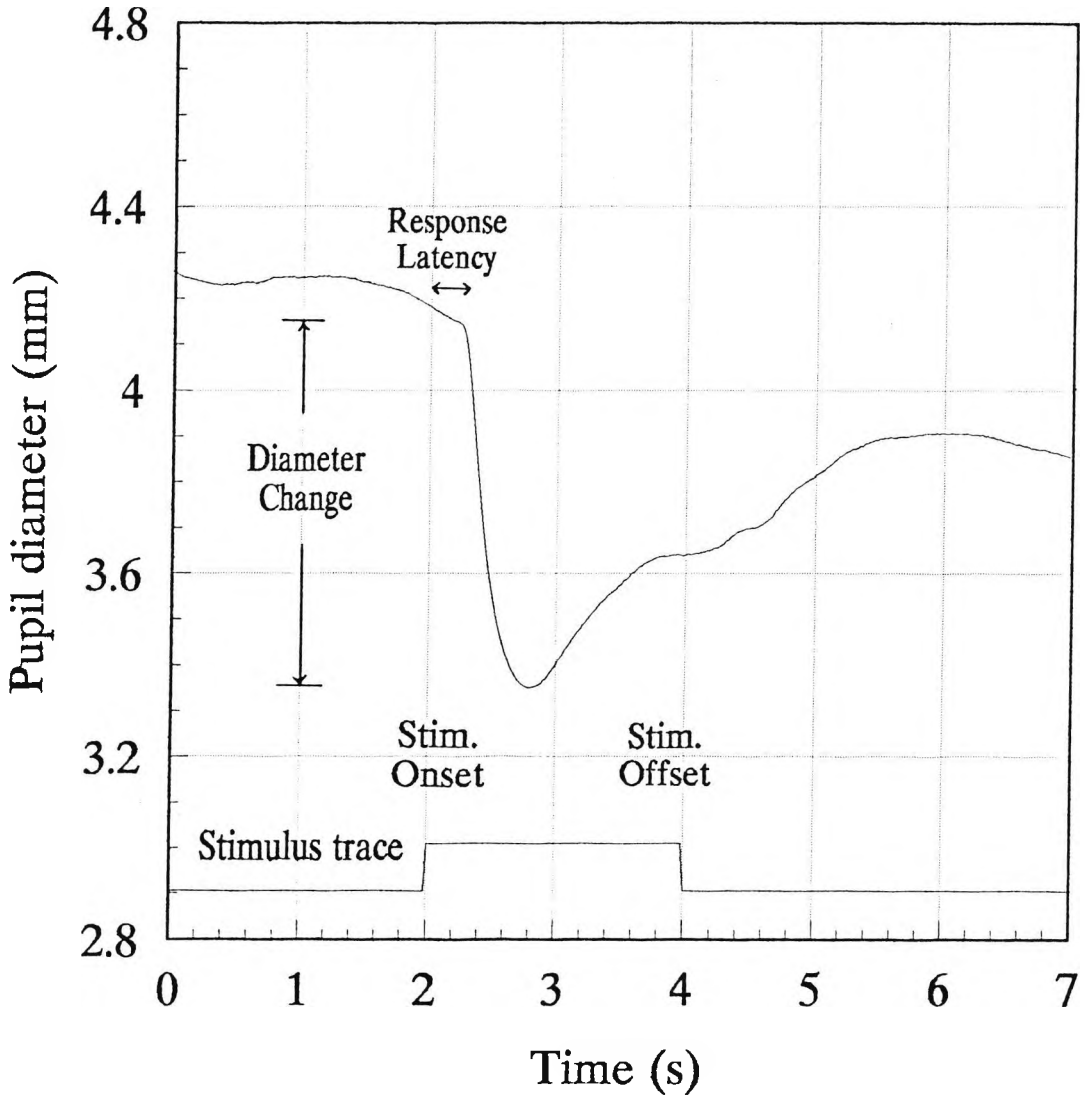


Figure 2.3: an example of a pupil response elicited to the onset of a ginen stimulus.
The response latency and diameter change referred to in the text, are indicated on the graph.
Pupil noise standard deviation associated with the average of 64 traces is 0.0053.

CHAPTER III
Is Processing of Motion Information Reflected in Pupil Response?

3.1 Processing of Movement Information

Physiological studies reviewed in sections 1.6-8 and 1.11-13 show that many neurones along the retino-geniculo-striate pathways respond to moving stimuli. The processing of motion information is continued in the extrastriate centres. Along this forward path, the resolution of parameters such as directional selectivity and retinotopic specificity does not appear to increase (see figure 3.1 for a schematic diagram of some cortical interconnections). The function of these visual areas appear to be of higher order of complexity.

The presence of orientation and direction selective cells, together with a powerful range of binocular interaction, would indicate that area V5 may have a variety of functions (Zeki, 1980). On average the receptive fields in V5/MT are much larger than in V1 and directional interactions occur over substantially larger distances than in V1 (Mikami et al., 1986b).

The major outputs of V5/MT appear to be relayed to the parietal cortex via intermediate areas including MST (Jones and Powell, 1970). In MST, some receptive fields cover a full quadrant of visual field (Tanaka et al., 1986). This loss of specificity in higher visual areas, is associated with the presence of cells with complex response properties.

Studies have shown that the directional interactions for neurones in area 7a can occur for spatial separations of 10° - 20°, indicating a large expansion of the spatial interactions underlying direction selectivity over those observed in V5/MT.

The antagonistic centre-surround receptive field of a cell was discussed in section 1.1. The response of a cell to a stimulus in its centre receptive field can be modulated if a second stimulus is placed in the surround. Several experimenters have investigated the influence of background movement on the responsiveness of neuronal cells to a moving object (Hammond and Mackay, 1977; Allman et al., 1985a; Tanaka et al. 1986).

MT and MST neurones with antagonistic surrounds responded well to local motion within the centre of the receptive field but not to global motion of texture and were well suited for distinguishing a moving figure from background (Allman et al. 1985a; Tanaka et al., 1986). MST contains neurones which are selective for higher

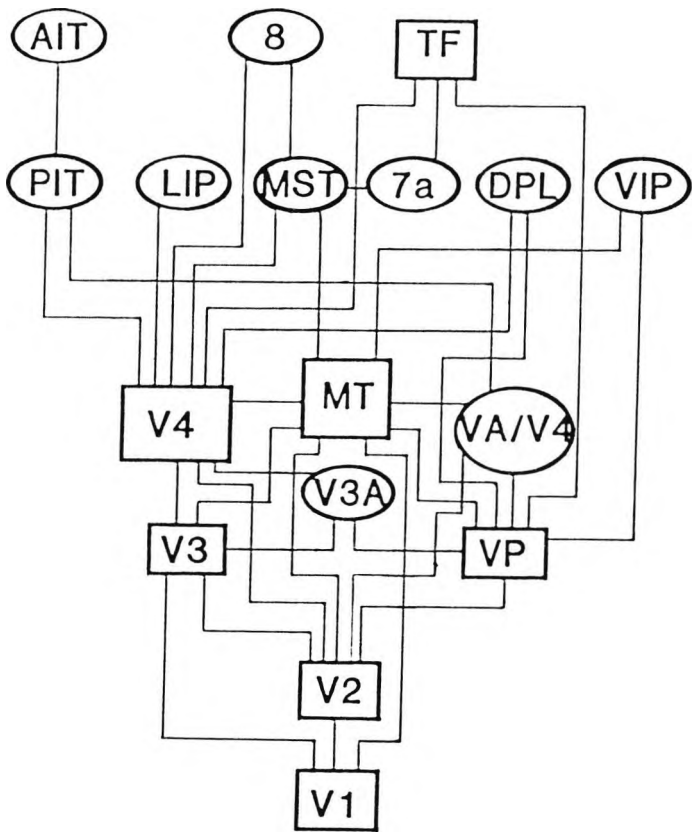


Figure 3.1: a hierarchy of visual areas in the macaque based on pattern of corticocortical connections. 7 well-defined areas (boxes) and 10 less well-characterised areas (ellipses)are arranged in seven hierarchical levels interconnected by 33 major linkages that are either reported or presumed to be reciprocal. Most minor connections have been omitted. AIT, anterior inferotemporal area; DPL, dorsal prelunate area; MST, medial superior temporal area; PIT, posterior inferotemporal area; VIP, ventral intraparietal area; 7a and 8, Brodmann areas (from van Essen, 1985).

order motion processing such as rotation and change in size. These properties were not observed in MT, whereas they were recorded in parietal cortex, frontal cortex and the superior temporal polysensory area (STP) (reviewed by Maunsell and Newsome, 1987). Neurones responding to rotation in depth have been found in MST and area 7a (Saito et al., 1986).

Neurones responding to the change in size of an image have been recorded in area V5 (Zeki, 1974) and MST (Saito et al., 1986) of the macaque monkey were the control experiments demonstrated that the responses where not elicited due to changes in light flux that may accompany the change in size, but responded only when two edges of the stimulus moved in opposite direction.

Neurones with opponent vector responses have been reported in the higher visual areas 7a and STP (Motter and Mountcastle, 1981). They have bilateral receptive fields in which the preferred direction of motion varies systematically from field subregion to subregion. For example, they respond to optical flow such that the neurones fire maximally to movement of stimuli in a direction towards or away from the fixation point.

The responses to rotation, changes in size and optical flow appear to represent the convergence of low-level motion cues in order to create higher level representation of important environmental events (Maunsell and Newsome, 1987).

3.2 Aims of the Study

Studies reviewed in section 1.5 demonstrated the existence of small transient pupillary constrictions to the sudden onset of some stimulus attributes such as stimulus structure and colour.
The hypothesis put forward to explain such findings states that "when a change in neural activity has taken place due to a stimulus attribute being presented to the eye, the steady state supranuclear inhibitory input to the pupillomotor nucleus is weakened transiently resulting in a pupillary constriction. The constriction amplitude appears to be proportional to the level of activity generated" (Barbur et al., 1986).
If the supranuclear inhibitory input to the pupillomotor nucleus is perturbed by a sudden change of neuronal activity in the visual cortex then in view of the large number of cells which respond to movement we postulate that the processing of movement information may also be reflected in the pupil.

The aim of this study was to investigate the presence of such responses in normal subjects. The effect of image quality and state of accommodation on these responses were also investigated.

In addition, the effect of lesions of the primary visual cortex on the pupil responses elicited to the onset of a moving stimulus was studied by carrying out similar experiments on a subject with damaged V1.

Possible pathways responsible for mediation of these responses are discussed.

3.3 Pupillometric Study of Motion Processing

Experimental Methods

When measuring the pupillary response to a stimulus attribute, it is essential to ensure that the presentation of the stimulus is not accompanied by any accommodation and convergence changes, eye movements and/or any additional local luminance flux changes on the retina, since such changes could give rise to a pupil response via the light reflex mechanism or the accommodation, convergence and pupil triad (see section 1.5).

Generation of the Test Pattern

A continuous movement is perceived from the sequential presentation of equi-distant targets at a short interstimulus time interval as explained in the apparent motion section 1.9. The target designed to investigate the pupil motion response (PMR), consisted of a set of bright dots positioned on a uniform background on a Video Graphics Colour Display (See chapter II). The pupil response amplitude may reflect the amount of perturbation in the neural activity generated, and therefore a large stimulus size is preferred. There are however restrictions on the stimulus size imposed by the equipment. That is, the larger the target area, the greater the number of pixels that must be manipulated between the consecutive frames. The height of the stimulus was thus limited by the time available for calculating and writing the new position of target pixels to the screen memory of the graphics board and the time taken for switching between graphics memory pages. In order to ensure a homogeneous distribution of the pattern dots and avoid possible non-uniformity of the luminance flux distribution across the test pattern, the test target area was divided into a grid, each grid element being a matrix of 16x16 pixels and a dot of 4x4 pixels was positioned at a random location within each grid element. The displacement between two sequential presentations is referred to as "*step-size*" and the time interval between the two presentations is termed "*inter-presentation*" time. The sequentially displaced presentations of each dot of the pattern stimulates the retina at a new position. In order to ensure that the onset of coherent movement does not cause any additional local luminance flux variations on the retina a masking technique was implemented. The coherent movement was generated in dynamic noise random dot kinematograms. During the preceding dynamic noise and the coherent movement intervals the step-size was kept constant. Thus, the only difference between these intervals was the fact that the dots were displaced in a random direction to form the dynamic noise, whereas

the coherent movement was achieved by movement of dots in the same direction. This is illustrated in Figure 3.2 & 3.3. This is important since any change in step-size during the transitions between different types of movement could cause visual artefacts (see section on: the design of optimum stimulus parameters). If the calculated subsequent positioning of a dot resulted in the dot falling outside the stimulus pattern area, then it reappeared at a location on the opposite side of the test target. This eliminated the possibility of a reduction in the overall target luminance during the stimulus as a consequence of loss of dots.

For a given inter-presentation time, different speeds of movement were achieved by altering the step-size. The direction and speed of movement were set prior to the experiment.

Two types of patterns were generated for investigation of the pupil motion response:

A) Single Patterns

Figure 3.4 shows the stimulus pattern dimensions set for the single pattern. The single pattern was used to study the motion responses in the peripheral visual field. For foveal measurements this pattern was considered inappropriate because of its masking effects of the fixation target and induced tracking movements of the eyes.

B) Twin Patterns

For foveal measurements, a different arrangement of the test pattern was therefore designed. Two patterns were positioned on either side of the fixation point and were set to move in opposite directions with the same speeds. Using this arrangement, good fixation stability was obtained. The dimensions set for the twin pattern are shown in figure 3.5.

The background and the target dot luminances were 15.4 cd/m^2 and 130 cd/m^2, respectively.

All the measurements were carried out at a viewing distance of 80cm and the movements of the subject's head were minimised using a chin rest and two head clamps (see chapter II). Subjects were instructed to fixate and the fixation points consisted of four yellow pixels. Blinks were also discouraged during the stimulus presentation. Subjects were either emmetropic or wore appropriate corrections.

The timing diagram for a typical stimulus presentation is shown in figure 3.6. As explained in section 1.5, the pupil also responds to audio stimuli. To prevent the synchronisation of the start of presentation of the visual stimulus and a possible audio clue a random delay period of (0 to 1) second was incorporated at the start. Because

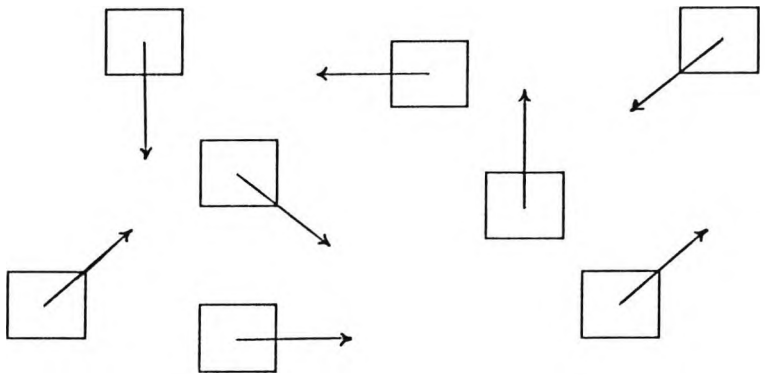


Figure 3.2: arrows indicate the next positioning of the dots during the dynamic noise interval.

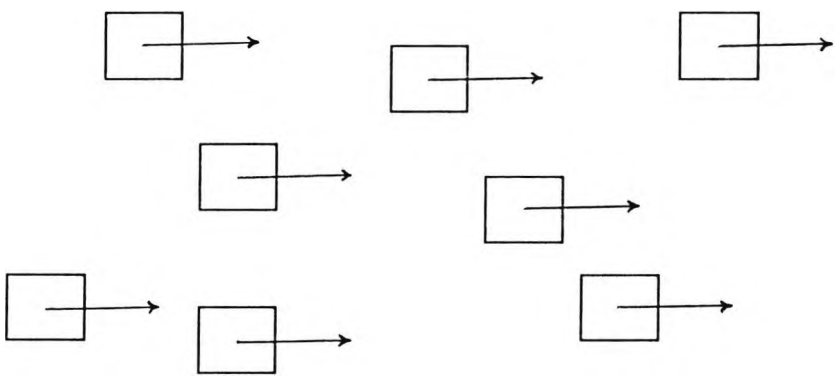
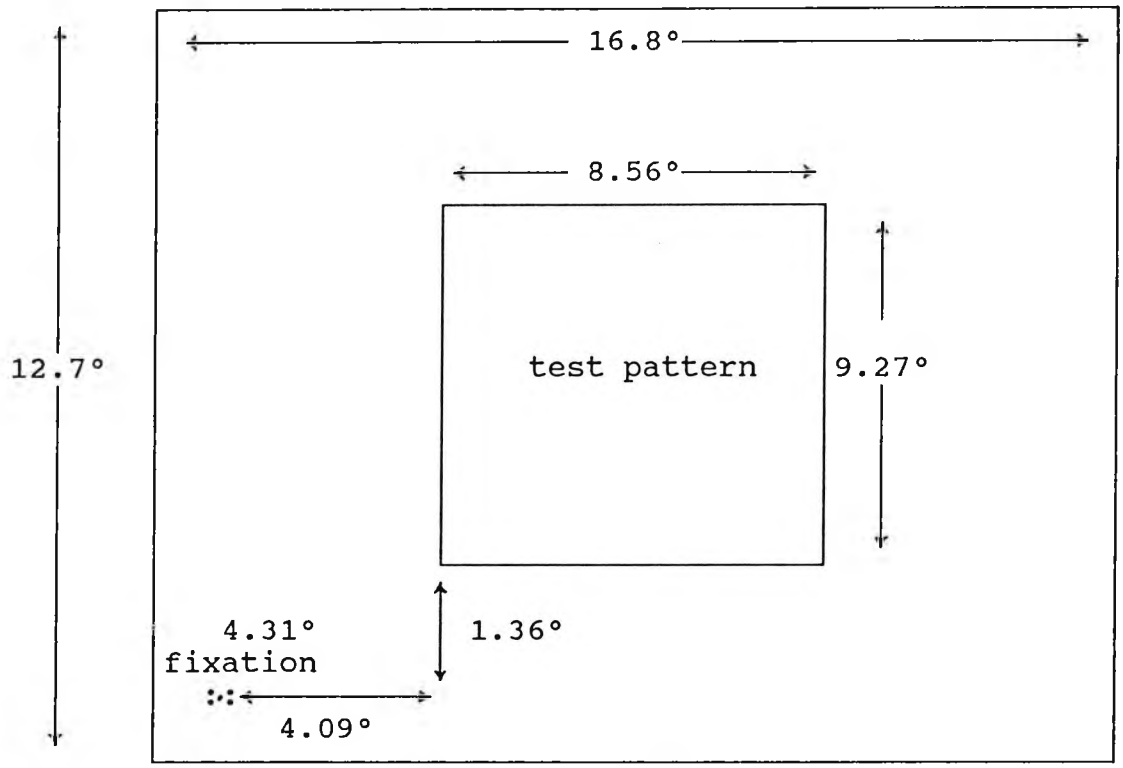
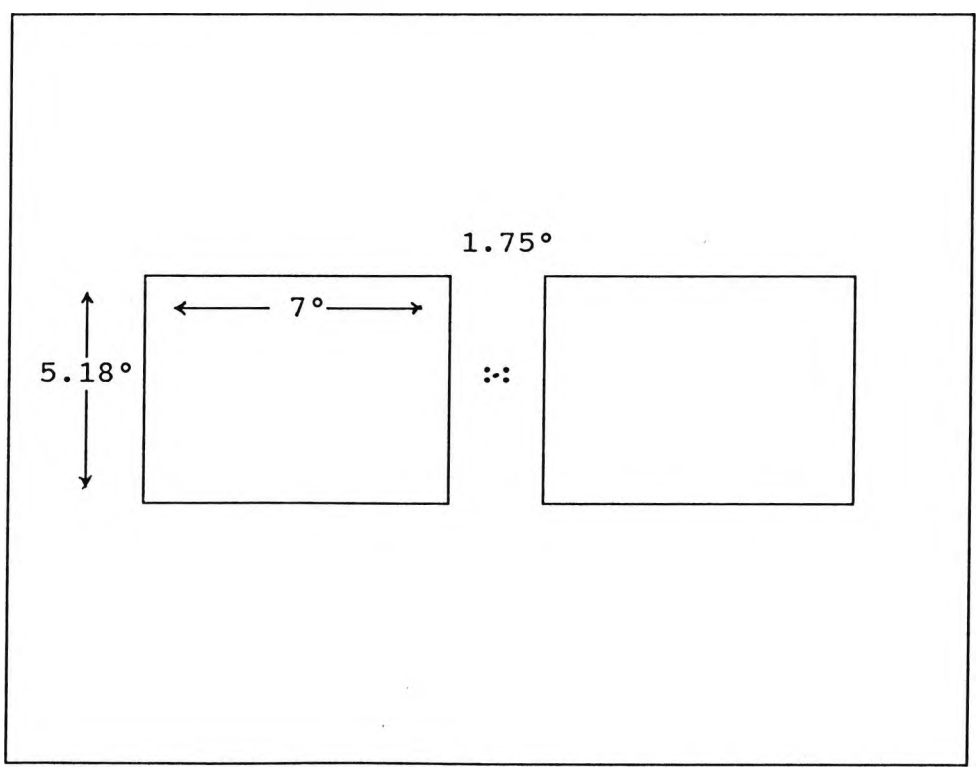


Figure 3.3: arrows indicate the next positioning of the dots during the cohernent movement interval.



Above: figure 3.4: schematic diagram of the single pattern.
Below: figure 3.5: twin pattern.



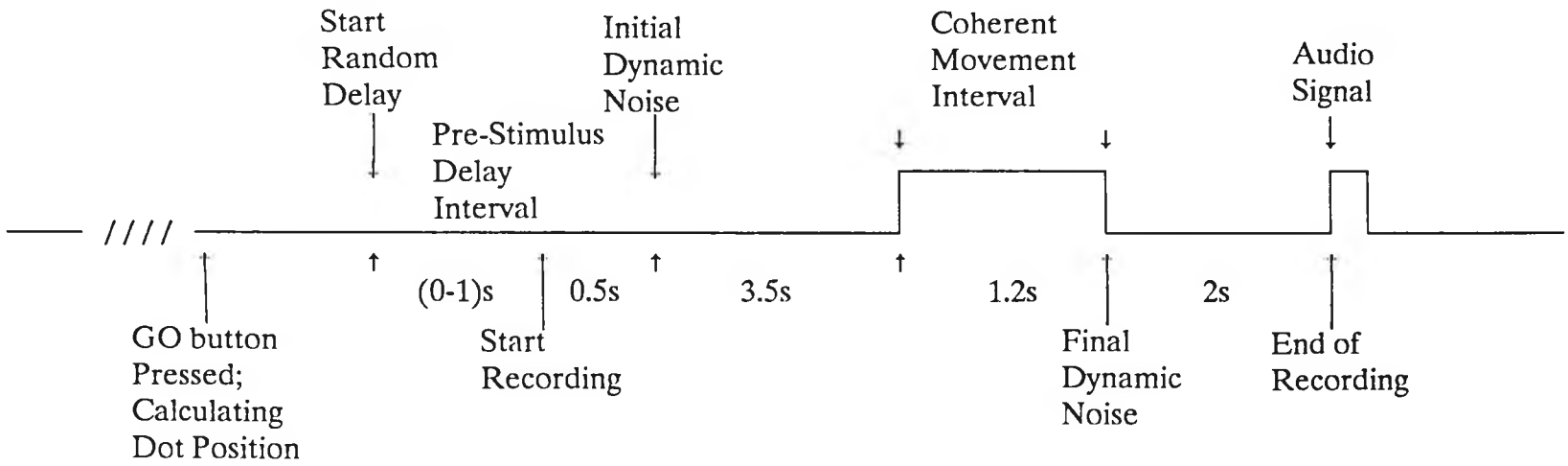


Figure 3.6: timing diagram for the PMR measurement experiments.

of the small signal to noise ratio involved, a large number of pupil traces were averaged for each stimulus.

The Design of Optimum Stimulus Parameters

Results from the first set of preliminary experiments are shown in figure 3.7. During these experiments each dot was displaced by a randomly selected step-size, in a random direction to generate the dynamic noise. This method of stimulus generation resulted in responses to both the on-set and off-set of the coherent movement as shown in trace A. It was important to investigate whether such responses were the result of a visual artefact, caused by a change in the type of stimulus. Trace B is a typical response measured when a constant step-size was used for the displacement of each dot, but here, the start position of the target dots in the first frame of the final dynamic noise interval did not coincide with the position of the last presentation of the coherent movement. The effect of this implementation was that the step size for displacement in the first frame of the final dynamic noise interval was not constant. When observing such a stimulus, a small discontinuity in the transition between the coherent movement and the final dynamic noise was almost detectable, which may be responsible for a small off-set response. When the stimulus was modified such that there was a smooth transition between the preceding dynamic noise interval and the coherent movement as well as a smooth transition to the final dynamic noise interval, pupil responses were elicited only to the on-set of the coherent movement, as shown in trace C.

To set a standard direction configuration for the coherent movement when using the twin pattern, experiments were carried out to compare the pupillary responses elicited to a speed of 3.82°/s when the coherent movement was along the horizontal meridian and in different directions with respect to the fixation. Figure 3.8 shows the results for movement towards and away from and to the left of the fixation point. There was no significant difference between the responses elicited to the onset of the coherent movement for these direction configurations. Hence the direction of movement along the horizontal meridian and away from the fixation point was set as the standard direction configuration for the twin pattern.

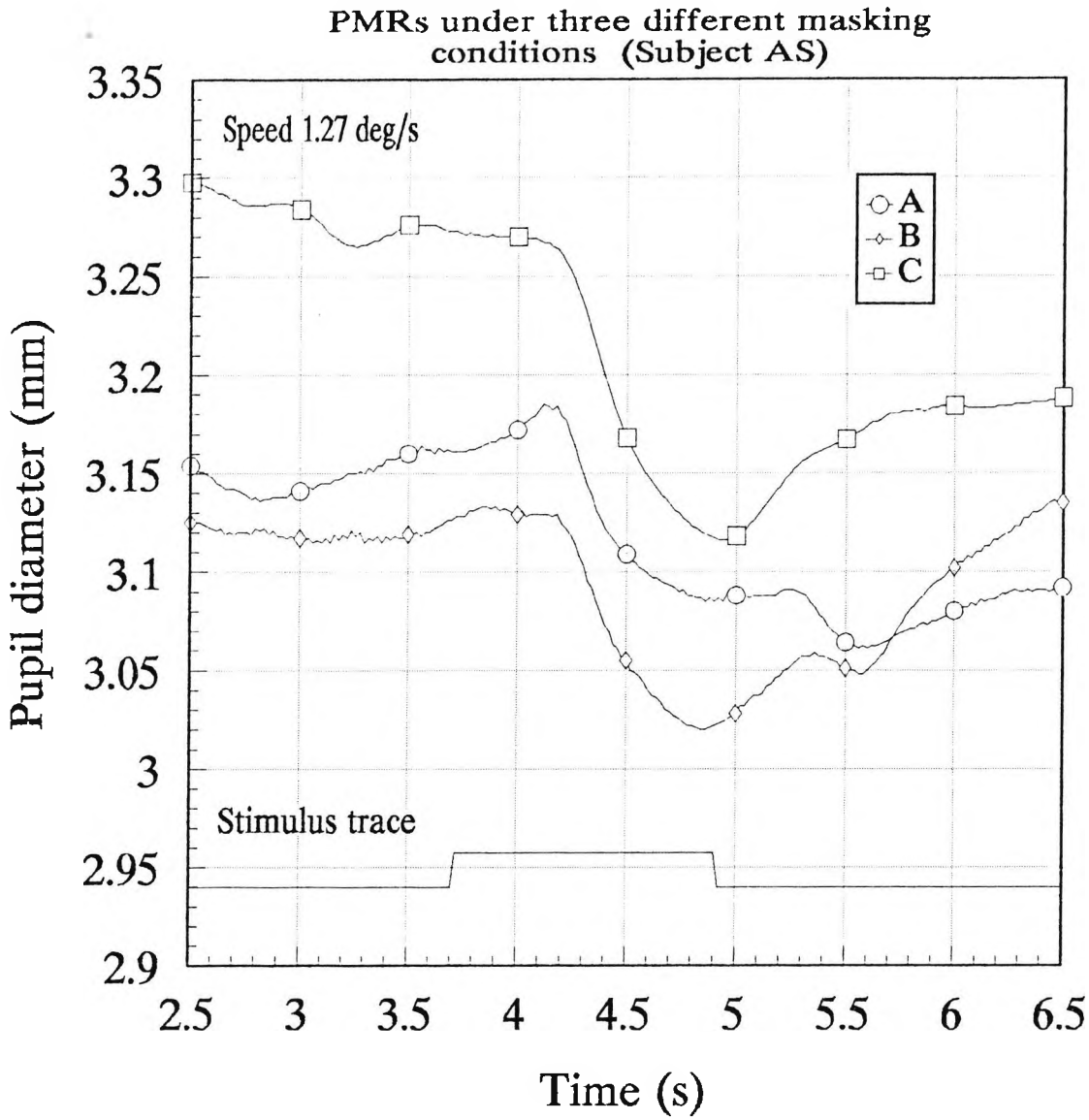


Figure 3.7: pupillary responses to coherent movement plotted as a function of time under three masking conditions. The traces show the responses obtained when the dynamic random movement formed by A: random step-size, in a random direction; B: constant step-size, in random direction with discontinuity on transition between the coherent and final random movement intervals; C: constant step-size in random direction and a smooth transition between the intervals. Each of the responses presented is the average of 64 measurements. The twin test pattern was viewed binocularly at a distance of 80cm. The dots and background luminances were 130 and 15.4 cd/m^2, respectively. Pupil noise standard deviation associated with the average of 64 traces is 0.00625.

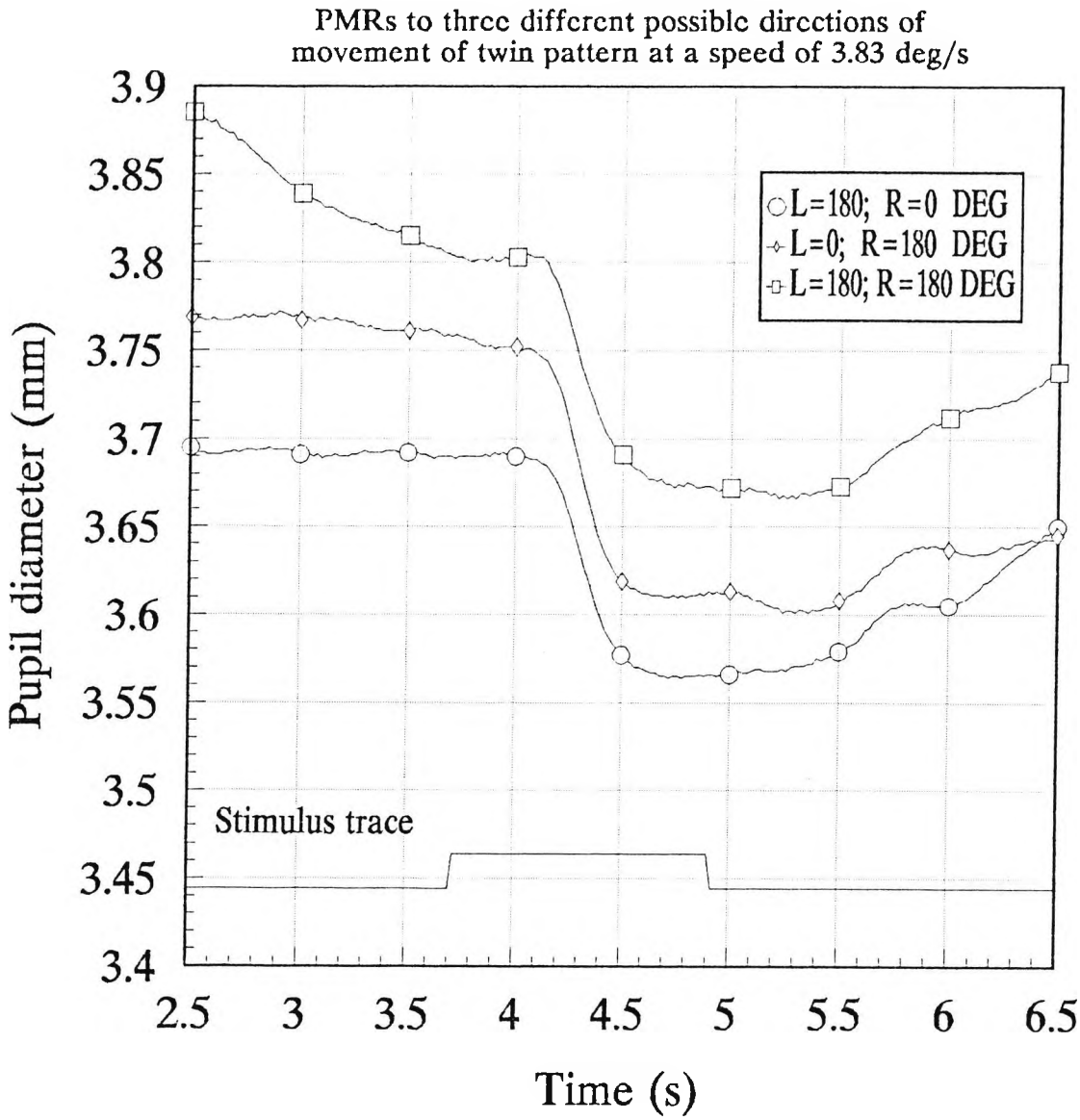


Figure 3.8: Showing the pupil motion responses to three different direction configurations using the twin pattern stimulus. Traces indicate the following conditions: open circles: coherent movement towards fixation; open diamonds: coherent movement away from the fixation points; and open squares: coherent movement in the horizontal direction for both left and right patterns. Each of the responses presented is the average of 64 measurements. The twin test pattern was viewed binocularly at a distance of 80cm. Pupil noise standard deviation associated with the average of 64 traces is 0.00707.

Results

Pupil motion responses were recorded in three subjects. The twin pattern was used as the stimulus and measurements were carried out for a range of coherent speeds. In all the measurements, the standard direction configuration was used, ie., movement along the horizontal meridian and away from the fixation points. Subjects viewed the twin test pattern binocularly at a viewing distance of 80cm. The background and test pattern dot luminances were 15.4 and 130 cd/m^2, respectively. The traces for these pupillary responses are shown in figures 3.9a,b &c. In all subjects and for each speed of movement, a small pupillary constriction was recorded at the onset of the coherent movement. Pupil motion responses are of a very small amplitude, therefore to obtain an adequate signal to noise ratio, a large number of traces need to be averaged. Each of the response traces shown is the average of 64 measurements.

Further experiments show that PMRs were also present when the test pattern was presented in the subject's peripheral visual field. These results are presented in the next chapter.

The response latencies for PMRs are in the range of approximately 400ms for the fast speeds to 500ms for the slow speeds. Pupil response amplitudes and latencies of the traces shown in figure 3.9a are extracted and plotted for a range of speeds in figure 3.9d. For the stimulus speeds above 1.27 °/s, neither parameter varies significantly for the range of speeds examined. It has been proposed that there are at least two distinct speed discrimination mechanisms, operating in slow (< 3 °/s) and fast (>3 °/s) speed range respectively (Barbur and Ruddock, 1980). The longer latency measured for the stimulus speed of 1.27 °/s, may have also been caused by the activity of a separate mechanism than those detecting movement at the high speed range. More measurements at the lower speed range are required to investigate this possibility. The best line fit through the data points shown on the response amplitude against latency graph, has a correlation coefficient of 0.73. The best line fit through the data points not including the 1.27°/s speed however has a correlation coefficient of 0.23. The low correlation coefficients show that there is no significant variation between the latency and pupil response amplitude for the range of speed examined.

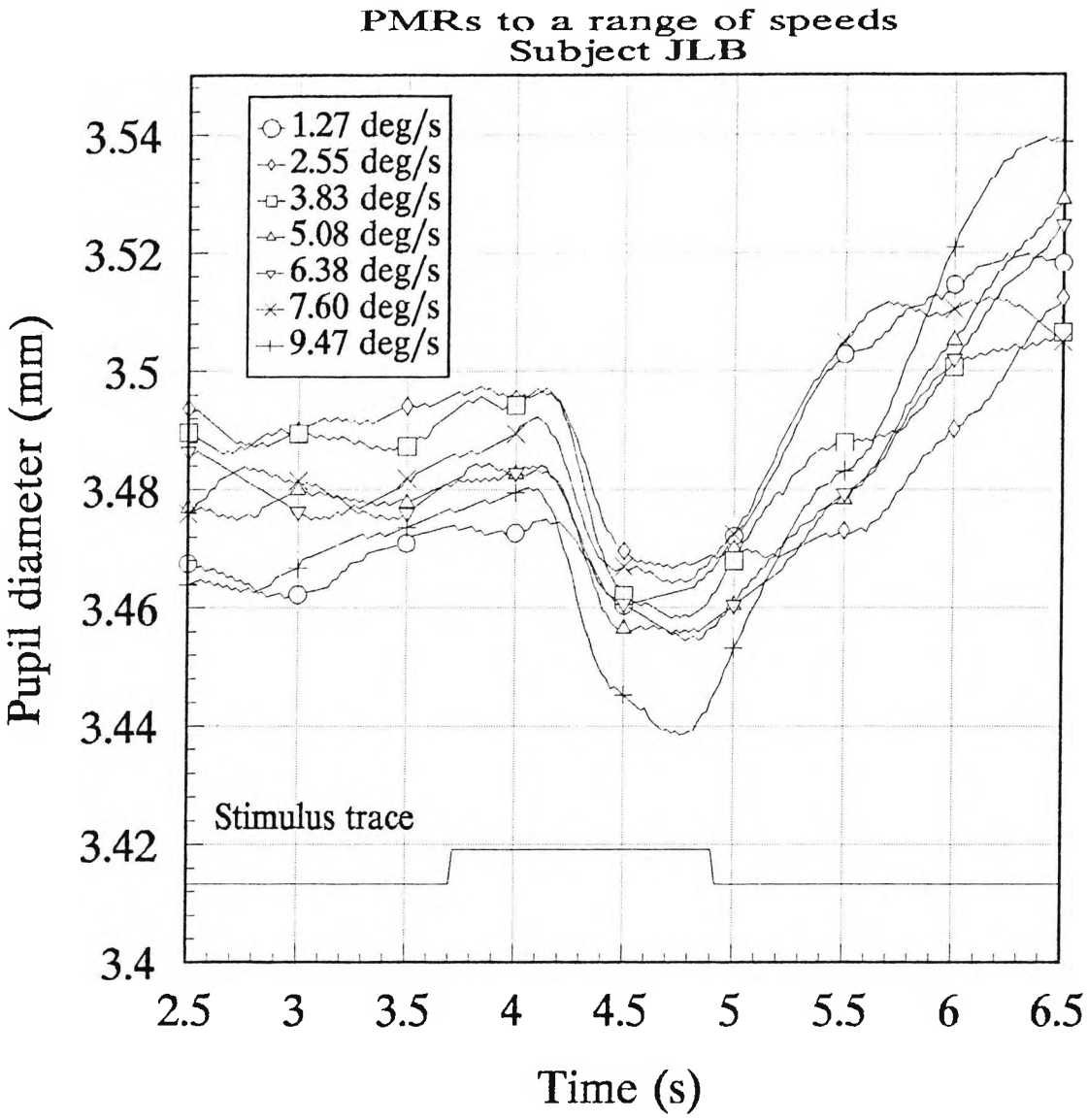


figure 3.9a: pupil motion responses plotted as a function of time for different speeds of movement. The twin test pattern was viewed binocularly at a viewing distance of 80cm. The dots and background luminances were 130 and 15.4 cd/m^2, respectively. The direction of the coherent movement was along the horizontal meridian and away from fixation. The duration of the preceding dynamic noise was 3.2s. The coherent movement lasted for 1.2s and was then followed by 2s of final dynamic noise. The rectangular pulse along the abscissa shows the time of stimulus presentation. Each of the responses presented is the average of 64 measurements. Pupil noise standard deviation associated with the average of 64 traces is 0.00612.

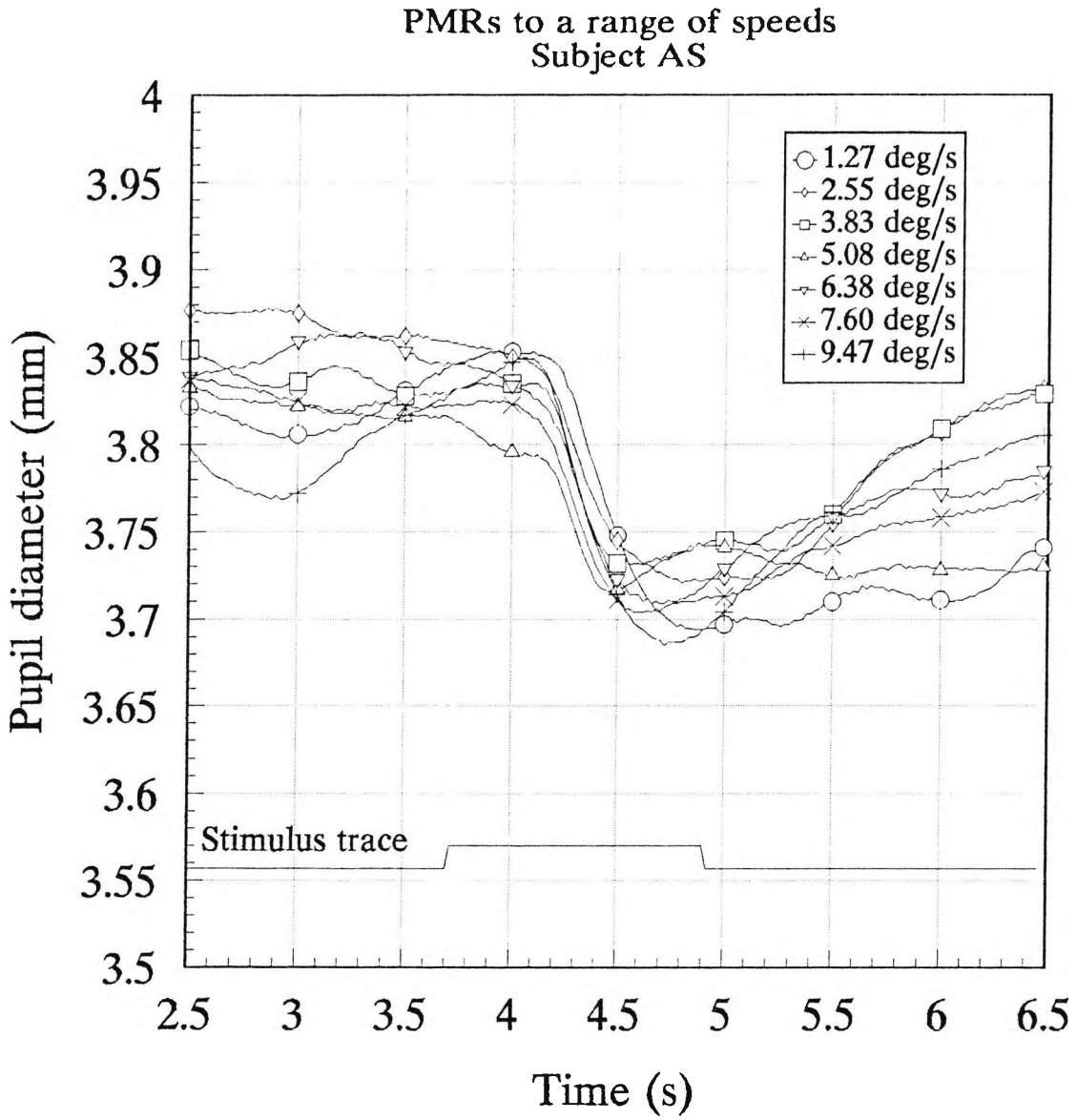


Figure 3.9b: pupil motion responses to a range of speeds (subject AS). The experimental conditions were the same as those described in caption to figure 3.9a. Pupil noise standard deviation associated with the average of 64 traces is 0.00685.

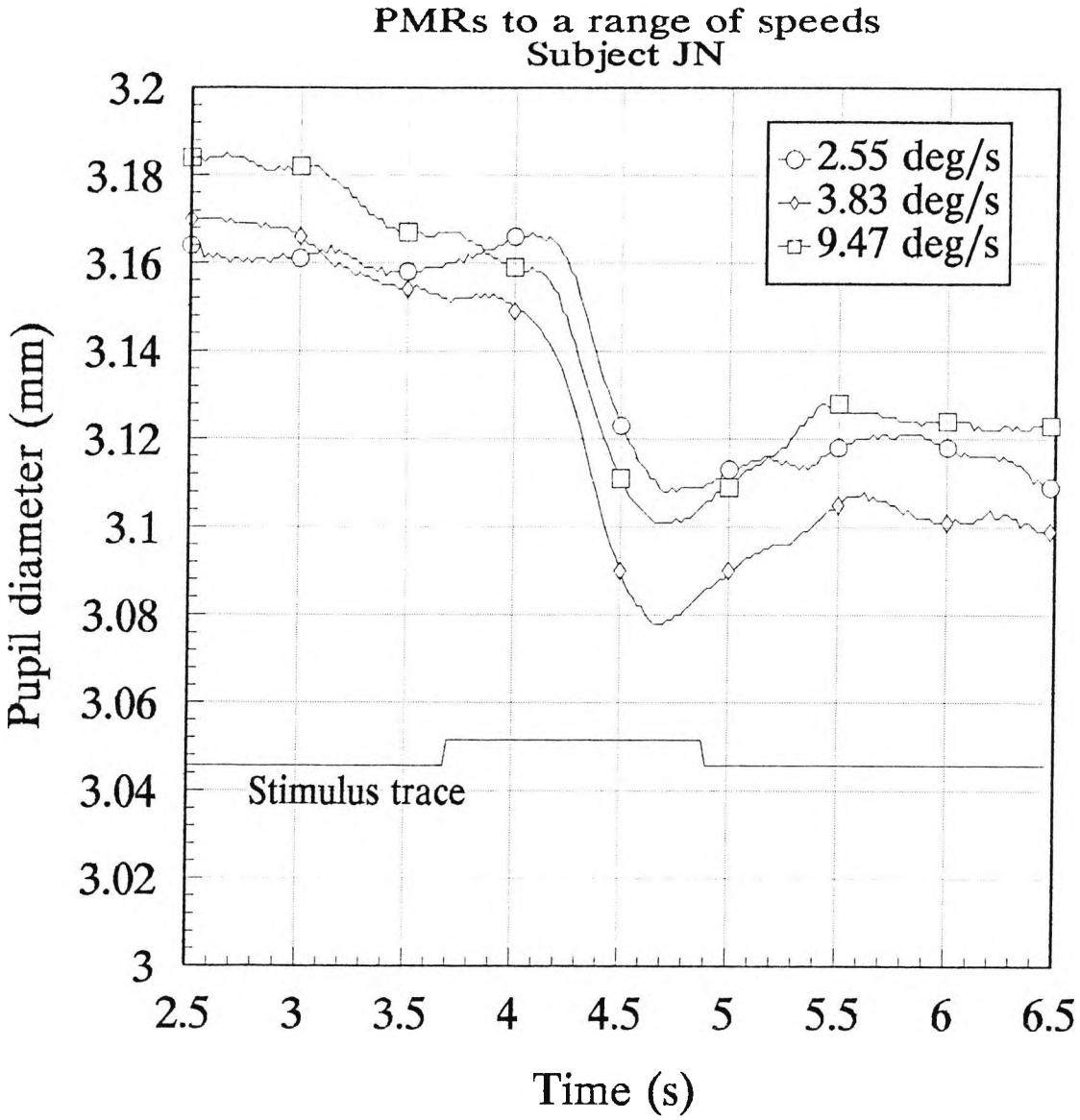
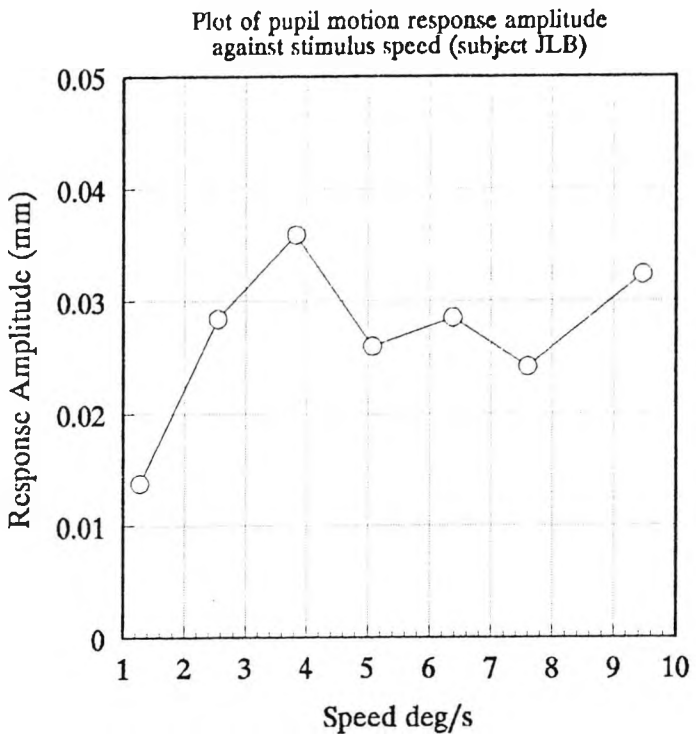
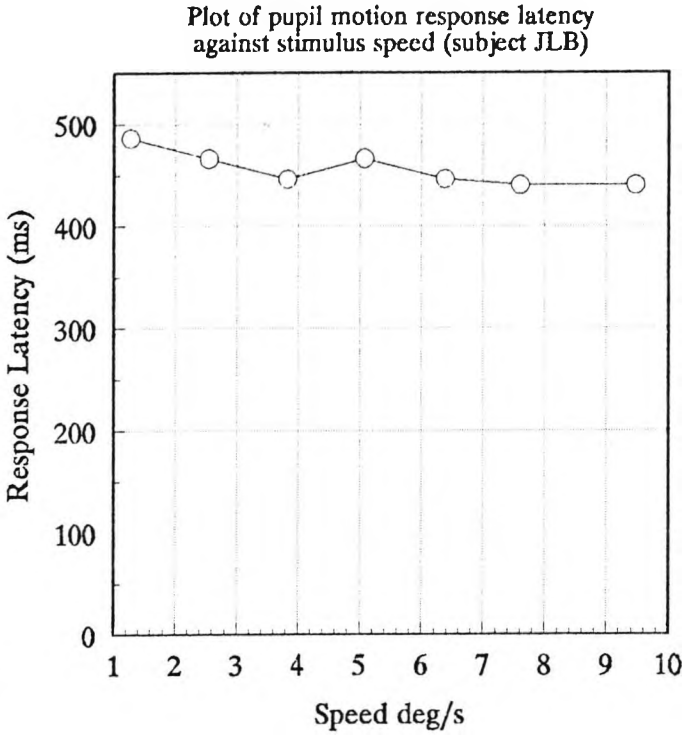


Figure 3.9c: pupil motion responses to a range of speeds (subject JN). The experimental conditions were the same as those described in caption to figure 3.9a. Pupil noise standard deviation associated with the average of 64 traces is 0.00354.





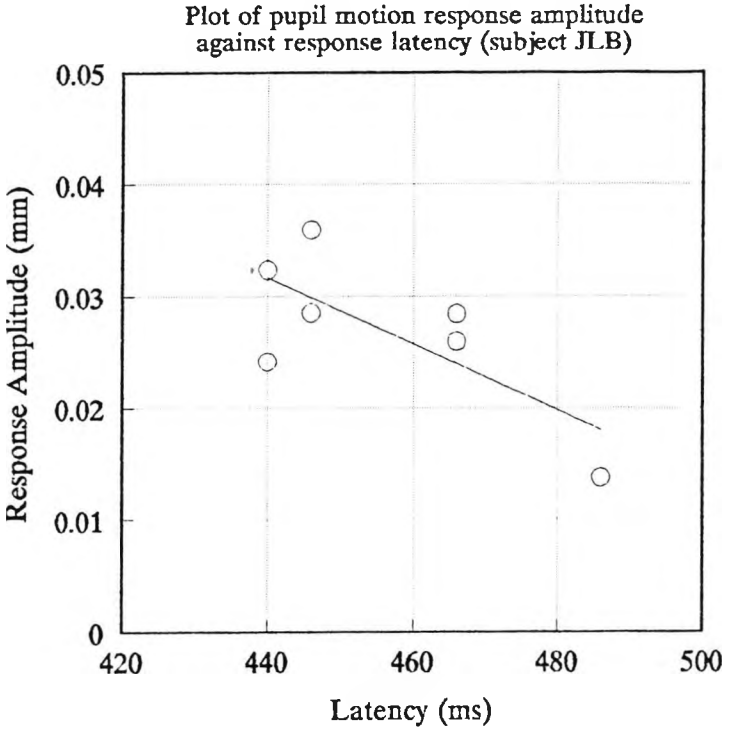


Figure 3.9d: plots of response amplitude and latency against speed, and plot of response amplitude against latency, extracted from the traces shown in figure 3.9a.

Effect of the State of Accommodation and Retinal Image Quality on PMRs

Experiments were carried out to investigate the effect of state of accommodation on PMRs. An observer, monocularly viewing the test pattern at a distance of one metre, wore a trial frame and various negative spherical corrections were placed in front of the subject's eye. PMRs were then measured for a range of spectacle correction. The results given in figure 3.10, show that the PMRs are independent of the state of accommodation.

The effect of placing positive spherical corrections in front of the subject's eye is one of blurring or degradation of the image quality. This however makes the fixation target blured and fixation unsteady. To study the effect of image degradation on PMRs therefore, an external fixation point was placed at various distances from the screen. At one metre distance an emmetrope would accommodate by one dioptre in order to obtain a sharp focus. By positioning the external fixation point at distances of 50cm and 30cm away, the subject was made to accommodate by 2 and 3 diopters, respectively resulting in degradation of the retinal image of the test pattern. The results given in figure 3.10, show that the presence of PMRs is independent of the image quality.

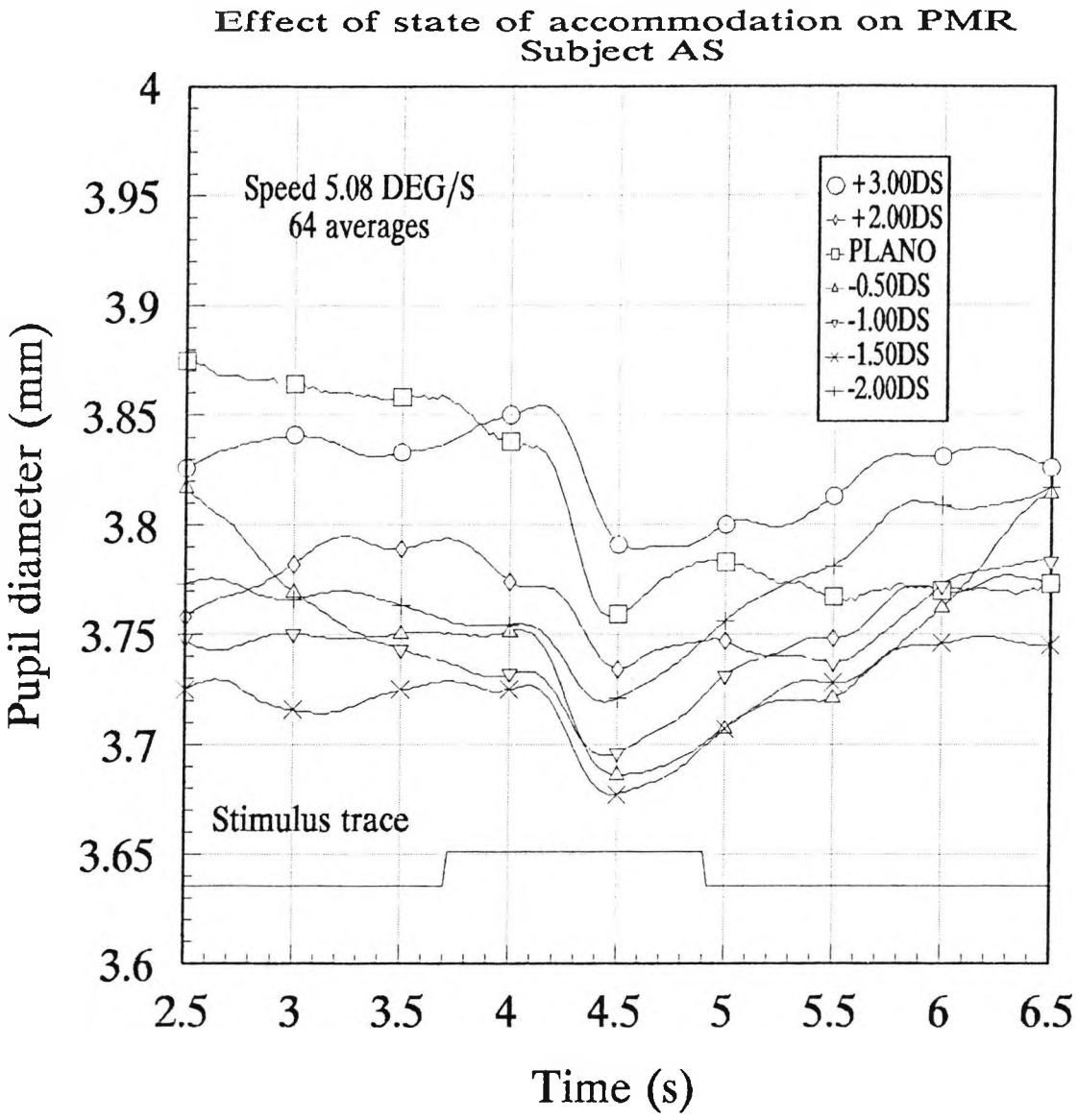


Figure 3.10: pupil motion responses under various states of accommodation. Subject (AS) wore a trial frame and PMRs were recorded for -1.00DS, -1.50DS and -2.00DS spectacle corrections. Using an external fixation at distance of 50cm or 33cm the subject was made to accommodate for +2D or +3D, respectively. The twin test pattern was viewed binocularly at a viewing distance of 1m. Other experimental conditions were the same as those described in caption to figure 3.9a. Pupil noise standard deviation associated with the average of 64 traces is 0.00685.

3.4 Pupil Motion Responses in a Hemianopic Subject

Having demonstrated the presence of a pupillary constriction to the on-set of coherent movement in normal subjects it is of great interest to investigate the possible mechanisms which mediate such responses. Whether the existence of PMRs is dependent on an intact geniculo-striate pathway was investigated by carrying out similar measurements on a subject with damaged primary visual area. The experimental methods and the results obtained are presented below.

Methods

Subject

The subject tested in this experiment, GY, has been investigated in several previous studies and his visual deficits have been documented (Barbur et al., 1980, 1988; Blythe et al., 1987; Weiskrantz et al., 1991). He has a complete right homonymous hemianopia with approximately 3° of macular sparing as a result of a road accident at the age of eight years. A comparison of field plots of the hemianopic field, taken immediately after the accident, some fourteen years later by Barbur et al. (1980) and in recent perimetric testing (Barbur, personal communication) show no significant change. A CT scan on this subject (Barbur et al., 1988) shows unilateral destruction of the left striate cortex.

GY is emmetropic and has no other loss of function following the accident.

Experimental Parameters and Results

The experimental conditions were similar to those used in the study of PMR in normal subjects (see section 3.3). A single pattern was placed in subject's blind field, the co-ordinates of which are shown in figure 3.4. The sighted field was tested by placing the fixation points on the right hand side of the pattern, at the same separation distances with respect to the centre of stimulus.

The stimulus speed was 9.47 °/s and the direction of coherent motion was horizontal, towards fixation, ie., towards the left and right when testing blind and sighted fields, respectively.

Figure 3.11 shows comparison of PMR measurements in the sighted and blind hemifields of GY. The traces shown for the blind and sighted hemifields are averages of 106 and 64 measurements, respectively. PMR measured in sighted hemifield was similar to those obtained in normal subjects. PMR is also present in GY's blind hemifield, although it is of smaller amplitude.

The pupil motion response in the blind hemifield is of low amplitude (ie., 0.02mm), but 3.8 times greater than the standard error of the measurement. The response amplitude is therefore statistically significant.

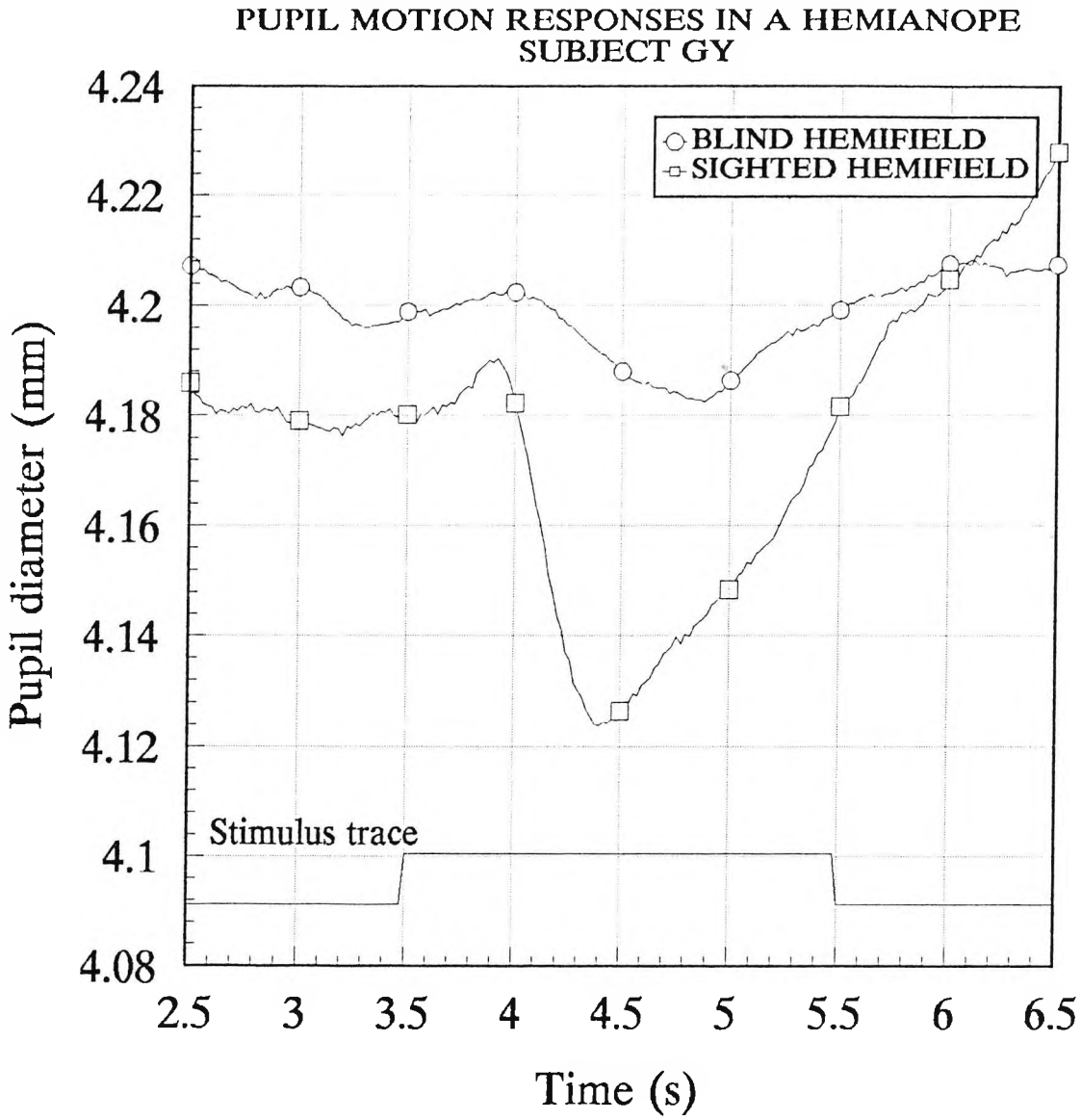


Figure 3.11: pupil motion responses in a hemianope (GY). The single test pattern was viewed binocularly at a viewing distance of 80cm. The speed of coherent movement was 9.47 °/s. Each of the responses presented is an average of 64 measurements. See text for the experimental conditions. Pupil noise standard deviation associated with the average of 64 traces is 0.00685.

3.5 Discussion and Summary

Recent investigations of vision in primates point towards a hierarchical model with multiple parallel and serial processors. Pupillometric studies show that changes of neuronal activity associated with many of these processes can effect the pupil size. The existence of these responses was postulated based on the hypothesis put forward to explain similar findings with respect to the onset of stimulus structure and colour (Barbur et al., 1986, 1987b). It may therefore be expected that changes in the neuronal activity caused by sudden onset of coherent motion could also give rise to perturbation of the supranuclear inhibitory input to the pupillomotor nucleus, resulting in a pupillary constriction.

As with any other pupillometric study, it was essential to ensure that the stimulus onset did not elicit a pupillary response via any other mechanisms, some of which are listed in section 1.5.

Two test patterns were designed in order to investigate the pupillary responses to movement information. It has previously been explained that changes in the temporal frequency of a uniform field could give rise to a pupillary response (see section 1.5). In order to ensure that the temporal contents of the stimulus were not altered at the stimulus on-set, dynamic noise intervals preceded and followed the coherent movement interval.

The existence of a pupil motion response in normal subjects was demonstrated. The results obtained show that the PMRs measured are elicited only to the onset of coherent movement. The response amplitude does not vary significantly for the range of speeds examined.

From the work carried out by Barbur et al. (1986, 1987a,b; see also Slooter and van Norren, 1980; Keenleyside, 1989) it was shown that the percentage change in pupil area was related to the spatial frequency of grating stimulus and that this could provide an objective measure of visual acuity. A pupillometric study of the processing of structure by a hemianopic subject (GY) showed no significant pupil grating responses (PGRs) in the blind hemifield (Barbur, unpublished observations). This suggests that an intact geniculo-striate pathway is necessary for producing PGRs (Keenleyside, 1989).

In order to determine whether the pupil motion responses were also dependent on an intact geniculo-striate projection similar measurements were carried out on a hemianopic subject (GY) with damaged primary visual area. The results obtained showedt blind hemifield, although the responses were of smaller amplitude when compared to those obtained in the normal hemifield.

Psychophysical evidence indicates that GY is sensitive to moving targets in his blind hemifield (Barbur et al., 1980, 1988; Blythe et al., 1987; Weiskrantz, 1990). He can localise moving targets and discriminate their speeds in forced-choice experiments (see section 1.4).
The pupillometric results obtained in this investigation parallel the extensive psychophysical data in movement sensitivity in blindsight.
There are at least two possibilities regarding the sources mediating PMRs. The first is that PMRs are of subcortical origin, ie., subcortical structures containing neurones which respond to moving stimuli, such as the superior colliculus and pulvinar may generate an inhibitory input to the pretectal nuclei resulting in a pupillary constriction. The second possibility is that PMRs reflect the activity of higher visual areas responsive to movement information such as V5 or MST. The coherent movement information may reach these areas via subcortical projections to the extrastriate cortex. It is not possible to distinguish between these two possible alternatives in GY. A distinction may however be possible, if similar experiments were carried out in hemispherectomised subjects.

Previous psychophysical findings relating to the effect of refractive error on the peripheral detection of motion and their interpretations are controversial. Some experimenters have shown that increasing the refractive error elevates the threshold for detection of a moving image (Leibowitz et al., 1972; Regan and Beverly, 1984) whilst others have argued that the effect is minimal (McKee and Nakayama, 1984). Leibowitz et al., (1972) noted that in the periphery, visual functions were generally degraded, but motion perception suffered least and small refractive errors could not eliminate the sensitivity to motion. The results presented in figure 3.10 show PMR traces obtained when the state of accommodation was altered.
At least two conclusions can be drawn from these PMR measurements. Firstly, the PMRs are not eliminated by degradation of image quality (refer to traces +2D & +3D) and secondly, they are not affected by the steady state of accommodation (refer to traces -0.5D, -1.0D, -1.5D & -2.0D). These findings together with those of Keenleyside (1989) which showed lack of accommodation and convergence changes with presentation of a range of visual stimuli (one of which was similar to those used in PMR experiments) suggest that the effect of accommodation and convergence changes cannot be used to explain the results obtained.
The PMR latencies are in the range of 400ms at fast speeds and are as high as 500ms at slow speeds.
The response latencies of 260-340 ms to achromatic gratings and 300-410 ms to

chromatic gratings have been reported (Barbur et al., 1986, 1987ab; Keenleyside, 1989). The longer latencies of PMRs possibly indicate the activity of more central visual areas.

In previous pupillometric studies longer latencies have been reported to stimuli of higher spatial frequencies. Similar effects have also been reported for visual evoked potentials (Parker and Salzmen, 1977) and reaction times (Breitmeyer 1975). In addition, adaptation to high spatial frequency stationary gratings elevates the contrast detection threshold of slow moving targets (Pantle 1970, see also section 1.12). It is possible that the processing of slow motion and the detection of high spatial frequencies may have similar or common neuronal processing.

CHAPTER IV

Effects of Changes in Stimulus Speed and Direction on the Pupil Motion Response.

4.1 Suprathreshold Measures of Visual Functions

Measures of visual performance are based usually on threshold responses whilst normal vision involves suprathreshold stimuli. At threshold levels, the responses of sensory mechanisms tend to be independent of one another, whereas, at suprathreshold levels they tend to interact (Sekuler and Levinson, 1974). Evidence for this interaction was demonstrated by the study of Levinson and Sekuler (1975) on direction specific mechanisms. They measured the threshold for a rightward moving grating after adaptation to two kinds of stimuli: a vertical rightward moving grating, and a combination of that same rightward grating with a similar grating, which moved leftward, forming a counterphase grating. Possible inhibition between mechanisms for opposite directions should make the counterphase grating less effective as an adapting stimulus than either of its components. They showed that the counterphase grating consistently produced less threshold elevation than was produced by its rightward component alone. This is evidence for direction specific inhibition.
Threshold measurements of adaptation produced by a moving target are consistent with the view that the threshold visual response is determined exclusively by the single most sensitive channel in a multiple channel system. The motion perception at suprathreshold levels is the result of activity in all the channels which respond above their individual threshold level, ie., the suprathreshold appearances result from the pooled activity of many or all responding channels (Sekuler, 1975). This pooled activity includes excitatory as well as inhibitory responses produced by the stimulus. Various methods have been devised to study the performance of visual mechanisms to suprathreshold stimuli. Some of these methods are outlined below.

Response Reaction Time Measurements
The reaction time of a subject to a change in a stimulus parameter is associated with the overall response of the visual mechanisms detecting the change (Ball and Sekuler, 1979; Sekuler et al., 1990).
Ball and Sekuler (1979) measured the reaction time to a change in the direction of

motion of random dot patterns in the presence of broadband and filtered directional noise. They found that the reaction time to the change in direction is elevated for all directions in the presence of directional noise. The directional tuning curve obtained for bandpass filtered noise showed that the reaction time is affected even for noise components 45° away, thus indicating that reaction time is affected by interactions between the direction selective mechanisms.

Sekuler et al. (1990) measured the reaction time to a change in the motion direction of a disc under two conditions; a) constant initial direction followed by a change in a random direction; b) random direction of motion followed by a change in a random direction. Experiments were carried out for various stimulus durations. The results showed that, for stimulus durations of <500ms, uncertainty about the initial direction can elevate reaction time for detecting a directional change. The visual system then extracts enough directional information within 500 - 700 ms stimulus durations to overcome the effect of this uncertainty. Thus, the visual system effectively normalises the perception of direction, so that the reaction times to many directions become equivalent to the reaction times to motion onset. They postulated that for short stimulus durations, the reaction time depends on the output of directionally specific mechanisms, a more time consuming process, whereas, at longer stimulus durations a temporal integration of directional information (normalisation) takes place which effectively reduces the task of detecting a change in the direction to a motion onset. The motion integration time of 500ms measured by Sekuler et al. (1990) is similar to the temporal integration in speed discrimination tasks obtained by Bowne et al. (1989) and Watamaniuk et al. (1989).

Interaction Between Moving Target and Grating Pattern (IMG) function

Measurements of threshold illumination levels for the detection of retinally non-localised moving targets show that the detection of a moving target is influenced by both the spatial and temporal modulation of the suprathreshold background field (Barbur et al., 1981). The relationship between the threshold illumination level and the spatial frequency of the suprathreshold background characterises the *interaction* between the *movement* detection and the background *grating*, and is designated the IMG function (Barbur and Ruddock, 1980).

Barbur and Ruddock (1980) showed that IMG functions have bandpass frequency responses and are found to be independent of other stimulus parameters such as target speed and size. IMG functions cannot be elicited by means of spatial frequency adaptation techniques, and they describe the spatial properties of the visual mechanisms which are at least partially different to those involved in the threshold

detection of grating patterns (Barbur, 1980, 1988).

Pupillary Responses to suprathreshold stimuli

Small systematic changes in the pupil diameter are elicited to a wide range of stimulus characteristics, some of which are attributed to a supranuclear inhibitory input to the pupillomotor nucleus (see section 1.5). Pupillary responses to changes in a stimulus parameter reflect the overall response of the visual system to the stimulus parameter examined. An example of this is demonstrated in the systematic pupillary constrictions associated with a shift in the chromaticity coordinate of the stimulus target in the x-y chromaticity space (Barbur et al., 1993; Birch et al., 1992). Using a random luminance modulation technique, the possible contribution of the pupil light reflex is eliminated. The amplitude of the pupillary response elicited is then proportional to the sensitivity of the subject to a shift in chromaticity in a particular direction. Measurements of these responses in colour anomalous subjects show that when the chromatic change is along the colour confusion lines, the pupillary responses are absent. Hence, when the visual system is unable to resolve the chromatic information, the pupillary responses diminish. This is strong indication that the response of the pupil reflects the overall performance of the visual system.

Barbur et al. (1987a,b) demonstrated the presence of pupillary changes in response to a stimulus structure. The interesting outcome of their experiments was that the pupil response amplitude varied systematically with the stimulus spatial frequency, such that, the shape of the pupil sensitivity function was comparable with the contrast sensitivity results. The contrast sensitivity data represent the overall performance of the visual system in detection of structures, and the results indicate that in a similar way the pupil response could be used to monitor objectively the processing of stimulus structure in human vision.

In the model described in section 1.12.1 and based on the psychophysical data cited, it has been hypothesised that to extract the motion information, the retinal image, in some stage of processing, is passed through orientation and direction selective filters. The velocity signal is also extracted by pooling outputs of a series of directionally selective velocity tuned mechanisms (see also Barbur, 1985).

The resolution of direction and speed tuning properties of the visual system can be demonstrated psychophysically (see section 1.11.1 and 1.12.1). It is of interest to investigate the existence of pupillometric correlates for these selectivities, using suprathreshold stimuli.

4.2 Aims of the Study

A large number of investigations have been cited, which show that the majority of neurones in the visual pathways are movement selective. The movement selective neurones can be divided into orientation, direction and speed selective categories, with the cells characteristically having one or a number of these properties (see section 1.11-13). The psychophysical literature cited supports the notion that the processing of motion information involves orientation, direction and speed tuned mechanisms. Since motion processing involves a large number of cells, it is possible that sudden changes in the pattern of neuronal activity caused by the onset of coherent motion could cause a transient perturbation of the inhibitory input to the pupillomotor nucleus, therefore, producing a small pupillary constriction. Indeed, the results of the experiments described in the previous chapter support this hypothesis.

Changes in stimulus parameters such as speed and direction of motion cause changes in the activity of neurones responsive to that parameter. Having demonstrated the existence of pupil motion responses, it was of interest to investigate whether these responses were also elicited in response to changes in stimulus direction and speed of movement. If such responses to suprathreshold stimuli existed then it may be possible to use these objective pupil motion response measurements to study the direction and speed tuning mechanisms with respect to changes in stimulus speed, direction and eccentricity.

4.3 Effect of Changes in Stimulus Direction on Pupil Motion Responses

Direction specific mechanisms must play an important role in the detection of the moving components of a complex image, and their interactions determine the global perception of moving stimuli. According to the hypothesis stated earlier regarding the presence of pupillary responses, a change in cortical activity would give rise to a small pupillary constriction, with the response amplitude proportional to the level of change in the neural activity induced.

A change in the direction of coherent movement results in a perturbation in cortical neural activity. In view of the presence of a large number of directionally tuned neurones in the visual system, the change causes the switching of activity from one set of neurones to another which in turn may be reflected in transient weakening of the supranuclear inhibition of the pupillomotor nucleus.

To study this hypothesis, the following experiments were carried out.

Methods

Isolating a pupil response to orientation from that to structure is not possible since it can be argued that the response to structure is a result of the pooled response of many orientationally selective cells. A moving grating would produce responses to a combination of motion and structure. In order to isolate the responses to direction and speed of motion therefore, random dot stimulus patterns similar to the ones used in the previous experiments were devised.

The stimulus pattern used to study the effect of change in the direction of motion on the pupil motion responses was the same as the twin pattern stimulus explained in chapter III. This stimulus configuration ensured a steady fixation and eliminated the possibility of any additional small involuntary eye movements being synchronised with the stimulus onset. As in the previous experiment, the speed of the dots was determined by changing the step-size at a given inter-presentation time interval. The step-size was determined prior to the experiment and was kept constant for both the pre- and post-stimulus dynamic noise intervals as well as the coherent movement intervals. The coherent movement interval was preceded and followed by dynamic noise intervals and was itself subdivided into two intervals, referred to as the initial and final coherent intervals. During the initial coherent movement interval, the movement of the twin pattern dots was set such that they moved along the horizontal meridian, and away from the fixation point. Motion along this direction was defined to be movement along the 0° axis. During the final coherent interval, the direction of motion of the dots was altered such that the dots were moving with the same speed but

along a different axis. The anti-clockwise rotation of the right hand pattern of the twin pattern stimulus was defined as the positive angle of rotation, and the clockwise rotation, a negative angle.

The movement direction of the left hand pattern was set to be along the same meridian as that on the right hand pattern but opposite in direction (see figure 4.1).

The durations of the initial dynamic noise, initial coherent interval, final coherent interval and final dynamic noise interval were 2014ms each. The timing diagram for the stimulus presentation is shown in figure 4.2.

To summarise, the experimental stimulus consists of the followings:

The initial dynamic noise interval, during which the dots move with the same speed but in random directions, followed by the initial coherent interval with the dots moving at an angle of 0° at the same speed for 2014ms. They then change direction and continue moving coherently along the new direction for a further 2014ms (final coherent interval) before changing to random movement at the start of the final dynamic noise interval.

Pupillary traces were recorded throughout the stimulus presentation.

Results

The pupil motion responses are expected to be elicited at the onset of the initial coherent movement interval as presented in the previous chapter. If the pupil also responds to the change in the direction of coherent movement, a second pupillary constriction would be expected.

The pupil motion responses to a change in the direction of coherent movement are shown in figure 4.3.

The pupil diameter is plotted against time for the eight traces, showing the responses to a range of direction changes from -90° to +90° at a stimulus speed of 6°/s. Each trace represents an average of 64 measurements. The subject viewed the twin pattern binocularly at a viewing distance of 80cm. The luminance of the dots and background were 130 and 15.4 cd/m^2, respectively.

The leading edge of the first step on the stimulus trace at the bottom of the graph represents the onset of the initial coherent interval and the leading edge of the second step represents the change in the direction of the coherent movement.

In all traces, there is a clear PMR to stimulus onset with a latency of approximately 450ms. As can be seen in the graph, there is clearly a small pupillary constriction associated with the change in the direction of motion. The latency of this small pupillary constriction is similar to the PMR latency.

In order to quantify the sensitivity of the pupil motion response to the change in the

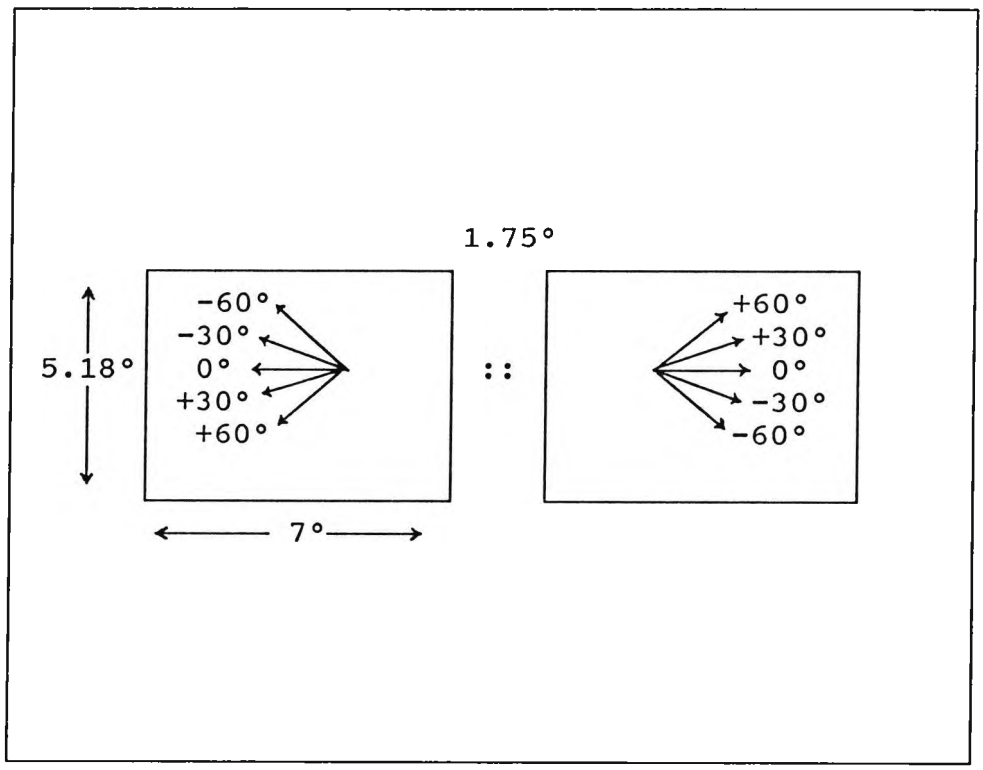


Figure 4.1: arrows show the direction of motion of the dots. During the initial coherent movement interval the direction of the dots was set to 0°. The direction was altered from 0° during the final random movement interval and pupillary responses were recorded.

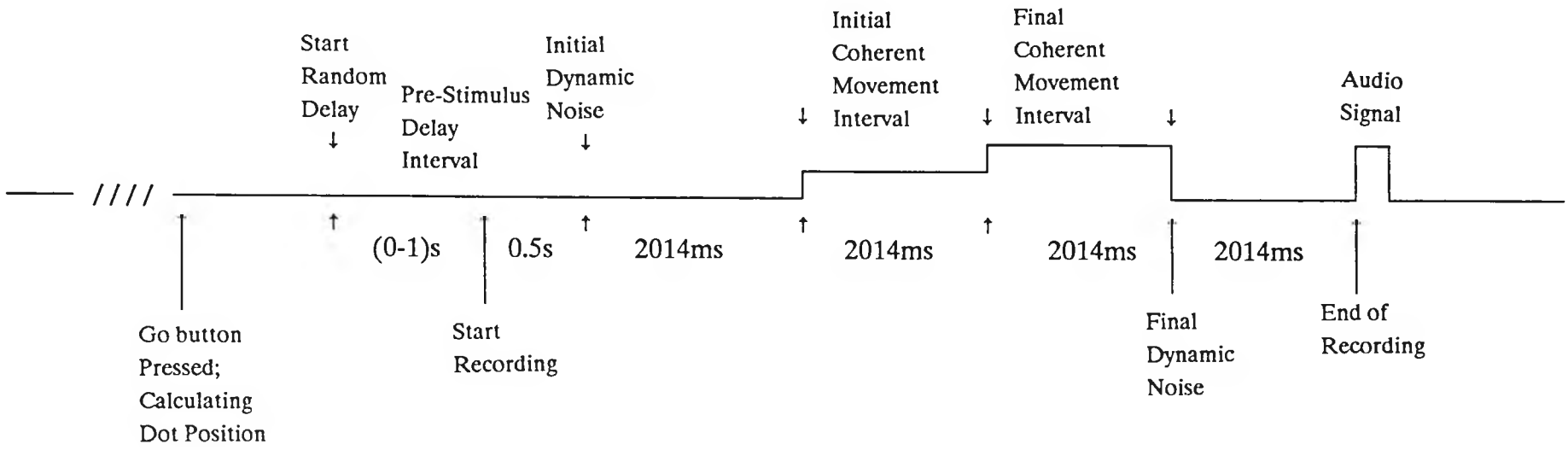


Figure 4.2: timing diagram of the experiments on the direction and speed tuning of PMRs

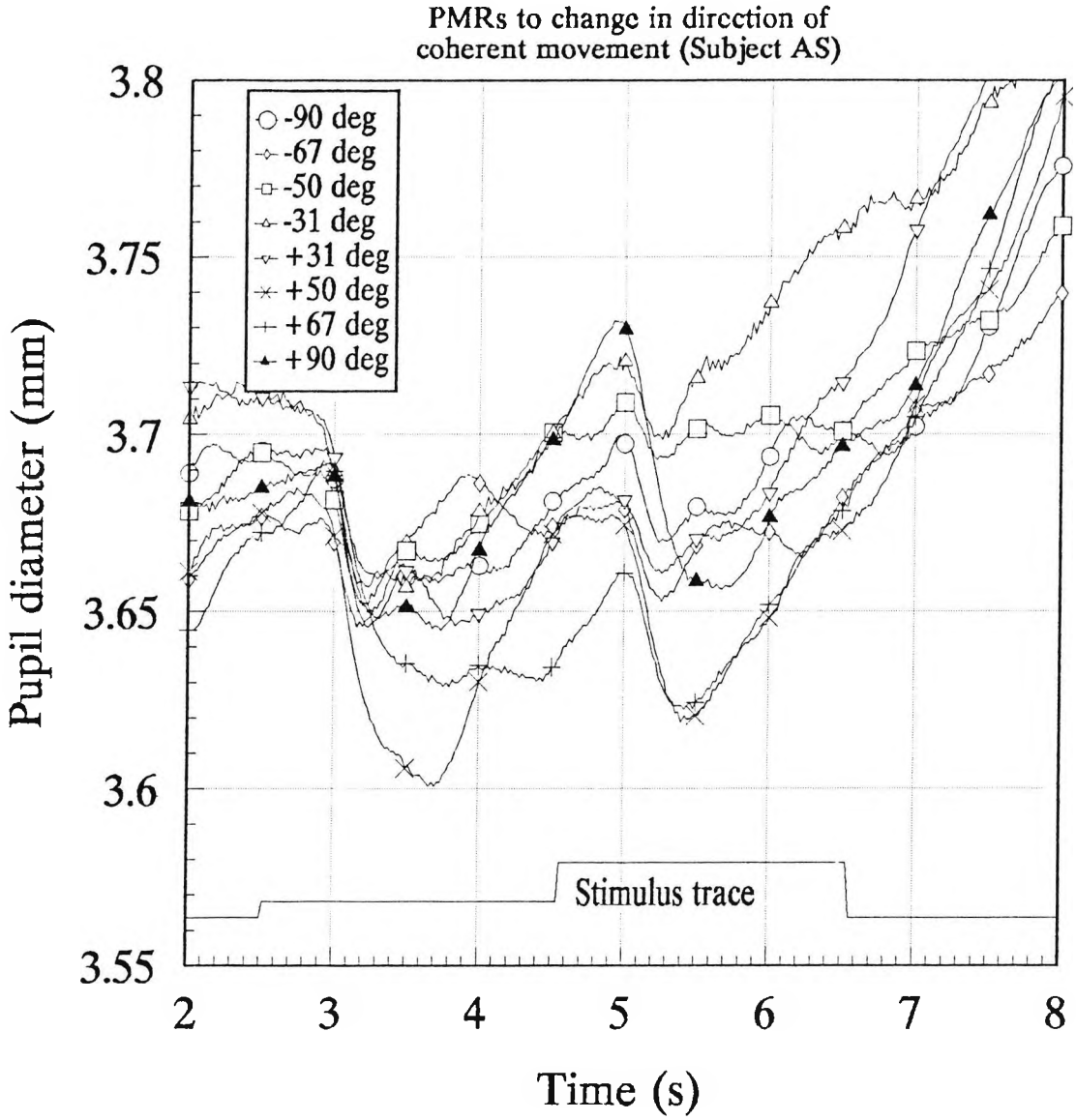


Figure 4.3: pupillary traces representing the pupil motion responses to a change in stimulus direction during the second part of the coherent interval. The pupil diameter is plotted against time. The direction of motion during the initial coherent movement interval was along 0° which was then altered for the final coherent interval. The altered directions are indicated on the graph by various symbols. The speed of the pattern dots was 6 °/s. Each trace shown is an average of 64 measurements. The twin test pattern was viewed binocularly at a viewing distance of 80cm (subject AS). The dot and background luminances were 130 and 15.4 cd/m^2, respectively. The first step on the stimulus trace at the bottom of the graph represents the onset of the initial coherent interval and the second step represents the change in direction of the coherent movement.

direction of coherent motion, a ratio of the response amplitude to the change in the direction, and the initial PMR amplitude can be calculated. The noise variance associated with each pupillary response can be calculated (Barbur, 1992). The variance of response ratios may then be calculated by standard statistical formula (Barford, 1967). A plot of the PMR ratios due to change in the direction of coherent movement for a range of directions is shown in figure 4.4 and the error bars represent twice the standard deviation. When there is no change in the direction of the coherent motion, then the second response is absent and consequently, the response ratio will be zero. Using the present experimental arrangement, it was not possible to measure the pupillary responses to directional changes of smaller angular intervals.

If a bandwidth for the sensitivity of the PMR to the change in direction is defined as the change which would give rise to a pupillary constriction with the response amplitude equal to 50% of that of the initial PMR, then the estimated bandwidth of the directional tuning of the pupillary responses would be less than 30°.

Experiments were also carried out to show that responses to a change in the direction of the coherent movement exist for a range of speeds. Such responses for a direction change of +50° was obtained for a range of speeds and is given in figure 4.5.

Using the single pattern described in chapter III, pupil motion responses to a change in the direction of coherent motion were investigated while the pattern was placed at 5° eccentricity in the right temporal field of the subject. The direction change of the coherent motion was from 0° to -90° and measurements were carried out for two speeds. The results are plotted in figure 4.6. They show that the PMRs are sensitive to the change in direction of motion, even when the pattern is at 5° eccentricity. In addition, from this measurement, it can be concluded that the change in direction does not have to be an axial change to produce a pupillary response.

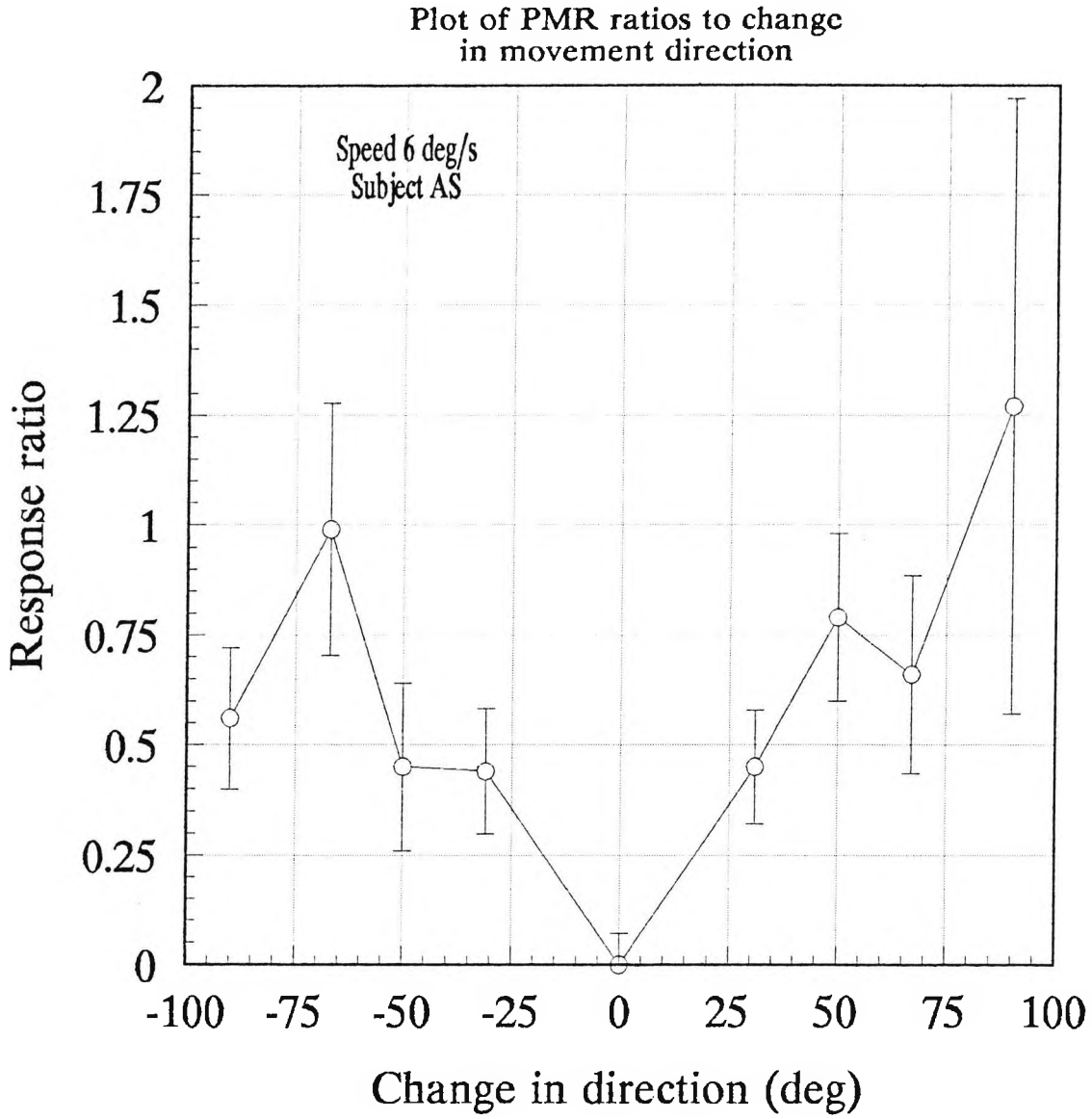


Figure 4.4: plot of the ratio of pupil motion response amplitudes of the second constriction due to the change in the direction, against that due to the coherent motion onset, for a range of direction changes (subject AS). These values were calculated from the traces in the previous graph. The error bar plots two standard deviations. The standard deviation of the ratio of the amplitudes is based on the noise variance extracted from the average of measurements and computed according to formula described by Barford (1967).

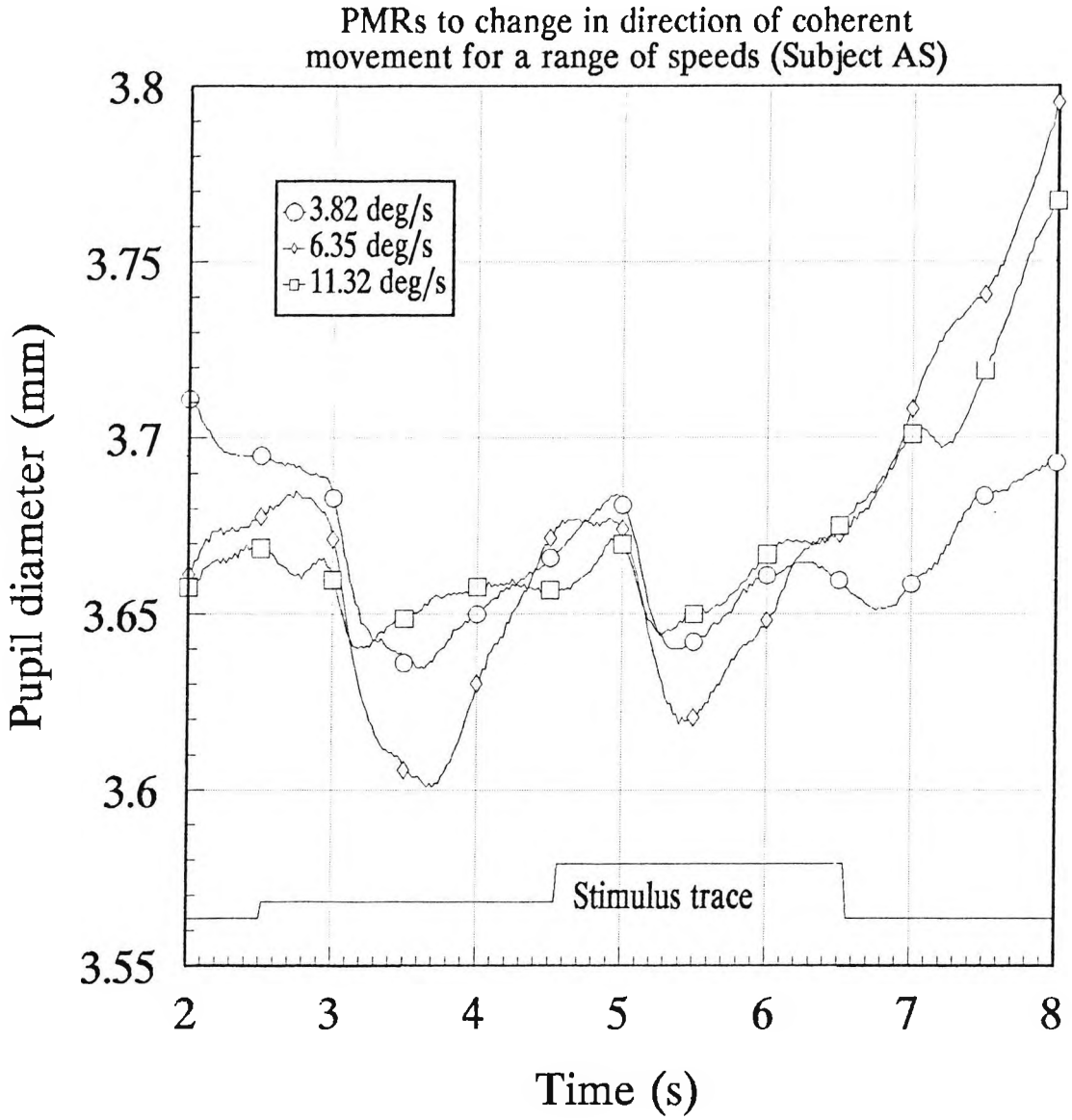


Figure 4.5: pupillary traces representing the pupil motion responses to a change in stimulus direction of +50° during the second part of the coherent interval for a range of speeds. For experimental conditions refer to main text. Pupil noise standard deviation associated with the average of 64 traces is 0.00901.

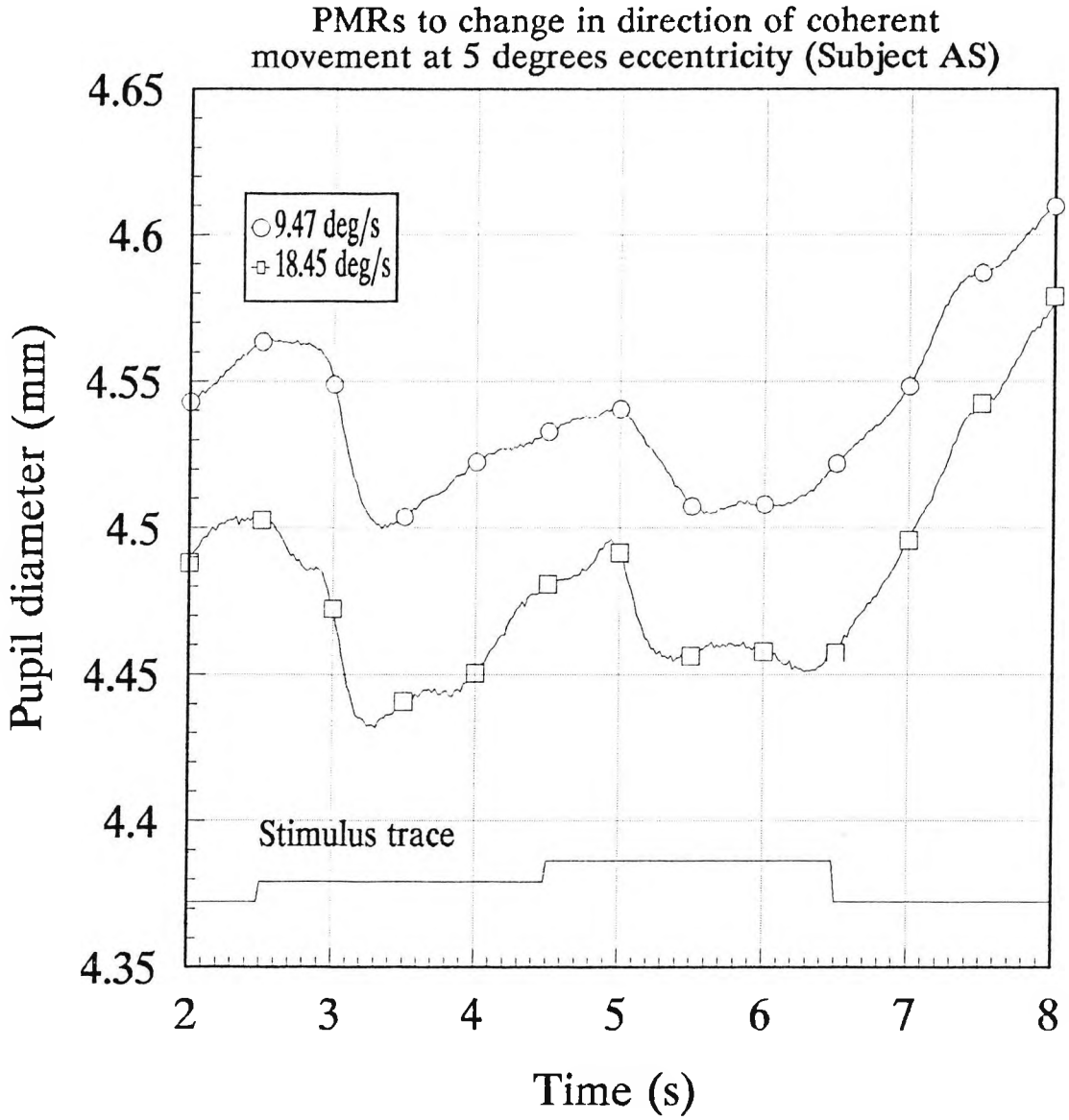


Figure 4.6: pupillary traces representing the pupil motion responses to a change in stimulus direction of -90° during the second part of the coherent interval for two speeds when the stimulus pattern was placed at 5° eccentricity. For experimental conditions refer to main text. Pupil noise standard deviation associated with the average of 64 traces is 0.00968.

4.4 Effect of Changes in Stimulus Speed on Pupil Motion Responses

Earlier, evidence was given in support of the notion that speed is a primary dimension of sensory coding (see section 1.13.1). In this chapter, some literature has been cited in support of a theory of motion perception which relies on the existence of many overlapping speed tuned detectors within each directionally selective mechanism. The stimulus speed is then pooled from the output of these detectors (see Barbur, 1985). Psychophysical data on the speed discrimination shows that a Weber fraction of 5% holds for a wide range of speeds. Physiological data also exist relating to the presence of these velocity tuned neurones. A change in the speed of a moving pattern would result in a change in the output of the speed tuned mechanisms. A change in the speed tuned mechanisms output is a result of alterations in the underlying neural activity.

Following experiments were carried out to investigate the effect of change in stimulus speed on the pupil motion response.

Method

The stimulus pattern used to investigate speed selectivity was similar to the one used in the study of PMRs and the pupillometric assessment of the directional tuning, except that the step-size was varied in order to change the speed of the coherent movement during the final coherent motion interval.

The stimulus consisted of an initial dynamic noise interval which was preceded by a random delay interval and followed by an initial coherent movement interval of the same step-size. After this, was the final coherent movement interval during which the speed of the dots was varied. The stimulus was then terminated with a dynamic noise interval of the same step-size as the preceding final coherent movement interval.

All the measurements were obtained with the stimulus patterns moving along the horizontal meridian and away from the fixation points during both coherent intervals. The step-sizes used during the dynamic noise intervals matched the ones in the neighbouring coherent movement intervals. The timing diagram and the duration of intervals were similar to those given previously in figure 4.2.

To increase the signal to noise ratio, 64 measurements were recorded and averaged for each configuration examined.

The subject viewed the stimulus pattern binocularly at a viewing distance of 80cm. The dots and the background luminances were 130 and 15.4 cd/m^2, respectively.

Results

Figure 4.7 shows the pupillary traces obtained. The pupil diameter is plotted against time, and the second step on the stimulus trace at the bottom of the graph indicates the second coherent interval, ie., the change in speed indicated by the leading edge of the step.

The stimulus speed during the initial coherent interval (primary speed) was 3.82 °/s and responses to a range of speeds of the final coherent movement (secondary speeds) were measured. A pupil motion response is associated with the onset of the coherent movement in the initial coherent movement interval.

The results show a clear constriction response to a change in the speed of the coherent movement. Responses exist for both decrement and increment in stimulus speed. The response latencies due to the change in stimulus speed are similar to those of the PMR.

In order to quantify these responses, a method similar to that used in the previous section was implemented. The ratio of the responses to the onset of the secondary speed and to the primary speeds was calculated for each speed change examined and these values were plotted against the percentage change in the speed, as shown in figure 4.8. The variance of the response ratio is also calculated as in the previous section and the error bars represent twice the standard deviation for each data point. The second response is absent when there is no change in stimulus speed during the final coherent movement interval. This is shown by the minimum point on the graph (response ratio= 0). In this experimental arrangement, the stimulus speed can have a set of discrete values as shown on the graph.

The experimental results show that the speed tuning properties of the visual system are also reflected in the pupil motion responses. It is shown that at a primary speed of 3.82°/s, the amplitude of the response to a change in stimulus speed reaches approximately 50% of the PMR amplitude when the change in stimulus speed is less than 30% of the initial speed.

Figure 4.9 and 4.10 show a set of results for a primary speed of 7.6°/s. Pupillary responses to a change in stimulus speed are also present at this speed. In this case the amplitude of the responses reaches 50% of the PMR amplitude at a 58% reduction in speed. Due to technical constraints it was not possible to measure responses to an increase in stimulus speed at a primary speed of 7.6°/s.

The two sets of results given demonstrate the existence of pupillary responses to a change in stimulus speed. The amplitude of the responses to a change in speed increases with a progressively larger deviation from the primary speed.

To demonstrate that the responses obtained are not due to luminance changes across

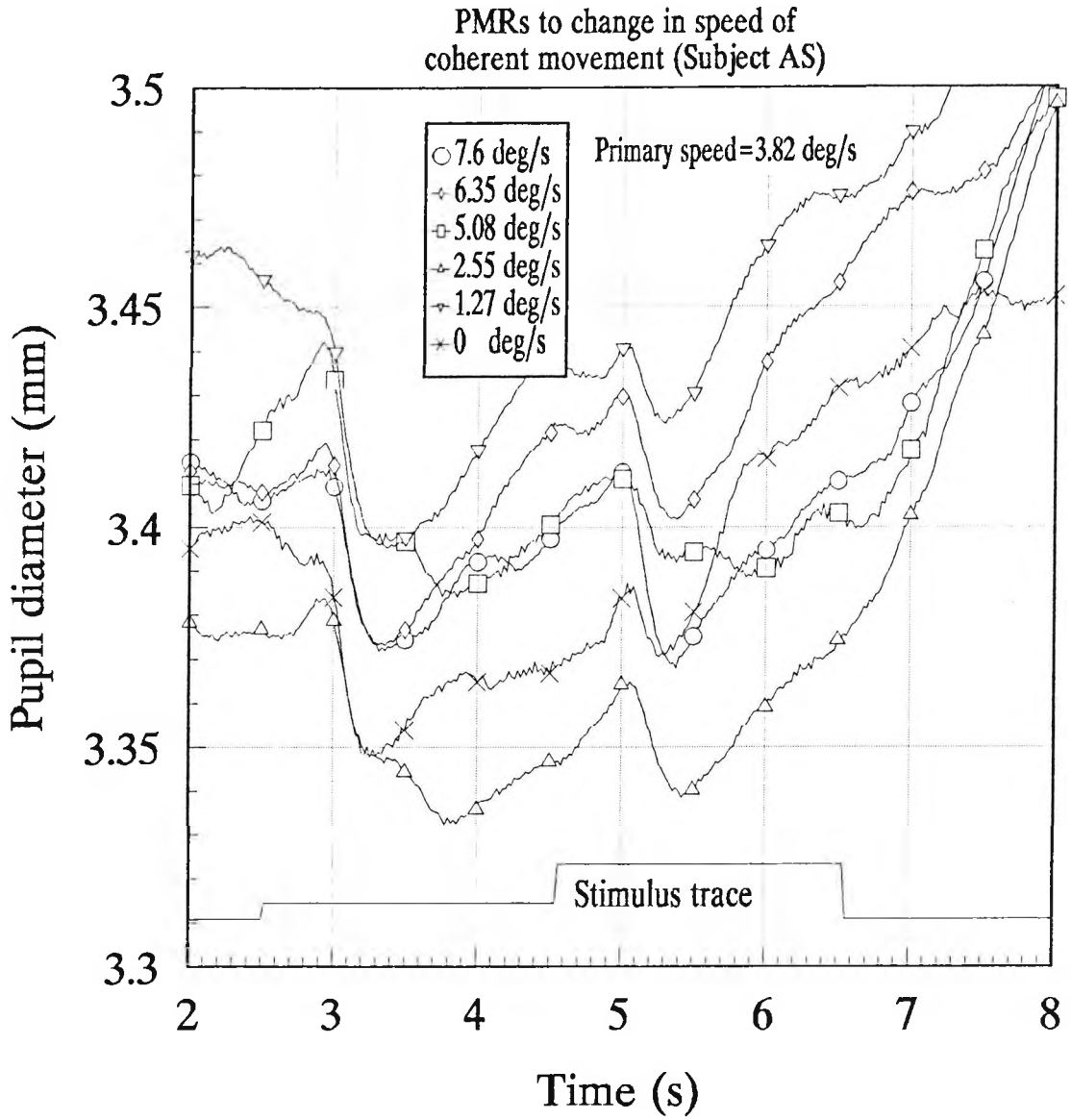


Figure 4.7: pupillary traces representing the pupil motion responses to a change in stimulus speed during the second part of the coherent interval. The pupil diameter is plotted against time. The direction of motion during both coherent movement intervals was along the horizontal meridian and away from the fixation points. The speed of the pattern dots was altered during the final coherent interval. The altered speeds are indicated on the graph by various symbols. The primary speed of the coherent pattern was 3.82 °/s. Each trace shown, is an average of 64 measurements. The twin test pattern was viewed binocularly at a viewing distance of 80cm (subject AS). The dot and background luminances were 130 and 15.4 cd/m^2, respectively. The first step on the stimulus trace at the bottom of the graph represents the onset of the initial coherent interval and the second step represents the change in speed of the coherent movement.

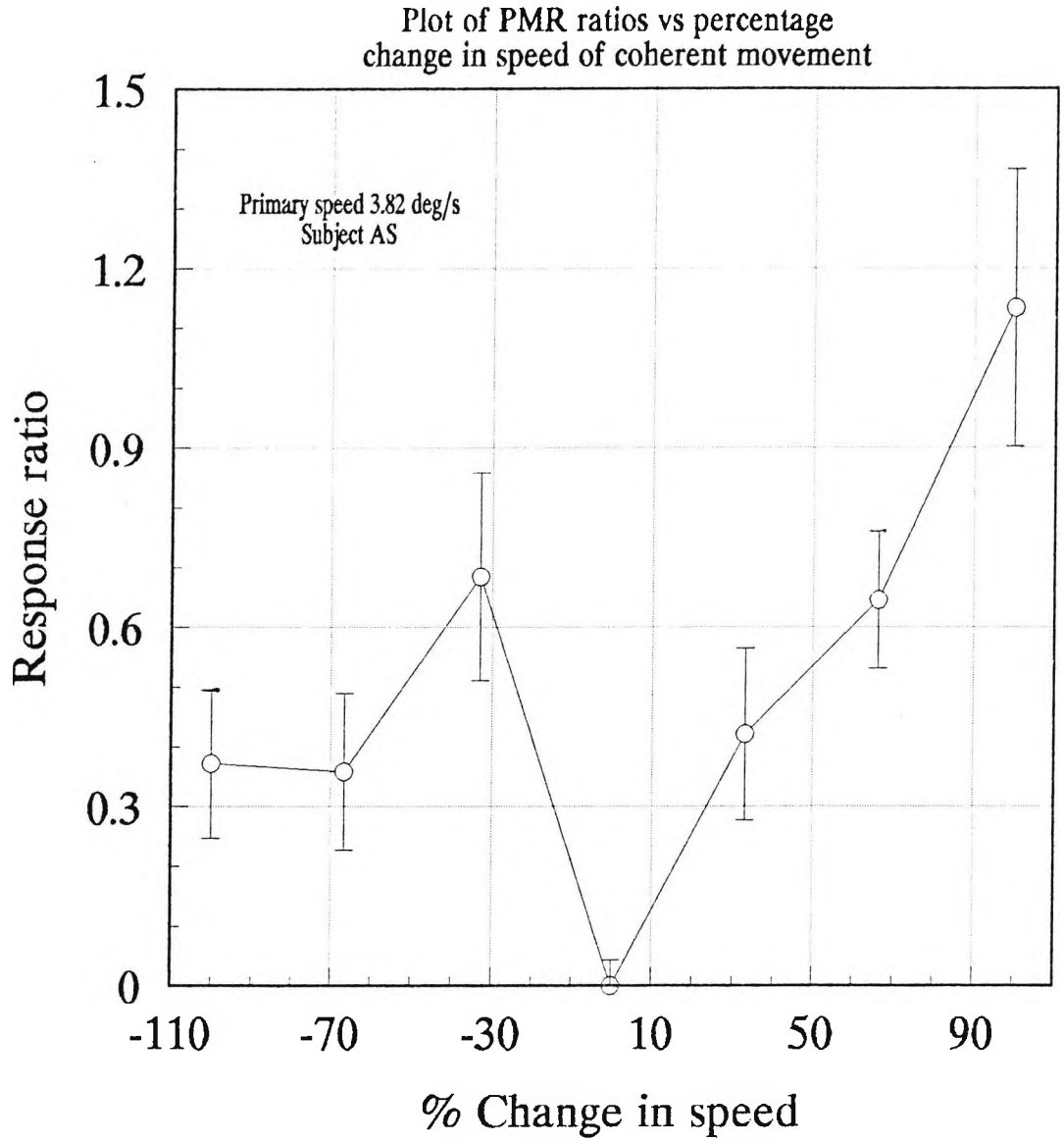


Figure 4.8: plot of the ratio of the pupil motion response amplitudes of the second constriction due to a change in the stimulus speed, against that due to the coherent motion onset, for a range of secondary speeds (subject AS). These values are calculated from the traces in the previous graph. The error bar plots two standard deviations. The standard deviation of the ratio of the amplitudes is based on the noise variance extracted from the average of measurements and computed according to formula described by Barford (1967).

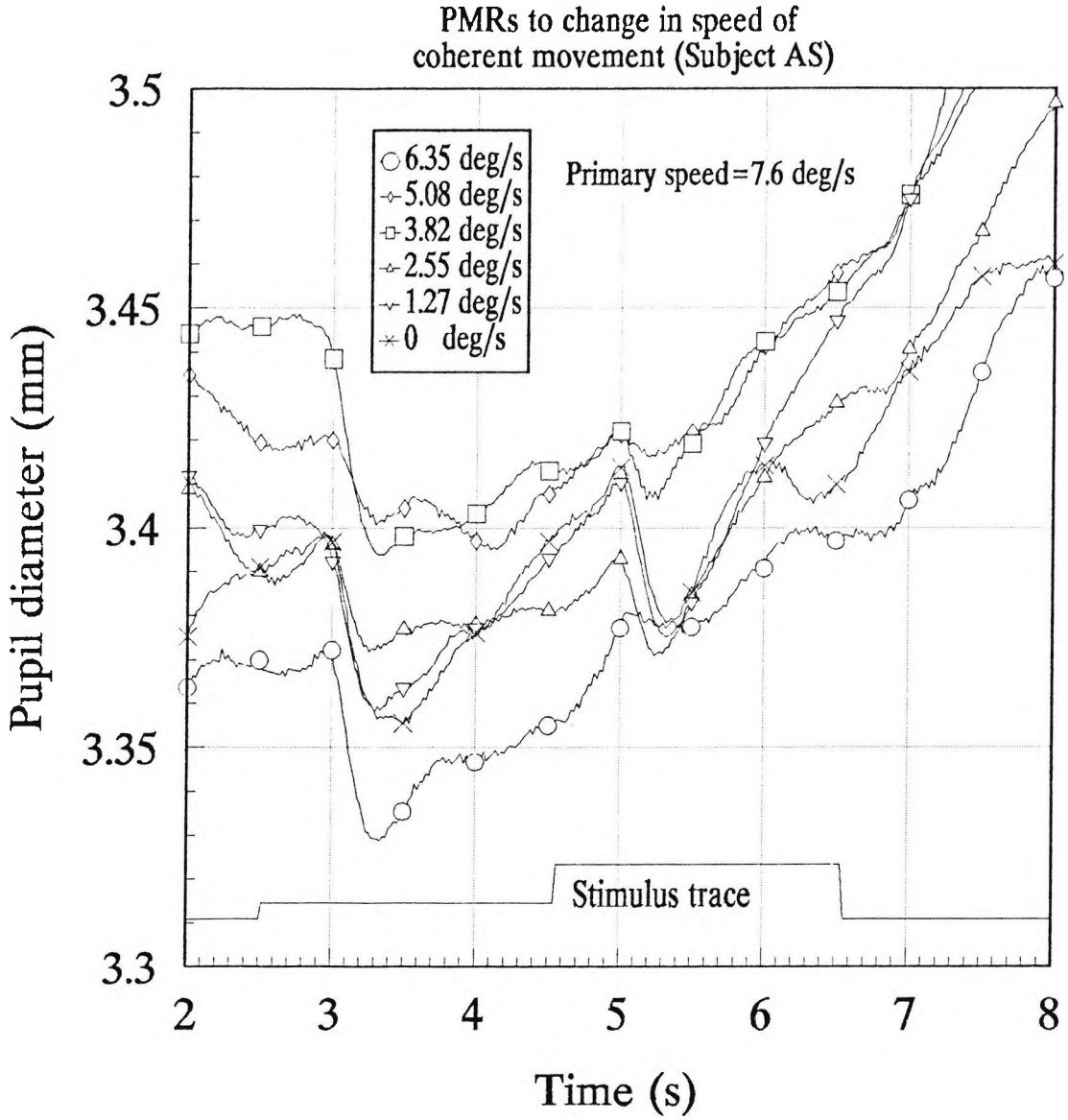


Figure 4.9: pupillary traces representing the pupil motion responses to a reduction in the stimulus speed during the second part of the coherent interval. Experimental conditions were the same as those described in figure 4.7.

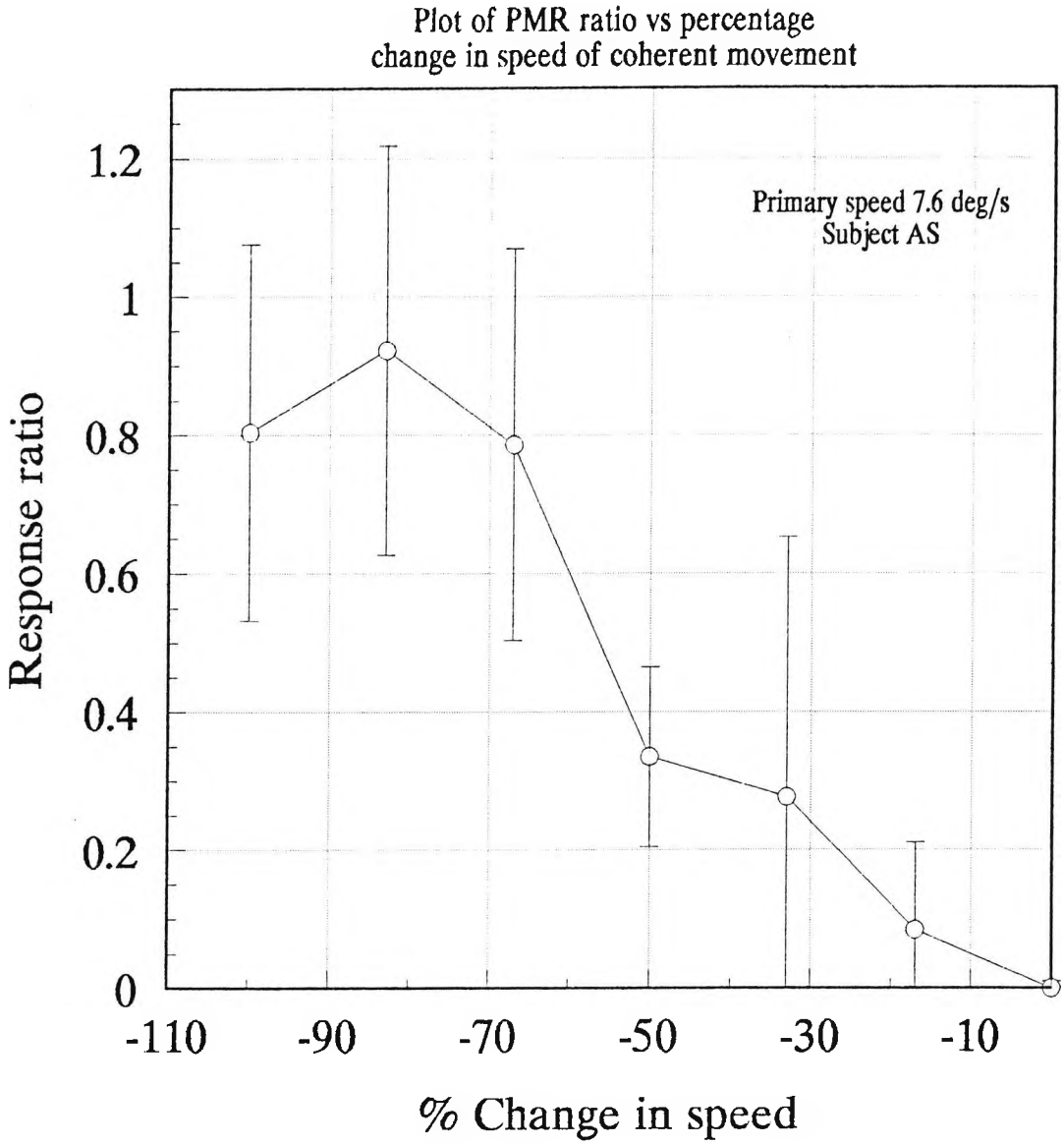


Figure 4.10: plot of the ratio of the pupil motion response amplitudes of the second constriction due to the change in stimulus speed, against that caused by the coherent motion onset, for a range of secondary speeds (subject AS). These values are calculated from the traces in the previous graph. The error bar plots two standard deviations. The standard deviation of the ratio of the amplitudes is based on the noise variance extracted from the average of measurements and computed according to formula described by Barford (1967).

the stimulus pattern giving rise to a pupillary constriction via the pupil light reflex, measurements were carried out for a change in the stimulus speed from 7.6°/s to 1.27°/s and vice versa. If any of the transitions caused an increase in the apparent stimulus pattern brightness resulting in a constriction of the pupil, then the inverse should result in a pupillary dilation due to a brightness reduction. The results shown in figure 4.11 demonstrate that pupillary constrictions occurred in both circumstances therefore, indicating that the responses obtained are not caused by a luminance change, and they reflect the activity of the speed selective mechanisms.
Collectively, the results obtained are in agreement with the prediction that a change in the speed of coherent movement should give rise to a systematic pupillary response due to changes in the underlying neural activity.

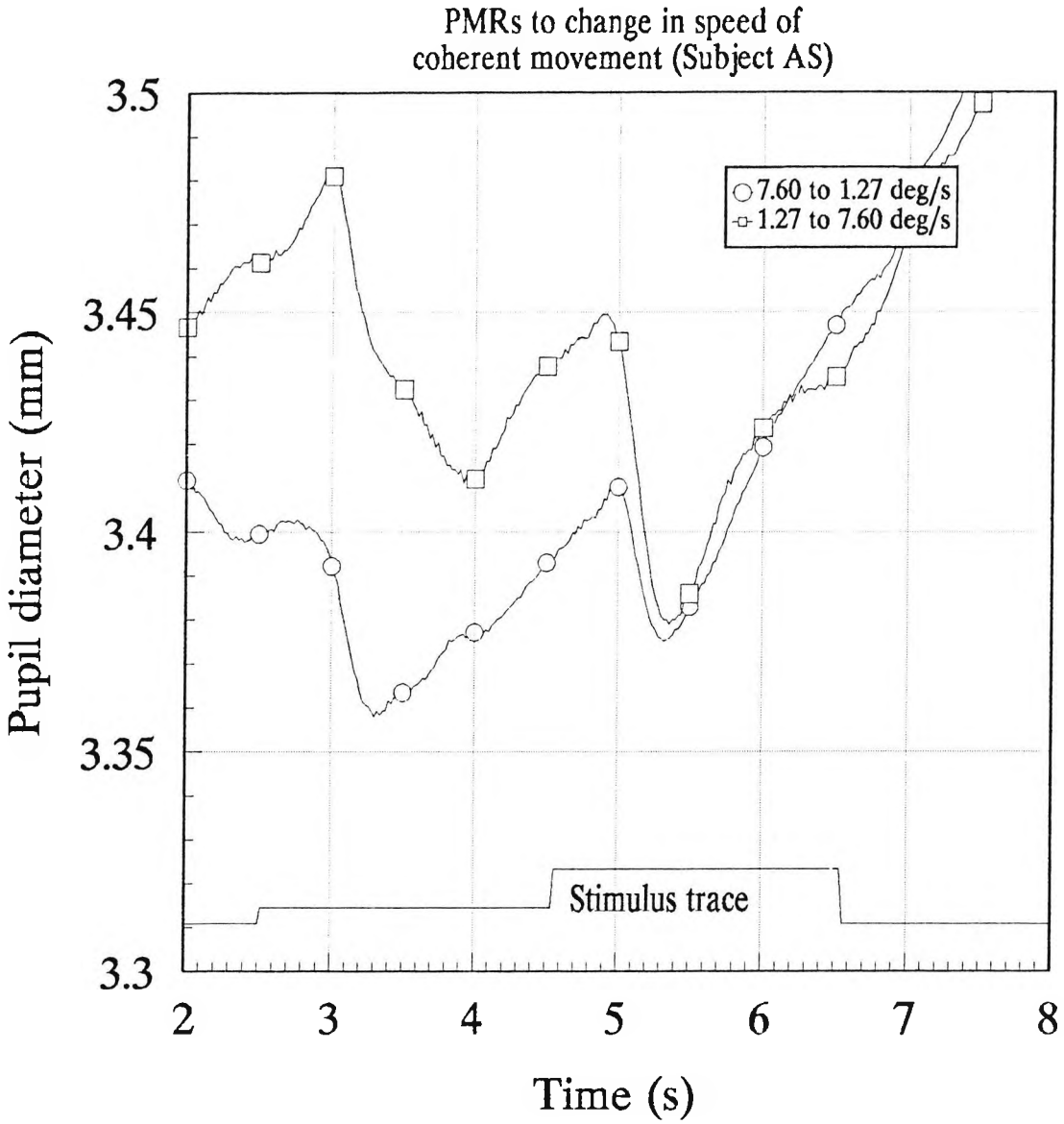


Figure 4.11: Pupillary traces representing the pupil motion responses to a change in the stimulus speed during the second part of the coherent interval. The responses shown are for the speed changes of 7.6 to 1.27 °/s and vice versa. For experimental conditions refer to main text. Pupil noise standard deviation associated with the average of 64 traces is 0.00791.

4.5 Discussion and Summary

Physiological data reveals an abundance of cells with orientation and direction tuning properties in the visual pathways. As far as the distribution of directionally tuned cortical cells is concerned, a small proportion ($\approx$ 25%) of V1 cells are directionally selective (Hubel and Wiesel, 1968; De Valois et al., 1982a; Orban et al., 1986). Some 40% of the neurones in V3 are directionally selective (Felleman and van Essen, 1987). In V2 the proportion may be lower (Zeki, 1978b). As orientation selectivity distinguishes V1, so the direction selectivity distinguishes V5. Some 40% of V5 cells are component direction selective and about 25% pattern direction selective (Dubner and Zeki, 1971; Movshon et al., 1985; Maunsell and Newsome, 1987) and the majority of V5/MT direction selective neurones respond well to random dot stimuli as well as to gratings (Tanaka et al., 1986; Mikami, 1991).

It was predicted that pupil motion response may be affected by changes in stimulus characteristics such as direction and speed. A change in direction of motion causes switching of activity from one set of neurones to another which in turn may be reflected in a weakening of the supranuclear inhibition of the pupillomotor nucleus. The results presented in figure 4.3 show the presence of PMRs to change in direction of coherent motion.

An account of direction specific mechanisms was given in section 1.12. Psychophysical evidence has been cited, showing the interaction between these mechanisms at suprathreshold levels (see section 1.11 & 4.1) and an overall response of the visual system is a result of pooled responses from these mechanisms. If pupil motion response is also the result of pooled activity of motion mechanisms, then a change in direction of motion of a suprathreshold stimuli may also affect the PMRs. Collectively, the results presented in figure 4.3 (ie., the PMRs to a change in stimulus direction) were in agreement with predictions based on psychophysical, physiological and pupillometric data.

With respect to the mean bandwidth for directional selectivity, physiological findings reported show that V1 cells are more narrowly tuned than V5/MT cells. The average bandwidth for V1 cells was found to be 68° (Albright, 1984); 65° (De Valois et al., 1982a); 50° (Poggio et al., 1977); and approximately 90° for MT cells (Albright, 1984). The Weber fractions measured psychophysically for discrimination of the direction of motion have been reported to be approximately 1°(Levinson and Sekuler, 1976).

The PMR bandwidth for direction and speed tuning was defined as the minimum change in each parameter required to elicit a pupil response of amplitude equivalent to 50% of that of the initial PMR. The bandwidth measured for PMRs elicited to a change in direction of motion was found to be less than 30°.

Having demonstrated the existence of PMRs to changes in the direction of motion, the results presented in figure 4.5 show that these responses were present for a range of speeds. In addition, similar responses were found for eccentric stimulus presentations (figure 4.6). This finding is consistent with the results of DeValois et al. (1982a,b) which show little or no variation in directionality of cells as a function of eccentricity.

The response latencies measured to change in direction of motion were similar to those of the motion responses reported in the previous chapter (400-500 ms). Sekuler et al. (1990) argued that a change in motion direction after a long period of adaptation to the initial direction of motion would reduce the task of direction discrimination to a detection of motion onset. The temporal integration time they measured was between 500-700 ms. All measurements reported in this chapter involved initial motion intervals of approximately 2s. Hence, the latencies measured were expected to have the same duration as those elicited to motion onset.

A large number of papers, cited in sections 1.13, have proposed the need for velocity tuned mechanisms to explain the results of velocity and displacement discrimination tasks. The need for two motion discrimination models operating at low speeds (<3°/s) and high speeds (>3°/s), respectively has been described by Barbur (1985). In common with both these models and those put forward by Thompson (1983, 1984), Adelson and Bergen (1985), Movshon et al. (1986, see section 1.13 for details) is a set of velocity detector units. The information regarding the speed of the stimulus is then pooled from these detectors and compared with the signals emerging from other adjacent velocity groups. The speed discrimination would then depend on the ratio of the pooled signals. It is therefore expected that a change in stimulus speed causes a switching of activity from one set of detectors to another. In neuronal terms a sudden change in speed is expected to cause a change in the neuronal activity within the cortex.

The physiological evidence for such velocity tuned neurones has been reported in studies of Movshon (1975), Orban (1985), Orban et al. (1981, 1986), Maunsell and van Essen (1983) and Mikami et al. (1986a) (see section 1.13.1 for details).

Considering the above psychophysical and physiological data, we hypothesised that

changes in stimulus speed may be reflected in the pupil motion response. Results presented in figure 4.7 and 4.9 show the presence of these responses. To obtain a quantitative analysis of the effect of change in stimulus speed, the ratio of response obtained to a change in speed to that elicited to the stimulus onset was plotted in figures 4.8 and 4.10 as a function of the percentage change in speed. This analysis shows that the PMRs are affected systematically, and the responses obtained are dependent on the initial stimulus speed and the degree of change.

The bandwidth measured for PMRs elicited to changes in stimulus speed was found to be narrower at slow speed (30% at 3.82°/s) than a faster speed (58% at 7.6°/s). Although the pupillometric bandwidth measured was dependent on the initial speed, the Weber fractions for the speed range 3-70 °/s measured psychophysically, have been reported to be approximately 5% (Nakayama, 1981; van Doorn and Koendrink, 1983; Orban et al., 1984; McKee and Nakayama, 1984).
Single cell recordings of velocity tuned cells in cat, shown figure 1.29a, show that at least for the cells measured the width of tuning is larger for cells with maximum sensitivity to faster speeds (50°/s) than those maximally responsive to slower speeds (<5°/s) (Orban et al., 1981).

The PMR latencies measured to a change in stimulus speed were again similar to those elicited to the onset of coherent motion at the range of speed examined. The temporal integration time for speed discrimination measured psychophysically yielded a value of 500ms (Bowne et al. 1989; Watamaniuk, 1989). Since the duration of the initial speed was much greater than the temporal integration time, it is possible that similarly to the reaction time measurements (see section 4.1), the change in stimulus speed had been reduced to a stimulus onset, therefore giving a latencies similar to those due to the motion onset.

The pupil traces obtained under the present experimental conditions in studies of the effect of changes in direction and speed have low signal to noise ratios, and a large number of measurements are averaged. Measurements were also carried out at a set of discrete speeds and directions due to technical limitations. The maximum speed generated and the minimum angle of rotation possible were limited to 10°/s and 30°, respectively.
Based on the results presented in this chapter, it is not possible to draw firm conclusions on the comparison of the pupillometric bandwidths to those of the average neuronal responses recorded electrophysiologically, or the perceptual psychophysical

performance. A larger set of measurements at a wider range of speeds and narrower angular change of directions is required which was not possible due to technical constraints. To obtain such data, modification of both the experimental conditions and measurement apparatus would be required.

The explanatory hypothesis put forward to explain the presence of the PMRs is strengthened further by the fact that the responses are affected by changes in speed and direction.

In summary, based on the psychophysical, physiological and pupillometric studies, we predicted that changes in motion parameters such as direction and speed may affect the pupil motion responses. This prediction was investigated using visual stimuli similar to those used in the previous chapter. The results obtained show that changes in speed and direction of coherent motion are reflected in pupil motion responses. A method for quantitative analysis of tuning properties of the pupil motion responses was described and parallels between the bandwidths measured and those reported in psychophysical and pupillometric studies were discussed.

CHAPTER V

Psychophysical and Pupillometric Assessment of Colour Processing in Blindsight

5.1 Colour Discrimination in Blindsight

Investigations of the effect of lesions of various parts of the visual pathways on wavelength and colour discrimination can provide an insight into the performance and connectivity of colour processes.

Lesions of the primary visual area or optic radiations produce homonymous visual field defects. When forced to "guess", subjects can discriminate some visual attributes in the absence of acknowledged awareness of the stimulus. This ability, termed blindsight, was explained in section 1.4 where a brief introduction of colour processing in these subjects was also included. An expansion of the literature cited involving studies on human subjects is given below.

Bender and Krieger (1951) recorded dark adaptation traces for monochromatic adaptive fields presented in a subject's blind field. Their results implied the involvement of more than one type of retinal receptor. They also reported that for sufficiently long and intense stimuli, subjects had an "appreciation of colour".

Correct colour identification of foveally presented large coloured stimuli at one incidence only, was reported by Perenin et al. (1980) for a subject with complete bilateral cortical blindness.

Barbur et al., (1980) measured the spectral sensitivity for threshold detection of a moving target in a blindsight subject and found that the rod signals dominated the responses when the stimulus was presented at an eccentricity of 30°.

Blythe et al. (1987) reported that only one out of 25 subjects studied could name correctly the colour of a stimulus presented in the blind field and identified consistently 635nm and 530nm flashes as red and green, respectively.

Stoerig (1987) reported that six out of ten subjects with central lesions tested had significant performance levels when asked to discriminate between red and green targets in a forced choice paradigm. The targets were small discs, subtending 44',with luminance of 16 cd/m^2, flashed for a duration of 200ms, and were positioned on a white background of luminance 1.6 cd/m^2. The red and green targets were perceived as having the same luminosity when presented at the same eccentricity in the sighted field. It was possible, however, that the subjects' blind

field spectral sensitivity was altered due to the lesions and that this resulted in the discrimination being based on luminance differences rather than chromaticity. This possibility was rejected since they could not discriminate between two achromatic targets of 16 and 160 cd/m^2, based on luminance differences alone.

Subsequently, the increment threshold spectral sensitivity was measured in three blindsight subjects by Stoerig and Cowey (1989b, 1991). They used a larger target subtending 116', presented for a duration of 200ms at 10° eccentricity positioned within the blind field and applied a forced choice procedure to obtain the threshold for detection of nine narrow band stimuli under both photopic and scotopic conditions. The results were then compared with the increment thresholds at the mirror symmetric position with respect to the vertical meridian within the subjects' normal field. Their main findings are listed below.

1. Under scotopic conditions, the increment threshold spectral sensitivity measured in the blind field had a peak between 500-550nm, declining steeply above 550nm. This indicates the activity of rods within the blind field.

2. Spectral sensitivity curves obtained under photopic conditions differed markedly from above and to a large degree resembled the normal response with a clear Purkinje shift, indicating the involvement of both rods and cones.

3. Increased sensitivity at 450nm and a notch at 480nm on a photopic increment threshold spectral sensitivity curve are indicative of the activity of blue/yellow opponent colour mechanisms in the blind field.

Stoerig and Cowey also claimed that the sensitivities measured at 580nm and peak at 600nm were further evidence of red/green opponency. The data however, are not convincing even for measurements of spectral sensitivity made for control subjects. The lack of a sharp trough at 580 and a peak at longer wavelengths in their measurements may be attributed to the small stimulus size presented at 10° eccentricity. In normal vision a large target is needed to enhance the activity of colour opponent mechanisms when measurements are carried out at larger eccentricities (Kuyk, 1982; Krastel et al., 1983).

The findings of Stoerig and Cowey (1989a, 1991) were the first evidence of both rod and cone activity in cortically damaged subjects. Moreover, opponent colour mechanisms or at least blue/yellow opponency were shown to contribute to the responses in the blind field.

Subsequently, Stoerig and Cowey measured the discrimination thresholds for two monochromatic wavelengths in the same three blindsight subjects, where the targets

had been equated for luminosity based on each subject's blind field increment threshold data (Stoerig and Cowey, 1992). They reported that the wavelength discrimination thresholds varied between subjects and were between 20-35nm in the blind field, being three to five times larger than the thresholds measured in the sighted field under similar conditions. To show that discrimination was based on the differences in wavelength and not in stimulus luminance, they measure the luminance discrimination threshold in subjects' blind field under identical conditions and found it to be in the range of 0.3-0.9 log units. This is the minimum luminance difference required for the subjects to be able to discriminate stimuli of the same wavelength on the basis of its luminosity. The values obtained ruled out discrimination based on brightness difference for all but one (yellow-orange) stimulus pairs.

Ruddock and colleagues have also measured wavelength discrimination in a blindsight subject (GY) using large monochromatic stimuli generated in a Maxwellian viewing system, and found evidence for cone activity and colour discrimination in the blind hemifield (Ruddock, 1993).

5.2 Aims of the Study

Recent investigations cited above, place emphasis on stimulus detection thresholds and wavelength discrimination in blindsight using narrow band stimuli. There is no evidence however, that colour discrimination ability in blindsight subjects is preserved in the absence of any luminance cues when broadband stimuli (ie., a mixture of three primaries with fixed spectral compositions) are employed. Indeed, in experiments where the presence of a stimulus bar formed by a small chequer-pattern, could only be detected based on its chromatic content, and any luminance changes were masked using random modulation technique (see section 1.5 and also Barbur et al., 1993 for explanation of the technique), then a blindsight subject could guess neither the presence, nor the colour of the stimulus. In these experiments the targets were not monochromatic and were produced on a high resolution monitor.

In experiments where a visual stimulus contained both colour and luminance components, the existence of a pupillary constriction despite large decrements in stimulus luminance, has been demonstrated (Barbur et al., 1987b; reviewed by Weiskrantz, 1990). The response amplitudes were found to be much reduced in the absence of any chromatic change, indicating the contribution of chromatic processes to the pupil responses.

The objective of the psychophysical experiments described in this chapter was to investigate whether the colour discrimination ability in blindsight persisted for a combined colour and luminance stimulus. If such persistence existed, then the subject's performance level in relation to the stimulus hue and saturation could be investigated systematically.
Similar stimuli were then presented in the blind and sighted fields of two blindsight subjects in order to investigate the existence of pupillometric correlates for the psychophysical measurements.

5.3 Psychophysical Assessment of Colour Processing in Blindsight

In order to study the activity of colour mechanisms, the experimental conditions can be optimised to enhance the performance of chromatic opponent channels. In order that the results of this study can be related to the pupillometric experiments (see section 5.4), the stimulus parameters selected in both studies must be comparable. These parameters must also be chosen such that the stimulus onset does not cause any pupil response via light reflex pathway or accommodation, convergence, pupil triad (see section 1.5).
The following points are considered when optimising the experimental conditions for colour discrimination (see 1.14 for references).

1. A white uniform background at photopic luminance levels, depresses selectively the activity of luminance channels.

2. A large stimulus area promotes the activity of colour opponent mechanisms due to the large spatial summation involved.

3. Long stimulus presentation times favour activation of the colour opponent mechanisms due to their long temporal integration (150-300 ms) compared with that of luminance channels (60ms).

An explanation of experiments carried out to investigate colour discrimination for a constant chromatic displacement in two blindsight subjects is given. Then, the results of a systematic study of the effect of saturation on a subject's colour discrimination performance are discussed.

Methods

Subjects

Two subjects (GY and FS) participated in these psychophysical experiments, both having suffered lesions of optic radiations and having blindsight. A resumé of case history of GY has been given in section 3.4.
Subject FS has been studied extensively by other experimenters (case F of Stoerig and Cowey, 1989b). FS is 56 years old and suffered a severe crainocerebral trauma resulting in optic radiation damage at the age of 42. As a result of the lesion, he has homonymous field defect of the right hemifield, visual field plots of which have been given in the paper by Stoerig and Cowey (1989b). In addition to the visual defect, he suffers from a mild aphasia when naming colours; a problem which can

be overcome if the time interval between stimuli are sufficiently prolonged. He is observant and does not suffer from any other visual defects.

Experimental Parameters

A description of the equipment used in the following experiments and an account of the experimental conditions are given in chapter II and only the experimental parameters are described below.

The subject viewed binocularly a high resolution monitor subtending 28° x 22° at a viewing distance of 0.7m. Assuming the bottom left corner of the screen to be the origin of a Cartesian coordinate, a box-cross fixation was displayed at coordinates (6,6)°. A circular test stimulus of radius 7° was placed such that the entire target area fell within the blind field of the subject. To achieve this, the coordinates of the centre of the test stimulus were set at (18,13)° for GY and (18,9)° for FS. A mirror symmetric location of these coordinates with respect to a vertical line at the centre of the screen was used to make corresponding measurements in subject's sighted field.

The background luminance was set to 18cd/m^2 and had the same chromaticity coordinates as those of MacAdam's white (x,y: 0.305, 0.323 see MacAdam, 1942). All the chromaticity coordinates in this chapter have been computed using the CIE 1931, x,y coordinate system.

The duration of a stimulus was 300ms which was preceded and followed by a 1s and 3s delay interval, respectively. The stimulus luminance at each presentation was chosen randomly with a value between 8.0-16.0 cd/m^2. The subject's fixation was monitored by imaging the pupils using the infra-red CCD cameras of P_SCAN 100 system (see chapter II).

The two alternative forced choice procedure developed for the measurements of colour discrimination was as follows:

When the subject was ready and fixating, the GO button of the response buttons was pressed. After a short random delay a single bleep signalling the start of the first interval was sounded followed by a 1s delay period. Subsequently, a stimulus was presented for 300ms followed by a 3s delay interval. A double bleep then served as an audio cue signalling the start of the second interval in which a second stimulus was presented in the same sequence as the first. At the end of the final delay interval a single bleep of a different tone signalled the end of the second interval. Either an achromatic or a chromatic stimulus was presented during each stimulus interval, the order and their luminance being chosen at random. The chromatic stimulus was chosen from a choice of three chromaticity coordinates.

The subject was instructed to guess at the end of each presentation the interval in which the chromatic stimulus was presented and to name the colour of the stimulus from a choice of "red, green and blue". If a subject is highly sensitive to the chromatic content of a target, then it is expected that he would score high in both discriminating the colour and the interval of presentation. If, for example, a subject is insensitive to one colour only, ie., he does not "see" its colour at the saturation level presented and therefore, is not able to distinguish it from an achromatic stimulus, but is able to discriminate the other two colours then given the choice of three colours he may consistently name the colour correctly by a process of elimination. The performance of the subject in guessing the presentation interval however would only be at chance level and would not parallel his colour discrimination, indicating an incorrect criteria.
In addition to the choice of three coloured stimuli, a fourth condition was added during both intervals of which consisted of an achromatic stimulus. Subjects were not informed of the presence of this fourth condition and their task remained that of guessing the interval and naming the colour of the stimulus. The score of naming the interval for the chromatic target would then indicate if the subject named the interval at random or had a tendency to favour a particular interval.

Constant Chromatic Displacement Experiments
The chromatic displacement (CD) given in x1000 units, represents the displacement from a neutral white on the x,y chromaticity diagram. In order to investigate the subject's colour discrimination, the chromatic displacement for all coloured stimuli was constant at CD=208 units, the coordinates of which have been denoted by stars on figure 5.1. Thus, for a normal observer and with the target presented in the subject's sighted field, all stimuli appeared to have approximately the same saturation.
Each of the four stimulus conditions was presented 32 times during each experimental run.

Colour Discrimination vs. Saturation
In a series of experiments, the luminance of the background was increased to 55 cd/m^2 and that of the stimulus was chosen at random in a range of 22.0-37.0 cd/m^2 for the red and blue stimuli and 22.0-42.0 cd/m^2 for the green and achromatic stimuli. The increase in the luminance level was selected to enhance the performance of colour mechanisms and to saturate further the rod responses (see pupillometric studies in section 5.4.2). The highest chromatic displacements

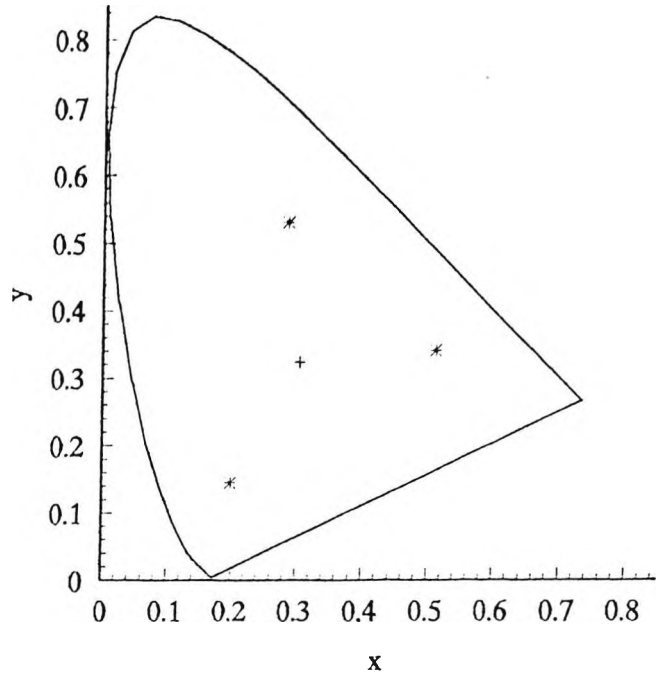


Figure 5.1: x,y chromaticity coordinate system. +, MacAdam's white (0.305, 0.323); points denoted by * all have equal chromatic displacement (CD=208). The coordinates are R(0.512, 0.340); G(0.285, 0.530); B(0.199, 0.145).

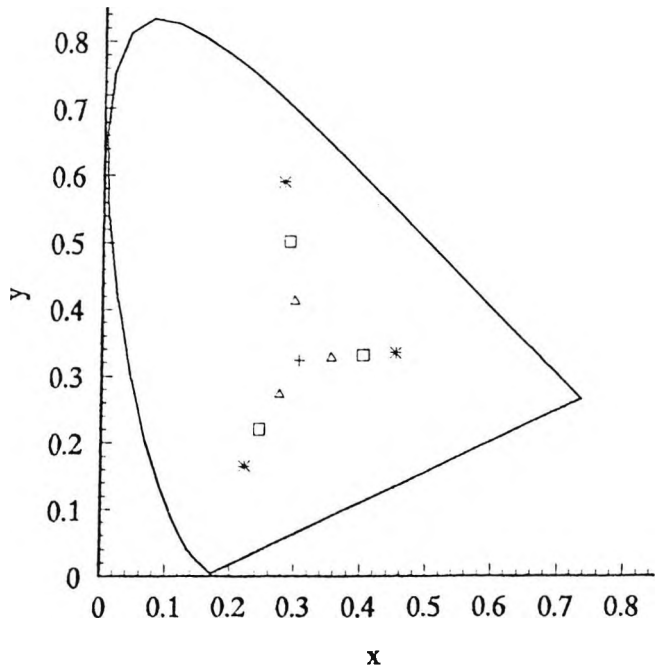


Figure 5.2: chromaticity coordinates for the high, medium and low saturation conditions. +, MacAdam's white (0.305, 0.323); Points denoted by * have chromaticities R(0.451, 0.335), G(0.279, 0.590), B(0.222, 0.165); : R(0.402, 0.331), G(2.88, 0.501), B(0.244, 0.220); : R(0.354, 0.327), G(0.297, 0.412), B(0.275, 0.272).

obtainable under the new photopic luminance level were calculated for displacements along the same axes as in the previous condition. The highest chromatic displacement value for each of the red, green and blue stimuli was then divided by three, to obtain the chromaticity coordinates for conditions of low and medium saturations as shown in figure 5.2.
For the cases of high, medium and low saturation levels, the colour discrimination ability was investigated using the same two alternative forced choice technique. Again each of the four stimulus conditions were presented 32 times except for the high saturation condition in GY where 64 stimulus presentations were recorded.

Results

Figure 5.3 shows the percentage correct discrimination scores for each of the three chromatic stimuli and also the scores for correct identification of the interval at which a coloured stimulus was presented. At the chance level, there was a probability of 1/3 for the subject to guess the correct stimulus colour and 1/2 for its presentation interval, indicated on the graphs by the horizontal lines.
At the chromatic displacement examined (208 units), both subjects could discriminate the blue and red coloured stimuli and guess the interval of their presentations with a high level of accuracy. For the green stimuli, GY could guess the colour of the stimulus, but his performance in guessing the presentation interval was at chance level. This result could be expected, if it is assumed that, he had a very low sensitivity to the green targets and where there was a lack of "colour", he guessed that it could not have been red or blue, hence naming green.
Subject FS also had low sensitivity to the green stimuli (see below). He could correctly identify the interval of presentation, but since his sensitivity to red and blue stimuli was not as high as GY's, he then guessed a colour at random, hence performing at chance level.
The results showing the effect of chromatic saturation of the stimulus on the psychophysical performance level are shown for both subjects in figures 5.4a,b & c. Figure 5.4a shows that significant performance levels were achieved for all coloured targets at the high saturation condition by both subjects.
Figure 5.4b & c show that, the subjects' performance level for both colour discrimination and correct identification of presentation interval declined with a decrease in saturation, the only exception being the discrimination of the red target at medium saturation for GY. This anomalous result may have been caused by the small number of presentations involved. Although the chromatic displacement for

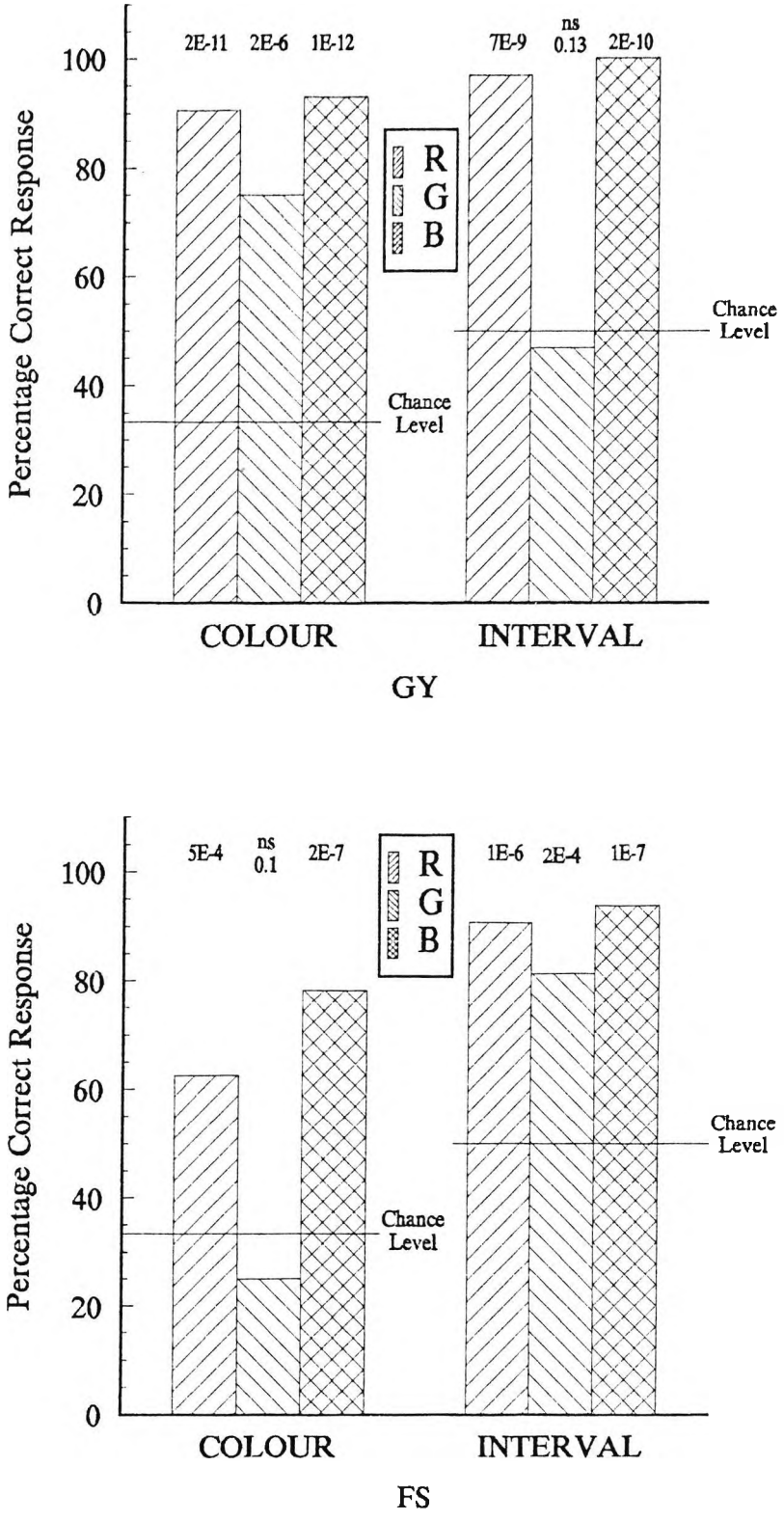
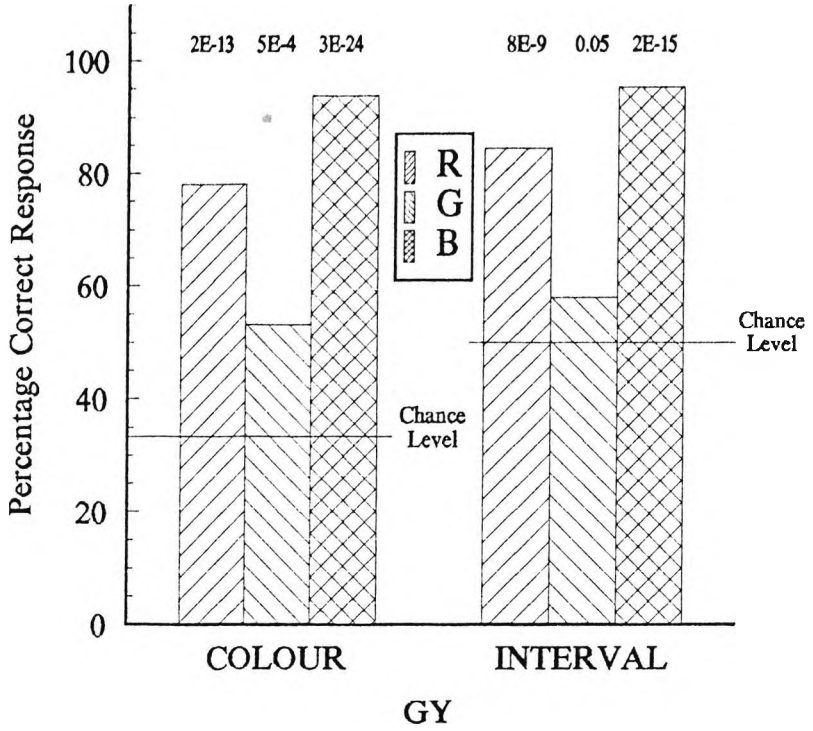


Figure 5.3: percentage correct responses for discrimination of the stimulus colour and interval of its presentation for two subjects. The chromatic displacements for all three stimuli were equal (CD=208 units). The background luminance was 18 cd/m^2. The chromaticity coordinates of the stimuli were the same as those denoted by * in figure 5.1. Figures above each column represent the calculated p value. See text for experimental conditions.



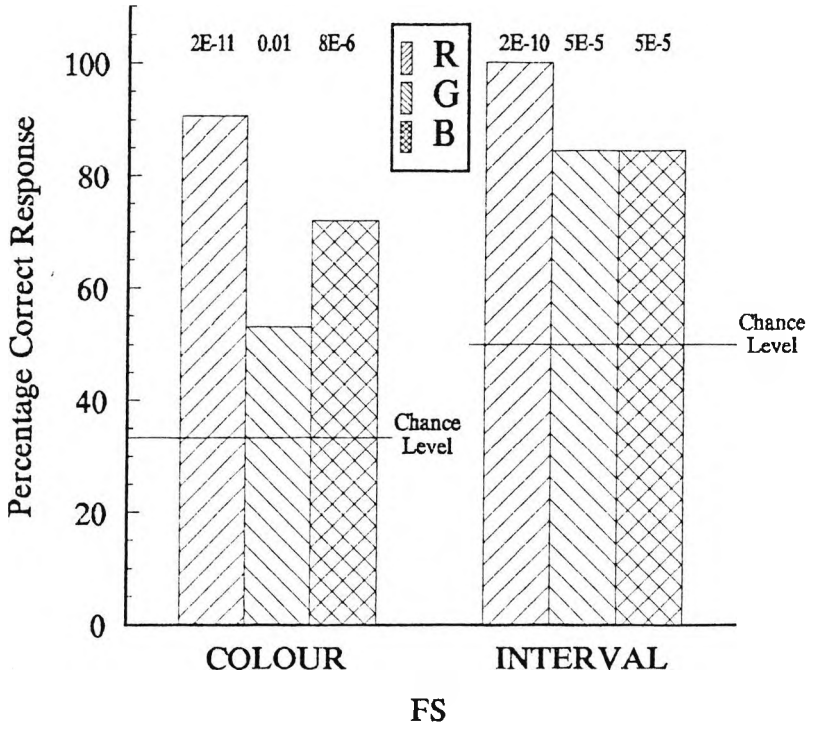
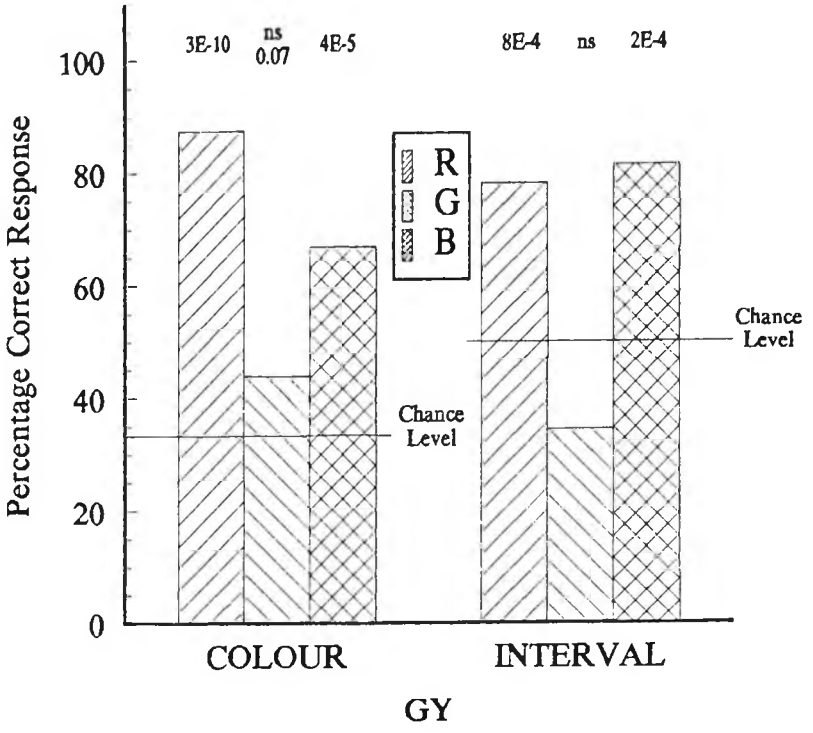


Figure 5.4a: percentage correct responses for discrimination of stimulus colour and the interval of its presentation for two subjects. The chromatic displacements were at their highest producible value under the photopic levels given, and denoted by * in figure 5.2. The background luminance was 55 cd/m^2. The number of presentations for each stimulus was 64 for GY and 32 for FS. Figures above each column represent the calculated p values.



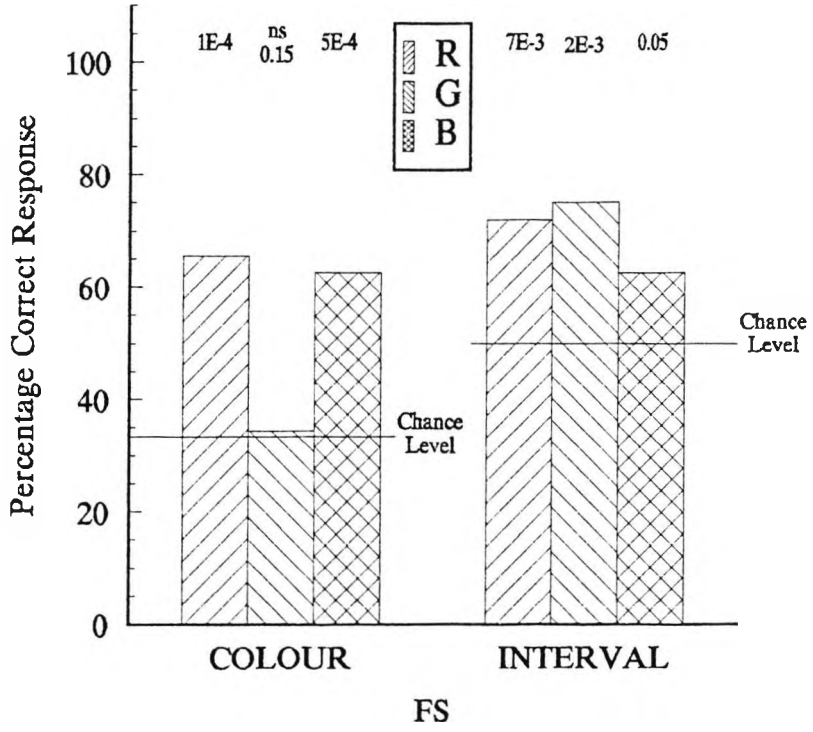
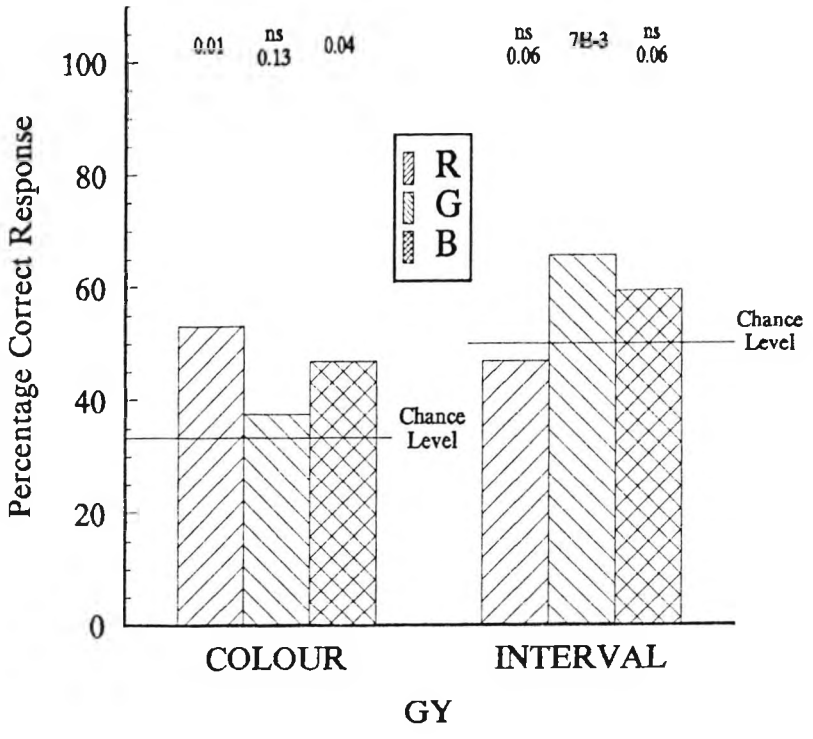


Figure 5.4b: as in (a). Stimuli had medium saturation, their chromaticity coordinates are denoted by squares in figure 5.2. 32 presentations of the stimulus was used for each subject. See text for experimental conditions.



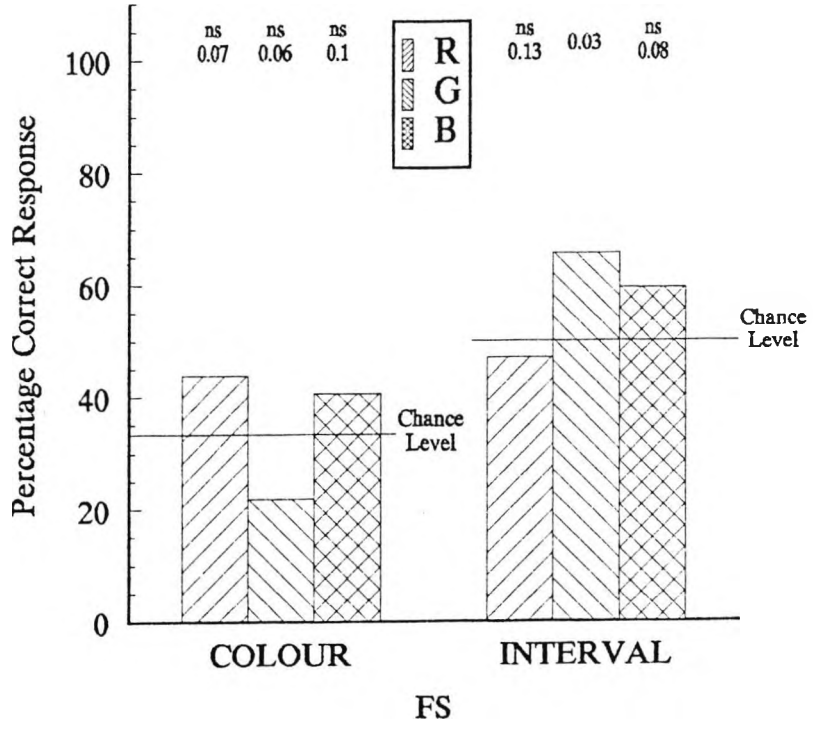


Figure 5.4c: as in (b), for low saturation stimuli. The stimulus chromaticity coordinates are the same as those denoted by triangles in figure 5.2.

the green stimuli was larger than those for the other stimuli at each saturation condition, the subjects' were least sensitive to its presentation.
An interesting feature of the results shown in figure 5.4a,b & c is that the identification of the stimulus interval follows the same trend as the discrimination of its colour for both subjects. This feature plus the high significance values indicated on the graphs in the absence of luminance cues demonstrate clearly the existence of residual colour discrimination ability in blindsight. The variations of colour discrimination with saturation for both subjects are extracted from the graphs 5.4a, b & c and are shown in figure 5.5a & b.

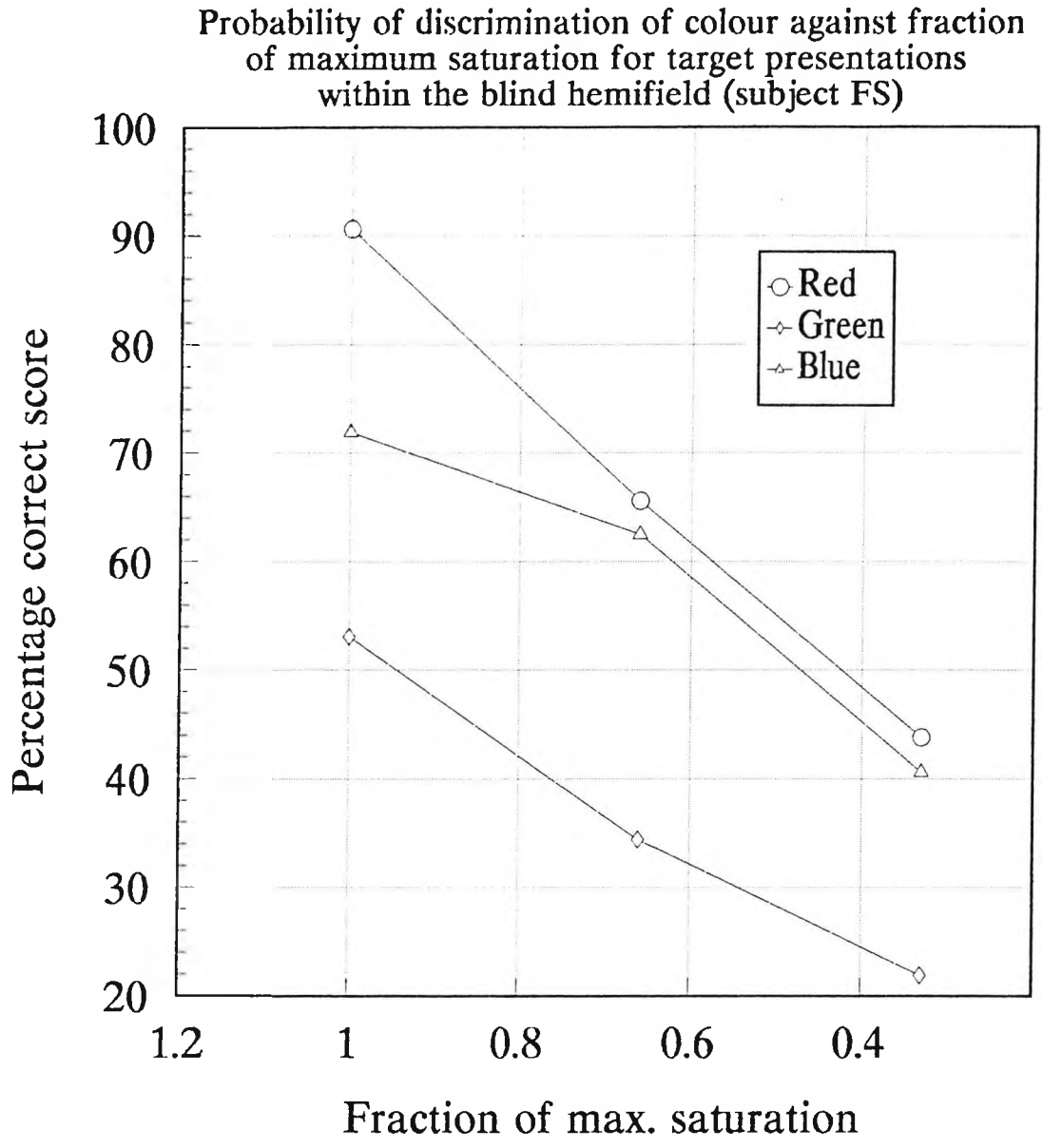


Figure 5.5a: psychophysical performance scores of the subject FS in discriminating the stimulus colour extracted from figures 5.4a,b&c and plotted as a fraction of the maximum stimulus saturation. The chance level is 33.3%.

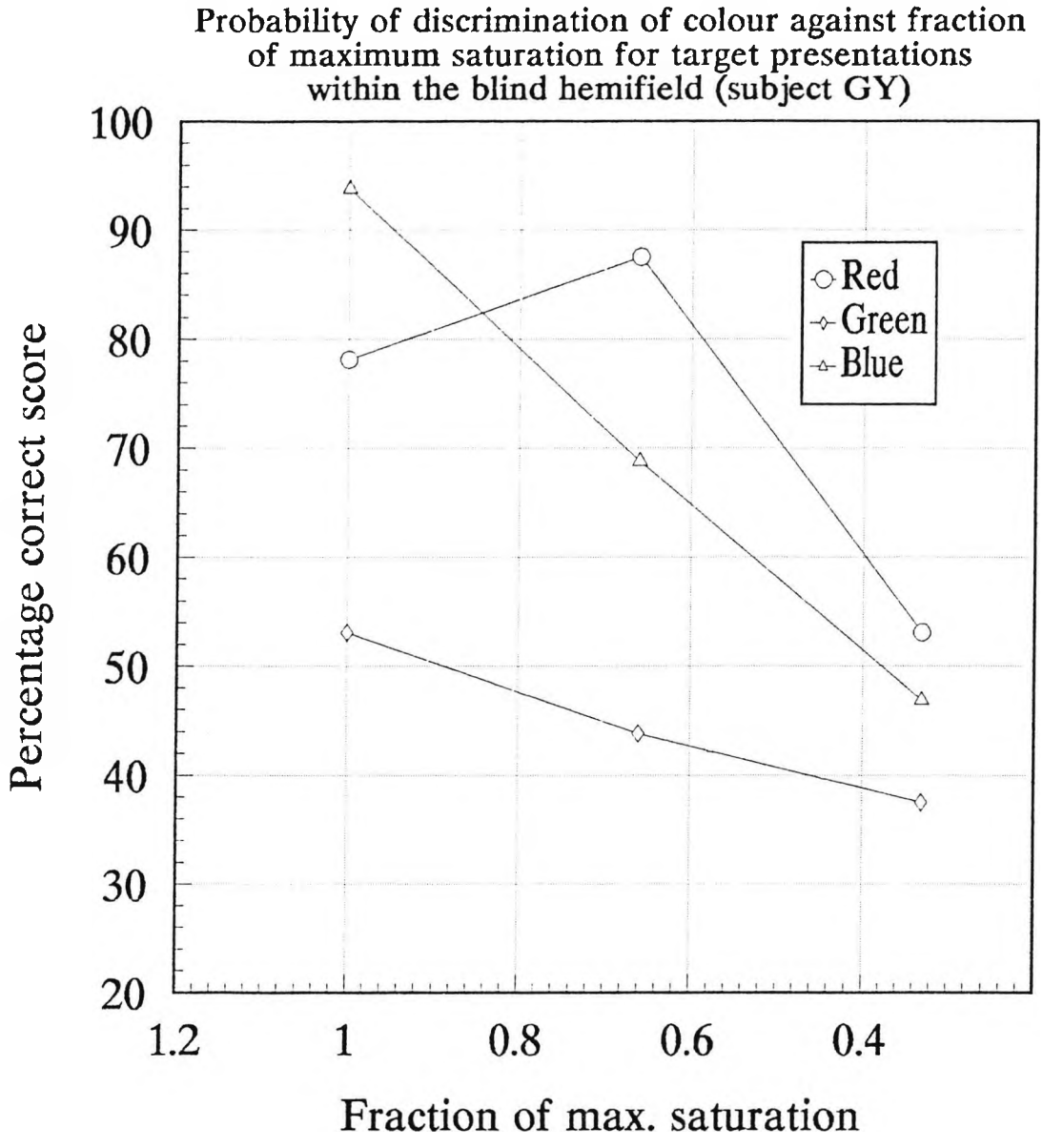


Figure 5.5b: as in (a) for subject GY.

Discussion

When colour discrimination was tested for stimuli of equal chromatic displacement away from the neutral background at lower photopic levels in the blind field, both subjects show clear evidence of chromatic discrimination ability. The experimental procedure implemented insured that the subjects could not make use of luminance cues in discriminating the stimulus colour. The precautions taken to avoid cues due to scatter light (see chapter II) ensured that the amount of scattered light from the surround and all the instrument surfaces was minimised and that it could not account for the high performance levels obtained. In addition, at the background and stimulus luminance levels used in these experiments, the high performance levels could not be attributed to forward scatter in the eye (Barbur et al., in press). For both subjects, the ability to discriminate green stimuli was lower than those for the red and blue targets of the same saturation. Stoerig and colleagues, when measuring the spectral sensitivity in the same subjects found that the green monochromatic targets were also poorly discriminated compared with coloured stimuli in the red and blue regions of the spectrum (Stoerig and Weiskrantz, personal communication). In order to investigate the colour discrimination ability, the chromatic displacements were set to the highest level possible under the given photopic conditions. The results shown in figure 5.4a,b,c and 5.5a,b indicate that the performance levels of both subjects for discriminating the colour of a stimulus target and the interval of its presentations are reduced at lower chromatic displacements (low saturation condition), emphasising that it was the saturation of the colour with respect to the background that was the main factor determining colour discrimination performance in blindsight. Subjects commented that for an equal chromatic displacement condition, the green stimulus when "seen", was not as saturated as both the red and the blue which parallel the results of figure 5.3. The psychophysical findings given above in support of the colour discrimination ability in blindsight are in good agreement with the findings of Stoerig (1987), Stoerig and Cowey (1989a, 1991, 1992) regarding wavelength discrimination and increment thresholds. However, they are not the same as the discrimination results obtained using a random luminance modulation technique (Barbur, in press). This may be attributed to the two major differences in experimental conditions. Firstly, it is possible that a large number of luminance fluctuations (every 50ms) may produce noise or increased neural activity in those mechanisms used by blindsight subjects for colour discrimination which could elevate their threshold or render them passive to any other stimulus attribute. Secondly, the surface area of the test

stimulus used in these experiment was larger than those used in random luminance modulation experiments. King-Smith and Carden (1976) have demonstrated the large spatial summation of chromatic channels. The importance of stimulus size and extensive spatial summation in midbrain pathways have also been demonstrated (Barbur et al., 1980; Weiskrantz, 1986; Weiskrantz et al., 1991). The larger stimulus area therefore, may result in increased discrimination capability.

Neurobiology of Colour Discrimination in Blindsight

What neural processing and pathways are involved in mediating residual colour discrimination in blindsight? At the retinal level, beta ganglion cells have high spatial resolutions, colour opponent properties, and they project to the parvocellular layers of LGN (Schiller and Malpeli, 1978; also see section 1.1). Both of the blindsight subjects tested had suffered post-geniculate lesions. After lesions of the occipital cortex or optic radiations, transneural retrograde degeneration takes place, affecting neurones both at LGN and the retina. The presence of a direct projection from LGN to the extrastriate visual areas has been reported (Yukie and Iwai, 1981; Benvento and Yoshida, 1981; Bullier and Kennedy, 1983). Primate studies have shown that eight years after a striate lesion some 20% of retinal beta ganglion cells and a small number of LGN neurones may survive (Cowey and Stoerig, 1991b). Retrograde HRP labelling (see section 1.2) of the visual cortex has shown that the surviving LGN cells project to the extrastriate areas including area V4 (Cowey and Stoerig, 1991b). Retinal beta ganglion cells have been found to project to the surviving LGN neurones either directly or via interneurones (Cowey and Stoerig, 1991b; Stoerig and Cowey 1992; Cowey, 1993). This pathway may then allow the colour information to be transmitted to the extrastriate area giving rise to the colour discrimination ability in blindsight. In addition, beta ganglion cells may project to the pulvinar where colour opponent cells have been reported (Felsten et al., 1983). The pulvinar has extensive connections to many other cortical and midbrain structures, hence, may act as a relay to allow for colour information to pass onto other areas for further processing (see section 1.1). Almost an equal number of alpha and gamma retinal ganglion cells also survive the retrograde degeneration. Alpha ganglion cells have high temporal and low spatial resolutions and broad band spectral sensitivity. They are not normally associated with colour processing although some of them and their corresponding magnocellular LGN neurones are not completely unresponsive to chromatic boarders (Derrington et al., 1984; Hubel and Livingstone, 1990). Their role in mediating colour discrimination is unlikely and they are mostly concerned

with luminance discriminations (Lee and Stromeyer, 1989).
Gamma cells are not colour opponent, but in the superior colliculus, where they mainly project, neurones with spectral bandpass characteristics have been reported (Kadoya et al., 1971, cited by Stoerig and Cowey 1992). Colour discrimination based on these bandpass characteristics is alone insufficient, but if the subsequent projections of the inferior pulvinar to the surviving projection neurones in the degenerated LGN were combined in an opponent fashion, wavelength discrimination based on gamma ganglion projections to the superior colliculus could be possible (Stoerig and Cowey, 1992).

In summary, psychophysical evidence for residual colour discrimination in blindsight has been demonstrated. Statistically significant colour discrimination scores were recorded in two blindsight subjects using a "guessing" paradigm. It was shown that their sensitivity for a given chromatic displacement was different along the three discrete axes tested. In addition, it was demonstrated that the colour discrimination along a given chromaticity axis is dependent on saturation. Possible pathways involved in mediating such responses have been discussed.

In the next section, the pupillometric parallels of the present study are discussed.

5.4 Pupillometric Assessment of Colour Processing

Sudden changes of neuronal activity in visual cortex caused by changes in a given stimulus attribute results in a small transient pupillary constriction. The constriction amplitude is related to the level of activity generated (see sections 1.5, 3.3, 4.3 & 4.4).

In view of the large number of neurones in the visual pathways being sensitive to chromatic information, a pupil response is expected to follow any chromatic change. Indeed, the pupil colour response (PCR) has been defined as a transient constriction of the pupil, triggered by chromatic changes in the visual field (Barbur, 1991) and their presence upon the presentation of a uniform pattern, chromatic gratings and isoluminant red/green gratings has been demonstrated (see review in section 1.5 and the discussions below). It has been hypothesised that such pupillary responses reflect the overall change of neuronal activity in the visual system to a given stimulus attribute. This has been demonstrated in normal subjects with respect to stimulus structure (Barbur et al., 1987a), colour (Barbur, 1991) and motion (see chapter III).

Blindsight subjects cannot discriminate the stimulus structure when the target is restricted to their blind field, and the pupil grating responses are also absent in these subjects. They are however, able to "guess" correctly the presence of a moving target and to discriminate its direction and the pupil motion responses have also been demonstrated. In the previous section, it was shown that blindsight subjects performed well above chance in discriminating stimulus colour.

It is of interest to investigate the existence of pupillometric parallels to the subjects' high psychophysical performance.

An initial study of pupillary responses elicited to the presentation of chromatic and achromatic test patterns in normal subjects was carried out and has been described below.

5.4.1 Pupil Responses to Coloured Stimuli in Normal Subjects

To demonstrate pupil responses to coloured stimulus in normal subjects, the stimulus parameters were chosen such that a comparative analysis between the results for normal and blindsight subjects was possible.

Methods

Subjects

Experiments were carried out on three normal observers DD, AS and JLB. All subjects were emmetropic, had normal colour vision and had no ocular pathology.

Experimental Parameters

The following parameters were identical to those used for the psychophysical experiments: viewing condition and distance; stimulus and fixation coordinates and dimensions; background chromaticity coordinates.

Pupillary traces were recorded using P_SCAN 100 system described in chapter II. The subject's fixation was monitored using the infra-red cameras of P_SCAN 100 system. With the subject fixating steadily, the pupillary measurements were initiated by pressing the GO button on the response box. After a short random delay period (0-0.5)s, the recording commenced. The stimulus presentation interval was 2s long and it was preceded and followed by fixed delay intervals of 2 and 3 seconds respectively. The long stimulus duration was used to allow the recovery of the pupil diameter after the stimulus onset. A bleep at the end of the final delay served as an audio cue indicating the end of the recording. The luminance of the background and stimulus were 18 cd/m^2 and 12 cd/m^2, respectively. The target luminance was set at a lower level than that of the background to avoid pupillary constriction via the pupil light reflex. The chromatic displacement for all coloured stimuli was constant and the chromaticities are denoted by * in figure 5.1. To obtain an adequate signal to noise ratio, a large number of pupillary traces (32 measurements) for each stimulus were averaged.

Results

The results of the pupillary responses recorded for presentation of three chromatic and one achromatic stimuli in three subjects are shown in figure 5.6a,b & c. The pupillary responses are elicited to both the stimulus onset and offset for all stimuli. In all subjects the response to the onset of the achromatic stimulus has the lowest response amplitude. This constriction response is present despite the reduction in target luminance and may be attributed to the change in the visual field, ie., presentation of the uniform disc (Barbur et al., 1987b). In all the graphs, it has been shown clearly that the presentation of coloured stimuli resulted in a larger

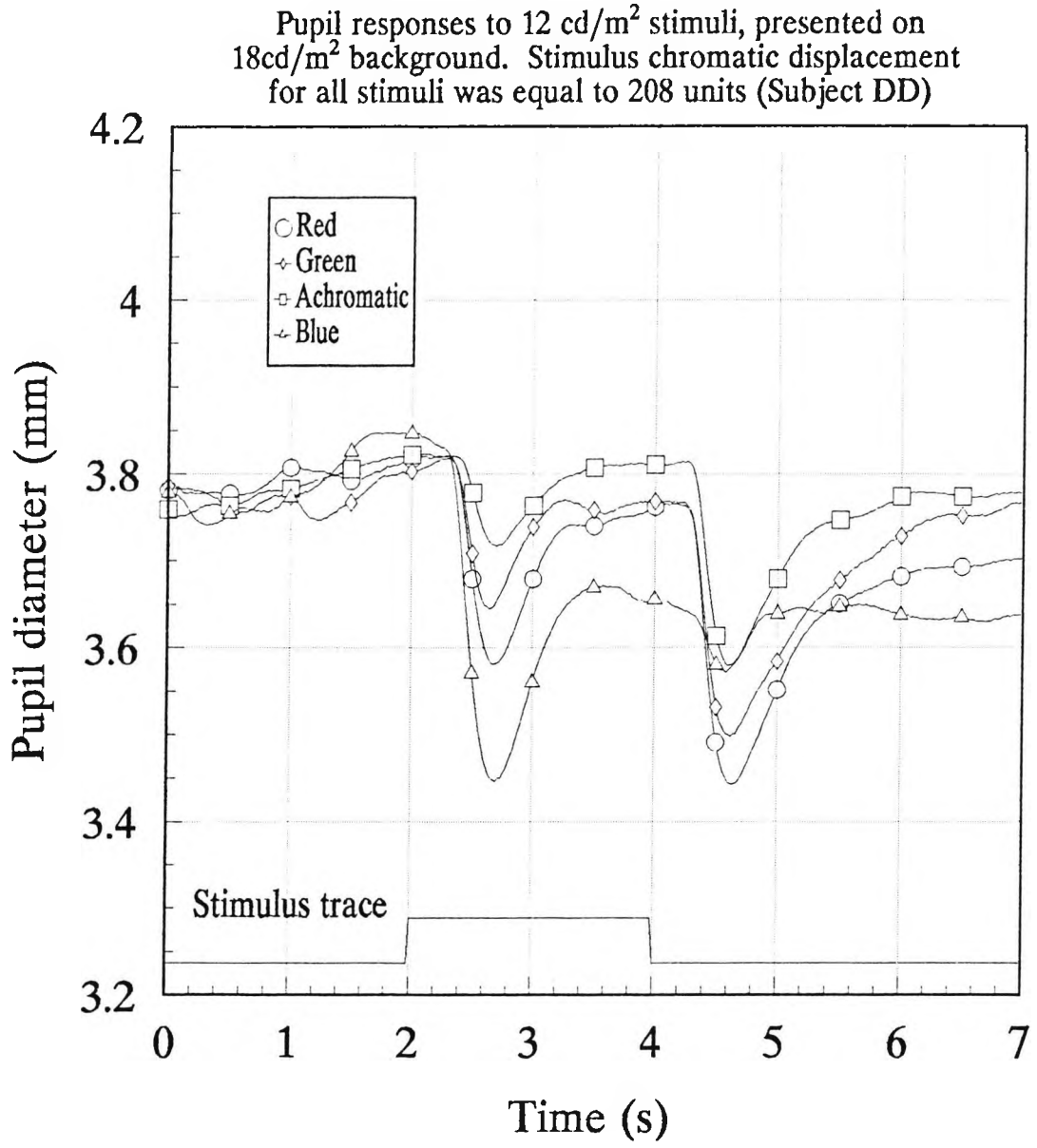


Figure 5.6a: pupil responses to a coloured uniform disc of lower luminance. uniform disc. The chromaticity coordinates of the stimuli were the same as those denoted by * in figure 5.1. See text for the experimental conditions.

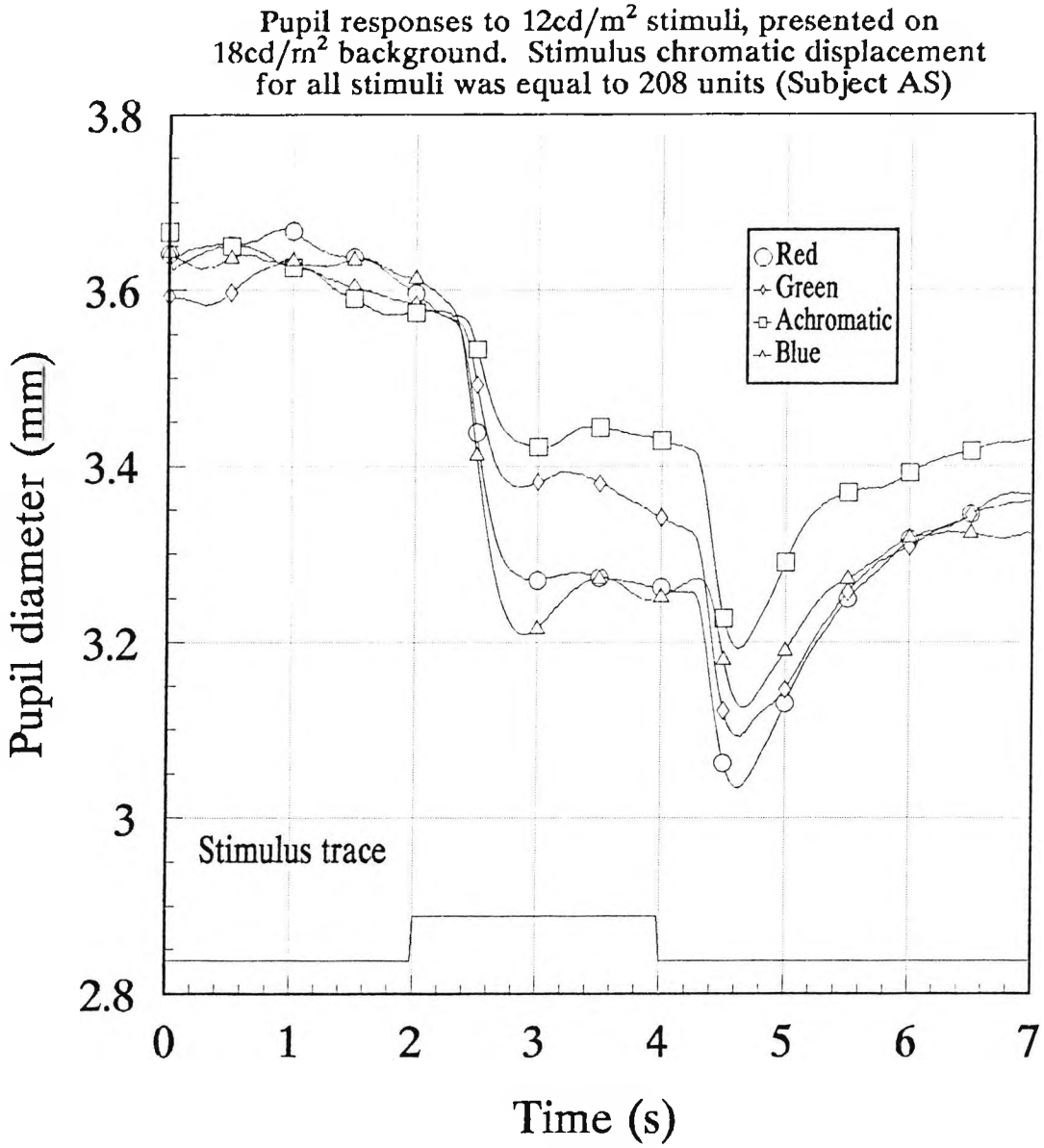


Figure 5.6b: as in (a) for subject AS.

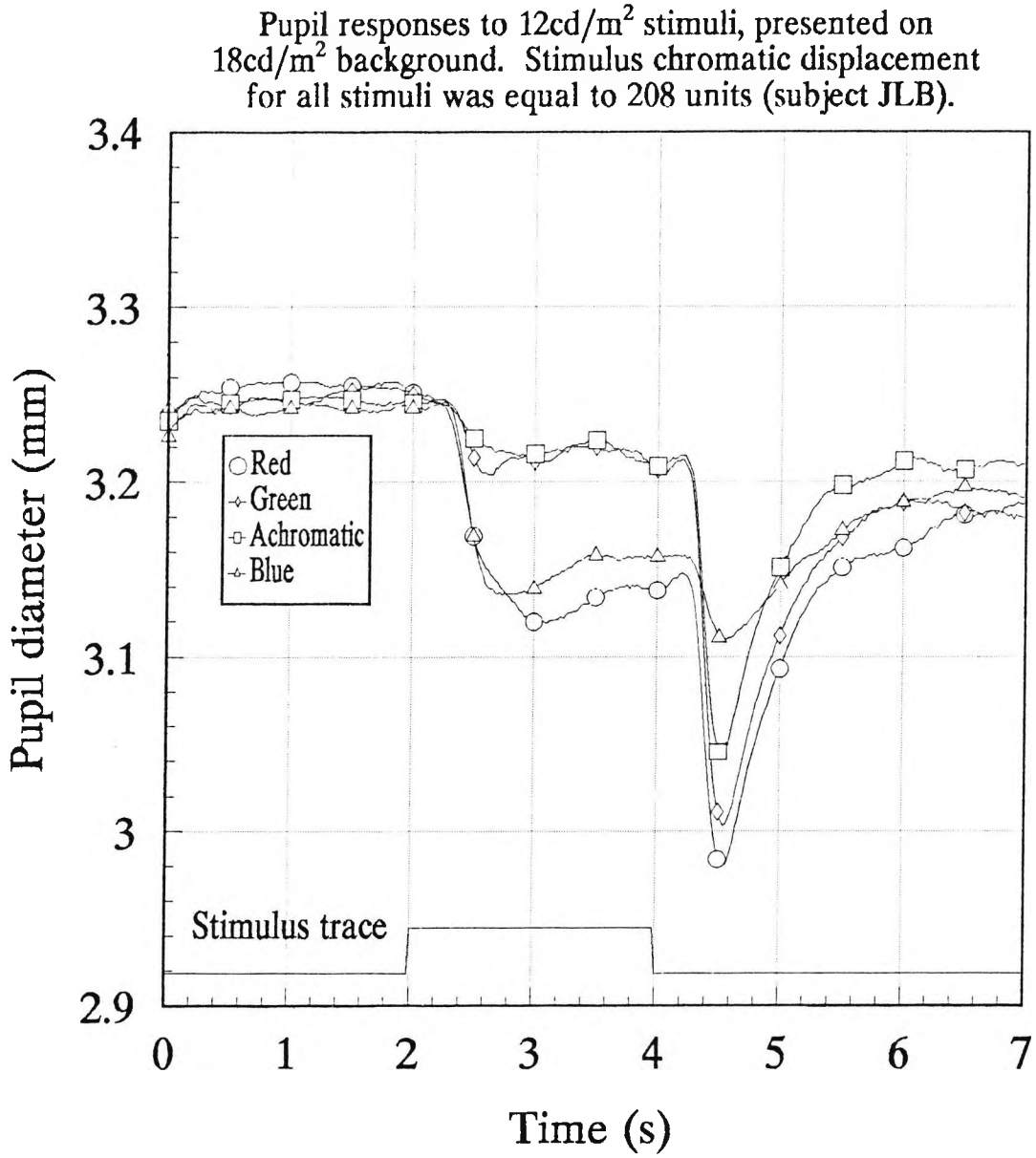


Figure 5.6c: as in (a) for subject JLB.

pupillary response. The response amplitudes of the pupil colour response elicited are highest for blue stimuli and lowest for green in all subjects.
The pupil responses elicited to the stimulus offset can be attributed to the light reflex response due to elevation of the luminance from that of the stimulus to the background level. The pupil light reflex has similar amplitudes for all stimuli except the blue.
To investigate whether the large amplitudes of pupil responses elicited to the red and blue stimuli compared with those to the green stimuli was a genuine stimulus characteristic or a possible artefact caused by longitudinal aberrations in the eye, experiments were carried out where the position of the plane of focus of the spectral rays with respect to the retina was altered. If similar responses were recorded, their presence could not be attributed to the longitudinal aberrations. Experiments were repeated at a viewing distance of 1.0m with and without +2.00D spheres placed in front of the eyes of one of the subjects (AS). At the viewing distance of 1m, the subject accommodates by 1.0D. By relaxing accommodation, the subject can compensate for 1D, hence leaving the retinal image 1D out of focus. This will result in a change in the position of the plane of focus for the spectral rays. The results of PCR recordings are shown in figure 5.7a &b. Since the increasing order of the PCRs response amplitude is not altered, their response can not be attributed to the longitudinal aberrations in the optics of the eye. The possible contributions of the transverse chromatic aberration may be discarded due to the large stimulus diameter (14°) and its presentation at relatively small eccentricities (10°) (Charman, 1992).

In summary, it was demonstrated that a large, uniform pattern with luminance lower than that of the background, presented at eccentricities equal to those used in psychophysical experiments could elicit a pupil response in normal subjects. The addition of chromatic information resulted in an increase in the response amplitude indicating that the processing of colour information was also reflected in the pupil responses measured.

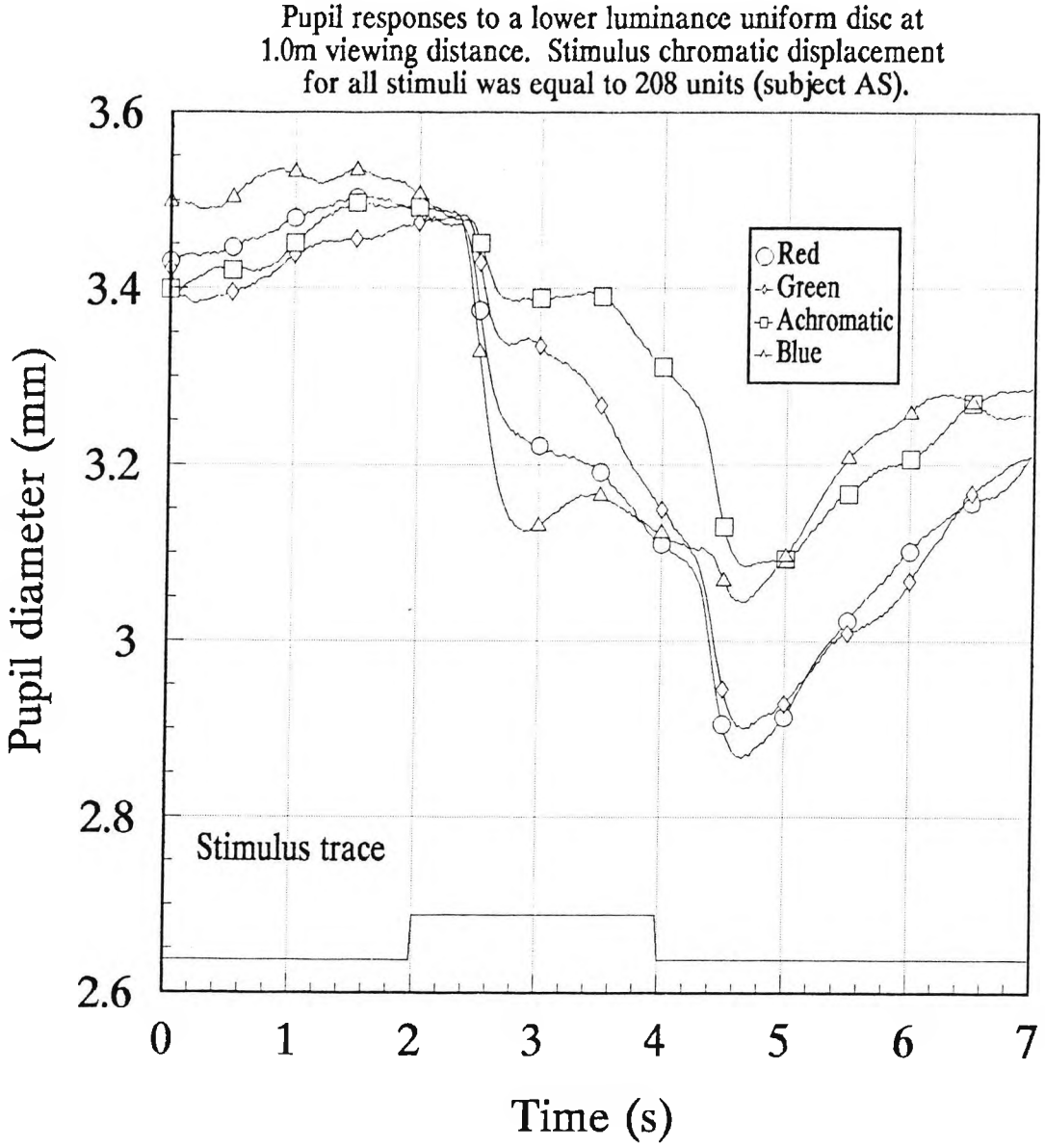


Figure 5.7a: PCRs to a lower luminance uniform disc. The viewing distance was increased from 0.7m to 1.0m. Other experimental conditions were identical to those of figure 5.6 and are given in the text.

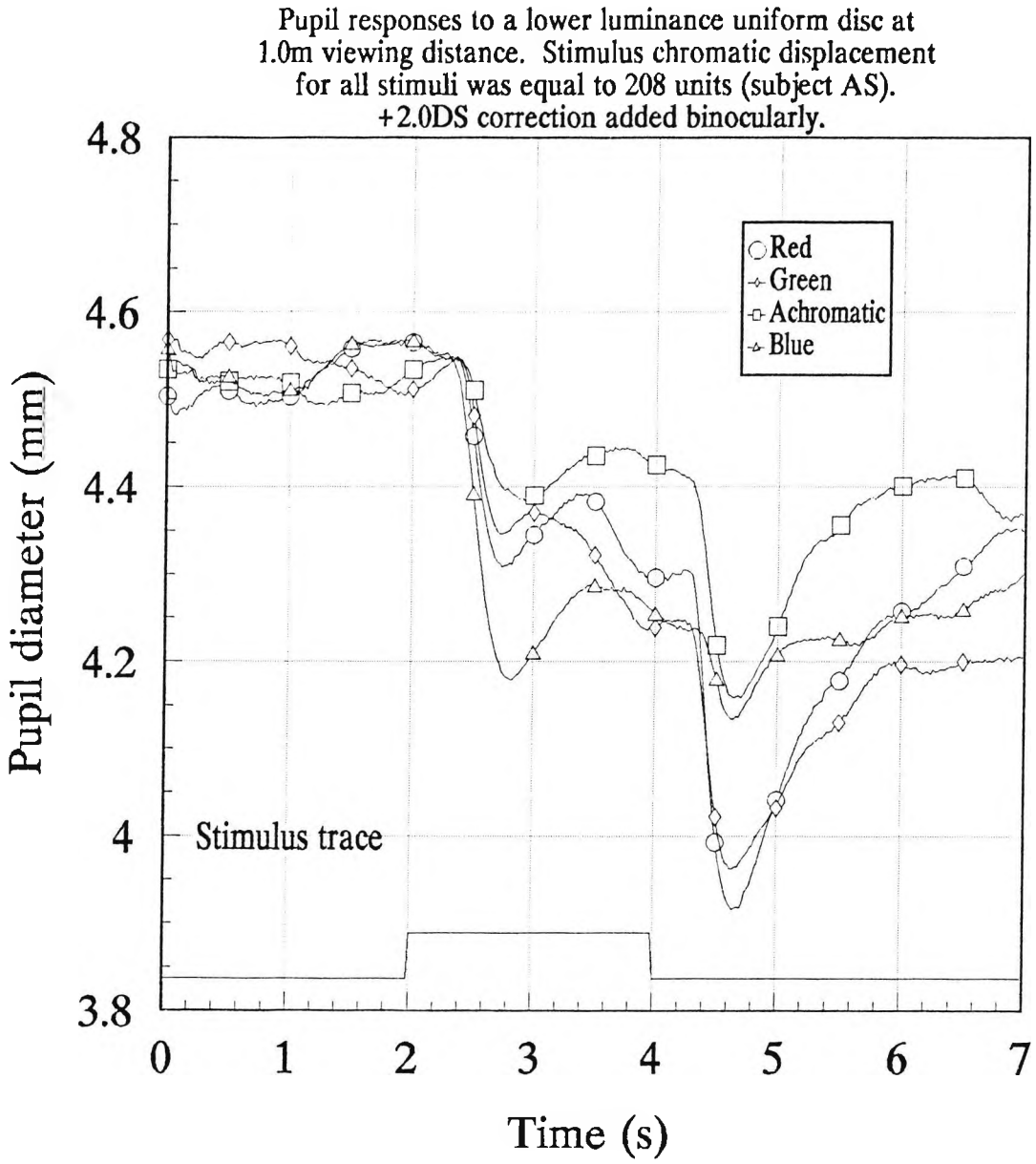


Figure 5.7b: the same as (a), in addition, +2.00D spheres were added binocularly.

5.4.2 Pupil Responses to Coloured Stimuli in Blindsight Subjects

A similar set of measurements were carried out on both blindsight subjects to investigate pupil responses elicited to coloured stimuli presented in their sighted and blind fields. These experiments were further extended to study these responses in relation to the subject's psychophysical performance in discriminating coloured patterns at various saturations. The findings are described below.

Constant Chromatic Displacement Experiments

The experimental methods and parameters were identical to those described for the normal subjects (section 5.4.1). All coloured targets had chromatic displacement of 208 units.
Measurements were carried out for both the sighted and blind field of the subjects.

GY
Figure 5.8a shows the recorded PCRs in GY's sighted field. These responses are similar to those measured in normal subjects. Figure 5.8b shows the corresponding traces for the stimulus presentations in the blind field. There is a very small response to the red and a good response to the blue stimulus onset. Normal responses to the stimulus offset, ie., the light reflex responses are present in both fields.
FS
Figure 5.8c & d show the same measurements in FS's sighted and blind fields respectively. A small response to the blue stimuli is recorded in his blind field. FS has smaller responses in his sighted and blind fields to the stimulus colour compared with GY and normal subjects. This may be attributed to his higher sensitivity to a reduction in luminance which normally causes a dilation response (seen more prominently in figure 5.8d). This response opposes the constriction due to the colour response. This point is investigated further in the section under "isoluminance condition".

Effect of Background Luminance on Pupil Responses in Blindsight

The larger pupil response and psychophysical discrimination score associated with the blue stimuli may have been due to the contributions of rod activity. In order to enhance the activity of cones and minimise the rod contribution to the pupil

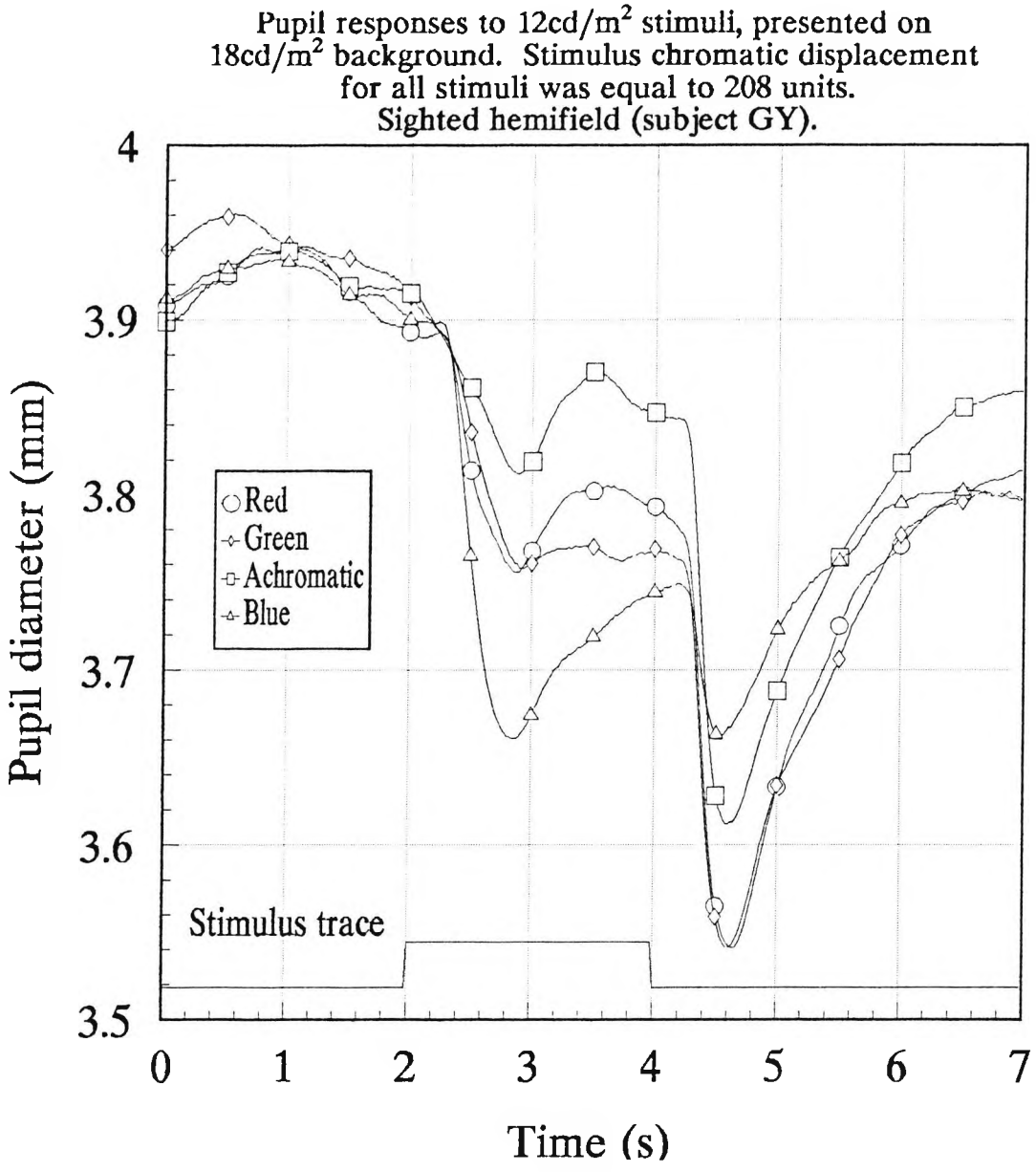


Figure 5.8a: pupillary traces obtained for sighted field stimulus presentation. Each trace is an average of 64 measurements. The chromatic displacements for all coloured stimuli were equal and the stimulus coordinates were the same as those denoted by * in figure 5.1. See text for experimental conditions.

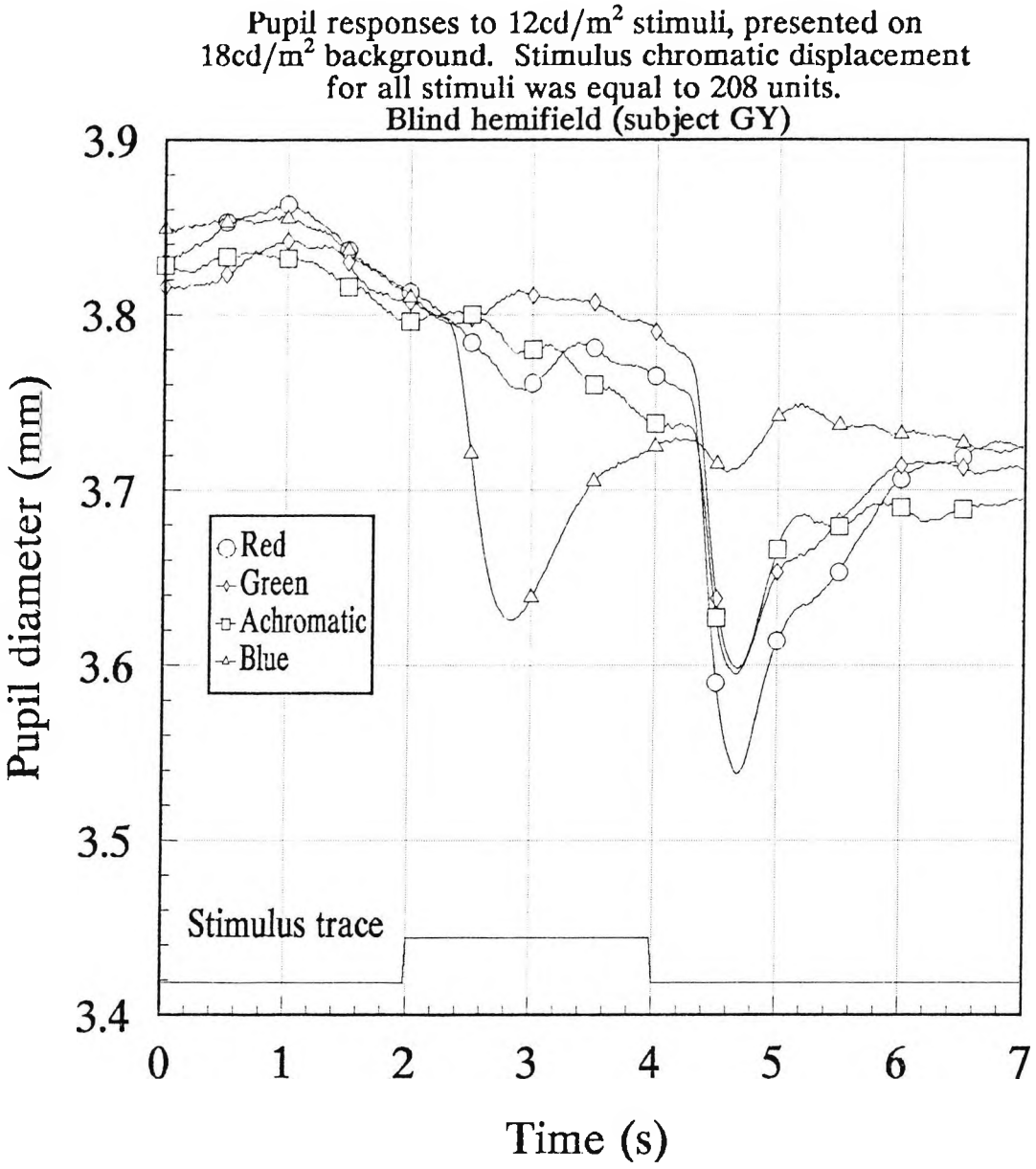


Figure 5.8b: pupillary traces obtained for blind field stimulus presentation. The stimulus chromaticities were the same as those described in (a). See text for experimental conditions.

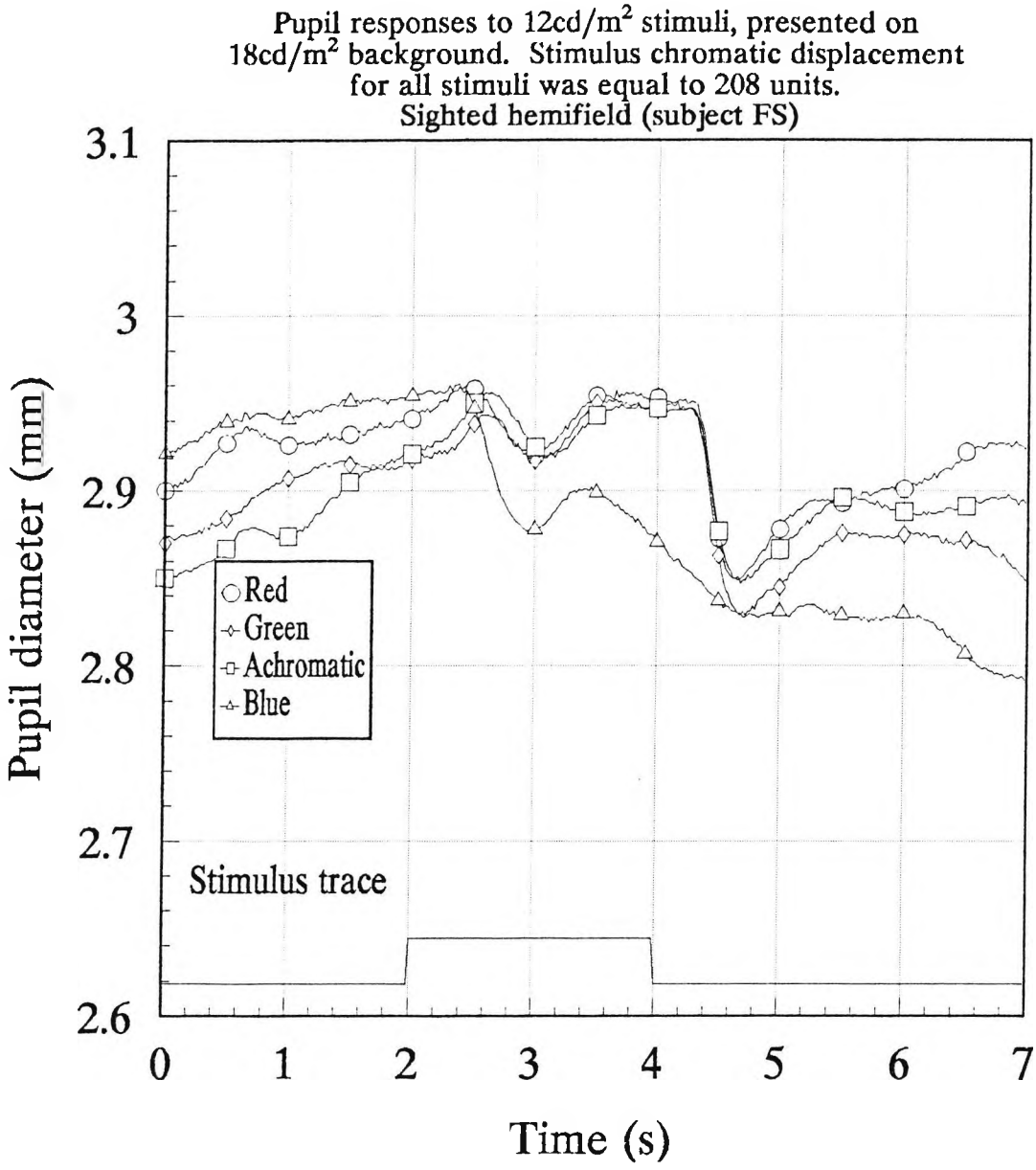


Figure 5.8c: see caption for (a). Each pupillary trace shown is an average of 32 measurements.

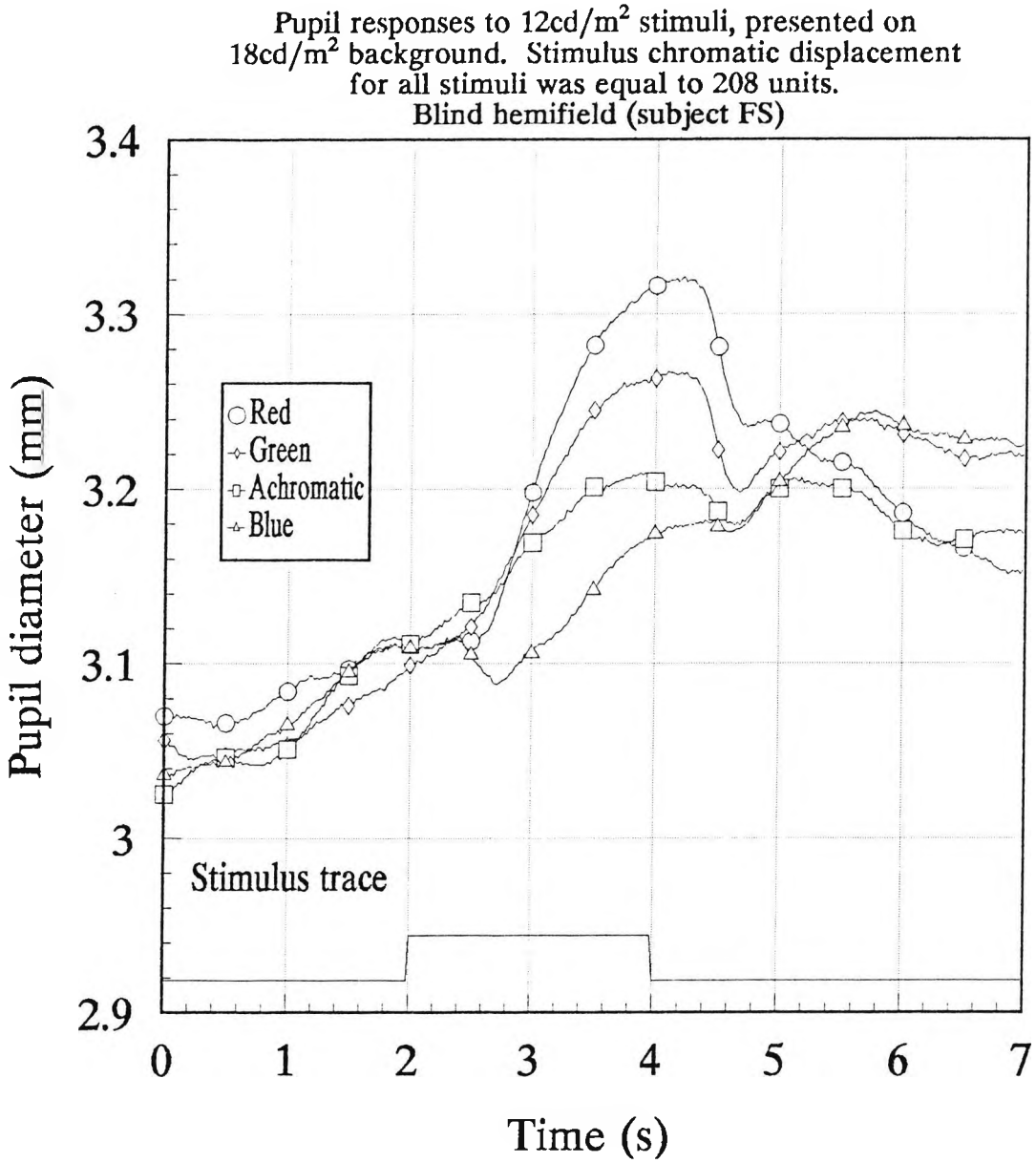


Figure 5.8d: see caption for (b). Each pupillary trace shown is an average of 32 measurements.

response, the background and stimulus luminances were raised to 55 cd/m^2 and 37 cd/m^2 respectively. The lower stimulus luminance was again selected to avoid pupillary constriction at stimulus onset via the light reflex. The pupillary responses were then recorded for the three saturation conditions used in the psychophysical experiments.

The chromaticity coordinates of the coloured stimuli used are denoted by stars, squares and triangles for high, medium and low saturation conditions, respectively (see figure 5.2).

High Saturation Condition

Figure 5.9a&b show the traces recorded for the largest chromatic displacement in GY's sighted and blind fields and the corresponding traces for FS are shown in figure 5.9c&d. Both subjects had normal pupil responses in their sighted fields. The same stimulus conditions also yield significant pupil responses in GY's blind field (figure5.9b).

The blind field responses of FS have been dominated by the dilation response due to a reduction in luminance, nevertheless, responses to the blue and red stimuli can be seen in figure 5.9d.

Medium Saturation Condition

Pupil responses measured in FS's sighted and blind fields are shown in figure 5.10a&b respectively. A small response to the blue stimuli was measured in the blind field. There is also a hint of a response to the red stimuli, but a larger number of recordings are required to establish its significance. At the same saturation level, GY had a pupil colour response to the red stimuli only (figure 5.10c), and did not respond to the blue and green stimuli.

Low Saturation Condition

At the lowest saturation level tested, FS had small pupil responses to the coloured stimuli presented in his sighted field (figure 5.11a). In the blind field, FS showed no pupil response to the presentation of the green and blue stimuli and showed only a very small response to the red stimuli (figure 5.11b).

GY however, showed no pupil response to any of the stimuli presented in his blind field as shown in figure (5.11c).

High Saturation Under Isoluminance

The amplitudes of the pupil responses in FS's sighted field were small compared to

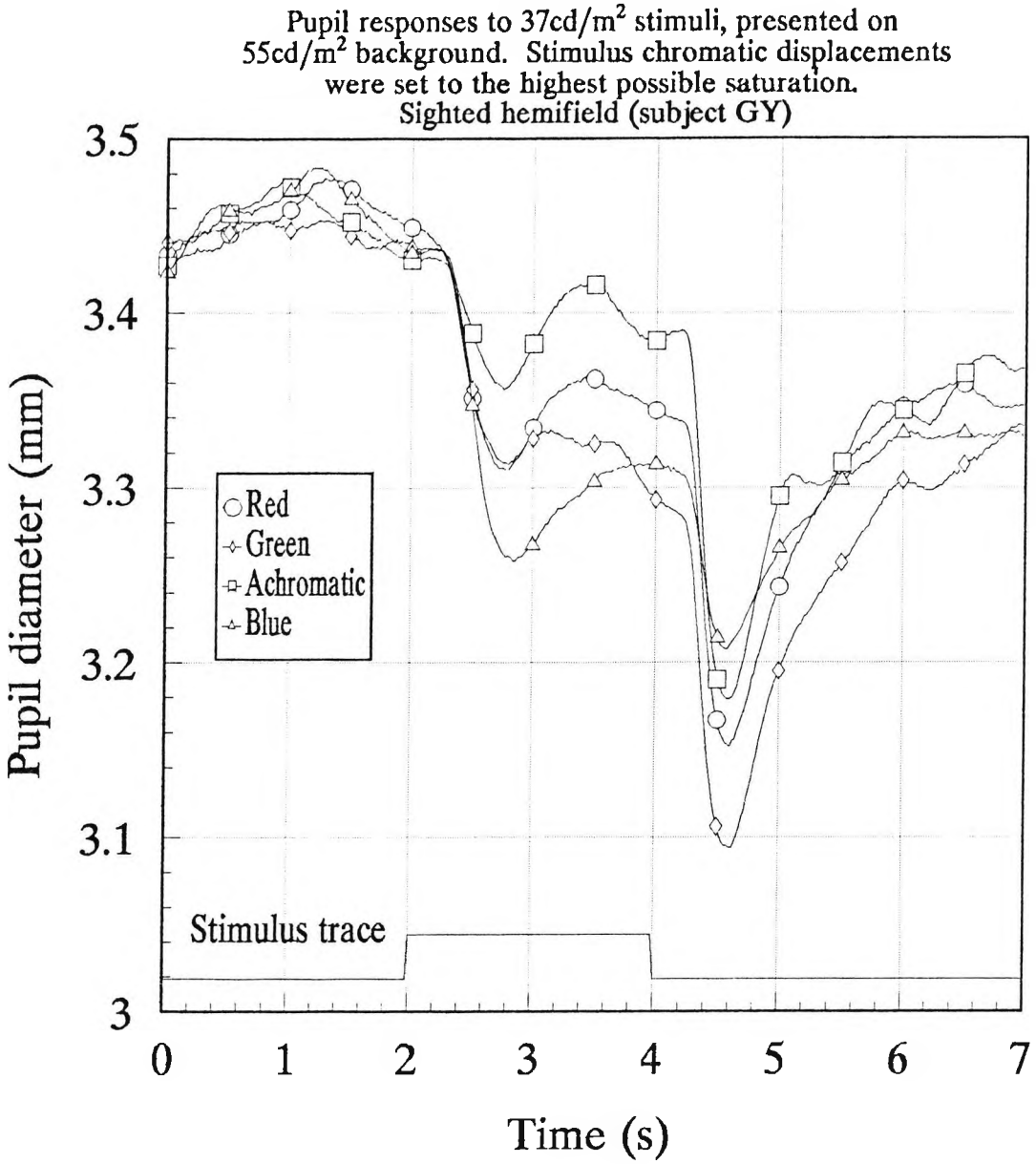


Figure 5.9a: pupillary traces obtained for sighted field stimulus presentation (high saturation condition). Each trace is an average of 32 measurements. The chromatic displacements were at their highest possible value under the photopic conditions given (see text). The stimulus chromaticity coordinates were the same as those denoted by * in figure 5.2. See text for experimental conditions.

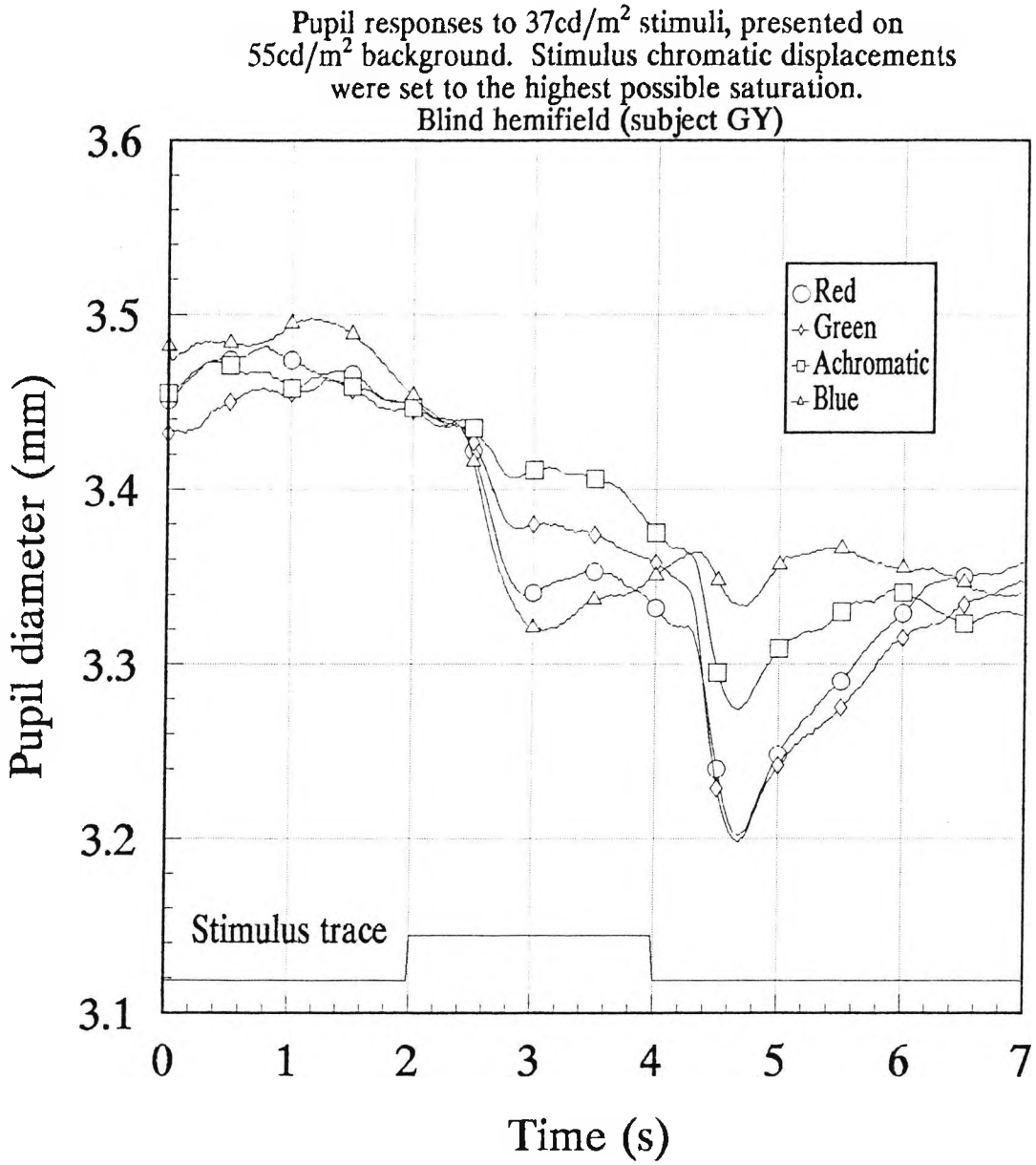


Figure 5.9b: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

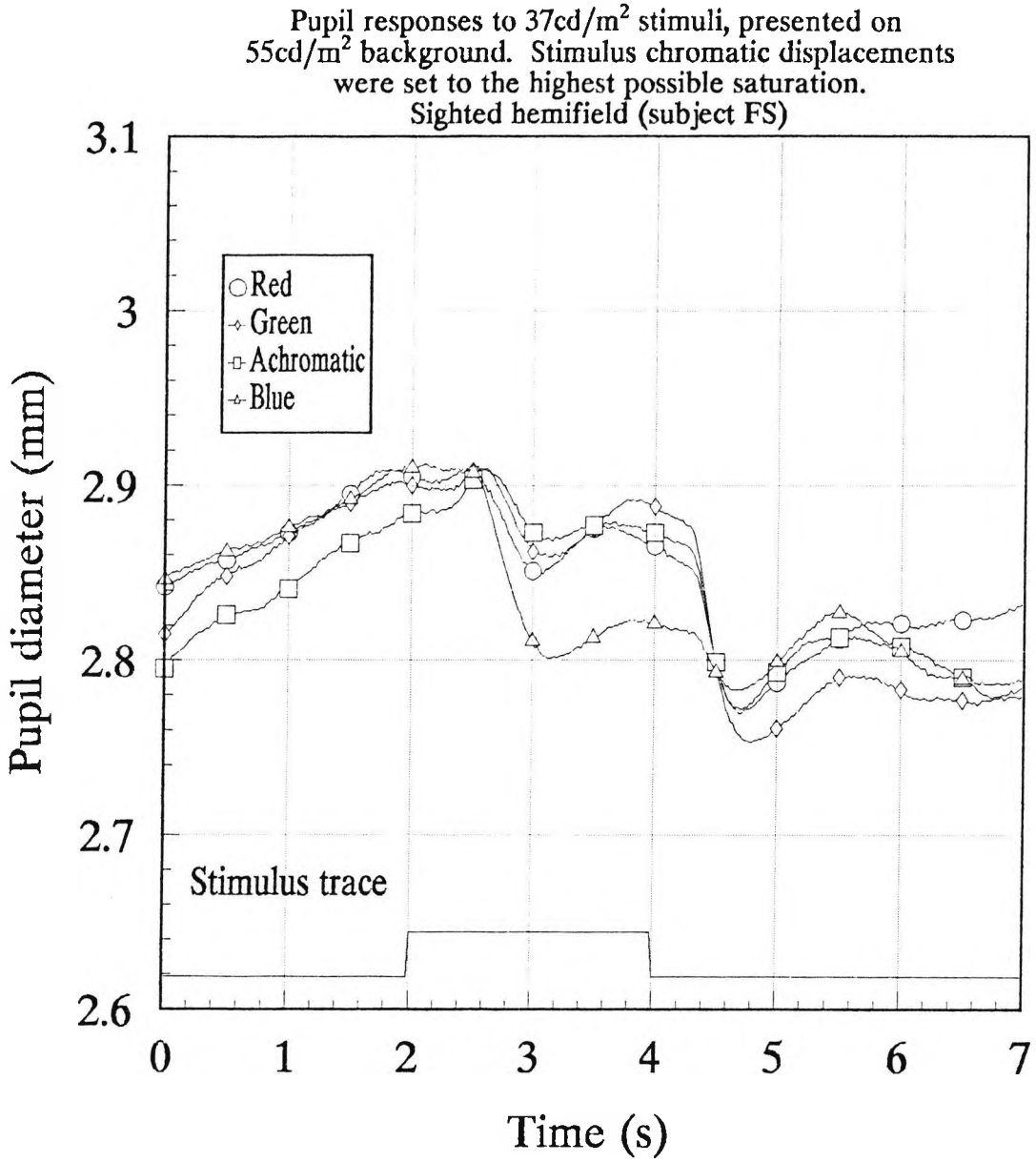


Figure 5.9c: pupillary traces obtained for sighted field stimulus presentation. See caption for (a).

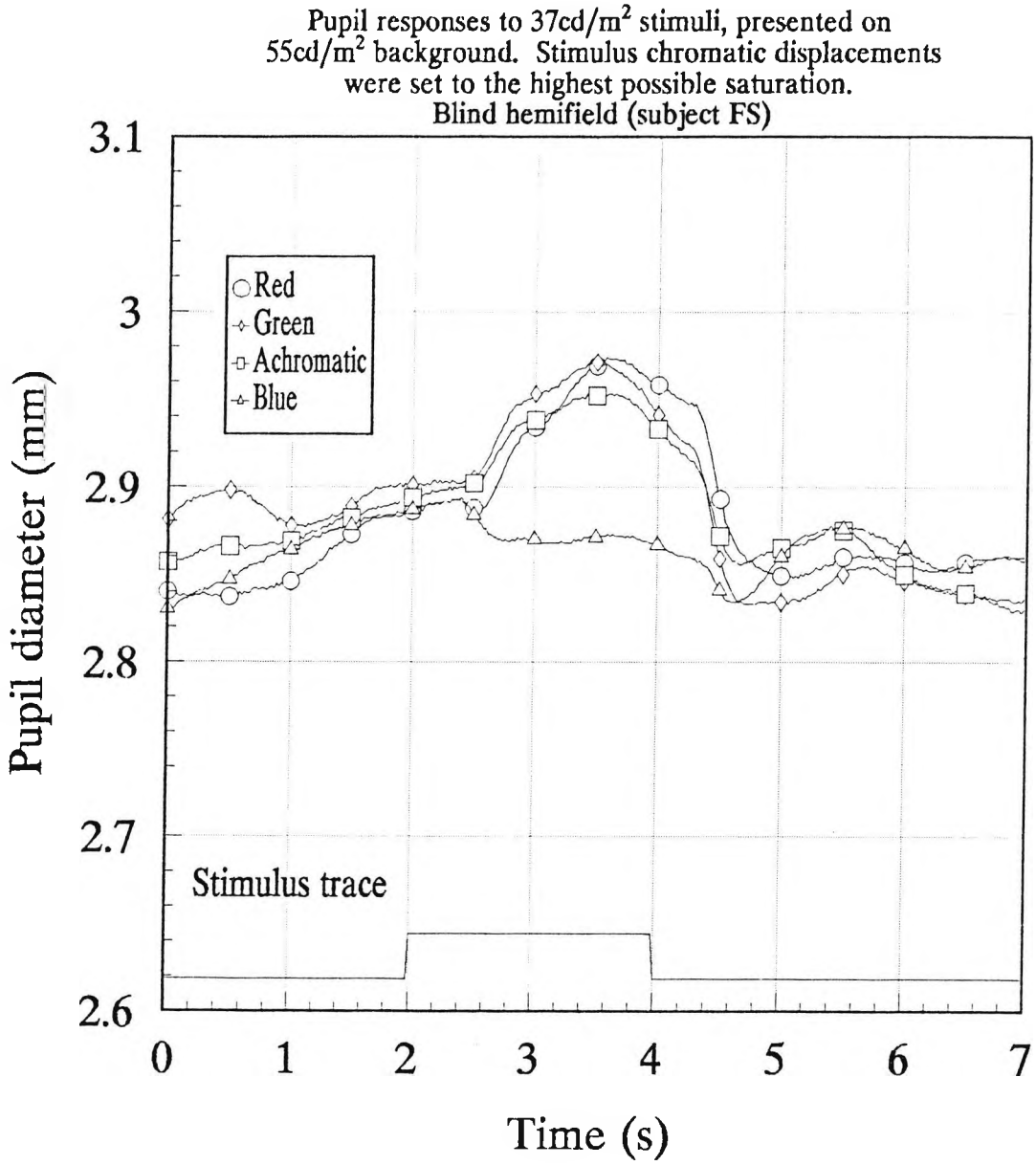


Figure 5.9d: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

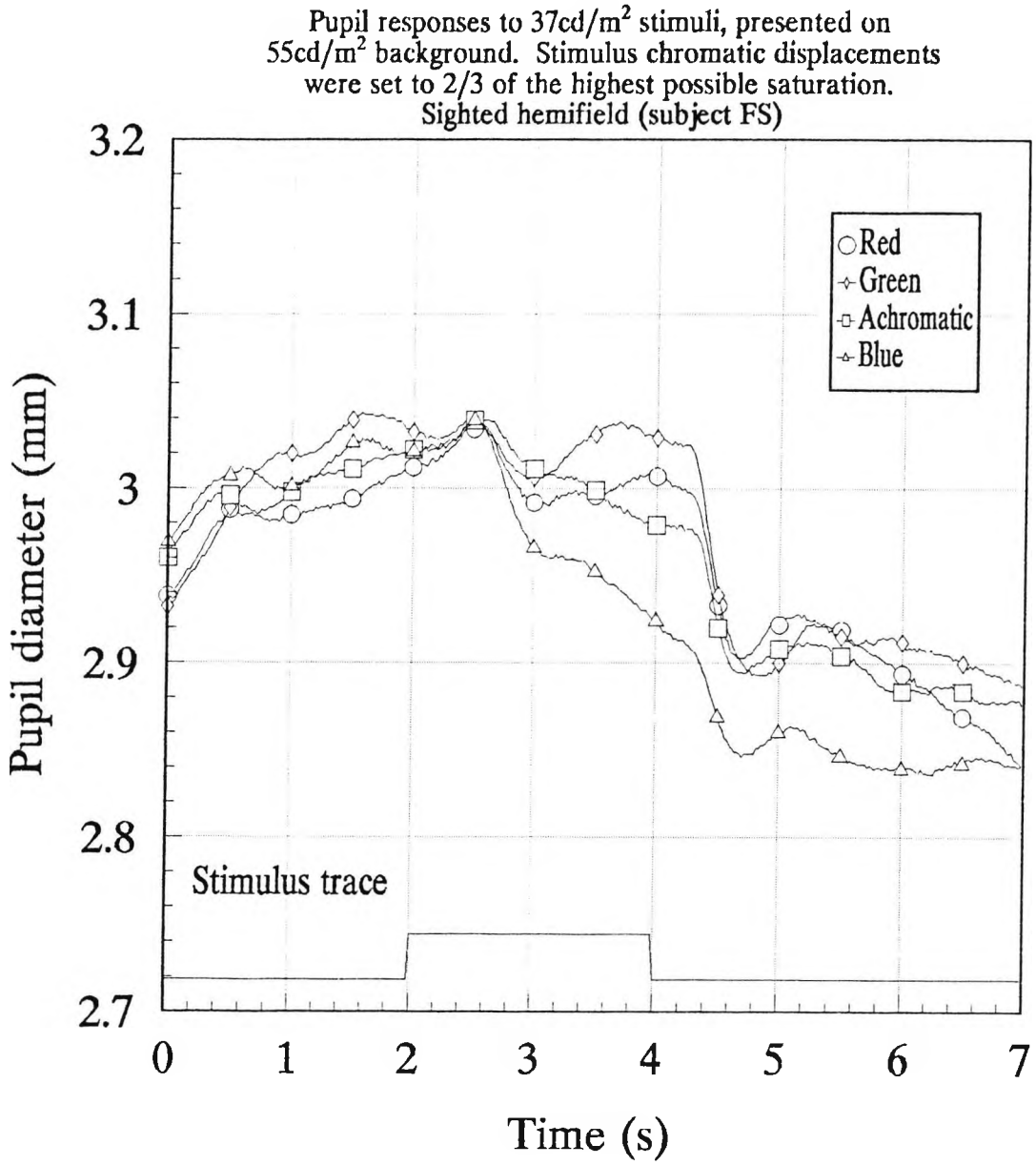


Figure 5.10a: pupillary traces obtained for sighted field stimulus presentation (medium saturation condition). Each stimulus trace is an average of 32 measurements. The stimulus chromatic displacements were set to 2/3 of their value for high saturation condition. The stimulus chromaticity coordinates were the same as those denoted by squares in figure 5.2. See text for experimental conditions.

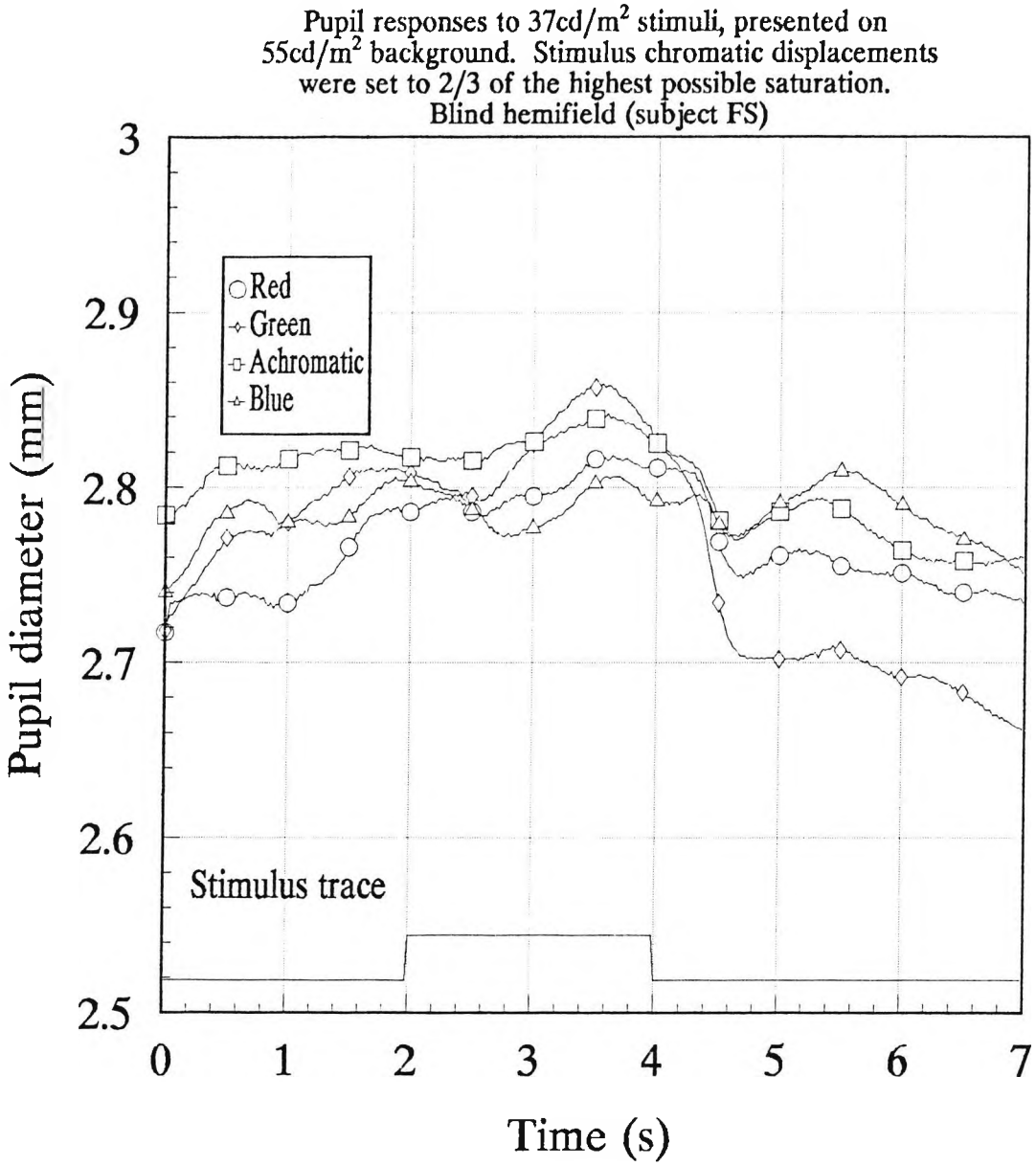


Figure 5.10b: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

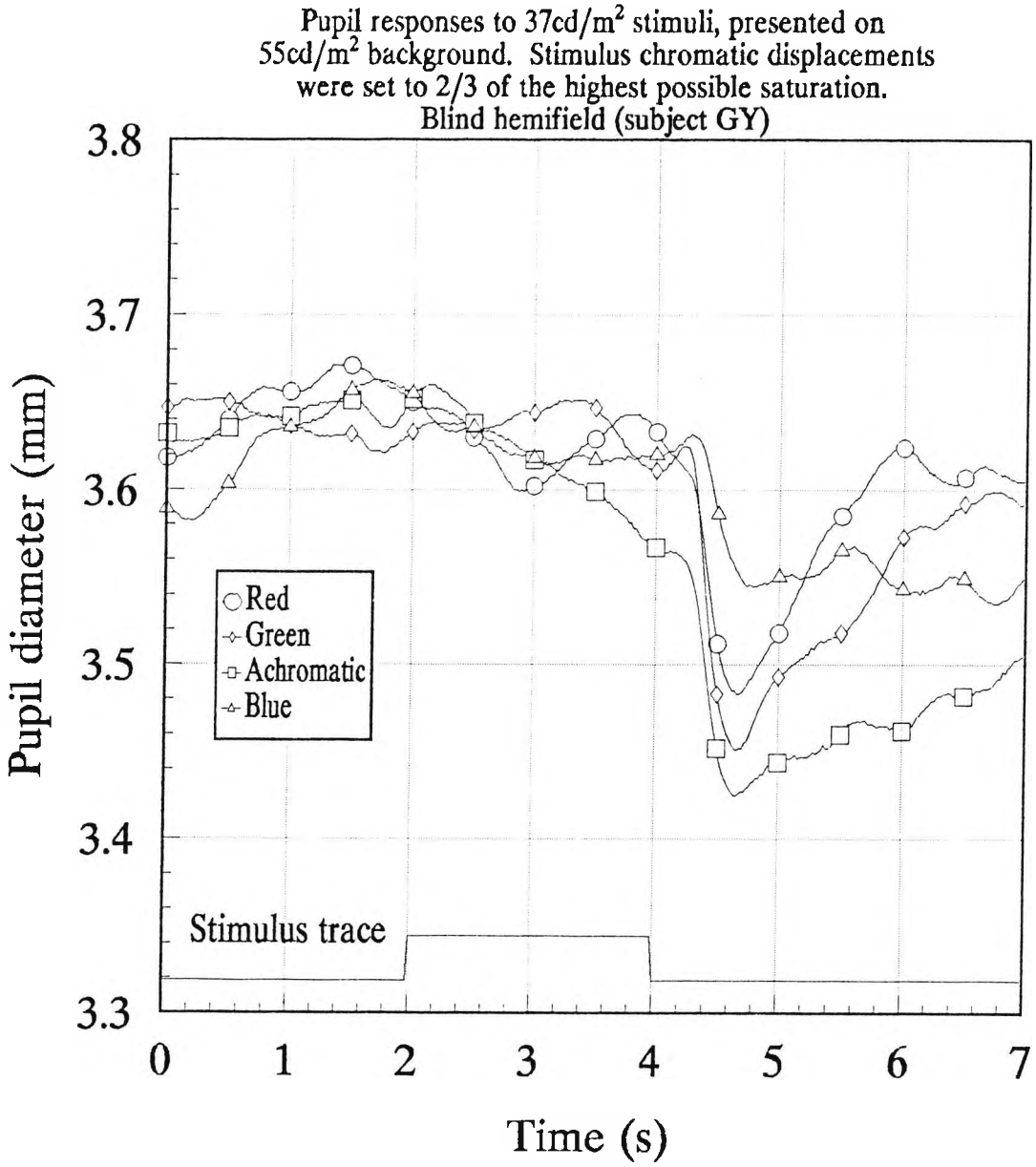


Figure 5.10c: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

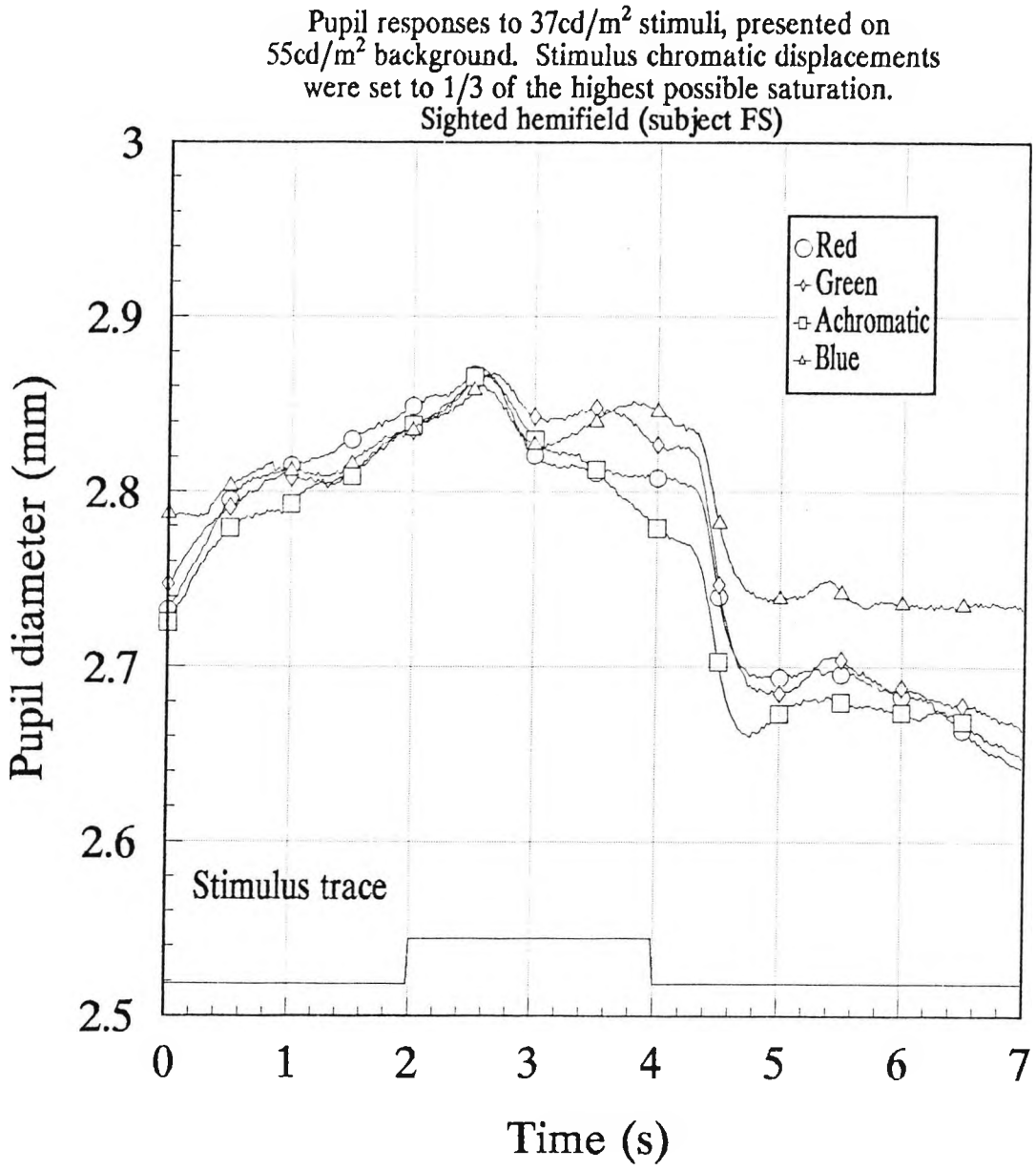


Figure 5.11a: pupillary traces obtained for sighted field stimulus presentation (low saturation condition). Each stimulus trace is an average of 32 measurements. The stimulus chromatic displacements were set to 1/3 of their value for high saturation condition. The stimulus chromaticity coordinates are the same as those denoted by triangles in figure 5.2. See text for experimental conditions.

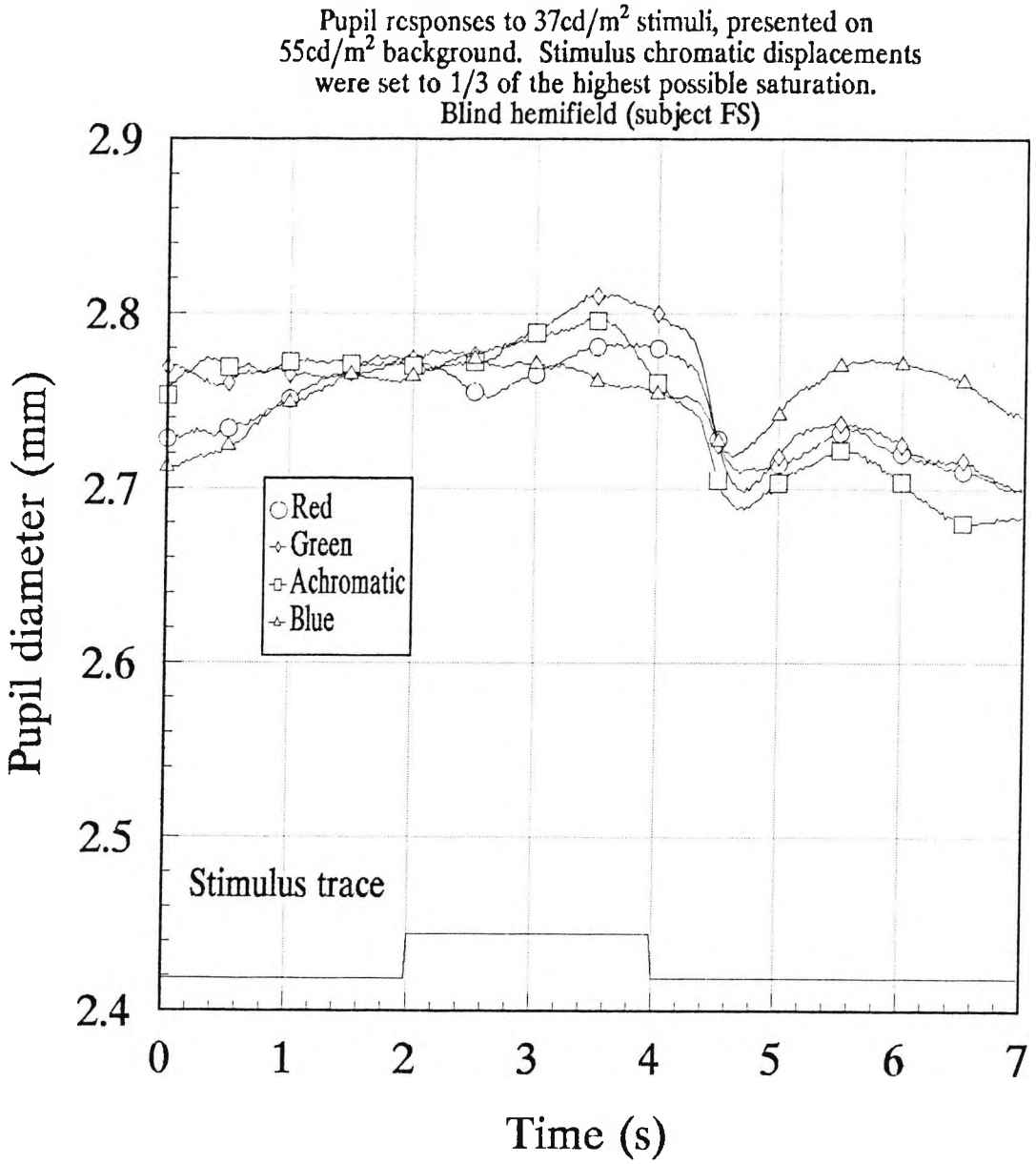


Figure 5.11b: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

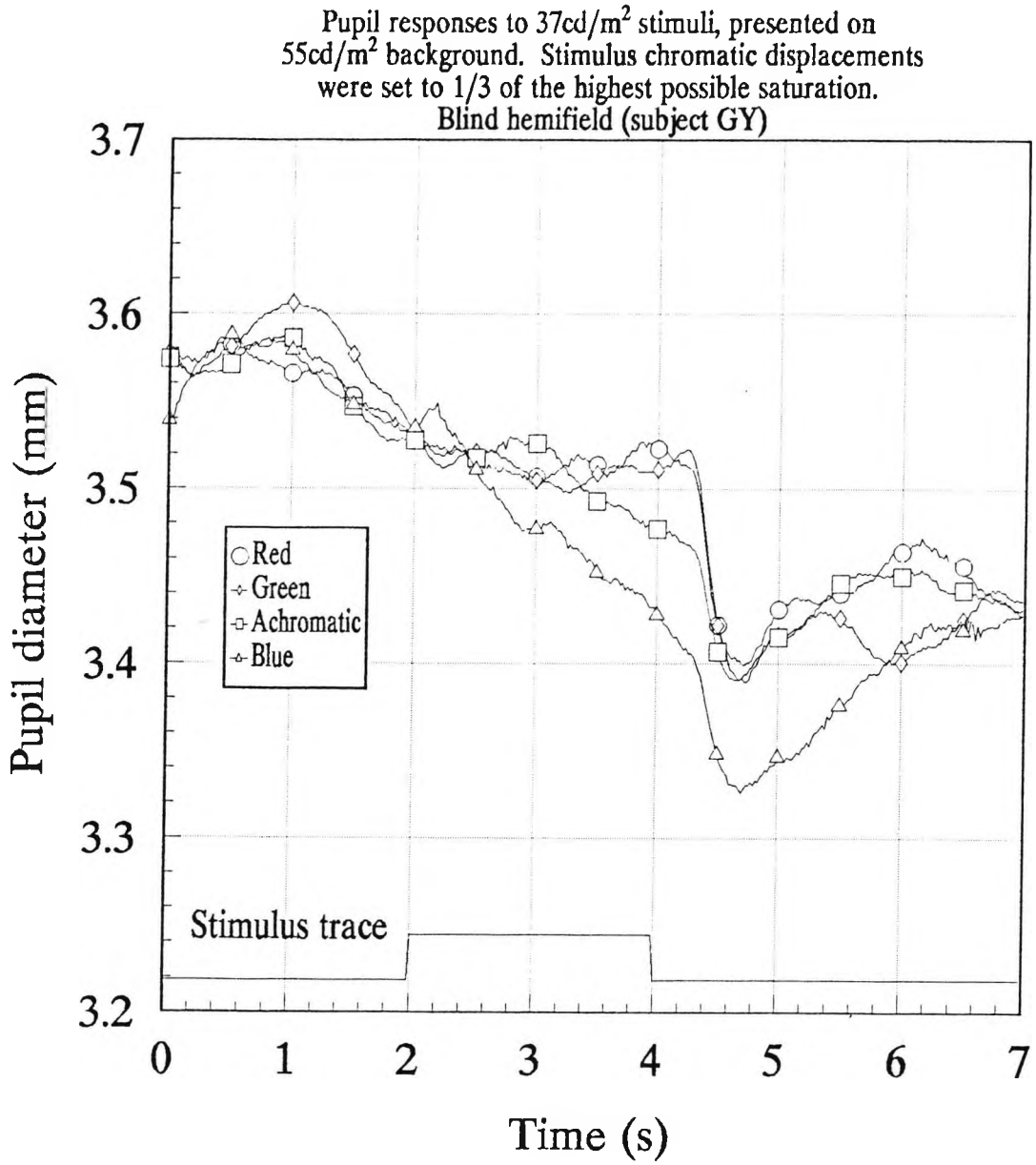


Figure 5.11c: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

the normal subjects. This observation was attributed to his high sensitivity to a reduction in stimulus luminance, giving rise to a dilation signal opposing the pupillary constriction due to the change in chromatic information. If this hypothesis is correct, then higher response amplitudes would be expected to be elicited for targets having the same luminance as that of the background.
Figure 5.12a shows the pupil responses for FS's sighted field under equal luminance conditions where the targets and the background luminances were equal to 37 cd/m^2. The chromaticities of the coloured stimuli were the same as for the high saturation condition. The responses measured have larger amplitudes than those shown in figure 5.9c. The response amplitudes for the blind field stimulus presentation given in figure 5.8b were also larger than those of figure 5.9d.
The "no-stimulus" trace of figure 5.12b was included to show that in the absence of any stimulus, no pupillary response is measured, ie., pupil responses elicited to the coloured stimuli are not as a result of an experimental artefact being synchronised with the stimulus presentation.

Since the background luminance (37 cd/m^2) was lower than those in the psychophysical experiments (55 cd/m^2) the colour discrimination was also examined at the background luminance of 37 cd/m^2 to investigate whether the subject could still perform above chance in guessing the interval and the colour of the test stimuli. The results are given below and show that FS's ability in the colour discrimination task was not altered by the reduction in background luminance.

Colour	% correct interval	%correct colour
red	93.8 (2E-7)	84.4 (3E-9)
green	68.8 (0.02)	56.3 (4E-3)
blue	71.9 (7E-3)	65.6 (2E-4)

The *p* values are given in the bracket.

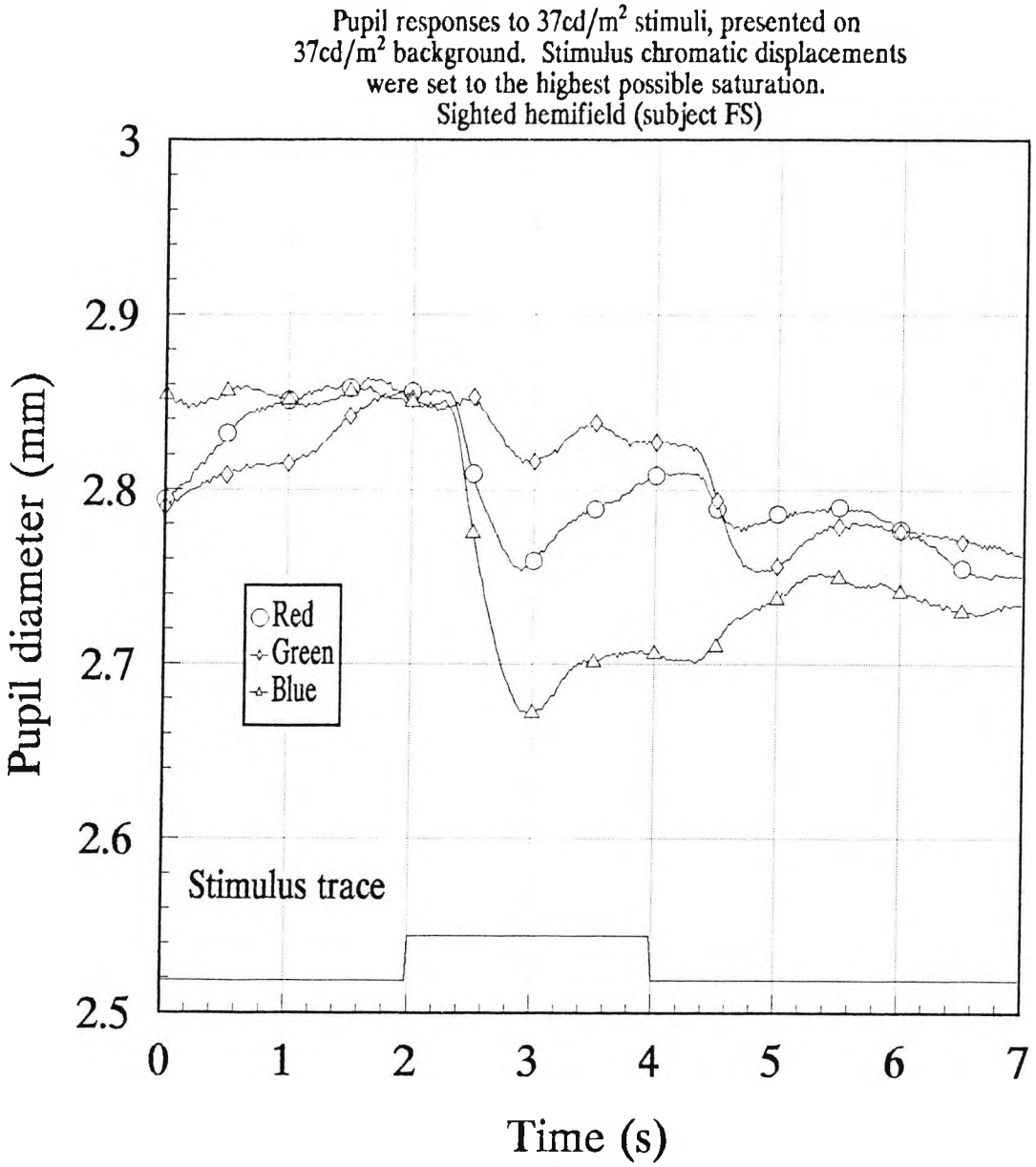


Figure 5.12a: pupillary traces obtained for sighted field stimulus presentation (isoluminance condition). Each stimulus trace is an average of 32 measurements. The stimulus chromatic displacements were the same as those described in figure 5.9a. See text for experimental conditions.

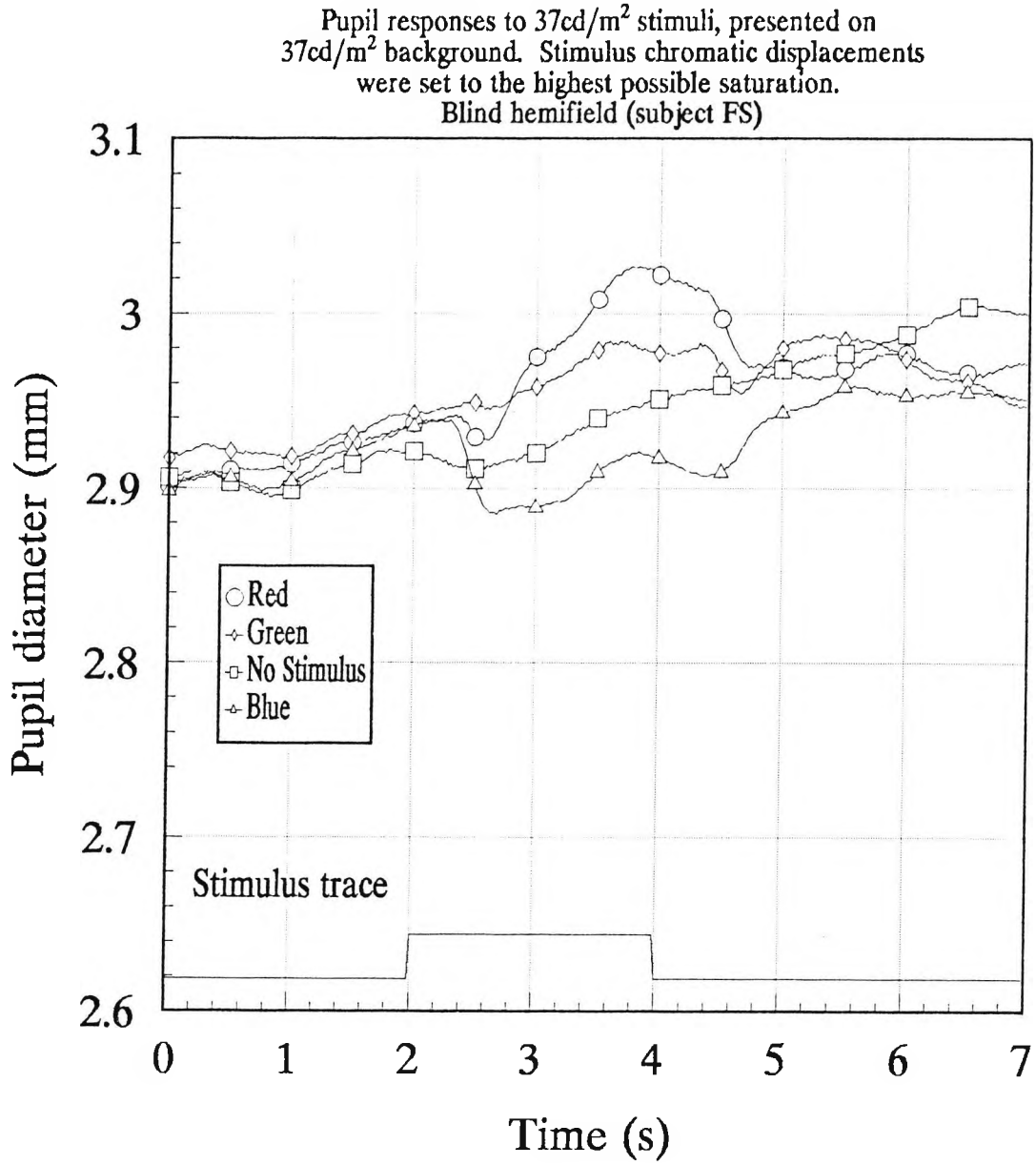


Figure 5.12b: pupillary traces obtained for blind field stimulus presentation. See caption for (a).

Discussion

Pupillary responses to pure chromatic signals have been attributed to a sudden change in neuronal activity when a coloured stimulus is presented to the eye (Barbur, 1991). A suprathreshold stimulus pattern similar to those described in this chapter is detected by both colour opponent and broadband luminance mechanisms. At suprathreshold levels, mechanisms detecting a stimulus attribute interact, and the perception of the stimulus is the result of pooled activity of the mechanisms. The presence of pupil responses to exchanges of isoluminant stimuli has been reported previously (Alpern and Campbel, 1962; Saini and Cohen, 1979; Young and Alpern, 1980). Pupil responses to the onset of colour of stimuli of lower luminance than the surrounding background field have also been examined (Barbur et al., 1987a; Barbur, 1991). Such observations have been extended by measurement of pupil colour responses in normal trichromats and in dichromats using a stimulus configuration which isolated the contribution of pure chromatic signals (Barbur et al., 1993; Birch et al., 1993).

The pupil spectral sensitivity obtained from changes in pupil size at photopic levels, parallels the sensory spectral sensitivity and exhibits the characteristic peaks and troughs associated with cone opponency indicating the effect of colour opponent mechanisms in pupillary responses (Krastel et al., 1985). Results of the pupillometric studies presented in this section show that when using large coloured stimuli of lower luminance than the background field small pupillary changes can be elicited both in normal subjects and in the sighted field of the blindsight subjects tested. In section 5.3, psychophysical evidence is presented demonstrating the existence of residual chromatic processing in blindsight. The pupillometric results parallel the psychophysical findings. The initial set of experiments (ie., the constant chromatic displacement condition), produced some indication of pupil responses in

both blindsight subjects. Pupil responses were however demonstrated clearly when the coloured stimuli had the highest possible saturations on a background of higher luminance, in both subjects. The response amplitudes decreased for the medium stimulus saturation condition. They were eliminated completely in one subject (FS) and were present for one stimulus colour only (red) in the other subject (GY), at the lowest saturation condition. Comparison of the psychophysical and pupillometric findings in subject FS show the following characteristics:

1. At the high saturation condition, discrimination was best for the red and blue stimuli. The pupillary responses to red and blue stimuli were also demonstrated.
2. At the medium saturation condition, discrimination of blue and red stimuli occurred and a small pupil response to the blue stimuli and possibly to the red were measured.
3. At the low saturation condition, colour discrimination was not significant for any of the coloured stimuli. A small pupillary response was elicited to the red stimuli only.
4. At medium and low saturation conditions, discrimination of green could not occur, and in none of the conditions was a pupil constriction elicited in response to the green stimulus.

Comparison of the psychophysical and pupillometric findings in subject GY show the following characteristics:

1. At the high saturation condition, performance was well above chance level for the discrimination of all coloured patterns. Pupillary responses were present for all coloured targets.
2. At the medium saturation condition, discrimination was best for the red stimuli and performance was above chance level for discrimination of blue. Pupillary responses were present for red stimuli only.

3. At the low saturation condition, chance level scoring occurred in "guessing" the interval of stimulus presentation and poorest performance achieved for guessing the colour of the stimuli. Significant pupillary responses could not be measured for any of the patterns presented.

Collectively , the PCRs could be elicited in the blind field of both subjects. Their response amplitudes were largest at the highest saturation condition and were either very small or absent at the low saturation condition.

Mechanisms mediating pupil responses to coloured stimuli and their neural connectivity in normal and blindsight subjects are not known. The presence of pupillary responses to pure chromatic change has been attributed to the weakening of the supranuclear inhibitory input to the pupillomotor nucleus in normal subjects, but the neurobiology of such an action has not yet been demonstrated.
The colour processing in blindsight is mediated either through functioning undamaged prestriate areas which receive input directly from the surviving LGN neurones, or through the activity of subcortical structures such as the pulvinar which may also send projections to prestriate areas (see section 5.3).

The pupil responses to large coloured stimuli in blindsight subjects may also be mediated via functioning cortical and/or subcortical structures. Such responses have much smaller amplitudes in the blind field compared with the sighted field. This may be attributed to the presence of a damaged primary visual area, thus indicating its direct role in generation of the normal pupil responses; or the destruction of the primary visual cortex may result in neuronal degeneration in many other cortical and subcortical structures (see section 1.1), thus affecting the generation of such responses indirectly.

Pupil responses to pure chromatic signals are absent in achromatopsic subjects when tested using random modulation technique (Barbur et al., 1993). This favours the role of the prestriate area in generation of PCRs. It is, however possible that their absence is related to characteristics of the stimulus. It is also possible that the large coloured patterns used in the present experiments, may also elicit pupillary responses in patients with cerebral achromatopsia.

Collectively, there are several candidate sites for the generation of pupil responses elicited to coloured stimuli in blindsight and the present results cannot be used to distinguish between them. Further psychophysical and neuroanatomical experiments are needed to investigate the contribution which the various pathways make to colour discrimination in blindsight and to the generation of pupil changes in response to chromatic stimuli both in normal subjects and in blindsight patients.

5.5 Summary

The ability of two blindsight subjects to discriminate the colour of a stimulus pattern was investigated using a two alternative forced choice procedure. We found that for a given chromatic displacement, their residual colour discrimination performance was not the same along the three axes tested. The performance of both subjects improved when the conditions were modified to obtain more saturated colours on a white background of higher luminance.

Pupil responses to the same stimuli used in psychophysical tests were also investigated. The results show that coloured stimuli elicit pupil colour responses in normal subjects and also when presented in the sighted field of subjects.
Pupil colour responses were demonstrated in both subjects when the stimulus was restricted to their blind fields. This was only the case for the high chromatic saturation condition and the responses obtained were also of significantly smaller amplitude when compared to those elicited in the sighted hemifields. The pupil response amplitudes varied with stimulus saturation. Significant responses were measured for all stimuli at high saturation condition. The responses were only significant for one stimulus colour and only in one of the blindsight subjects at low stimulus saturation level examined.

Both subjects scored poorly for the green stimulus in psychophysical experiments, responses being significant only in the high saturation condition.

Similarly, no pupillary response to the green stimulus was elicited in one subject (FS) under any of the conditions tested, and was present only for high saturation condition in the other subject (GY).

Collectively, psychophysical evidence for colour discrimination in blindsight has been presented. Pupillometric correlates for the psychophysical findings have been demonstrated. Possible pathways involved in mediation of such responses have been discussed.

CHAPTER VI

Concluding Remarks

Previous studies have shown that visual mechanisms may not act entirely independently of each other at suprathreshold levels, and that some facilitatory and inhibitory interactions exist between them. This has been attributed to the presence of common basic neuronal structures both at receptor and in post-receptoral levels (Sekuler and Levinson, 1974; Mollen, 1982).

Evaluation of the overall activity of the visual system as well as the assessment of specific mechanisms are of both clinical and scientific interest. The psychophysical procedures designed to achieve such tasks, rely mainly on a subject's response to changes in the visual field (Ruddock, 1977). Subjective responses however, cannot always be obtained as easily in infants or in primate studies. They may also be affected by parameters beyond the control of the experimenter such as changes in subject's response criteria. Thus, objective evaluation techniques can be of great value in such cases.

Small transient changes in the pupil diameter associated with presentation of some stimulus attributes, such as structure and colour have been demonstrated (Slooter and van Norren, 1980; Barbur and Forsyth, 1986). These pupillary responses have been attributed to a transient perturbation in the pattern of neuronal activity in the visual cortex (Barbur, 1991), therefore, reflecting the response of the visual system as an entity to the onset of the stimulus. Indeed the pupil response measurements using chequer-patterns and the pupil grating responses have been shown to mirror the contrast sensitivity function, hence, providing an objective measure of the performance of the visual system at suprathreshold levels.

A large number of neurones along the visual pathways either code movement information or at least respond to moving stimuli. It may therefore be expected that perturbation in their activity caused by a moving stimulus would give rise to a systematic changes of pupil size.

The results of experiments described in chapter III show that pupil motion responses (PMRs) can be elicited in response to the onset of coherent motion in dynamic random dot noise. PMRs are present for both foveal and eccentric

stimulus presentation and the response amplitude does not vary significantly with stimulus speed, at least for the range of speeds tested. PMRs are not eliminated by degradation of the retinal image quality or by changes in the steady state of the accommodation.

There are extensive psychophysical studies on movement sensitivity in blindsight (Barbur et al., 1980; Blythe et al., 1986, 1987; review by Weiskrantz 1990). Using guessing paradigms, it has been demonstrated that blindsight subjects have residual discrimination for both direction and the speed of a moving target. The ability to discriminate moving stimuli in the absence of a direct retino-geniculo-striate pathway can be attributed to the processing of motion signals either in extrastriate areas and/or in midbrain structures. Movement sensitive cells responding to apparent motion of a visual stimulus have been reported in the extrastriate area V5/MT (Dubner and Zeki, 1971; Maunsell and van Essen, 1983a; Albright, 1984; Newsome and Paré, 1988) as well as subcortical structures such as the superior colliculus and pulvinar (Peterson et al., 1985).

The existence of pupillometric correlates for these psychophysical findings was demonstrated in chapter III. The pupillary traces given in figure 3.11 show that PMRs were present when movement stimuli were presented in the blind field of a blindsight subject, although of smaller amplitudes compared to those measured in the sighted field. It is unclear which structures mediate PMRs in blindsight subjects since there are both cortical and subcortical candidate sites. Recent MRI/PET studies in GY (Barbur et al., in press) show that stimulation of the blind hemifield with moving stimuli results in increased activity in V5 and satellite areas. It is therefore likely that the residual PMR observed in GY originates from the same structures which are involved in mediating motion responses in normal subjects.

Neurones responding to the component and pattern motion along specific directions have been found in primates (Newsome et al., 1985, 1986; Maunsell and Newsome, 1987). The presence of narrow-band, bandpass and broadly tuned, speed selective neurones have also been reported (Orban et al., 1981a,b, 1986). It is highly likely that these neurones form the basis of motion analysers responsible for extracting movement information in the human visual system. The perception of a change in motion direction or speed may then occur as a result of a shift in activity ratios among these basic motion analysers.

Psychophysical studies reviewed in chapter IV have shown that human observers have small Weber-fractions for detecting a change in stimulus speed and direction at least for an intermediate speed range. Again, pupillometric correlates for psychophysical responses to a change in speed and direction of coherent movement were demonstrated in chapter IV. These pupillary responses were present for both foveal and peripheral stimulus presentations and their amplitudes varied systematically with the percentage change in the stimulus direction or speed over the range of values tested.

Further psychophysical evidence for colour processing in blindsight were described in chapter V. These results are in agreement with the findings of other experimenters, Stoerig and Cowey (1989a, 1991, 1992) and Ruddock and colleagues (Ruddock, 1993). The latter also demonstrated that colour discrimination ability remains even in the absence of V1. There are, however, differences between the stimulus conditions used in our experiments (see chapter V) and those of other experimenters. Stoerig and Cowey produced their 2°, 17-18 cd/m^2 stimuli using narrow-band filters projected onto various positions of a perimeter illuminated at low photopic levels (10 cd/m^2). Ruddock and colleagues used similar filters for generating a large (20°, 2.1 log td) narrow-band stimulus presented on a 1.7 log td white background, using a Maxwellian viewing system. In our experiments we used desaturated broadband stimuli. In discrimination tasks the stimulus luminance was chosen at random between 20-42 cd/m^2 and presented on a 55 cd/m^2 white background to minimise rod signals and to avoid the detection of scattered light. The results demonstrate that the blindsight subjects' ability in discriminating the colour of a stimulus pattern in a forced choice paradigm varies with the chromatic saturation of the stimulus (see discussions in section 5.3).

Pupillometric studies, using a similar stimulus pattern revealed the existence of small pupil responses which parallel closely the psychophysical performance under the experimental conditions used (see discussions in section 5.4.2).

Although in this report, experimental evidence has been given in support of the existence of pupil responses to the stimulus motion and colour as an indicator of the neuronal activity in the visual system, their evolutionary importance is not known. Since the pupil responds to a wide range of stimuli besides visual information, it is possible that the responses result from a "leakage" of neuronal activity to the pretectal nuclei. Fluctuations in the pupil diameter as a result of the stimulus

presentation are too small (max. ≈8%) to have a significant effect on the optical quality of the retinal image (Woodhouse, 1974). Their presence therefore, may indeed have little or no functional use.

Previous studies have shown that the pupil responses elicited to the onset of a stimulus structure have similar characteristics to those found using subjective contrast sensitivity measures. In this report correlates between the results of pupillometric studies and those of psychophysical performance and physiological recordings with respect to the processing of movement and colour in normal subjects have been reported. Evidence was also presented which suggests the existence of similar correlates in subjects with damaged geniculo-striate pathways. These findings support the explanatory hypothesis that relates the presence of pupil responses to the overall neuronal processing in the visual system. These pupillometric techniques therefore may be used as an objective assessment of performance in various visual functions where the subjective data is not readily obtainable. For example, the development of colour processing in infants and non human primates may be investigated by measuring the pupil responses elicited to presentation of chromatic stimuli.

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