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VISUAL THRESHOLDS AND DISCRIMINATIONS MEASURED
FOR SPATIAL PATTERNS

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ABSTRACT

The thesis describes an investigation of visual responses to spatially structured stimuli. Several different psychophysical methods were applied in the study of human subjects and both normal and abnormal patterns of response are examined.

Background perturbation techniques, applied in the study of normal vision, showed that in the early stages of processing, visual channels treat dark targets similarly to light ones. Efforts to show that mechanisms detecting the two target contrasts act independently were only partially successful. By studying the contribution of different spectral mechanisms (isolated using Stiles' two-colour increment threshold technique) to spatial channels sensitive to orientation, it was found that the blue-sensitive mechanism projects to a luminance channel, contrary to the conclusions of several earlier studies which suggest that they project solely to chromatic channels.

Investigations on a number of different kinds of abnormal visual function are presented, and their results are summarized as follows.

i) Discrimination of single targets embedded in multi-element backgrounds are, under some circumstances, abnormal in subjects with visual agnosia and strabismic amblyopia. In the latter case, performance appears to be limited by lack of spatial resolution, but cannot be attributed solely to the coarse spatial responses measured for early stages of visual processing. Experiments on a single agnosic subject revealed normal discrimination of orientation of lines, but impaired performance for all the pattern discriminations. It is shown that increasing the number of elements in the pattern reduces severely discrimination capacity.

ii) The direction of apparent motion, produced by two spots separated in space and time, could be discriminated with near normal accuracy by those hemianopes who exhibit residual vision although they have no spatial discrimination.

iii) In a case of visual perseveration, in which the subject experienced 'after-images' following brief presentations of relatively dim light stimuli, it was shown that there is a decrease in threshold sensitivity associated with the 'after-images'. This provides an objective method for assessment of response characteristics associated with the condition.

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CHAPTER ONE INTRODUCTION

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The average human brain weighs 1450g, is composed of 18×10^{10} cells of which 6×10^{10} are directly engaged in information processing and each of these 6×10^{10} cells make up to 15×10^3 physical contacts with other cells. There are differences of detail between human brains but in all normal subjects the cells are arranged into the same gross structures, the visual system being one of them. [Boddy, 1978].

1.1 Anatomy and Electrophysiology of the Visual System

(a) Gross Structure

The structure of the human brain has been studied with anatomical techniques. These have revealed the gross structure of the brain – that the nerve cells (neurones) of the brain form a network and that a major part of the brain, the cerebrum, is divided into two similar hemispheres which connect through the corpus callosum and anterior commissure. By projection mapping, tracing the axons of neurones from the eyes into the brain, the visual areas of the brain have been located. Most of these axons (about 90%) project to the lateral geniculate nucleus (LGN) of the thalamus and then to the visual cortex which is situated in the occipital lobes of each cerebral hemisphere. Those of the remaining 10% which terminate in the midbrain and subcortical regions, project to the superior colliculus, the accessory optic tract nuclei, pretectum, pulvinar and ventral lateral geniculate [Weiskrantz, 1972], see figure 1.1.

As can be seen from figure 1.1(b) some axons from one eye project to the opposite half brain. This phenomenon of the 'crossed brain', whereby one

half of the brain responds to signals from the contralateral half of the body, is found for visual, auditory and somatosensory stimuli. Each cerebral hemi-

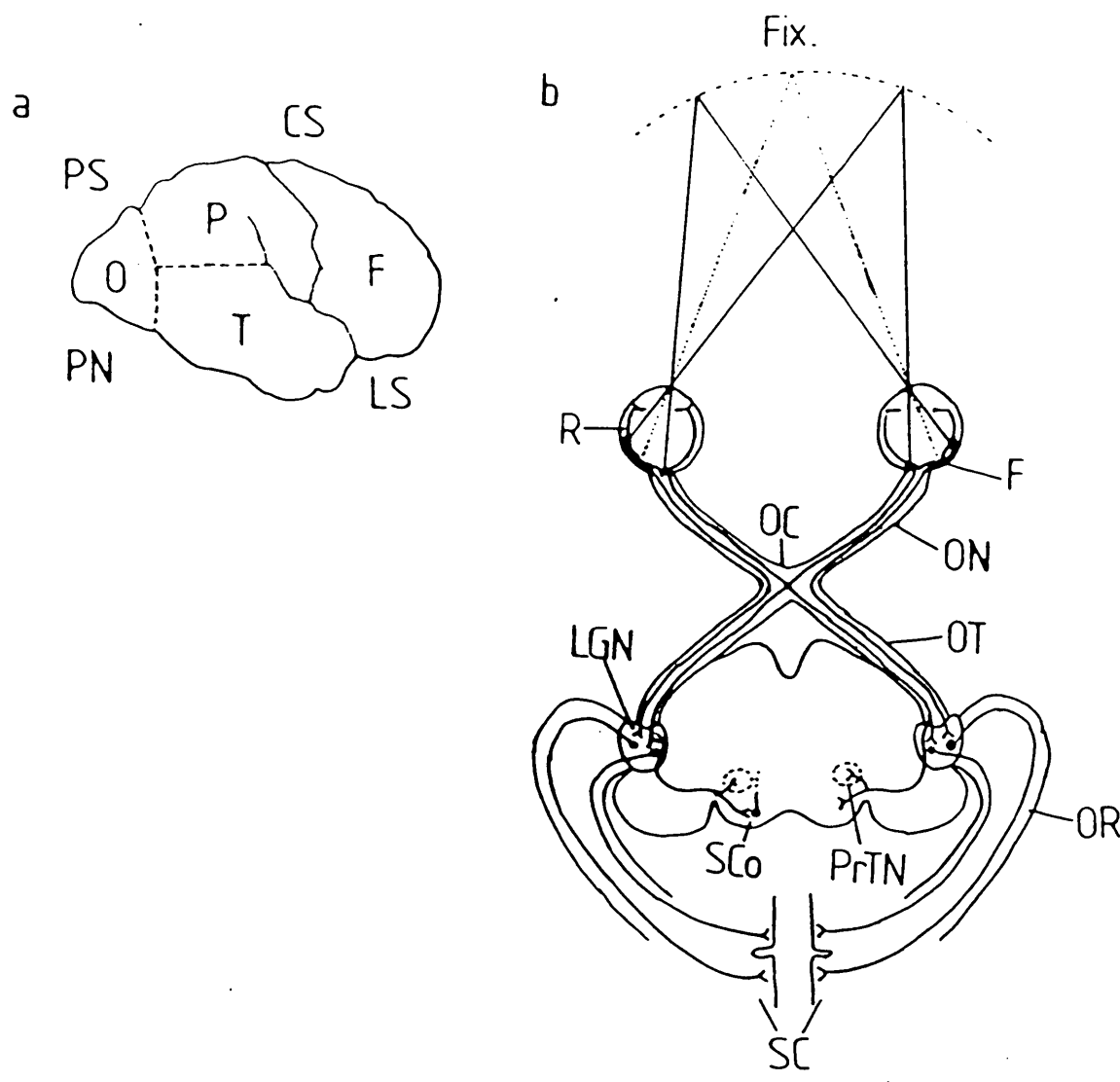


Figure 1.1 (a) Side view of the brain showing the lobes of a cerebral hemisphere. O, occipital; P, parietal; T, temporal; F, frontal; PS, parieto-occipital sulcus; PN, preoccipital notch; LS, lateral sulcus; CS, central sulcus. (b) Schematic diagram of a horizontal cross-section through the brain showing the primary visual pathway from the eyes to the visual cortex. Also shown are the pathways to the superior colliculus and the pretectal area. Fix, fixation; R, retina; F, fovea; OC, optic chiasma; ON, optic nerve; OT, optic tract; LGN, lateral geniculate nucleus; SCo, superior colliculus; PrTN, pretectal nucleus; OR, optic radiation; SC, striate cortex.

sphere also controls the musculature on the contralateral side of the body. When looking at an object the optical components of the eye form an image on the retina, the nervous tissue which covers the internal, rear surface of the eye. The part of the object to the right of the observer's fixation point is focused onto the left half of the retina, the fixation point is focused at the centre of the retina (or fovea) and the left part of the object is focused onto the right half of the retina. All of the fibres from the left halves of both retinae then project to the left hemisphere, those from the right eye crossing over at the optic chiasma to join those from the left eye. The fibres from the right halves of both retinae are similarly arranged so that they project into the right hemisphere and the fibres from around the vertical mid-line of the two retinae may project to either hemisphere. In this way the visual information from the right half of the field of view is processed in the left hemisphere and that from the left half of the field of view in the right hemisphere. Support for these findings comes from the work of Holmes [1918] on soldiers who suffered brain trauma during the First World War. Localized damage to one or other occipital cortex, which caused the death of neurones in that area, led to blindness in the corresponding visual field area of the contralateral hemifield.

The first stage of the visual pathways is the retina (figure 1.2). This is a layered structure with the photoreceptors forming the first layer, followed by a bipolar cell layer and then a ganglion cell layer and these three types of neurones form a direct pathway to the brain. The horizontal and amacrine cells form laterally directed pathways, the horizontal cells at the level where photoreceptors and bipolar cells synapse (the outer plexiform layer) and the amacrine cells at the level where bipolar and ganglion cells synapse (the inner plexiform layer). The retina covers the inside of the eyeball, with the

photoreceptors located on the inner margin, which means that light must pass through the other layers before reaching them. The ganglion cells form the

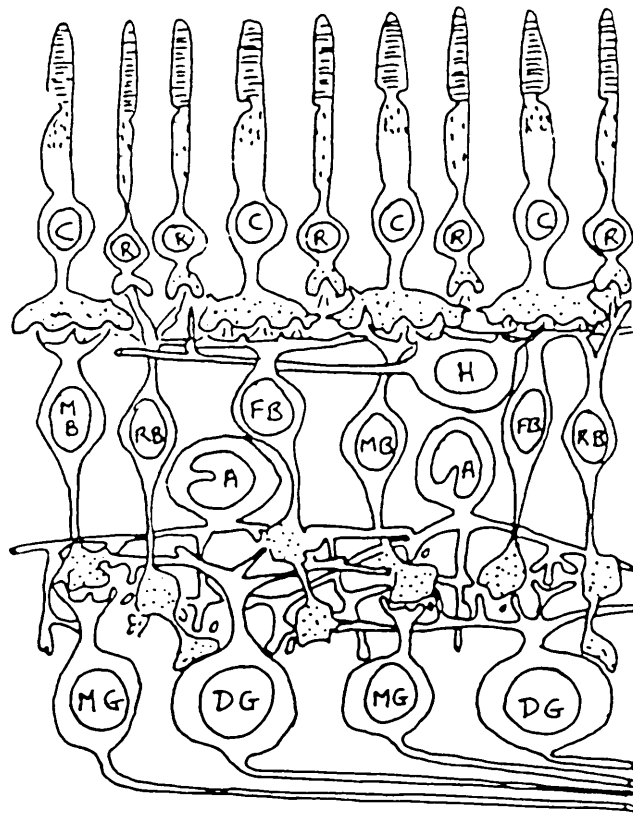


Figure 1.2 Schematic section through the primate retina. R, rod photoreceptor; C, cone photoreceptor; H, horizontal cell; MB, midget bipolar cell; RB, rod bipolar cell; FB, flat bipolar cell; A, amacrine cell; MG, midget ganglion cell; DG diffuse ganglion cell.

(from Dowling and Boycott, 1966)

outermost layer and their axons leave the eyeball at the blindspot, where there are no photoreceptors. The photoreceptors contain pigments that are chemically changed by the absorption of light incident on them and this change initiates an electrical signal, with hyperpolarization of the photoreceptors (this process is known as transduction). This hyperpolarization reduces the

rate at which the photoreceptors release excitatory neurotransmitter [Trifonov, 1968], thereby changing the electrical potential in the post synaptic bipolar and horizontal cells. The bipolar cells in turn drive synaptically the amacrine cells and the ganglion cells. The axons of the ganglion cells form the optic nerve and optic tract which transmit the signal from the retina to the LGN and other visual areas

There are two types of photoreceptors, rods and cones, differentiated by their shape. The rods have high sensitivity to light and provide low resolution black and white, night vision, whilst the cones operate at higher illumination and mediate high spatial resolution and colour vision. In man, the rods all contain the photopigment rhodopsin whereas cones are divided into three groups, each containing a photopigment with a different spectral sensitivity and peak responses at 565nm, 530nm and 445nm. Light absorption in the different spectral classes of cone is determined by the wavelength distribution of the light energy and the comparison of the relative rates of absorption in the three cone types, by post-receptoral neurones, enables the visual system to discriminate stimuli by their spectral composition.

The LGN is a laminated structure and the ganglion cells which project from the retina to the LGN synapse with cells in specific layers, those from the ipsilateral eye in layers 2, 3 and 5 and those from the contralateral eye in layers 1, 4 and 6. The topographical relation of the visual field is maintained with the central portion of the LGN representing the central visual field and peripheral portions the peripheral visual field. Fibres from cells in the LGN then project, through the optic radiation, to layer IVb of the primary visual cortex, also called the striate visual cortex, visual area V1, or area 17. Again, the topography of the visual field is maintained with the central part of each half visual field represented at the back of the brain and the peripheral

parts in the calcarine fissure, but the representation of the central area is grossly exaggerated, the central 10° occupying some 60% of the area. Cells project from the primary visual cortex to the secondary (or pre-striate) visual cortex where there are many more visual areas, V2, V3, V3A, V4 etc. each containing maps of the visual field and receiving inputs from the striate cortex (figure 1.3).

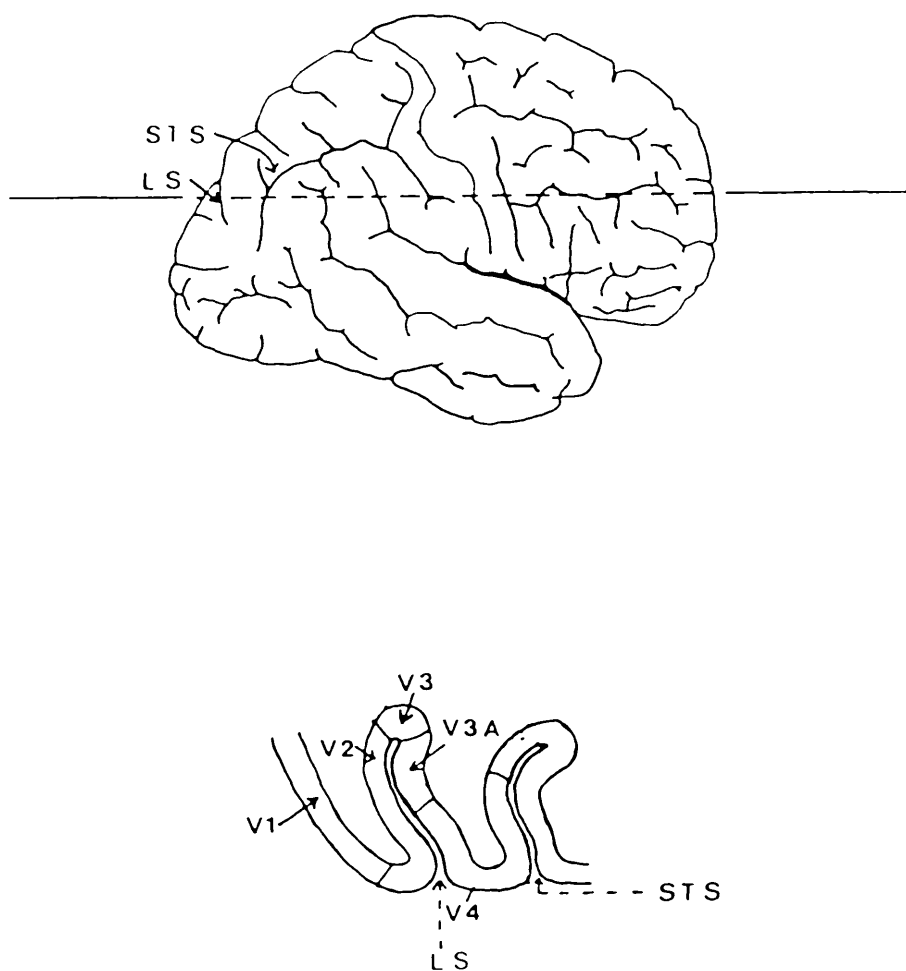


Figure 1.3 (a) Side view of the brain of the rhesus monkey, showing the positions of the lunate sulcus (LS) and the superior temporal sulcus (STS). (b) Horizontal section through the prestriate cortex along dotted line shown in (a). (from Zeki, 1977)

Brains of certain mammals, particularly the cat and other primates such as the macaque monkey, possess many of the same structures as human brains, including the visual system, and it is possible to study the processing of visual information in these animals by methods which cannot be applied to man. The network of neurones communicate by electrical activity and synaptic transmission and the former can be observed with extracellular (or rarely, intracellular) electrodes in order to study their functional organisation. The area of visual space within which presentation of a stimulus causes changes in the electrical activity of a neurone is defined as its visual or receptive field, and a cell is classified functionally according to its response to various stimulus parameters. Cells of the outer retina respond to light with maintained potential changes, the amplitude of which varies with illumination level (amplitude modulation). Amacrine cells exhibit isolated spike potentials superimposed on the maintained potentials and ganglion cells respond with trains of spike potentials, typical of all CNS neurones.

(b) X- and Y-Type Ganglion Cells

The retinal ganglion cells can be divided into two broad groups on the basis of the linearity of spatial summation within the receptive field of the cell. For one group of cells, the X-type, a position of a grating can be found such that it can be exchanged for a uniform field of the same mean luminance without evoking a change in response, whereas for the second group, the Y-type, no such position can be found. Both have similar shaped receptive fields that consist of two concentric circles, a centre and a surround whose responses are antagonistic. A spot of light in the centre of the field causes an increase in firing rate for 'on' centre receptive fields and a decrease for 'off' centre receptive fields, while an annulus of light in the surround

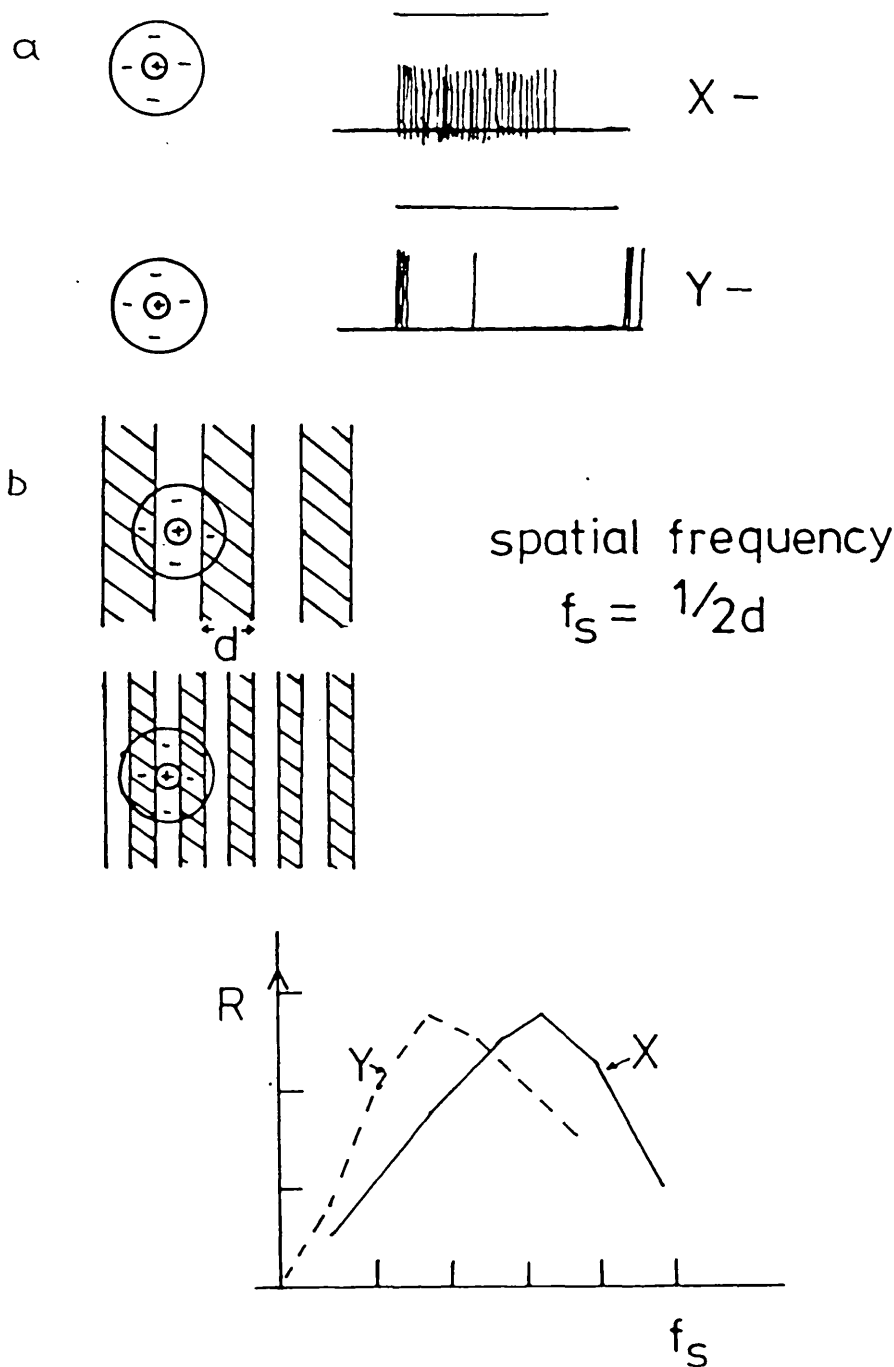


Figure 1.4 X- and Y- type cell responses. (a) Two schematic 'on' centre receptive fields with their responses to a spot of light flashed at the centre of their receptive fields. The X-type cell responds throughout stimulation, shown by the horizontal line above the trace, whereas the Y-type cell responds transiently at onset and offset of stimulation. (b) Stimulation of a cell by gratings, the second grating is of optimal spatial frequency. The graph shows idealised curves of the response, R , of the cell as a function of grating spatial frequency for X- and Y-type cells. As X-type cells tend to have smaller receptive fields they respond to higher frequencies than Y-type.

causes the firing rate to decrease for 'on' centre receptive fields and increase for 'off' centre receptive fields. X- and Y-type cells may have either 'on' centre or 'off' centre receptive fields, but the Y-type cells have larger receptive fields, about 2.5 times the size of X-type cells at any eccentricity [Peichl and Wässle, 1979]. Y-type cells also exhibit a transient response firing at onset and offset of a stimulus while X-type cells have a sustained response and fire throughout stimulation. Most X-type ganglion cells have concentric centre surround antagonistic receptive fields which are also colour coded so that centre and surround receive signals from different cone types. Y-type cells conduct signals along their axons more quickly than X-type cells and there is evidence [in cat, Rodieck, 1973; in monkey, De Monasterio, 1978 a,b] that there is a third class of ganglion cell, W-type, which conducts signals slower than X-type cells. In monkey, X- and Y-type ganglion cells project to the LGN and the cells which project from the LGN to the striate cortex show a similar division of response characteristics. Both Y- and W- type ganglion cells project to the superior colliculus [Schiller and Malpeli, 1977].

(c) Striate Cortex Cells

The cells of the striate cortex can be classified by their receptive field type as simple, complex and hypercomplex [Hubel and Wiesel, 1962]. Simple cells have receptive fields with spatially distinct on and off areas separated by parallel straight lines and are selective to bars and edges of particular orientation. Complex cells show no separation of receptive fields into excitatory and inhibitory parts, but similarly to the simple cells a line stimulus (bar or edge) at a particular orientation evokes optimum response. Whereas for the simple cell the position of the stimulus is crucial, in complex cells a response is evoked by a correctly orientated line on any part of the receptive

field and they respond strongly to stimulus movement, many of them for movement in a specific direction. Hypercomplex cells, more recently termed 'simple end-stopped' cells [Hubel, 1982], respond to correctly orientated line stimuli, but extending the line beyond the activating part of the receptive field in one or both directions causes a marked decrease in response.

Colour-opponent cells have also been found in the striate cortex. Gouras [1974] found that the majority in layer IVb are colour-opponent and do not show orientation or direction selectivity whereas the majority of cells in the outer layers exhibit considerable spatial selectivity without apparent colour-opponency. Unlike simple and complex cells, they are monocularly rather than binocularly driven.

(d) Prestriate Cortex

The prestriate cortex of the monkey contains many different visual areas each receiving inputs from the striate cortex and different areas are specialised for the analysis of different features [Zeki, 1978] (figure 1.3). Area V2 seems to be involved in depth perception as some cells in this area are sensitive to differences in position of the images from the two eyes [Fischer and Poggio, 1979]. V4 has a large proportion (60%) of cells which are colour specific in their response [Zeki, 1980], whereas 90% of cells in V3 are orientation sensitive, and 90% of those in V5 are selectively sensitive to movement in some preferred direction [Zeki, 1978].

1.2 Psychophysical Methods for Studying the Visual System

Sight is one of the senses for detection of the outside world by the brain. We can exploit the fact that we are conscious of what we see in order to develop psychophysical techniques for the study of the visual system.

In a psychophysical experiment visual stimuli are presented to an observer; as a parameter of a stimulus is varied the change in the observer's response is recorded. An 'everyday' example of this technique is the eye test carried out by an optician where by noting the response of the patient to a variety of stimuli e.g. different sized letters, the optician can assess the quality of the image that the optical components of the eye form on the retina.

This thesis reports experiments carried out using psychophysical techniques to study the image processing by the visual pathways and several of the basic techniques are described below.

(a) Increment Threshold Measurement

In this psychophysical technique a test spot is flashed on a background field of fixed illumination and the increment threshold illumination of the test spot is measured. In figure 1.5 the threshold illumination of a test spot, I_t , is plotted against the illumination, I_b , of the background field on which it is superimposed. The curve, typical of the results obtained by normal observers, has two distinct parts. At low background illuminations the test threshold has a constant value, irrespective of I_b , whilst for higher background illuminations the threshold for the test spot increases as I_b increases and the gradient of the line is near to 1 i.e. I_t is proportional to I_b . In the first case, threshold is limited by noise in the visual system whilst in the second, threshold is set by the background illumination I_b , against which the test flash is to be detected. In the latter range, the increment required for detection is proportional to I_b , and this relationship is known as the Weber–Fechner Law.

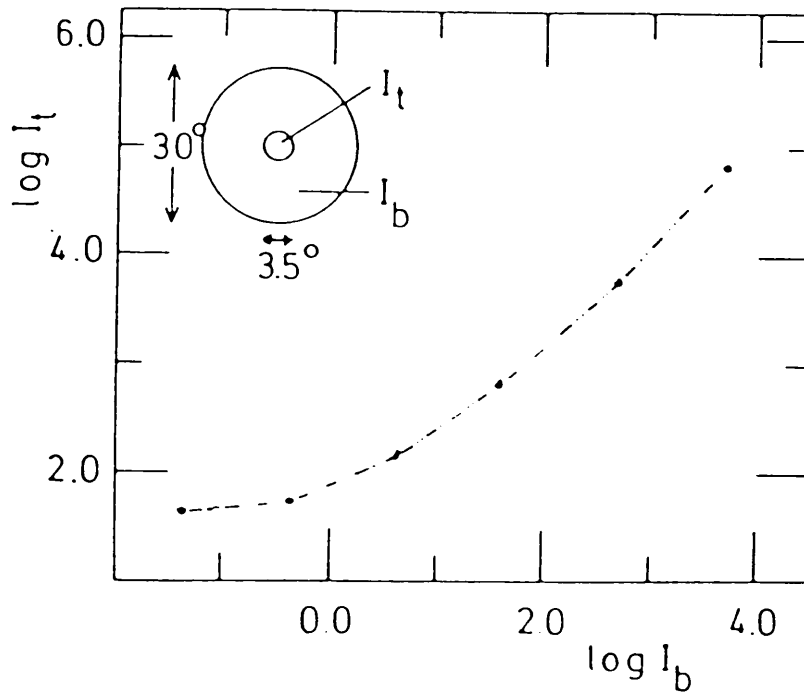


Figure 1.5 Threshold illumination, $\log I_t$, for a 3.5° diameter, circular target flashed for 0.1s every 1s at the centre of a 30° diameter, spatially uniform background. (Data taken from figure 5.21 of Chapter Five)

(b) Stiles's Two Colour Increment Threshold Technique

The visual system's spectral sensitivity is derived from the different spectral responses of four types of photoreceptors. The response of a particular type of photoreceptor can be enhanced relative to the others by selectively suppressing the responses of the other photoreceptors with a suitable background. This method was used by Stiles in his two colour increment threshold technique [Stiles, 1949, 1959]. He obtained selective suppression of two of the three cone types by the use of a bright, conditioning background of wavelength μ , strongly absorbed by both of them. The bright background field also suppressed the rod response. When a small, circular target of near monochromatic wavelength λ is flashed on such a background, it is detected mainly by the activity in the cone type whose spectral sensitivity is to be

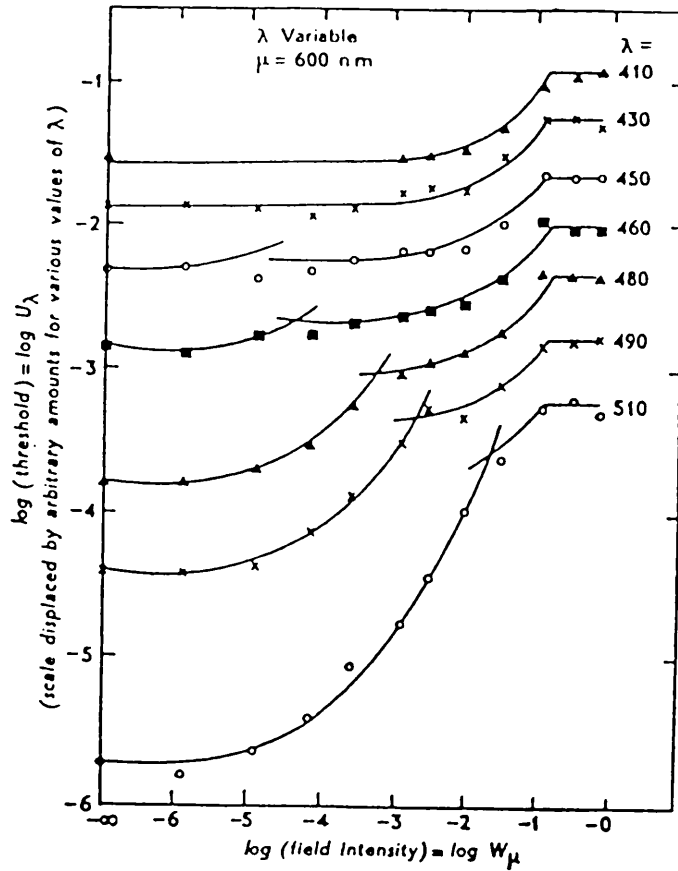


Figure 1.6 Effect on the curve of $\log(\text{threshold})$ against $\log(\text{background intensity})$ of changing the wavelength of the test stimulus, λ , and keeping the background wavelength, μ , constant. Foveal test stimulus of 1° diameter.
(from Stiles, 1949)

measured and not by the other photoreceptors whose sensitivity has been reduced by the conditioning field. A target flash of wavelength λ and 1 log unit above threshold, is presented against the background of wavelength μ , and threshold is determined by increasing the background illumination, I_μ , until the target is just no longer detected. Repeating this measurement for different

values of μ yields a sensitivity curve $(I_\mu)^{-1}$, which describes the mechanism responsible for detection of μ . Alternatively, the illumination I_λ , required for detection of the target can be measured for different values of I_μ (see figure 1.6), and by repeating this for different wavelengths, λ , the spectral sensitivity can be derived. By these methods, Stiles found three spectral sensitivity curves which were blue-sensitive (maximum sensitivity near 440nm), green-sensitive (maximum sensitivity at 540nm) and red-sensitive (maximum sensitivity between 570 and 590nm), but he emphasized that these responses describe psychophysical mechanisms since factors other than photopigment absorption cannot be excluded. He called the mechanisms responsible π_3 , π_4 and π_5 (blue-, green- and red-sensitive). In addition to the three 'basic' cone responses, five other spectral responses are obtained, the rod response, π_0 , two blue-sensitive responses, π_1 and π_2 , and for high background illuminations, modified π_4 and π_5 responses denoted π'_4 and π'_5 respectively.

(c) Spatial Vision

The visual system's ability to resolve fine detail can be measured using a Snellen chart. This consists of rows of high contrast letters, the size of which decreases going down the chart. With each line the size of the gaps in the letters decreases so that they subtend 1 minute of arc at different, specified viewing distances and the letters on each line themselves subtend 5 minutes of arc at each viewing distance. Visual acuity is recorded as a fraction where the numerator is the testing distance, usually 6m, and the denominator is the distance at which the gaps in the letters would subtend 1 minute of arc. A visual acuity of $6/6$ is 'normal' acuity and means that an observer can just resolve 1 minute of arc. A visual acuity of $6/18$ means that the gaps in the last resolvable line would subtend 1 minute of arc if viewed at

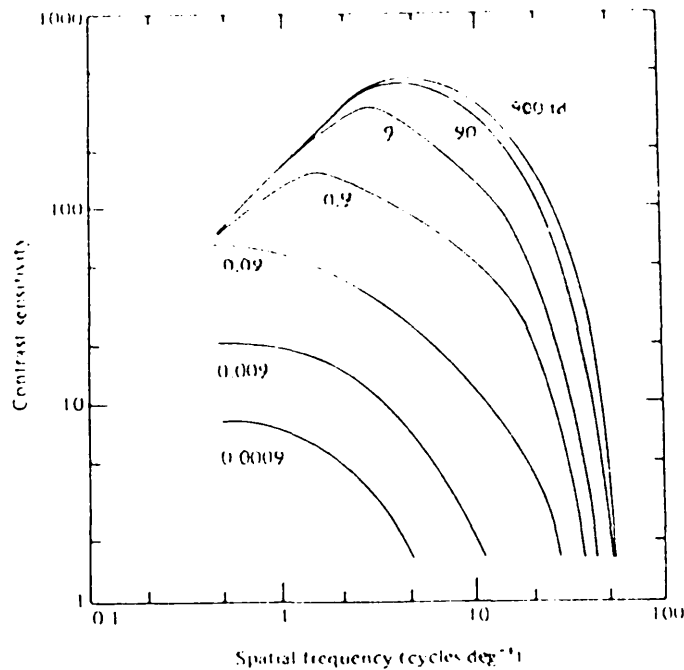


Figure 1.7 Spatial contrast sensitivity curves at seven different illumination levels between 0.0009 and 900 trolands (td.). (from Woodhouse and Barlow, 1982).

18m and that the observer's visual acuity is three times worse than normal and their minimum gap resolution is 3 minutes of arc. Normal visual acuities of $6/5$ and $6/4$ are found and imply an ability to resolve gaps of $5/6$ and $2/3$ minutes of arc. Lower than normal visual acuities are usually due to a refractive error in the optical components of the observer's eye but they may have a neuronal basis and this is discussed in 1.3(c).

The Snellen chart measures spatial resolution at high contrast and frequency. In order to measure resolution for the entire range of spatial frequencies, contrast sensitivity for a one-dimensional, sinusoidally varying distribution of illumination (a 'sine-wave' grating) is measured. The contrast of a grating, defined as $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$ where $I_{\max}$ and $I_{\min}$ are the maximum and minimum illumination levels respectively, is varied until

threshold is found. Results such as those in figure 1.7 are obtained where sensitivity, the inverse of contrast threshold, is plotted for a range of grating spatial frequencies and for a range of different illumination levels. The response depends markedly on illumination level with the range of detected spatial frequencies increasing with average illumination. At low illumination levels, the response is low pass, whereas at higher illumination levels it is band pass with a peak in the range 1 to 7 cycles/degree. This second characteristic is evidence of neuronal processing of spatial information as contrast sensitivity for a passive optical system is always low pass in nature.

(d) Measurement of Temporal Responses of the Visual System

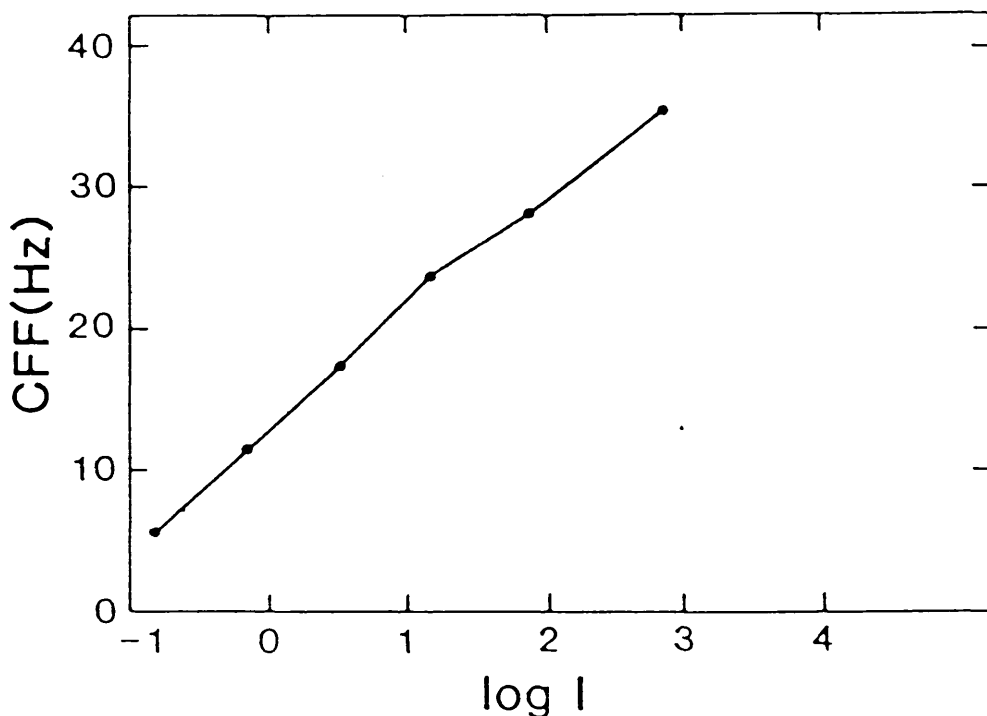


Figure 1.8 The limiting frequency at which flicker is just no longer detectable, the critical fusion frequency (CFF), in a 100% temporally modulated field as a function of background illumination, I . The background field was presented foveally. (Data taken from figure 6.11 of chapter six).

A temporal response of the visual system can be found by measuring the limiting frequency at which temporal flicker can just no longer be detected in a background of mean illumination level I . Figure 1.8 shows that the critical fusion frequency varies linearly with mean background illumination. The Ferry–Porter Law [Porter, 1902] describes the variation in critical fusion frequency (CFF) with intensity (I) as:

$$\text{CFF} = a \cdot \log I + b$$

The measurement of spatial contrast sensitivity (1.2(c)) describes the spatial characteristics of visual detection at threshold and similarly the measurement of temporal modulation sensitivity defines the corresponding temporal characteristics. Figure 1.9 shows temporal modulation sensitivity, the inverse of the modulation level at which flicker can just no longer be detected in a uniform, sinusoidally flickering field, as a function of the flicker frequency for a number of mean background illuminations. Such curves were first measured by de Lange [1954]. The maximum frequency at which the eye can detect flicker is ^{about} 60 Hz and this occurs at the brightest background illumination and for 100% modulation. The high frequency cut-off points on all the curves correspond to the critical fusion frequency at that illumination level (figure 1.8). At high illumination levels the sensitivity peaks at between 10 and 20 Hz but with decreasing mean illumination of the background field, sensitivity for high frequency flicker decreases. Between 2 and 5 Hz, the mean illumination of the background field has little effect on modulation sensitivity.

The visual system's ability to detect real motion can be measured by finding the threshold illumination of a moving test stimulus as a function of its velocity and figure 1.10 shows results obtained by a normal observer.

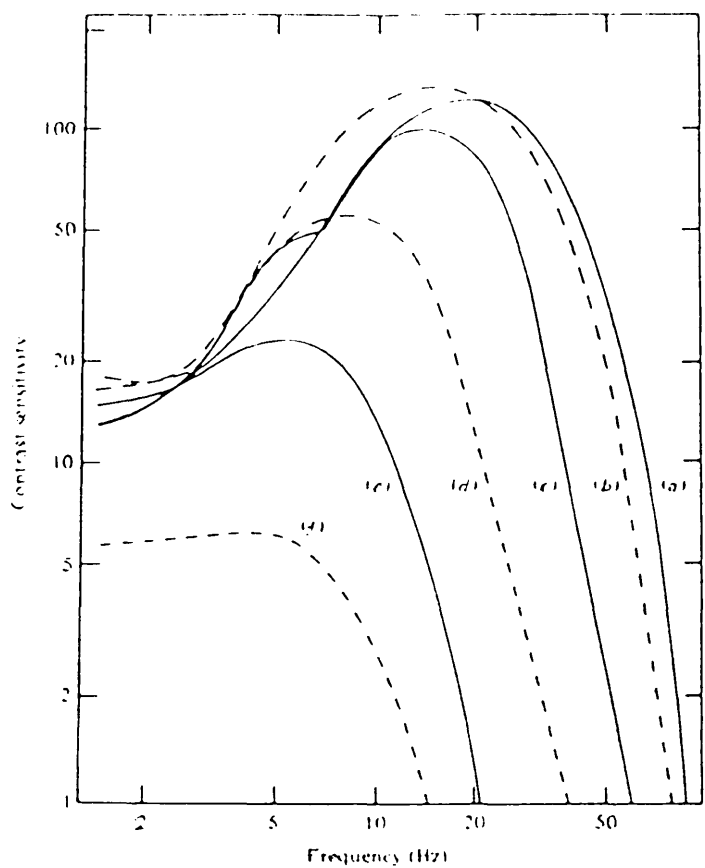


Figure 1.9 Temporal contrast sensitivity curves at six different illumination levels: (a) 9300td. (b) 850td. (c) 77td. (d) 7.1td. (e) 0.65td. (f) 0.06td.. (from Woodhouse and Barlow, 1982).

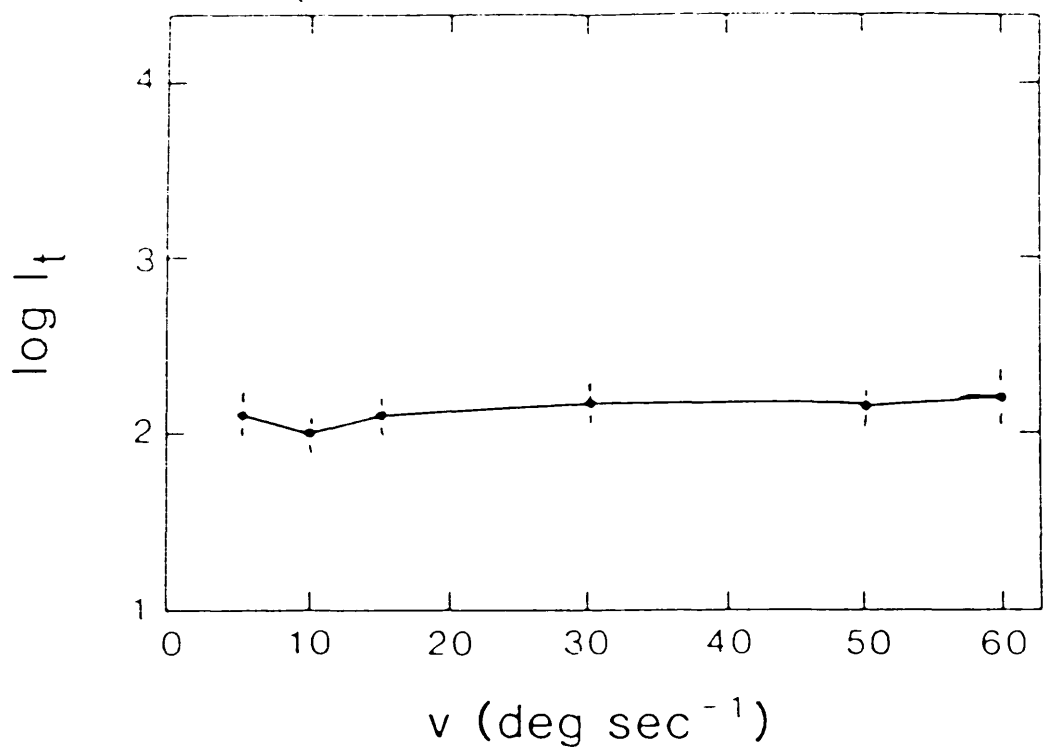


Figure 1.10 Illumination, $\log I_t$, for threshold detection of a circular target (3.5° diameter) moving at velocity v degrees/second through the central 8.5° of the circular background field (diameter 30° , illumination level $2.6 \log \text{ td.}$). (Data taken from figure 6.9 of chapter six)

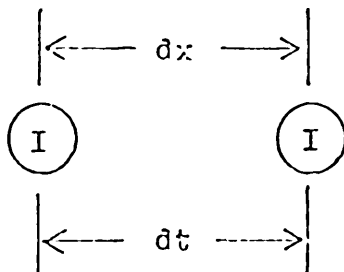


Figure 1.11 Stimulus for producing apparent motion. I , illumination of source; dx , spatial separation of sources; dt , time lag.

The appearance of motion can also be given by stationary, flashed lights. The sensation of a single object moving can be given when two discrete, stationary sources of light are flashed on and off with an appropriate time lag (figure 1.11) [Wertheimer, 1912].

(e) Background Modulation Techniques

These techniques can be used to study psychophysical mechanisms sensitive to visual stimuli which contain spatial and/or temporal modulation. The activity of the mechanism is determined by its sensitivity to the modulation of the background field. The activity level of the mechanism is determined by ^{measuring} threshold illumination for detection of a test stimulus, superimposed on the modulated background, and the greater the activity of the mechanism the higher is the threshold for the test stimulus. The type of responses which can be obtained from this form of psychophysical measurement are illustrated in figure 1.12. Section 2.2(a) contains the results of

experiments carried out using this technique which show that, by suitable choice of the background spatial and temporal structure, and of test stimulus, the responses of two different psychophysical mechanisms are found.

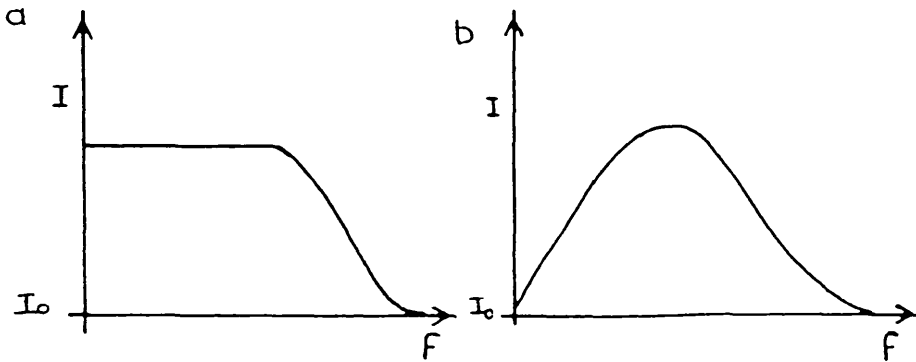


Figure 1.12 Responses of psychophysical mechanisms sensitive to spatial and/or temporal background field modulation. (a) Low pass response where threshold for the test stimulus, I , is raised compared to its value, I_0 , for a uniform field of the same mean illumination, by low frequencies f of background spatial or temporal modulation. (b) Band pass response where threshold for the test stimulus is raised by a band of frequencies, f .

1.3 Abnormal Functions and their Classification

The methods of psychophysics discussed above have been applied to the study of normal vision and in this thesis Chapters Three and Four contain the results of such types of experiments. The characteristics of abnormal vision also contribute to the understanding of visual processing and Chapters Five, Six and Seven consist of studies on subjects with abnormal visual function.

The study of functional losses in subjects suffering well defined lesions can provide significant evidence on the organisation of the visual pathways. There are a number of ways in which such lesions can occur, for example, by vascular disorders, where blood flow is interrupted; by traumatic head injuries, which can cause direct damage to the brain, disrupt blood flow, cause swelling

and allow infection to enter; by tumours which kill nerve cells directly or by pressure; by degenerative disorders which cause progressive deterioration of brain tissue e.g. multiple sclerosis. When a lesion leads to selective loss of visual function it is possible to study how the normal visual system operates in isolation from the damaged components.

(a) Lesions of the Striate Cortex

As explained previously, the human striate cortex contains a topographical map of the visual field on its surface and damage to the striate cortex causes a field defect, usually permanent blindness, in the corresponding visual field position [Holmes, 1918]. If the left striate cortex is damaged the blind area (called scotoma) is in the right half visual field and if the right striate cortex is damaged the scotoma is in the left half visual field. If the entire striate cortex is damaged on one side, blindness covers all the half visual field, a condition known as homonymous hemianopia, although there may be sparing of vision around the fovea since ganglion cells from the fovea project to either hemisphere. The extent of the blind area can be measured by conventional perimetry.

A surprising finding was reported by Riddoch [1917] who found that in some cases of striate cortical lesion, flashed and moving lights located within blind areas of the visual field could be detected. Since then a number of other authors have also reported detection of lights located in blind areas [Pöppel, Held and Frost, 1973; Weiskrantz, Warrington, Sanders and Marshall, 1974; Perenin and Jeannerod, 1978; Zihl, 1980; Barbur, Ruddock and Waterfield, 1980]. The reports have split between those whose subjects have no conscious visual sensation and for whom visual discrimination can be shown only as forced-choice judgements between alternatives, termed blindsight, and

others who report a sensation, usually described as a 'dark shadow' in response to bright, transient lights presented within blind areas, termed residual vision. Blythe, Kennard and Ruddock [1987] suggest that since both types have been observed in subjects suffering damage to the geniculo-striate pathway, it is probable that they are expressions of similar neural activity and merely represent differences in degree of responsiveness.

The primary visual pathway in primates is that from the retina to the LGN and hence to the striate cortex. There are several other non-striate pathways carrying signals from the retina including a projection to the superior colliculus in the mid-brain, and it has been established that similarly to V1 there is a point-to-point mapping of the visual field onto its superficial (upper) layers [Schiller and Koerner, 1971; Goldberg and Wurtz, 1972]. Y-type ganglion cells project to the superior colliculus [De Monasterio, 1978a; Weller, Kaas and Wetzell, 1979] and, like the Y-type ganglion cells, those in the superficial layers of the superior colliculus are responsive to flashed and fast moving targets [Goldberg and Wurtz, 1972]. The superior colliculus itself projects, via the pulvinar, to the pre-striate cortex. Observations on non-human primates suggest that there are two principal visual pathways working in parallel, one to the striate cortex which provides fine discrimination of stimulus parameters and the other to the superior colliculus which controls eye movements in response to light stimuli. Mohler and Wurtz [1977] have shown that after ablation of either the superior colliculus or the striate cortex alone, recovery of visual function occurs in macaque monkeys. Damage to corresponding regions of both brain areas leads, however, to permanent impairment of visual function. So, in non-human animals, there is considerable flexibility in the organisation of function following damage to visual centres in the brain. It has been suggested [Barbur, Ruddock and

Waterfield, 1980] that since the superior colliculus shows characteristics similar to those of residual vision, blindsight and residual vision may be mediated by this pathway.

Other pathways could be responsible for residual vision/blindsight, for example, the projection from the LGN to the pre-striate cortex described by Fries [1981], Yukie and Iwai [1981] and Bullier and Kennedy [1983]. Spear [1985] suggests that the posterior lateral suprasylvian visual area of cortex is involved in behavioural recovery from damage to cortical areas 17, 18 and 19 in cat.

It has been argued that residual visual function in hemianopes is caused by light scattered into the normal field [Campion, Lattin and Smith, 1983] but a number of experiments [Barbur, Ruddock and Waterfield, 1980; Zihl and Werth, 1984; Stoerig, Hübner and Pöppel, 1985] have shown that scattered light cannot explain the observed responses.

It has been suggested by Blythe, Kennard and Ruddock [1987] that the age at which brain damage occurs, may be the significant factor in determining whether a subject will have residual vision. Three out of five of their subjects received lesion at eleven years of age or less, one at twenty three years of age and the fifth did not know when the blind area appeared and therefore it may have been present from an early age. Thus all five subjects received lesion early in life. There is support for this proposal from some data [Perenin and Jeannerod, 1978] but not from others, where the lesion occurred at a considerably greater age [Weiskrantz, Warrington, Sanders and Marshall, 1974; Zihl and Von Cramon, 1979; Ross Russell and Bharucha, 1984]. Studies on a larger number of subjects will be required to resolve this question.

(b) Visual Agnosia

Visual agnosia is a disturbance of visual recognition without disturbance of elementary sensory processing. Lissauer [1889] identified two types, one, apperceptive, in which visual objects cannot be distinguished because of distortion in visual perception and the other, associative, in which despite intact visual perception, visually presented objects cannot be recognized. The first type is purely a visual problem, and the degree of difficulty in recognizing objects can vary from subject to subject, while the second type is not solely a visual problem; subjects suffering from associative agnosia could have equal difficulty recognizing an object presented visually or tactually, or they may recognize an object as familiar but have a problem in associating the shape with its function. Associative agnosia is a problem involving stored knowledge and its recall and cannot be studied by visual psychophysical techniques, whereas the defective visual processing in apperceptive agnosia can be studied with such techniques. The latter type of visual agnosia is caused by lesions of the cortex.

Lesions in a variety of cortical areas have been described in the literature as causing degrees of loss of visual recognition. Benson and Greenberg [1969] described a subject who suffered multiple, small, cortical lesions caused by carbon monoxide poisoning. His visual recognition ability was severely affected and he could not identify objects, pictures of objects, geometric objects or letters of the alphabet. In fact, the only visual identifications that he could make were of a few simple letters (O and X) and only under certain presentation modes. He was also unable to copy letters or simple figures and could not describe or trace the outline of common objects. He could distinguish colours, follow stimulus movement and had no field loss and he could also write a few letters or numbers, but frequently reversed and

inverted them. Other subjects with similar lesions and a complete inability to discriminate on the grounds of spatial form have been described by Adler [1944, 1950] and Campion and Latta [1985]. In another group of subjects, damage of the parietal region in the right hemisphere disrupts visual recognition only slightly and they are unable to recognize objects seen under unusual viewing conditions, particularly those which foreshorten the long axis [Warrington and Taylor, 1973, 1978; Warrington, 1982; Humphreys and Riddoch, 1984]. Subjects suffering bilateral, occipito-parietal lesions, usually caused by vascular disturbances, show visual discrimination abilities intermediate between the two groups described above [Albert, Reches and Silverberg, 1975; Mack and Boller, 1977; Wapner, Judd and Gardner, 1978; Ratcliffe and Newcome, 1982]. They can recognize local image features of an object, finding silhouettes the most easy to extract features from, but are unable to integrate the parts into a whole visual image. The subject of Chapter Five, H.J.A., appears to belong to this particular group and he is able to read letters of the alphabet but finds it difficult to read script because he cannot recognize more than one object at a time. The subjects of this group can copy objects, but only in a 'slavish', line-by-line manner, and can draw objects from memory.

There are a number of other visual recognition defects which can occur in isolation or in combination with others. These include prosopagnosia, the inability to recognize faces; topographical agnosia, the inability to find directions in the environment; alexia, the inability to read and simultanagnosia, the inability to name pairs, as opposed to single stimuli, which is described by Kinsbourne and Warrington [1962] for four subjects. These, like the subject H.J.A. discussed in Chapter Five, were unable to read and had difficulties in picture interpretation.

As this review shows, disturbance of recognition, visual agnosia, can take many forms and the study of individual cases contributes to the knowledge of neuronal processing in normal visual recognition.

(c) Amblyopia

Blurred vision is usually due to refractive error and can be corrected with appropriate lenses but amblyopia is neuronal in origin and the blurred vision cannot be improved in this way. It can be caused by a squint (strabismic amblyopia) or refractive error (anisometropic amblyopia) occurring during post-natal visual development. An uncorrected refractive error causes blurred vision in that eye, while a squint, which may be convergent or divergent, causes the point of fixation on an image to be focused eccentrically, nasally or temporally, not at the fovea. This means that fixation is eccentric under binocular viewing and may also be eccentric under monoptic viewing in which case the 'false fovea' is always used. An image of an object is not focused onto corresponding points of the two retinae and suppression of the signal from the squinting eye may occur in order to prevent diplopia.

The defective vision that these conditions produce during visual development is thought to cause an abnormal pattern of neuronal development which results in permanently reduced resolution when the subject is older, even if the squint or refractive error is corrected. Support for this theory, that there is abnormal neuronal development, comes from electrophysiological studies on cat. Wiesel and Hubel [1963] and Hubel, Wiesel and LeVay [1977] demonstrated that neuronal responses and innervation of the striate cortex by fibres from the two eyes are modified by suturing one eye, and Ikeda, Treisman and Eimon [1978] and Jacobson and Ikeda [1979] have shown that normal, high visual acuity is based on the activity of X-type cells. Using

several techniques e.g. daily application to one eye of an agent causing pupil dilation which produces image blur, or severance of the eye balance muscles, they produced amblyopia in kittens and showed that X-type retinal ganglion and LGN cells in the pathways from the amblyopic eye have abnormally low visual acuity. They also showed, behaviourally, that high visual acuity develops post-natally and that there is a correspondence between age of onset of the condition producing amblyopia and the resulting visual acuity, with the visual acuity being halted at the stage it reached in normal kittens of the same age. In normal eyes, defocusing an image by 6 to 8 diopters causes a drastic decrease in the response of X-type cells [Ikeda and Wright, 1972] therefore, the degree of development in X-type cells may relate to the amount of activity in them. In all these electrophysiological studies Y-type cells were virtually unaffected by the conditions producing amblyopia in the X-type cells. Data from human subjects with amblyopia, determined psychophysically, is described in 2.2(a) and this supports the idea that X-type but not Y-type cells are affected.

(d) Visual Perseveration

Visual perseveration is the term used to describe visual perception which exhibits abnormal temporal persistence or spatial spread [Critchley, 1951]. Chapter Six contains a study of a subject F.B. who suffers from prolongation of visual sensation, i.e. abnormal temporal persistence. This is known as palinopsia and it is also divided into two types [at least by some authors — Critchley, 1951; Bekény and Péter, 1961; Swash, 1979 and Cummings, Syndulko, Goldberg and Treisman 1982]. In one type there is a continuation of visual sensation after cessation of the light stimulus and the perseverated image is like an after-image, whereas, in the other, there is

episodic reappearance of images without immediate visual stimulation.

Palinopsia has been found to occur in association with brain lesions of the parieto-occipital cortex [Critchley, 1951; Bender, Feldman and Sobin, 1968; Cummings, Syndulko, Goldberg and Tremain, 1982], the right posterior parietal cortex [Cleland, Saunders and Rosser, 1981], the right occipito-temporal cortex [Meadows and Munro, 1977] and the occipital cortex [Michel and Troost, 1980]. It has also been observed following temporal lobe surgery [Bynke, 1984], in association with field loss and, sometimes, in association with seizures in which instances it can be suppressed by treatment with anticonvulsant drugs [Jacobs, Feldman and Bender, 1972]. The idea that there are two distinct types of palinopsia seems to be supported by the subject of Chapter Six who fits into the first category well, having after-images invariably associated with the primary light stimulus, several characteristics in common with other such subjects and little similarity to the subjects who have episodic palinopsia.

CHAPTER TWO EXPERIMENTAL APPARATUS

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The majority of the experiments reported in this thesis have involved the use of one or other of two sets of equipment. The first, used for pattern discrimination experiments, consists of a microcomputer connected through a graphics board to a colour monitor [Ike, Skinner and Ruddock, 1987]. A program written by Peter Skinner, a former research student in the vision research group, allows for the production of patterns on the monitor, the measurement of the time an observer takes to find a target element amongst a background of similar elements and the display of results. Any pattern elements currently in the program's repertoire can be displayed but the program also allows for the development of new patterns by using a joy-stick connected to the computer to draw them on the screen. These new pattern elements can then be saved for later use.

The second set of apparatus is a four channel, Maxwellian view, optical system which has facilities for monocular and binocular viewing [Barbur and Ruddock, 1980a]. This can be used to present, within a large field of view, well-defined, moving or stationary targets. It also provides high illumination, monochromatic or broad-band light and two or more stimuli can be superimposed. The amount of light reaching the observer's eye can also be accurately controlled. The control and data-logging of this system is carried out by a microcomputer.

2.1 The Maxwellian View Optical System

(a) Maxwellian Viewing

In this method of viewing a light source, called Maxwellian viewing

after J.C. Maxwell who first reported it and used it in his experiments on colour mixing, a lens is used to image a light source in the observer's eye pupil. This uniformly illuminates an area of the retina much larger than is covered when the observer looks directly at the source. The area covered depends on the lens used and its distance from the source. Using a lens, the retina is uniformly illuminated whereas, when viewing with the unaided eye, the light falling on the retina is spatially modulated, see figure 2.1. The luminous flux per steradian reaching the observer's retina is known as the

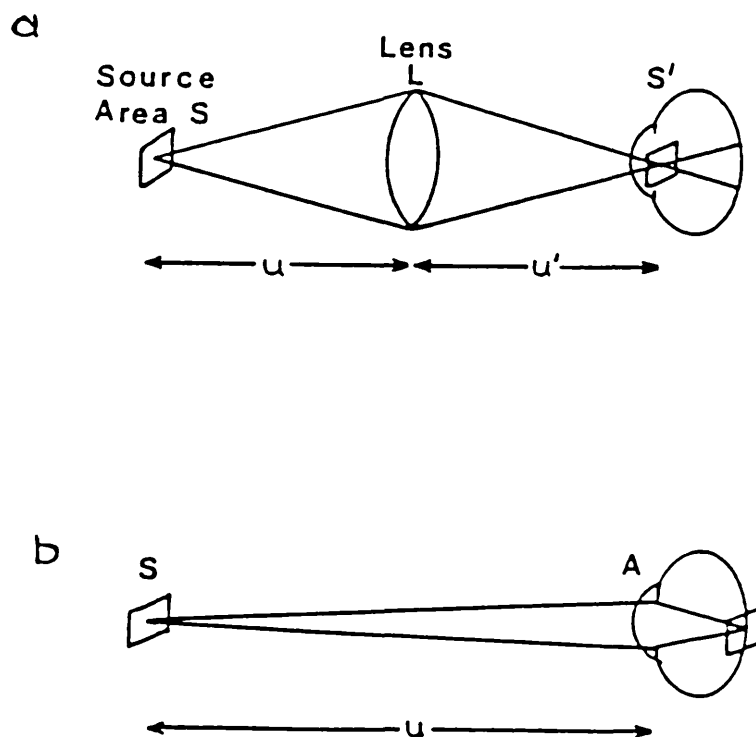


Figure 2.1 (a) Schematic diagram of the principles of Maxwellian viewing. A source of area S is imaged by a lens in the pupil of the eye. The image of the source has area $S' = Su'^2/u^2$.
 (b) Ordinary viewing of an extended source of area S placed at a distance u from an eye, whose entrance pupil has area A .
 (from Westheimer, 1966)

retinal illuminance which is an important stimulus parameter. Although the level of retinal illumination produced by a source will differ from eye to eye due to variation in their light losses, a conventional retinal illumination can be defined, assuming no light losses, by taking the product of the luminance of the light incident on the eye and the area of the pupil. A problem with direct viewing of a source is that as its luminance varies so does the pupil size. In the Maxwellian view system the retinal illuminance can be controlled precisely by the experimenter if the source image is smaller than the minimum pupil size of 2 mm. With the Maxwellian view system the retinal illuminance is the same as in the direct viewing case if the source image is the same size or larger than the pupil (although some light is lost in the optical components of the system); in both cases it is $(\text{source luminance}) \times (\text{area of pupil})$. However, the advantage of being able to control the retinal illuminance when the source image is smaller than the pupil outweighs the decrease in illumination and in this case the retinal illuminance is $(\text{source luminance}) \times (\text{area of source image})$. The actual retinal illuminance cannot be measured and, because of differences in the amount of light lost in different eyes, absolute visual thresholds will vary between observers when specified in conventional retinal illuminance. In this thesis relative visual thresholds are measured under a variety of conditions and these may be compared between observers.

The apparatus with which the experiments of this thesis were carried out employs two lenses to image the light source in the eye pupil: the first lens produces a collimated beam from the source and the second one focuses the beam to form an image of the source in the eye pupil. A stimulus object (the target), which is a mask of opaque and transmitting areas, is placed in the parallel beam between the two lenses, nominally at the back focal plane of the second lens. The target's position between the two lenses

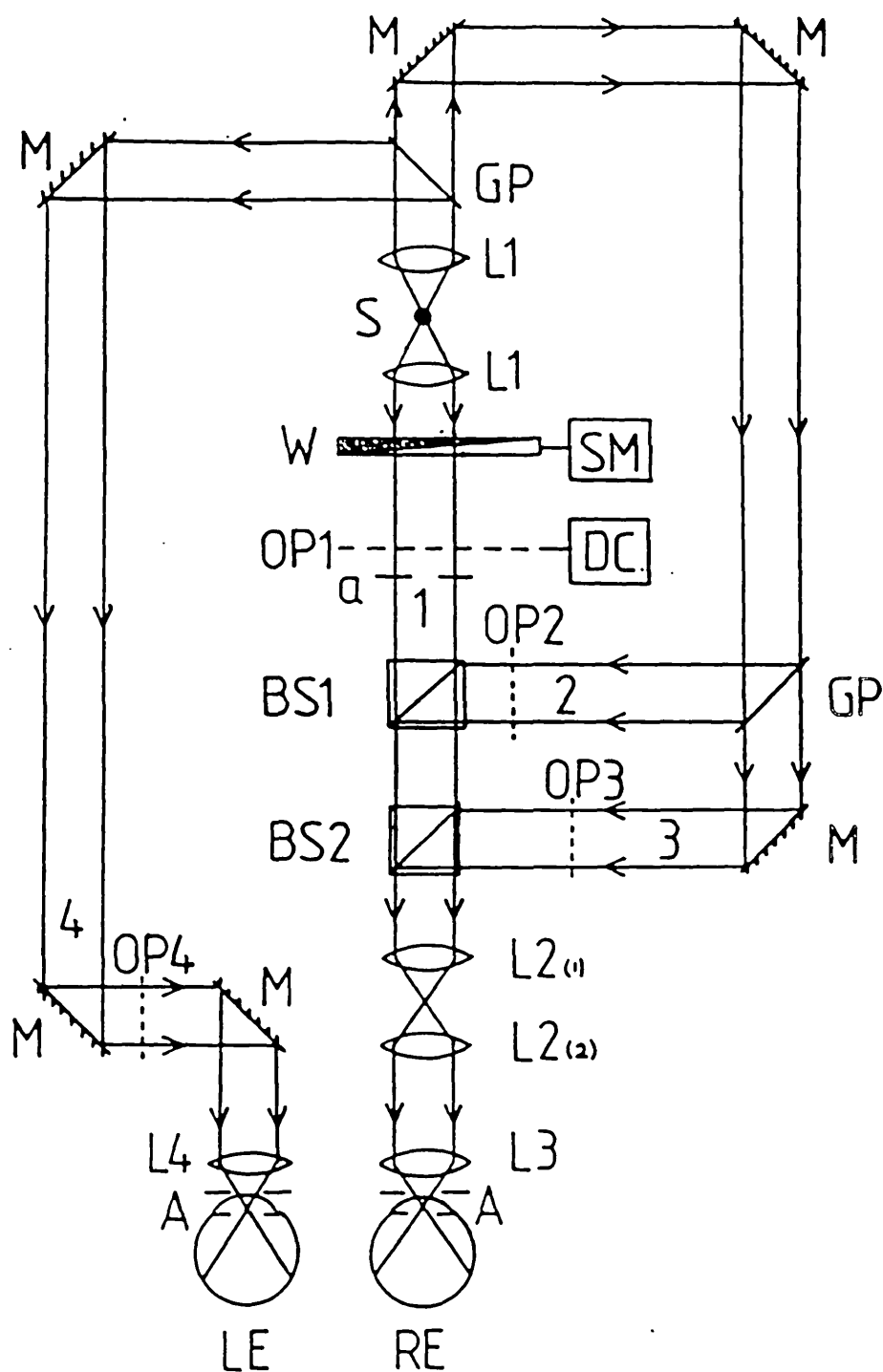


Figure 2.2 Schematic diagram of the four channel Maxwellian view apparatus. See text for explanation of symbols used.

does not affect image size or retinal illuminance but does affect the accommodative state of the observer. In the experiments, the target is always placed so that the observer is not accommodating when it is viewed. If the observer is emmetropic this is achieved by placing the target at the first focal plane of the second lens. Observers with refractive errors view with uncorrected eyes and their errors can be compensated by changing the target position between the lenses. The relationship between the size of the target and the angle it subtends at the eye is constant and is fixed at a value depending on the focal length of the second lens. By splitting the parallel beam formed after the first lens and recombining the various beams so formed before the second lens, any number of channels can be produced, each with its own focal plane. This allows for superimposed stimuli in the field of view of the observer.

With a suitable choice of lenses and source size, the Maxwellian view apparatus provides a large, uniformly illuminated field of view in which sharply defined targets of known retinal illuminance can be presented.

(b) Description of the Maxwellian View Optical System

Figure 2.2 shows a schematic diagram of the four channel Maxwellian view apparatus with binocular viewing configuration. The light source (S) is a 100W/12V quartz-halogen lamp with a small, flattened tungsten filament of dimensions 5mm x 2.5mm. The spectral radiant exitance distribution of tungsten approximates that of a black body, in this case with colour temperature of 3,100 K, and the lamp is driven by a stabilised power supply (Roband electronics model 67-10A/12V). The source voltage was increased and decreased gradually at the beginning and end of each experimental session by means of a rheostat, in order to increase the lamp's lifetime. After being

turned on the lamp was left to stabilise for at least 15 minutes before an experiment was carried out. Fluctuations in the voltage across the lamp, as shown on a voltmeter connected in the power supply circuit, or deterioration in the source filament, visible in the source image at the exit pupil, both of which signal deterioration of the lamp, were regularly checked for and, if detected, the lamp was changed. One lamp lasts for many hours and all the experiments except those of Chapter Four were carried out with the same lamp. Light from the source is collimated with achromatic doublet lenses (L1) into two separate parallel beams. The beam from one of the lenses forms channel 1, the other beam is split using two glass plates (GP) to form three further channels 2, 3 and 4. Channels 2 and 3 are combined with channel 1 by beam splitters (BS) and this composite beam is then focused by the final lens (L3), a 50mm f1.2 Pentax camera lens, to form an image of the source in the observer's right eye pupil. The pair of Takumar 135mm f2.5 lenses (L2) in this beam provide object planes OP1, OP2, OP3, all at the first focal plane of lens L2(1), conjugate with the first focal plane of L3. Thus the optical planes of the three channels are 135mm behind the lens L2(1) instead of 50mm behind L3. This allows more room for the manipulation of the three channels with beamsplitters and for positioning targets. The fourth beam, which provides binocular viewing, is focused by lens L4 (focal length 18cm), forming an image of the source in the observer's left eye pupil. The optical plane of channel 4 (OP4) is at the front focal plane of this lens.

The size of the field of view from any channel is controlled with masks of the required aperture dimensions. The mirrors (M), used to manipulate the beams, are all front-silvered, made by the vacuum deposition of aluminium onto optically flat glass.

The luminance of each channel can be adjusted stepwise by the

insertion of neutral density filters into the beams. These are Kodak Wratten gelatine filters mounted in two plates of glass and this assembly attenuates the beam equally for all wavelengths. The luminance of channel 1 can also be varied continuously by a neutral density wedge (W) (Kodak) mounted in a frame and moved through the beam under computer control by a stepping motor (SM) (Sigma Instruments, model 20-2220D200-F5.1) via rack and pinion gearing. The wedge's position in the beam, and hence the attenuation of the light incident on it, is known by the number of steps made by the stepping motor from its zero position. The zero position is on the extreme left (as seen by an observer), of the wedge's movement. At the beginning of an experiment, the neutral density wedge moves to the left, until it touches a button at the end of the rack in which it moves. On touching this button a signal is sent to the computer which then stops the neutral density wedge and signals that this is the zero position from which step counting should start.

In the experiments of Chapter Four, a different neutral density wedge is used. This wedge is connected, via gears, to a linear coil motor which can be driven in either direction through channel 1. The motion of the wedge is controlled by the observer. A 10-turn potentiometer, with a constant applied voltage, is connected via gears to the wedge. The voltage from the potentiometer is displayed on a digital multimeter (Dana, model 3800B) and can be printed by a digital printer (Credshire, model DP100). This value corresponds to the position of the neutral density wedge and thus defines the illumination of channel 1. Recordings of the voltage are printed onto paper when the observer presses a button. The light provided by the system is white light but the wavelength of light provided by each channel may be controlled by the insertion of interference filters (Balzer, type B40, half-bandwidth $\pm 5\text{nm}$).

Targets for use with this system are made by running a program on the Imperial College mainframe (CDC, Cyber series computer) which plots the required target stimuli onto 35mm film. Contact prints of these are then made onto Kodalith film which gives high optical density in the exposed regions and almost zero elsewhere. These slides are then mounted in Gepe double glass slide-binders. The most frequent target types used in the experiments are gratings of alternately transmitting and opaque (light and dark) bars and circular spots, both light spots on a dark background and dark spots on a light background (see figure 2.10). Three different modes of target presentation were studied; i) continuously, ii) flashed for a fixed duration determined by electromagnetic shutters, under computer control and iii) moving, when the target is presented in channel 1. For mode ii), a signal from the computer to a specially constructed power supply [Holliday, 1982] causes it to supply current to the shutters. The circuit provides a voltage pulse of the required duration, which is initially at 90 volts but drops within 10ms to a steady 10 volts for the rest of the timing period. The 90 volt signal ensures rapid shutter opening, while the 10 volt signal avoids unnecessary heating of the shutter solenoid and large back EMF generation at the end of the timing period. A minimum opening period of 30ms can be achieved, and the maximum opening period is unlimited although, in practice, for a single presentation of more than 30 seconds, shutters are not used, but the beams blocked and unblocked by hand and timing carried out with a stopwatch. The target in channel 1 (placed at OP1, figure 2.2), can be presented moving by mounting the target slide in a carrier which is moved perpendicularly across the beam, via gears, by a DC servo-motor (Electrocraft 586-5A) fitted with a 30:1 ratio gearbox (McLennar Engineering, AM 5020). The motor is controlled by the computer which supplies, via a power supply,

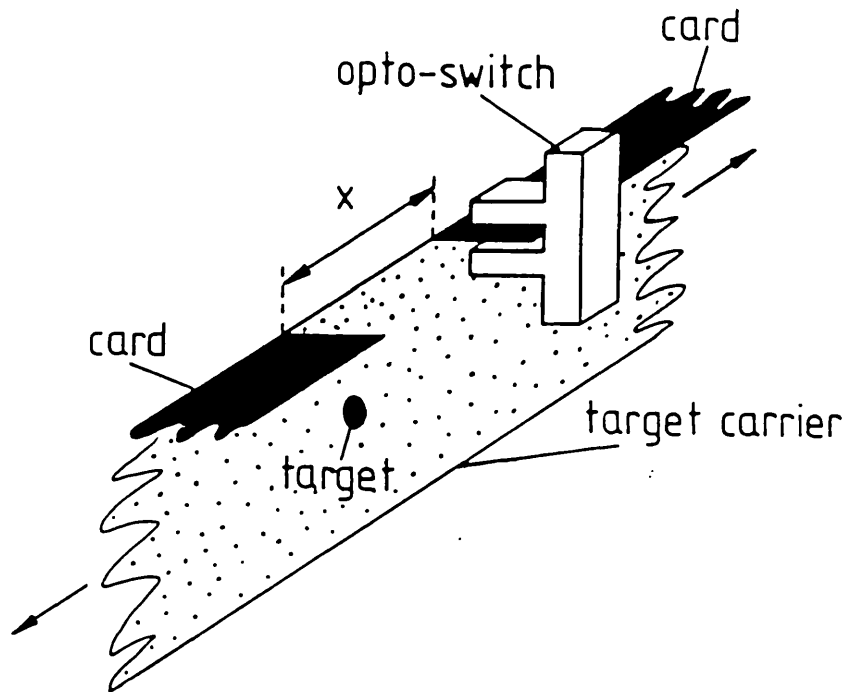


Figure 2.3 Diagram of the slotted opto-switch used to measure target displacement.

a voltage whose magnitude determines the target carrier's speed and sign determines its direction of motion. The velocity range available goes from 0 to 50 degrees/second. The displacement during motion is also controlled by the computer, using a slotted opto-switch fixed to the carrier frame to signal the target carrier's position (see figure 2.3). Two pieces of card are attached to the carrier and as the carrier moves they move in and out of the arms of the opto-switch, blocking and unblocking the infra-red beam passing between the two arms. The separation (x) of the two pieces of card on the carrier corresponds to the extent of motion required. The carrier starts with one piece of card in the slot breaking the beam and keeps moving until the second piece of card breaks the beam again, when a signal is passed to the computer which stops the target carrier moving. When the carrier starts moving again it

goes back in the opposite direction. By using the slotted opto-switch the target carrier is prevented from moving too far thus shortening the time between presentations of the target. The angle of target displacement seen by the observer is controlled by the size of the aperture placed just in front of its plane of movement (at OP1, figure 2.2).

A temporally modulated field of view is produced by placing a sheet of Polaroid (called the analyser) in the beam to polarise the light, while another sheet of Polaroid, attached via a 1:15 gearbox (McLennan engineering), to the shaft of a d.c. servomotor (Electro-craft 586-5A) is rotated in the beam. This produces a field of view whose illumination varies as the square of the cosine of the angle between the polarising axes of the two sheets.

The size of the image of the filament produced in the right eye pupil by this optical apparatus is $1.5 \times 0.75\text{mm}$ and to assist the observer in positioning the eye so that the image of the source is within the pupil, an artificial eye pupil with diameter of 4mm is placed just in front of the required eye position. When viewing binocularly, another artificial eye pupil is provided for the left eye. To keep the observer's head still once it is in the right position, a mouth piece is used. This consists of an impression of the observer's teeth made in Stents thermoplastic and mounted on a metal plate, the position of which is adjustable in all directions.

Different experiments require different fields of view and the Maxwellian view apparatus can be arranged to provide a variety of fields of view. The channels and stimuli used for the experiments carried out in this thesis will be described later in this chapter, together with background information on the experiments.

(c) Calibration of the Maxwellian View Optical System

In this section, the calibration of the Maxwellian view system is described. A second Maxwellian view system was used for the experiments presented in Chapter Four, and where the procedures or data for this system differ from that of the main system, they are also described.

The source

The source, a tungsten filament quartz lamp, produces a total flux of 3000 lumens and has an approximate colour temperature of 3100K. One lamp was used for the majority of the experiments and its average source brightness was constant varying by only 0.2 log units over 60 hours of use. The spectral output of this type of source has been determined by measuring the radiant energy in spectral bands. The radiant energy was measured using a digital radiometer/photometer (Macam, model PR3010) and the spectral bands were isolated by placing narrow bandwidth interference filters (Balzer B40), whose transmission characteristics had been measured in a Beckman DK-2 recording spectrophotometer, perpendicular to the collimated target beam (figure 2.4). The radiant exitance of the source is decreased by only 0.7 log units at 400nm relative to the value obtained in the red part of the spectrum.

In the experiments to be described, it is necessary to define the retinal illuminance of the field of view. To determine the retinal illuminance, the source image luminous intensity at the exit pupil is measured in candelas (cd), the luminous flux/solid angle, using the digital photometer/radiometer fitted with a filter so that its spectral sensitivity closely matches that of the eye, as defined by the CIE photopic curve. Since the source image in the artificial pupil of the apparatus is smaller than the minimum pupil size for the human eye, the retinal illumination is the number of candelas in the areal image [Westheimer, 1966]. The unit of retinal illuminance used throughout this study

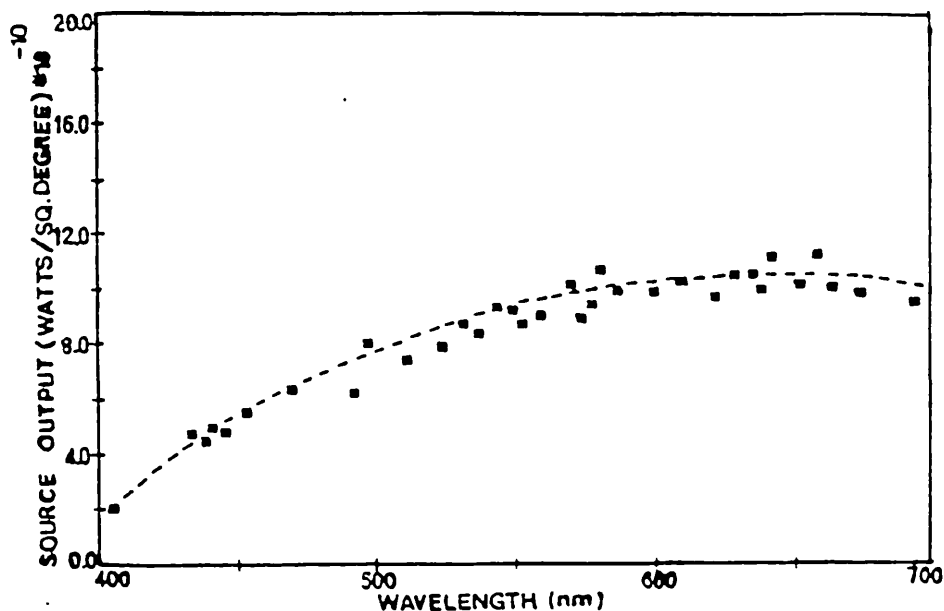


Figure 2.4 The spectral distribution of the light from the source, measured at the exit pupil. [Barbur, 1980]

is the troland (td.). One troland is defined as the retinal illumination level produced by a surface of luminance 1 cd/m^2 viewed through a pupil of 1 mm^2 area; that is, 1 troland is equivalent to 10^{-6} lumens/steradian (candelas). Retinal illumination levels in trolands are obtained from the intensity measurements in candelas by multiplication by 10^6 and the base 10 logarithm of these values is normally used. Measurements were made regularly for all channels and the results for the target channel are incorporated in the data analysis program for use in computation of the channel's light level.

Magnification of the system

The conversion factor relating the object size to the angle it subtends at the observer's eye is found for each of the viewing lenses L3 and L4 by measuring the size, $y \text{ mm}$, of a linear image produced at a distance of $a \text{ mm}$ from the artificial pupil, by an object, of size $x \text{ mm}$, placed at the focal

plane of the lens (figure 2.5). Then the angle θ , subtended at the eye is given by

$$\theta = 2 \tan^{-1} (y/2a)$$

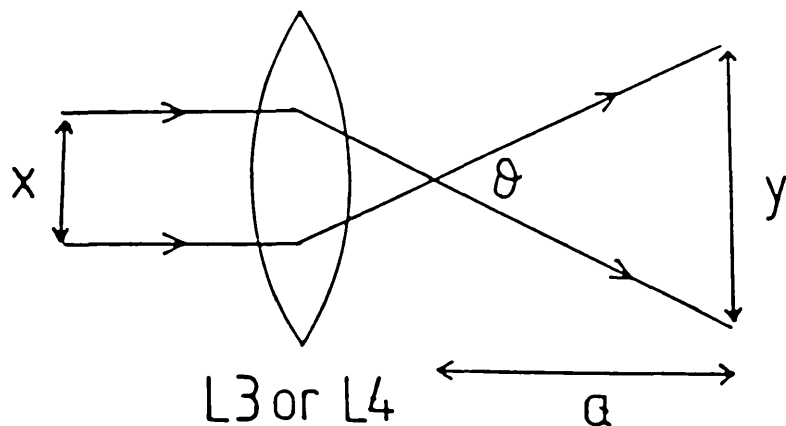


Figure 2.5 Schematic diagram showing the visual angle that an object of size x mm subtends at the eye when viewed through lens L3 or L4.

Each millimeter of object space subtends m degrees of visual angle where $m = \theta/x$. A grating of bar width d has a spatial frequency in cycles per mm of object space of $(2d)^{-1}$ and a spatial frequency in cycles per degree of visual angle of $(2md)^{-1}$.

For L3, one millimeter in object space subtends $m = 1.14^\circ$ of visual angle and for L4, $m = 0.32^\circ$. The maximum field of view obtainable with this apparatus is limited by the lens L3 or L4. Lens L3 gives a maximum field of view of 47° . The field of view produced by L4 is somewhat smaller but large fields were not required in the binocular experiments.

Neutral density filters

Using the photometer, the optical densities of the neutral density filters were found by measuring how much they attenuate the light from one channel when inserted into the beam. The filters were also checked for neutrality by

inserting interference filters into the beam, and measuring the transmission of the neutral density filters as a function of wavelength. The optical density of each of the filters was found to vary by only ± 0.05 log units over the visible wavelength range tested.

Neutral density wedge

The neutral density wedge was calibrated to find the relation between the transmitted luminous intensity and the wedge position in channel 1 measured by the number of steps made by the stepping motor to move the wedge from its zero position to that position. Figure 2.6 shows the relation obtained. The vertical scale shows the change in luminous intensity of light passed by the wedge as it moves from one position to the next. As can be seen from the graph, the luminous intensity of light passed by the wedge does not increase linearly as it moves from its zero position, however the graph profile was the same each time it was measured. Also, when movement was from left to right different values were obtained than when the wedge's motion was from right to left. The four different regions identifiable on the graph are described with four different equations (as shown on figure 2.6) where equations 1 and 2 describe left to right motion of the wedge and equations 3 and 4 right to left motion. All four equations are included in the data analysis program for use in computation of channel 1 light levels.

In the experiments of Chapter Four a different neutral density wedge is used. The calibration curve of luminous intensity transmitted versus position is given in figure 2.7. Its position in the beam is determined by the voltage applied to the motor driving it. The calibration is not completely linear, but was found to be unchanged each time it was repeated.

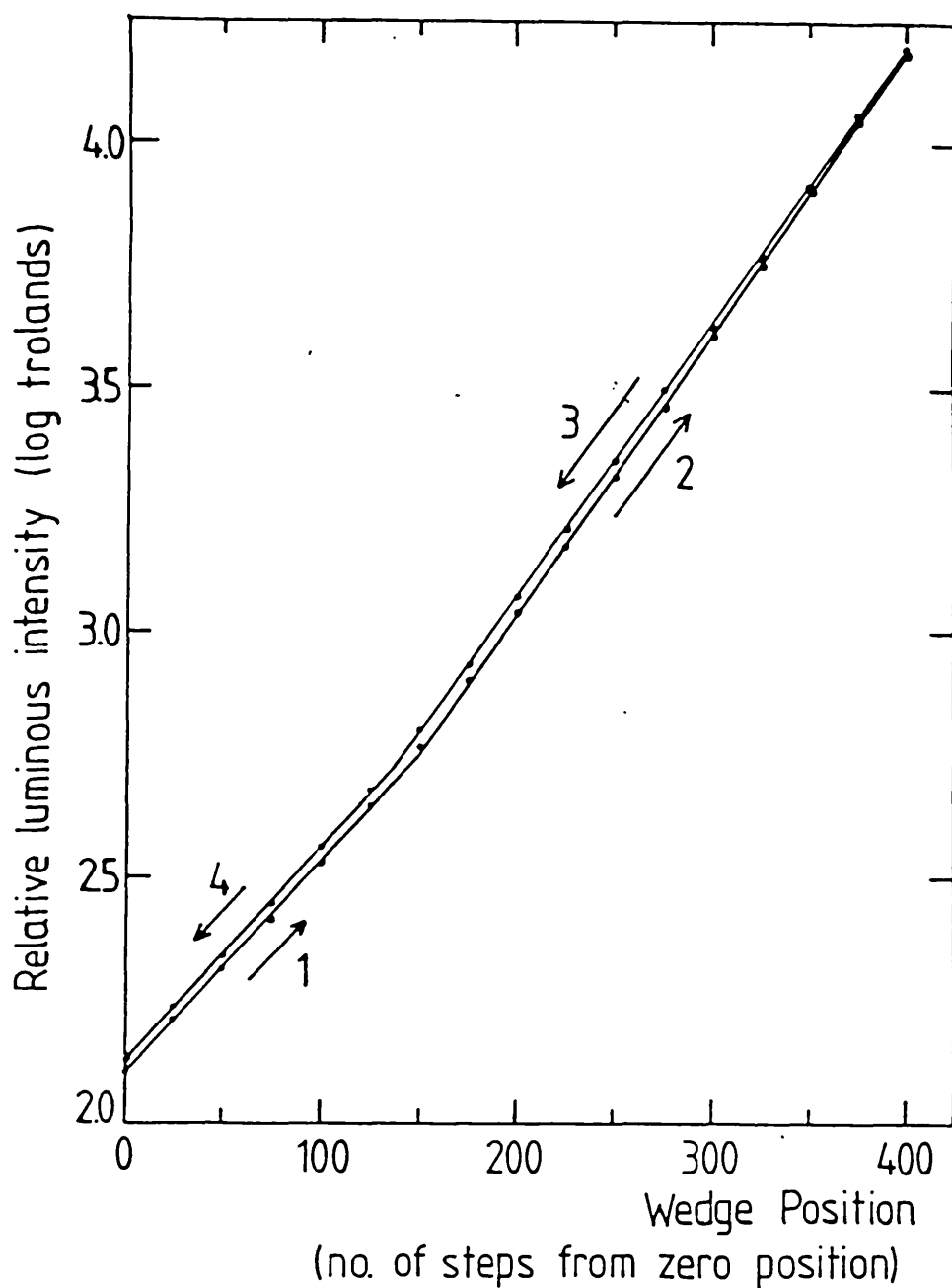


Figure 2.6 The relative luminous intensity of light transmitted by the wedge plotted against its position measured in steps of the stepping motor from zero position. Left to right motion 1. positions 25 to 150 $y = 0.0043x + 2.10$ 2. positions 150 to 400 $y = 0.0057x + 1.90$, right to left motion 3. positions 400 to 150 $y = 0.0056x + 1.96$ 4. positions 150 to 25 $y = 0.0044x + 2.13$

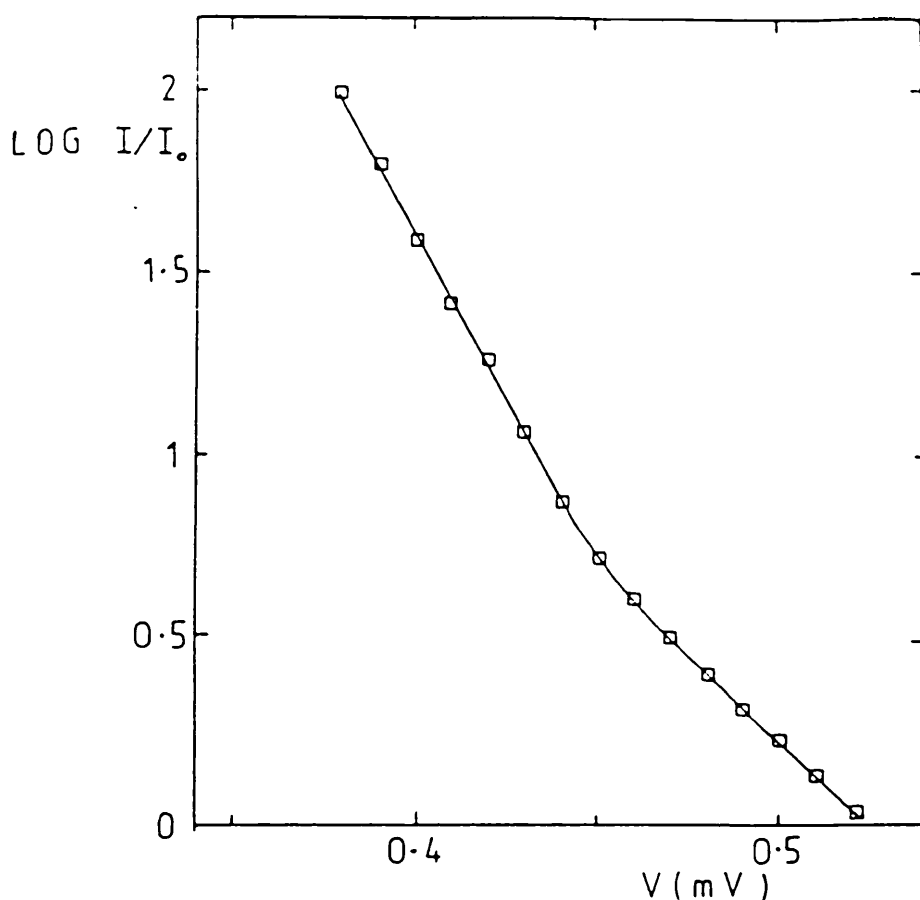


Figure 2.7 Calibration curve for the neutral density wedge used in the experiments of Chapter Four. Relative luminous intensity of the light passed by the wedge as a function of the wedge's position in the beam measured by the applied voltage (mV).

Target velocity

The velocity of the target holder, perpendicular to the beam, was measured as a function of the voltage applied to the motor. To carry out this calibration a program was written to run on the Macsym2 computer. The program caused a known voltage to be applied to the motor and then timed how long the target holder took to move a set distance. The beginning and the end of timing was signalled to the computer by two pieces of card

separated by 7.5cm fixed to the target carrier; as the first moved out of the arms of the opto-switch timing started and as the second piece moved in timing stopped. The resulting velocities, measured for a series of different voltages, are plotted in figure 2.8, and they show that the velocity increases linearly with applied voltage up to a value of 53.5 degrees/second at an applied voltage of 10 volts. This calibration was included in programs running on the Macsym2 computer which performed experiments requiring a moving target. The velocity required can then be entered at the keyboard before an experiment and the computer translates this into the corresponding voltage to be applied to the motor driving the target holder during the experiment.

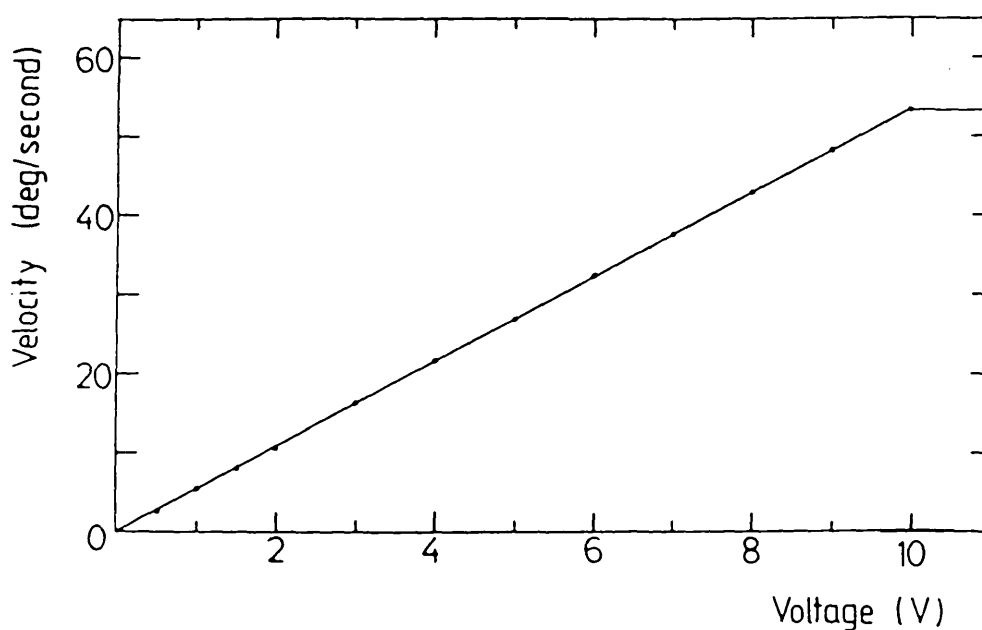


Figure 2.8 Velocity of the target through channel 1 as a function of the voltage applied to the motor driving the target holder

Rotating Polaroid

The rotating polaroids, which consist of two pieces of polaroid film,

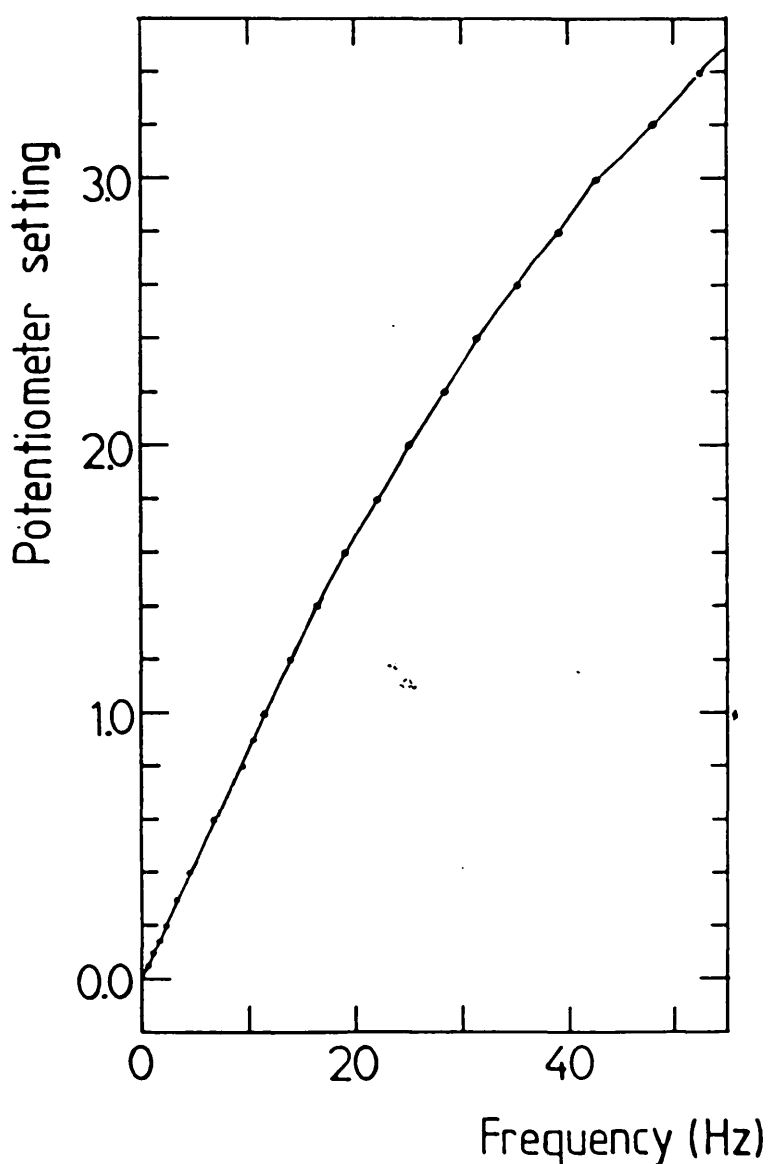


Figure 2.9 Calibration of the polaroid rotation. The potentiometer setting is plotted versus the temporal modulation frequency of the light transmitted by the rotating polaroid and analyzer combination.

one in a fixed position in the beam and the other rotated on the shaft of a motor through a 1:15 gearbox, was used to produce sinusoidal temporal modulation of the light beam. The intensity of the light produced by this arrangement fluctuates from approximately zero to a maximum, twice in each

revolution of the moving polaroid – i.e. it varies as the square of the cosine of the angle between the polarisation axes of the two sheets. The frequency of the change in light intensity was measured as a function of the voltage applied to the motor via a potentiometer, by timing a number of revolutions of the motor shaft. Figure 2.9 shows the graph obtained.

When temporally modulated light is used in an experiment the experimenter sets the potentiometer to the voltage corresponding to the required flicker frequency.

2.2 Experimental Procedures Requiring the Maxwellian View System

(a) ST1 and ST2 Spatio–Temporal Visual Filters

The Maxwellian view system of Figure 2.2 was originally designed for the determination of the spatial characteristics of visual filters [Barbur and Ruddock, 1980] and subsequently for spatio–temporal filters [Holliday and Ruddock, 1983]. The method they used for their investigations, the background modulation technique (see section 1.2(b)), is based on the hypothesis that the response of a psychophysical mechanism to a particular stimulus parameter can be revealed by superimposing a constant test stimulus upon a background stimulus, and obtaining the threshold for detecting the test as a function of the background parameters. Four different configurations of the background stimuli were used to elicit the spatial and temporal properties of the two filters. The background field was always circular and its diameter subtended 17° of visual angle. Its spatial and temporal features will be described in detail further on in this section. The test stimulus was a circular spot, either moving at 15 degrees/second through the central 8° of the background field or presented stationary and flashed at the centre of the background field. The observer viewed the visual field with one eye usually their right. For trans–foveal

presentation of the target the observer was instructed not to track the target, but to maintain gaze towards the centre of the background field, and for non-foveal measurements a red light emitting diode was used to provide a small fixation point. The observer was required to determine the target illumination at which it could just no longer be detected i.e. its threshold value. For this purpose the target illumination was controlled automatically by the computer. The original experiments employed targets of light (positive) contrast, but in the present study targets of dark (negative) contrast were also investigated (see Chapter Three).

The Threshold Program

This program controls both the timing of presentation of the target, either moving or stationary and flashed, on the background field and also the illumination according to the observer's response in a forced choice detection task. The program used two, randomly interleaved, staircases to control the test illumination [Cornsweet, 1962]. Each staircase produced threshold values, bracketing the threshold region, at the points where the target just disappeared and appeared. The size of the change between successive steps on a staircase is initially large (0.5 log units) becomes smaller (0.25 after the first turning point and 0.05 after the second). Twelve turning points, six on each staircase, are normally obtained for each threshold determination and the first two from each staircase, which are obtained with the larger step sizes, are discarded. The program calculated the mean and best estimate of standard error from these values.

Background Field Configurations

The background field configurations used by Barbur and Ruddock [1980a]

and by Holliday and Ruddock [1983] in their studies, were applied in the experiments to be described in Chapters Three and Five for the determination of spatial and temporal characteristics of the ST1 and ST2 filters.

ST1 – Background Field for Spatial Responses

The background consists of a 1-dimensional periodic, square-waveform, grating with bar-width d , giving a fundamental spatial frequency, or period, of $f_s = 1/2d$. Figure 2.10 shows the test stimulus, a circular target moving on this background. The grating image is produced by placing one of the photographic transparencies with a grating pattern on it in channel 2 (figure 2.2) and its contrast can be controlled by superimposing a uniform field from channel 3. If the illumination of the light beam from channel 2 is I_2 and

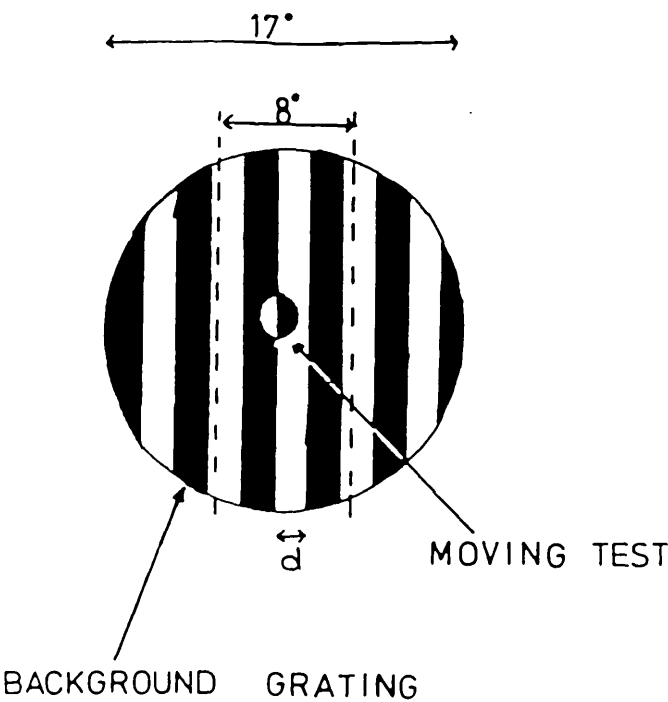


Figure 2.10 The field of view presented to the observer when performing the ST1 spatial experiment.

that of the beam from channel 3 is I_3 , the average spatial illumination level is $I_b = I_3 + I_2$ and the modulation depth M is $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min}) = I_2 / 2I_b$.

ST1 – Background Field for Temporal Responses

This background consists of two gratings with the same dimensions, and also with the same contrast and mean illumination level, arranged in spatial antiphase and modulated in temporal antiphase. Figure 2.11 illustrates the background field when both gratings have 100% contrast. The background field is formed by placing grating slides with spatial frequency, f_s in beams 2 and 3, superimposing the two images so that they are in spatial antiphase, and shutting the two beams alternately at a temporal frequency f_t cycles/second. If the illumination level of the light bars of both gratings is I and there is 100% contrast between dark and light bars, the average spatial and temporal illumination level $I_b = I/2$.

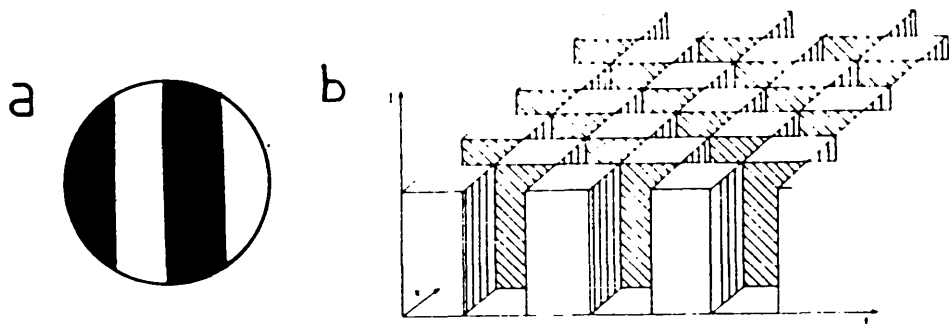


Figure 2.11 Field of view presented to the observer when performing the ST1 temporal experiment. (a) Field of view at an instant in time, (b) Diagram showing evolution of field of view with time.

ST2 – Background Field for Spatial Response

This background also consists of two identical gratings arranged in spatial antiphase and whose light bars have the same average illumination level.

The illumination level of the light bars of one grating is varied in time, those of the other grating are constant, giving the spatial and temporal distribution of illumination shown in figure 2.12. This field is produced by placing grating slides with spatial frequency f_s in beams 2 and 3 and superimposing the two images in spatial antiphase. The illumination level of one set of light bars is made to vary temporally with a frequency f_t by the use of the analyzer and rotating polaroid in channel 3. If the maximum illumination level from this channel is I_3 , its evolution with time is described by $I_3 \cos^2(f_t t)$. The illumination level of the light bars produced by channel 2 is I_2 and $I_2 = I_3 / 2$. Hence the total illumination level of the field of view is $I_2/2 + I_3 (\cos^2 f_t t)/2$ and the spatial and temporal average background illumination level, I_b , is I_2 .

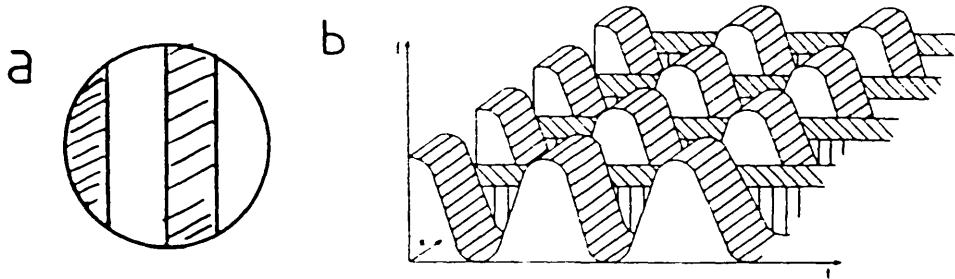


Figure 2.12 Field of view presented to the observer when performing the ST2 spatial experiment. (a) Field of view at an instance in time, (b) Diagram showing evolution of field of view with time.

ST2 – Background Field for Temporal Response

This background (figure 2.13) is spatially uniform and temporally modulated at frequency, f_t . This is obtained by placing the analyser and rotating polaroid in channel 2 and, for variable modulation depth, combining this with a uniform field from channel 3. Thus if the modulated beam has an output illumination $I_2 \cos^2(f_t t)$ and the uniform beam has illumination I_3 the average temporal illumination of the background is $I_b = I_2/2 + I_3$ and

the temporal modulation depth is $M = I_2 / 2I_b$.

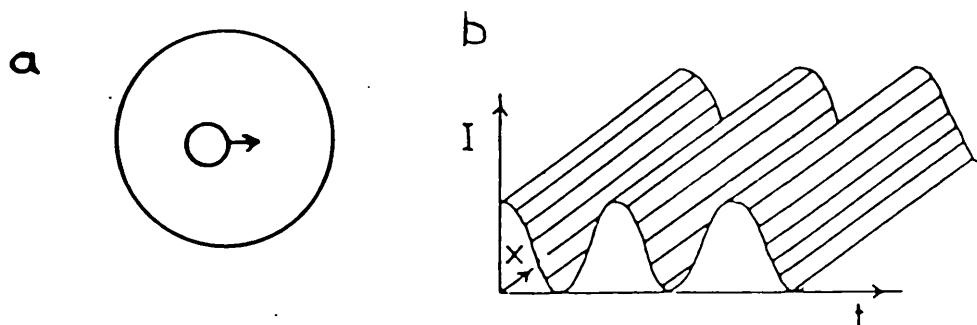


Figure 2.13 Field of view presented to the observer when performing the ST2 temporal experiment (a) Field of view at an instant in time (b) Diagram showing evolution of field of view with time.

Review of the ST1 and ST2 Filters' Characteristics

The spatial properties of the ST1 filter, originally called the IMG filter, were determined in the study of Barbur and Ruddock [1980 a and b]. The ST1 spatial response is obtained by measuring test threshold illumination I_t for a 3.5° circular, light target flashed in the centre or moving at $15^\circ/\text{s}$ over the central 8° of a 17° diameter circular grating background (figure 2.10) as a function of the fundamental spatial frequency of the background grating. The types of spatial tuning curve obtained are illustrated in figure 2.14. For foveal presentation of the target the response peaks around 4 cycles/degree with mean background illuminations below $2.0 \log \text{td.}$ and shifts to around 8 cycles/degree with illuminations above about $2.5 \log \text{tds.}$ The peak position moves to lower spatial frequencies for non-foveal test presentation, for example a peak is obtained at 1 to 2 cycles/degree for 30° eccentricity. The response is also independent of the background orientation, the same tuning curve being obtained when the target moves horizontally across vertical or horizontal orientation gratings. The amplitude of the effect is the same for all

background illuminations of 1.0 log td. and above, but at low illumination the amplitude is smaller. The amplitude varies linearly with the contrast of the background field, reaching a maximum of 0.5 to 0.6 log units for 100% spatial modulation depth. Changing target parameters also affects the response; if the target diameter is less than 0.1° the amplitude becomes smaller and if it moves at less than 0.5 degrees/second the peak shifts to lower spatial frequencies. The remaining responses of the ST1 and ST2 filters were determined in the study of Holliday and Ruddock [1983].

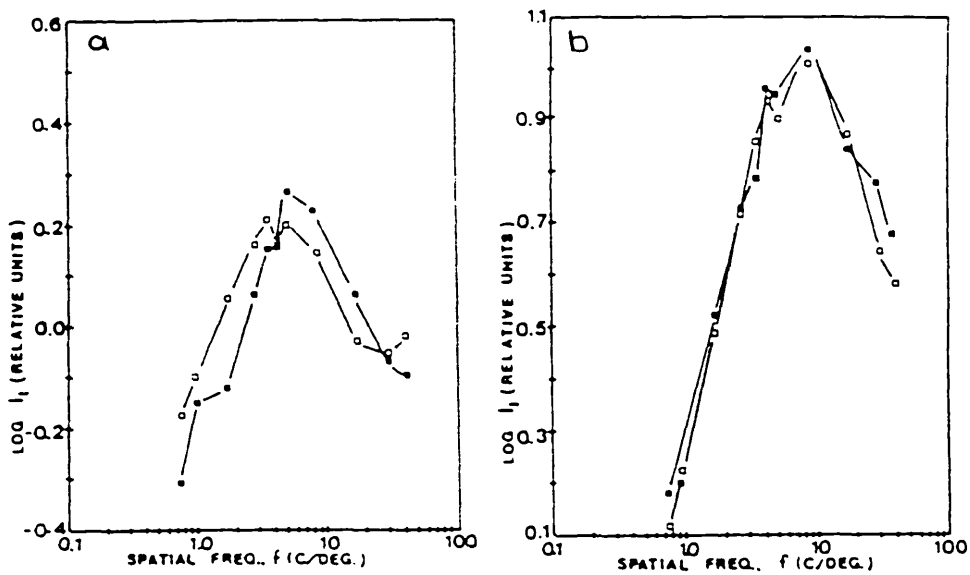


Figure 2.14 ST1 spatial response obtained using the grating background of figure 2.10. (a) Background field illumination of 1.4 log td. (b) Background field illumination of 3.4 log td. Two observers, $\square$ V.W. and $\blacksquare$ J.B. (from Barbur, 1980)

The ST1 temporal response is obtained using the background field shown in figure 2.11. The response obtained when the test threshold illumination I_t is measured, for a 1.4° diameter circular light target flashed for one second every three seconds at the centre of this background, as a function

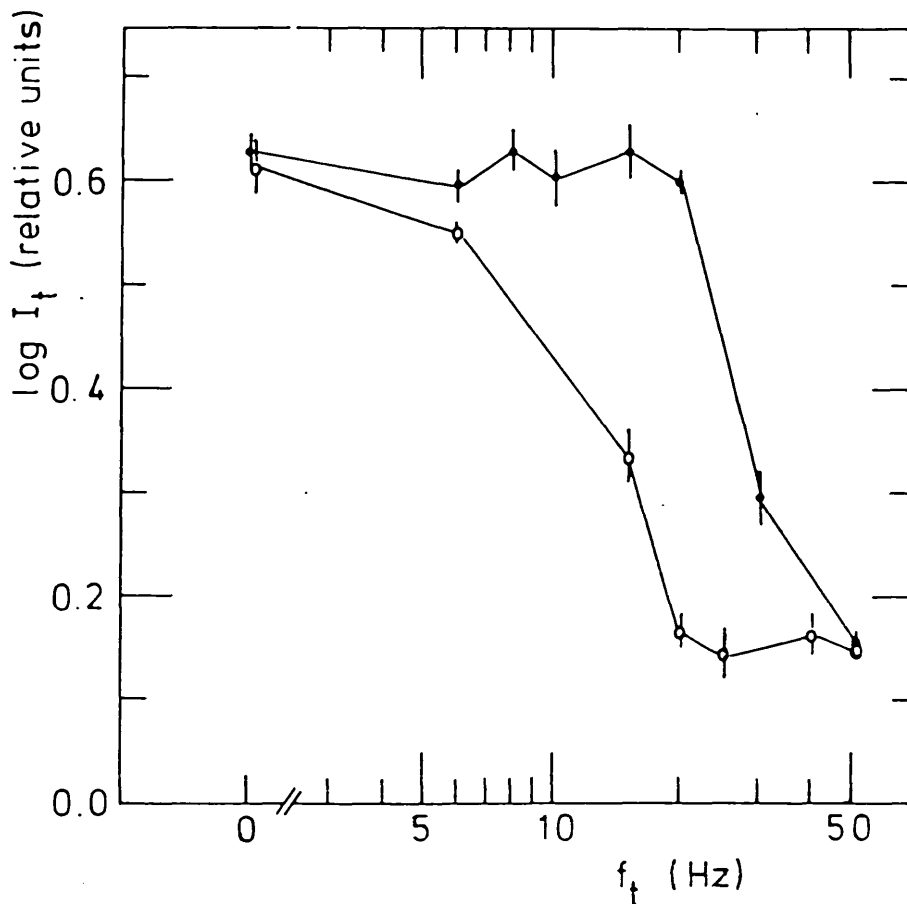


Figure 2.15 Low-pass temporal response of the ST1 filter for two values of background field illumination. Target threshold illumination, $\log I_t$, is plotted against the modulation frequency of a 17° diameter circular background of figure 2.11. (The target was a 1.4° diameter, light contrast circle presented flashed for 1 second every 3 seconds in the centre of the background). The grating was 100% spatially modulated and had spatial frequency 4.3 cycles/degree. Mean background illumination was 2.6 log td. (•) and 1.7 log td. (◦).
(from Holliday and Ruddock, 1983)

of the frequency of temporal modulation is shown in figure 2.15. The responses, which are low-pass, were obtained with background illuminations of 1.7 log td. and 2.6 log td. and background spatial frequency of 4.3 cycles/degree. With increasing background illumination the corner frequency and cut-off frequency increase. This low-pass temporal response is associated with the ST1 filter because like the spatial tuning response above, the amplitude of the threshold elevation increases linearly with the contrast of the

spatial component of the background. In addition the amplitude of the threshold elevation for the background configuration of Figure 2.11 is maximum for a background spatial frequency of around 4 cycles/degree, which is the spatial frequency which produces maximum threshold elevation for the ST1 spatial response. If the response with the background configuration of figure 2.11 is measured with a moving target rather than a flashed target, then as this velocity is increased from 0 to 15 degrees/second, the responses change from low-pass to band-pass, but the high frequency response is similar to that of the original low-pass response obtained for the stationary target.

The ST2 temporal response is obtained by measuring test threshold illumination, I_t , for a circular, light target moving over the central 8° of a spatially uniform but temporally modulated 17° diameter circular background field (figure 2.13) as a function of the temporal modulation frequency. The type of band-pass temporal tuning curve obtained is illustrated in figure 2.16. The position of the peak of the tuning curve moved to higher frequencies as the background illumination increased whilst the amplitude of the response is constant for all background illuminations above 1 log td. As the flicker modulation depth increases the response amplitude increases, reaching a maximum at 40% modulation. For non-foveal presentation of up to 25° eccentricity the response remains the same but at 30° eccentricity the peak is displaced to higher flicker frequencies for all background illumination levels. Varying the target parameters also affects the response obtained; thus the maximum amplitude response is obtained with targets moving at speeds greater than 10 degrees/second and of size 1° to 2° .

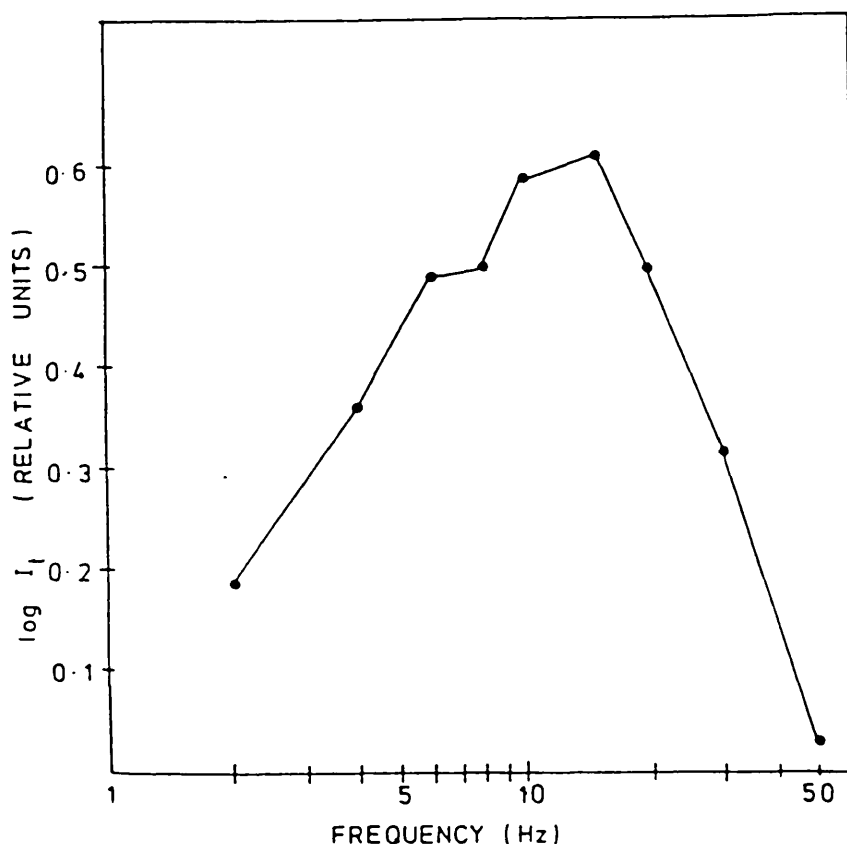


Figure 2.16 The temporal frequency response of the ST2 filter. Target threshold illumination, $\log I_t$, plotted on a relative scale, for a 1.4° diameter circular light target moving at 15 degrees/second across the central 8° of a 17° diameter circular flickering background (figure 2.13) plotted against flicker frequency of the background. The mean background field illumination was 1.4 log tds and the modulation 25%. Results for observer IMH with transfoveal presentation. Mean standard deviation = 0.05 log units.

(from Holliday, 1982)

The ST2 spatial response is obtained by measuring test threshold illumination for a circular, light target moving over the central 8° of a 17° diameter, circular background field modulated temporally and spatially as a function of background spatial frequency (figure 2.12). The response illustrated in figure 2.17, peaks in the region of 1 cycle/degree for all background illumination levels and is of constant amplitude for background illuminations greater than 0.0 log td. Similar responses are obtained for either horizontal or vertical orientation of the background grating thus, like ST1, they are not

orientation selective. This spatial response shares many of the parametric properties of the ST2 temporal response suggesting that the two sets of data are associated with the single filters, ST2. For any particular background illumination level, the amplitude of the response is a maximum for the same flicker frequency that produces the peak threshold level for the corresponding temporal response curve. As temporal modulation depth increases so does the amplitude of the response up to 30% modulation. Similarly, for eccentricities up to 30° the response curve remains the same and the response is optimal for target diameters in the range 1° to 2° and for velocities greater than 5 degrees/second.

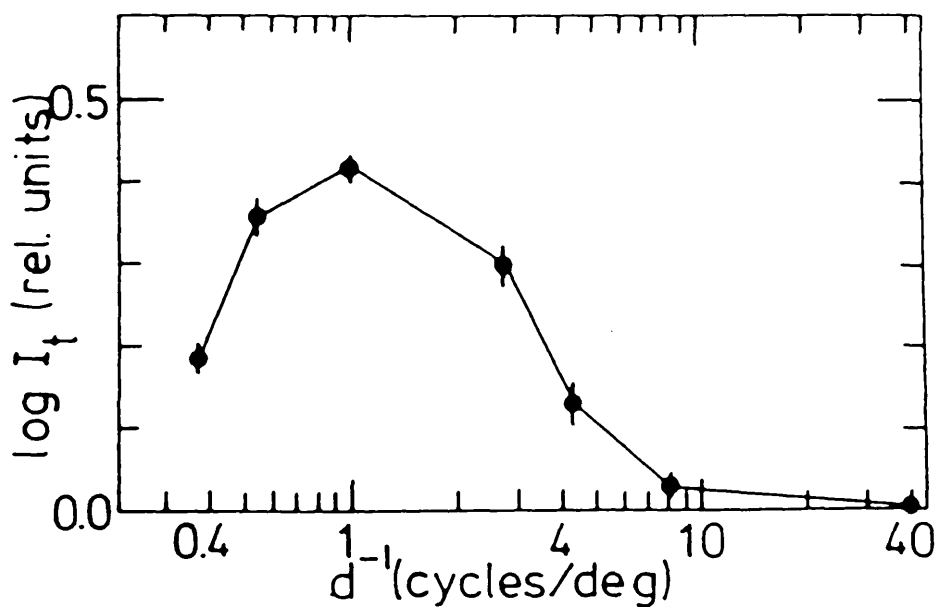


Figure 2.17 The ST2 spatial response obtained using the background of figure 2.12 and mean background illumination $1.4 \log \text{td}$.

It is important to note that neither ST1 nor ST2 responses can be obtained under dichoptic presentation with the background in one eye and target in the other, thus the response mechanisms do not appear to be

binocularly controlled. Spatial distributions corresponding to the spatial frequency responses of the two filters have been estimated. Because the amplitude of the ST1 spatial response varies linearly with background grating contrast, transform methods can be used to compute its spatial mechanism. The response amplitude of the ST2 spatial filter is not, however, linearly related to the modulation depth of the flickering bars so its spatial distribution was found with a linear approximation. Both filters are shown to have circularly symmetric, antagonistically organised spatial distributions which can be interpreted as the receptive fields of physiological response units. Figure 2.18 shows the computed spatial distribution for the ST1 filter obtained with an average background illumination level of 1.4 log td. The circular symmetry is implicit in the non-orientation specific properties of both filters. The centre widths of the receptive fields are 0.4' for the ST1 foveal spatial response which has its peak around 4 cycles/degree and 25' for the ST2 spatial response which peaks at a lower spatial frequency of 1 cycles/degree. The circularly symmetric antagonistic nature of the receptive fields of ST1 and ST2 and their monocular control suggest that they are associated with pre-cortical neuronal mechanisms. The ST1 filter with its smaller receptive field centre and sustained (low-pass) temporal response was associated with X-type mechanisms and the ST2 filter with its larger receptive field centre and transient temporal response was associated with the Y-type mechanism.

X- and Y-type ganglion and geniculate cells also exhibit 'on' centre and 'off' centre responses and it is thought that the data reviewed above, obtained with light targets, reflect the activity of the 'on' centre cells. It is the aim of Chapter Three to obtain ST1 and ST2 responses with a dark contrast target in order to determine whether the results are similar to those

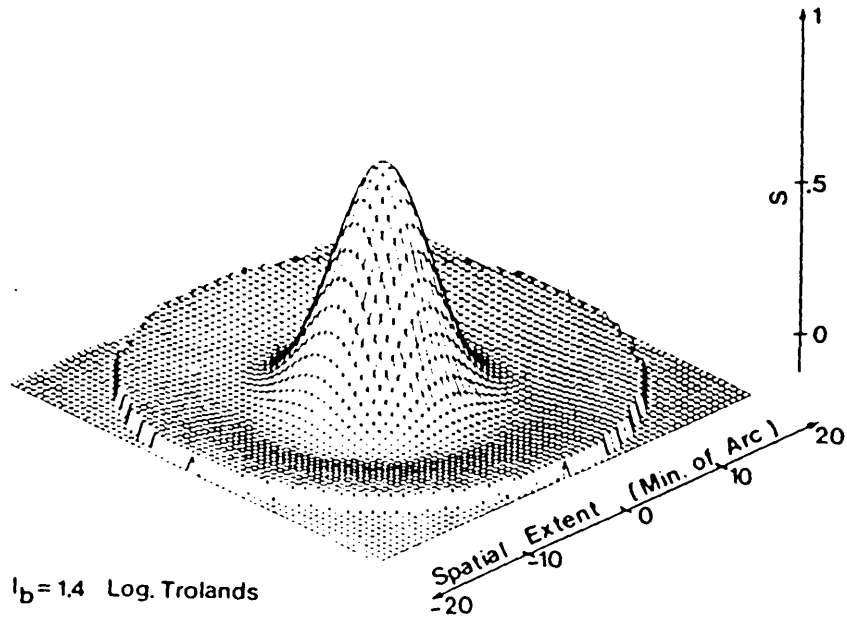


Figure 2.18 Spatial two-dimensional sensitivity function derived from foveal ST1 data for average background illumination level of 1.4 log td. x-y plane is the spatial extent of the filter and the z co-ordinate is the sensitivity of the filter. The shape is of a sharply peaked central lobe surrounded by a shallow negative trough. (from Barbur and Ruddock [1980a]).

obtained with a light contrast target and to test for independent activity of 'on' and 'off' centre mechanisms.

Grounds, Holliday and Ruddock [1983] also measured with bright targets the spatial and temporal characteristics of the ST1 and ST2 filters for subjects suffering amblyopia. They established that the ST1 spatial response for both the 'normal' and 'amblyopic' eyes of observers with strabismic amblyopia is displaced to low spatial frequencies compared with the normal curve. In Chapter Five data are presented which describe amblyopic responses to dark targets.

(b) Adaptation Mechanisms Sensitive to Orientation and Bar Size

Following adaptation to a one-dimensional grating composed of alternate light and dark bars of given width and orientation the contrast required for detection of the bars of a similar 'test' grating is raised [Gilinsky,

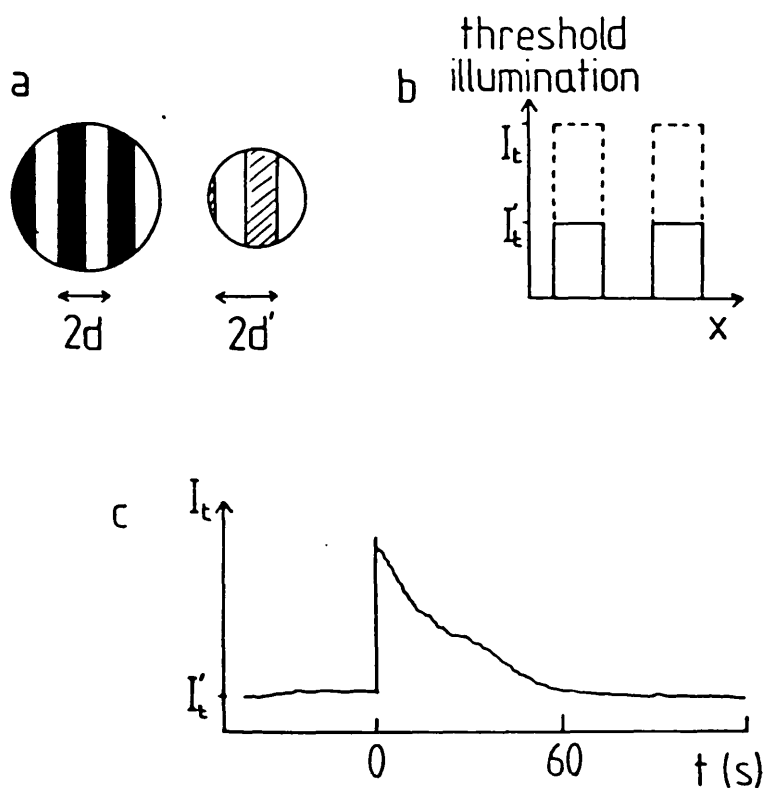


Figure 2.19 Diagram of the visual stimulus used to elicit contrast threshold elevation, the effect of adaptation to a high contrast grating on threshold illumination level of the test grating, and the time course of the effect. (a) On the left is the high contrast adaptation grating which the observer views for 2 minutes and on the right is the test grating of similar orientation and spatial frequency, $(1/2d')$, for which observer's threshold illumination level is raised. (b) Threshold illumination level of the test grating before and following adaptation, I_t' and I_t respectively. (c) Threshold illumination level, I_t , immediately after viewing the adaptation grating for 2 minutes and the subsequent fall in this level, over the period of a minute, until the pre-adaptation level I_t' is reached.

1968; Pantle and Sekuler, 1968, 1969; Blakemore and Campbell, 1969]. The effect, called the contrast threshold elevation effect, is transient of duration one minute and the amplitude of the effect depends on the mean illumination level and contrast of the adaptation grating (figure 2.19).

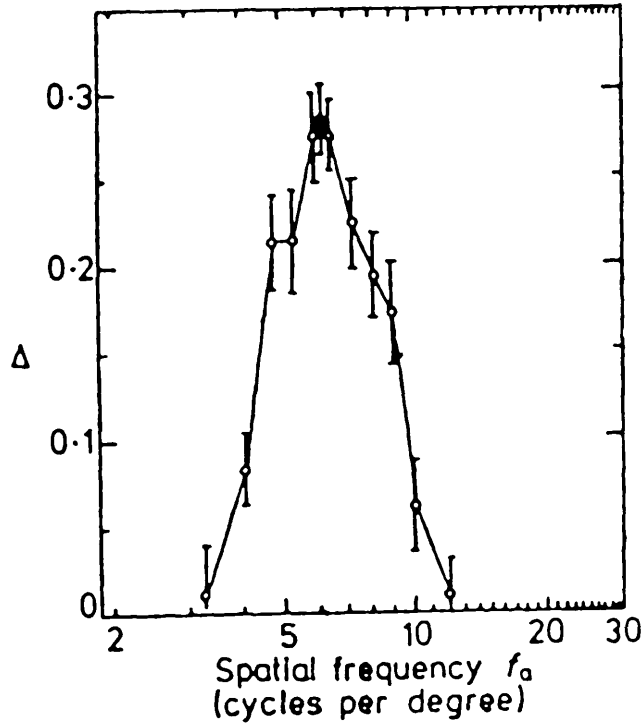


Figure 2.20 Tuning curve showing the adaptation spatial frequencies, f_a , which produce a raise in threshold illumination level for a test grating of spatial frequency, $f_t=6.1$ cycles/degree. The range of adaptation spatial frequencies producing elevation covers 2–3 octaves. (From Maudarbocus and Ruddock, 1973a)

The effectiveness of the adaptation grating can be determined by taking the difference between the illumination level required to detect the test grating following adaptation to a grating and following adaptation to a uniform field of the same illumination level. The effect of the adaptation grating relative to the uniform field is called Δ . If the average threshold illumination values following adaptation to a grating and to a uniform field are I_t and I_0 respectively, the grating adaptation effect can be expressed as

$$\Delta = \log I_t - \log I_0$$

The adaptation effect is spatial frequency specific, the amplitude depending on the relative widths of the test and adaptation bars. The effect

is maximal when the spatial frequency of the adaptation grating is the same as that of the test grating and for a particular test spatial frequency only a limited range of adaptation spatial frequencies produce elevation (figure 2.20). The effect is also orientation specific, being maximal when the adaptation grating is of the same orientation as the test [Maudarbocus and Ruddock, 1973a] (see figure 2.21)

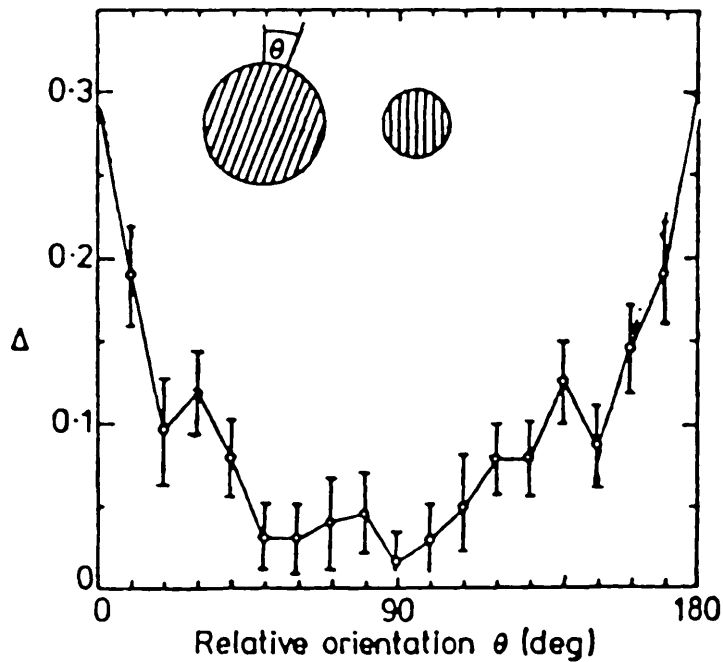


Figure 2.21 Graph showing the variation in the adaptation grating's effect, Δ , as a function of θ , the relative orientation angle of the test and adaptation fields. (From Maudarbocus and Ruddock, 1973a).

The effect is obtained for all resolvable gratings (figure 2.22) and the amplitude of Δ is constant up to a grating spatial frequency of 15 cycles/degree. Above this value Δ becomes smaller.

The adaptation effect, Δ , increases linearly with the log illumination level of the adaptation grating as is shown in figure 2.23. It starts with $\Delta = 0$ when the adaptation grating is set at threshold illumination level and increases until the adaptation grating is about 5 log units above threshold level, above

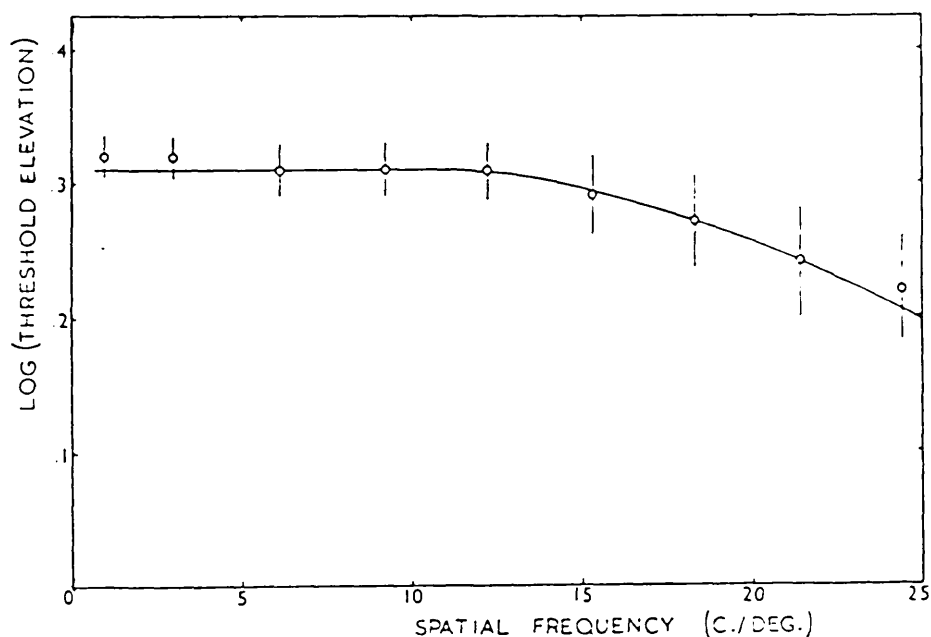


Figure 2.22 Graph showing the maximum values of Δ (when $f_a = f_t$) obtained with test gratings in the range 1.0 to 24.4 cycles/degree. The amplitude of the effect decreases for $f_t > 15$ cycles/degree. (from Maudarbocus, 1973).

which point saturation occurs and Δ remains constant. Maudarbocus and Ruddock [1973a] found that the relation between Δ and the illumination level of the adaptation grating, I_0 , up to saturation level can be described by

$$\Delta = k \log I_0 / I_c$$

where I_c is the threshold illumination level for the adaptation grating, k is equal to 0.056 ± 0.04 and I_0 is the mean illumination of the adaptation grating.

The effect can be transferred dichoptically, so adapting one eye raises threshold illumination level for a matched test grating viewed by the other eye. Δ values obtained in this way are slightly lower than in the case of monoptic viewing. The fact that the effect can be dichoptically transferred implies that the mechanism responsible for it must be centrally located so that it receives signals from both eyes. The characteristics of the mechanism discussed above

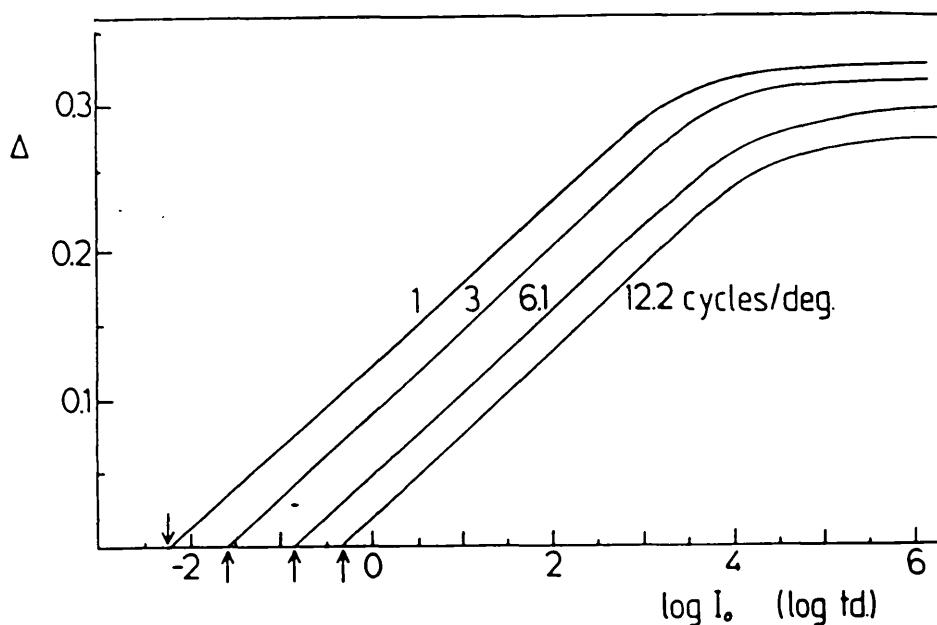


Figure 2.23 Graph showing the relation between Δ and the illumination level of the adaptation grating for four adaptation gratings. The adaptation and test gratings have the same spatial frequency ($f_a = f_t$) and I_c is the threshold illumination level for the adaptation grating, marked with an arrow for each grating used. (From Maudarbocus, 1973)

are similar to those found by electrophysiological measurement of striate cortical neurones [Hubel and Wiesel, 1968].

For dichoptic viewing only, all adaptation wavelengths are equally efficient at producing threshold elevation as long as they are adjusted to be at the same supra-threshold illumination level. Figure 2.24 shows the result of experiments by Maudarbocus and Ruddock [1973a] where adaptation grating wavelengths of 632.8 nm and 476.6 nm both produced similar contrast threshold elevation for a test grating of wavelength 632.8 nm. So the mechanism responsible for the elevation of threshold illumination level is characterised by a broad-band (luminance) spectral response.

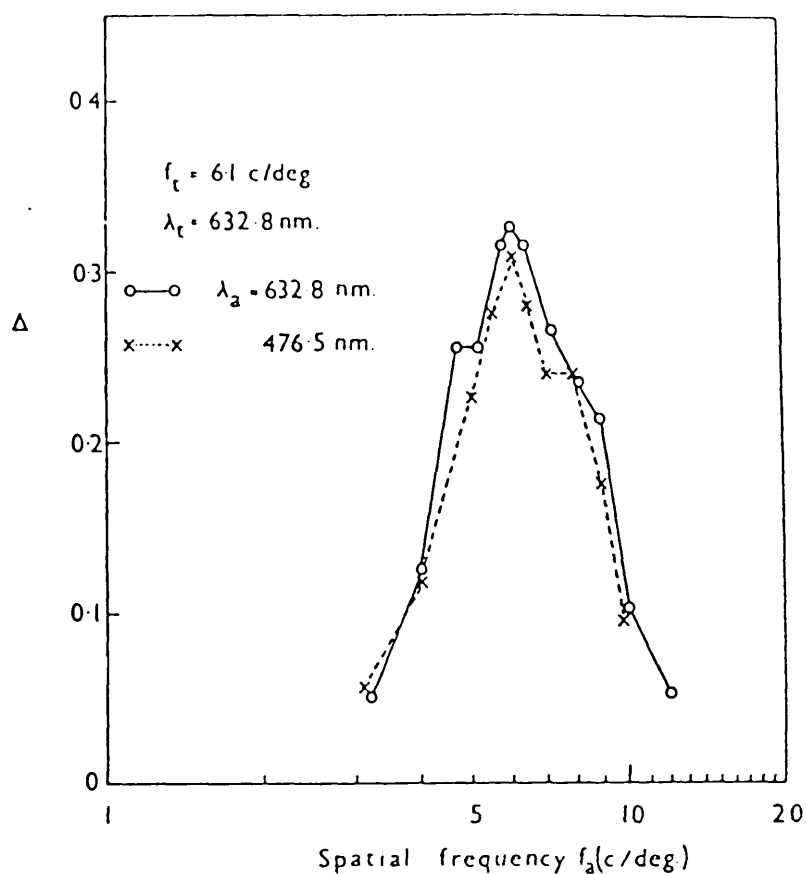


Figure 2.24 Tuning curves for a test grating of wavelength $\lambda_t = 632.8 \text{ nm}$ and $6.1 \text{ cycles/degree}$ following adaptation to gratings of wavelength 632.8 nm (full line) and 476.5 nm (dotted line), both of equal supra-threshold illumination level. (From Maudarbocus, 1973)

In Chapter Four the contrast threshold elevation effect is examined binocularly using the Maxwellian view system. The high-contrast adaptation field was formed by placing a square-waveform grating of bar-width d° and fundamental spatial frequency $f_a = 1/2d \text{ cycles/degree}$ in channel 4. Its illumination level I_a could be adjusted with neutral density filters and set to the required by monitoring the output from the left artificial pupil with the photometer. The low-contrast test field was produced by placing a grating of spatial frequency, f_t in channel 1 and superimposing a uniform field from

channel 2. The illumination level of this uniform field could be adjusted with neutral density filters and set to the required level by monitoring the output from the right artificial pupil with the photometer. The fields of view are as shown in figure 2.25.

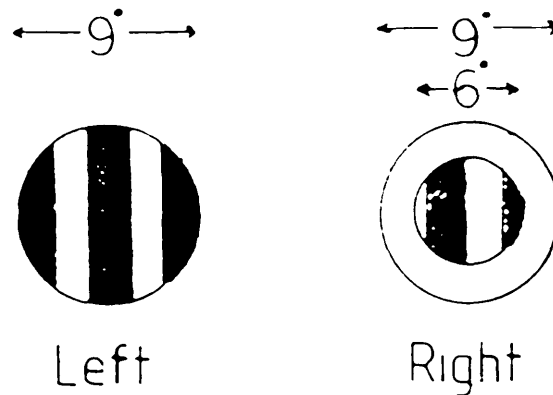


Figure 2.25 Visual fields presented to the left and right eyes during the contrast threshold elevation experiment.

Before an experiment the observer dark adapted for 15 minutes. This was followed by grating adaptation of the left eye for two minutes. The test field and the adaptation field were then presented alternately to the right and left eyes for 2 seconds and 20 seconds respectively, by means of shutters in the three beams. The positions of the two fields were adjusted for the observer so that, with their eyes relaxed and looking into the distance, the images of the fields fell on corresponding parts of the retina in the two eyes. The neutral density wedge used in this experiment was positioned by the observer. The aim was to set the test grating to threshold, I_t . It started at some supra-threshold value and after each presentation of the test the observer decreased its illumination level until threshold was reached. This was done a number of times for each adaptation grating and the average taken. Between

each setting of the threshold, the test illumination was increased to an arbitrary supra-threshold value.

(c) Examination of the Contribution of Different Spectral Mechanisms to the Adaptation Mechanism

The experiments reported in Chapter Four combine the Stiles's two-colour increment threshold technique (section 1.2(b)) with that of spatial adaptation (section 2.2(b)) in order to examine the contribution of different spectral mechanisms to the adaptation mechanism. Contrast threshold experiments have been performed with the test grating superimposed on a coloured background. By choosing appropriate wavelengths of the test grating λ and background μ , measurements were made with the test grating detected by the blue-sensitive, π_3 -mechanism and the red-sensitive, π_5 -mechanism. μ was chosen as 582.5 nm for isolation of π_3 , and 495 nm for isolation of π_5 . In order to check the effectiveness of these background wavelengths in isolating the appropriate π -mechanisms the energy, E_λ , required for detection of the target grating was measured as a function of the test wavelength and the spectral sensitivity curves obtained compared with those obtained by Stiles [1953, 1959] tabulated by Wyszecki and Stiles [1982]. In the first set of experiments the wavelength of the adapting field was chosen to be similar to that of the conditioning background and in the second set a variety of different wavelengths were used for the adapting field. The monochromatic fields were produced by placing interference filters of the required spectral transmission properties in the beams of the apparatus. The wedge had been calibrated to find its optical density for the test wavelengths used.

(d) Increment Threshold Measurements

Threshold measurements were made for detection of both flashed, stationary targets and for targets moving at constant velocity. A background field of fixed illumination level, I_b , is provided by channel 2 of the Maxwellian view apparatus and the test stimulus, usually a small circular light target, by placing an appropriate photographic negative in the target slide of channel 1. The threshold program described in section 2.2(a) is used to present the target and to find its threshold illumination as parameters such as I_b or velocity of the target are changed.

(e) Measurement of Time Periods

Experiments reported in Chapter Six required the measurement of the time duration following viewing of a conditioning primary stimulus for which a flashing target was presented until it became visible to the observer. The primary stimulus, a circular uniform field of 30° diameter, was produced by channel 2 and the flashing target was formed by a photographic negative and shutter in channel 1. A program running on the computer set the target to the required illumination level, flashed it for 0.1 second every 1 second, and timed from primary stimulus offset until the flashing target became visible and the observer pressed the reply button.

(f) Critical Fusion Frequency

Measurements were made of the frequency at which the flicker of a small, circular target of illumination I , just disappears. The flickering target was provided by an appropriate photographic negative at OP2 (see figure 2.2) for the circular field and the rotating polaroid apparatus to give flicker with squared-cosinusoidal temporal modulation. For each value of I the flicker

frequency was set to a supra-threshold value for the observer and slowly decreased, by adjusting the potentiometer, until threshold was reached. The observer looked away and then looked back to check that no flicker was visible and from the potentiometer setting flicker fusion frequency was found. For each value of I this process was repeated 3 times and the average value of critical fusion frequency found.

(g) Apparent Motion Experiment

By flashing sequentially two identical targets which are spatially separated in the visual field an illusion of movement from the first flashed target to the second is produced (figure 2.26). This phenomenon is called apparent motion [Wertheimer, 1912]. A program was written for the Maxwellian view system for the presentation of such a stimulus with the direction of apparent motion randomized between presentations. After target presentation the observer indicated the direction of apparent motion by pressing one of the two reply buttons and this result was recorded by the computer, which at the end of the experiment displayed the number of correct responses.

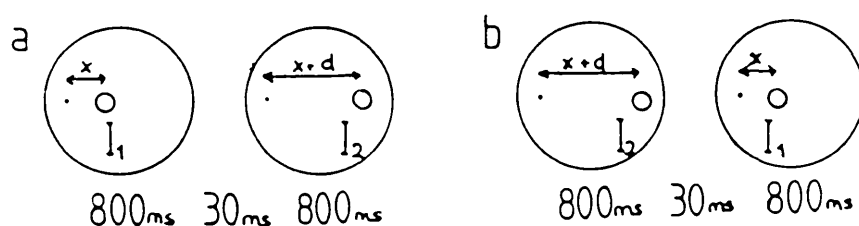


Figure 2.26 Visual field in apparent motion experiment. Motion shown here is in the horizontal direction and in the right half visual field. Targets are of illuminaiton I_1 and I_2 and the fixation point is shown by $\cdot$. The target appears to move (a) to the right from x to $(x + d)$ or (b) to the left from $(x + d)$ to x . Whilst looking at the fixation point the observer is asked to judge whether apparent motion was from left to right or from right to left.

The targets are produced by putting slides with small, circular transmitting areas in channels 2 and 3 and then shutters in these 2 channels control the duration of their presentation. By using a small red LED to provide a fixation point the two stimuli can be presented anywhere in the visual field and by altering the targets' separation the apparent movement can be generated over any chosen displacement. Targets were presented for 800 ms and the gap between presentations was 30 ms, so the separation of targets also controls the apparent velocity of movement.

Blindness for stimuli presented in one half of the visual field is called hemianopia, and when associated with cortical damage is homonymous for the two eyes. Some subjects suffering hemianopia are able to detect and locate moving and flashed targets in their blind field e.g. Barbur, Ruddock and Waterfield [1980] and Blythe, Kennard and Ruddock [1987]. Experiments utilizing stimulus configurations such as that in figure 2.26 have been carried out in order to study the ability of such subjects to detect apparent movement, and their results, which are recorded in Chapter Seven, have been compared with those of normal subjects.

2.3 The Colour Monitor Apparatus

The second set of equipment used in the experiments reported in this thesis is a colour monitor controlled by a microcomputer (Sharp MZ-80B) via a colour graphics board (IO Research, Pluto board). The microcomputer has its own integral monochrome monitor used by the experimenter and attached to it are two floppy disc drives on which programs and data are stored, a printer (Sharp MZ-80P6) used to produce copies of the experimental data, and a reply box. The reply box which is connected to the computer via a universal interface card (MZ-80I02) consists of a metal box with two reply

buttons for use during experiments, a joy-stick, a push button switch and toggle switch (the last 3 items are used in creating new experiments).

This apparatus was used to perform experiments for the measurement of visual discrimination between simple patterns. A program called 'last' written in Z-80 assembly language for speed of execution, was used to carry out these pattern discrimination experiments. On the colour monitor a single target embedded in a background consisting of multiple, identical elements is displayed, none of the targets overlapping (figure 2.27); the various background and target types used are displayed in Figures 2.30 and 2.31. Existing targets saved in data files on one of the discs could be modified, and new targets could be created, by using a part of the program Last called Learn. This part of the program had been specially written to allow the experimenter to draw and amend targets on the screen using the joystick and buttons on the reply box. New targets could be saved onto a floppy disc for use in later experiments. Eight different colours could be used for drawing the targets and each of these colours could have any value between 0 and 255 inclusive for the red, green and blue guns, giving a possibility of 16.7 million different hues. In the experiments of this thesis, only green targets were used and the screen background was black (red, green and blue guns all at zero).

The time elapse between presentation of the pattern and observer response is recorded by the computer and at the end of each set of measurements, the computer displays both the distribution of the response times and the cumulative number of responses as a function of time. The background elements for each experiment, and their number N , were fixed, and the target was one of three different elements (e.g. for orientation ∇ , $\triangleright$ or $\triangleleft$). A single set of measurements uses a block of 100 patterns with each of the three targets being presented on 25 occasions the other 25 being

'null' patterns in which an additional background target was included. The observer responds by pressing one button when a target was detected, and another for 'no target', the latter responses providing a measure of the subject's accuracy. The positions of the target and background elements and the type of target element are chosen randomly by the computer for each presentation. Successive presentations were made immediately following the observer's response and at the end of a set of 100 presentations, the results could be displayed as a time distribution or cumulative response of the probability of detection of the target as a function of time (figure 2.28) up to a limit of 1.5 seconds. Three cumulative response curves are displayed, one for each target type and a fourth curve displays the total number of 'yes' replies to the null target presentation (figure 2.28). A measure of the subject's response was provided by $T_{\frac{1}{2}}$ the time required to obtain 50% probability of detection of the target, this is also shown on figure 2.28.

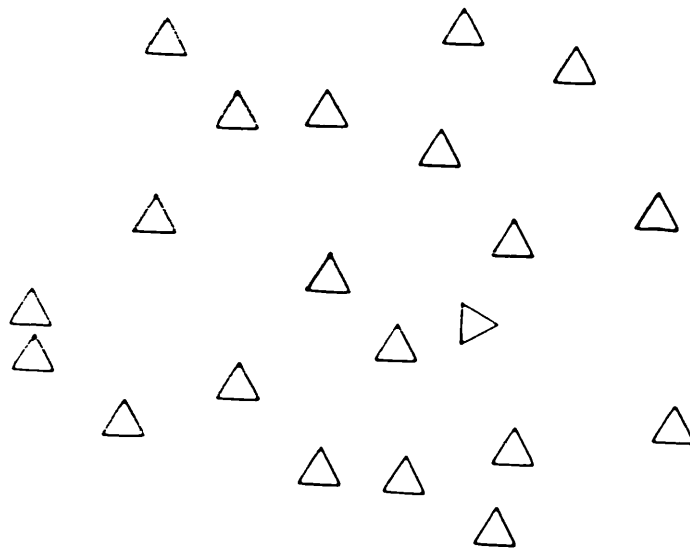


Figure 2.27 Typical visual field configuration used in these experiments.

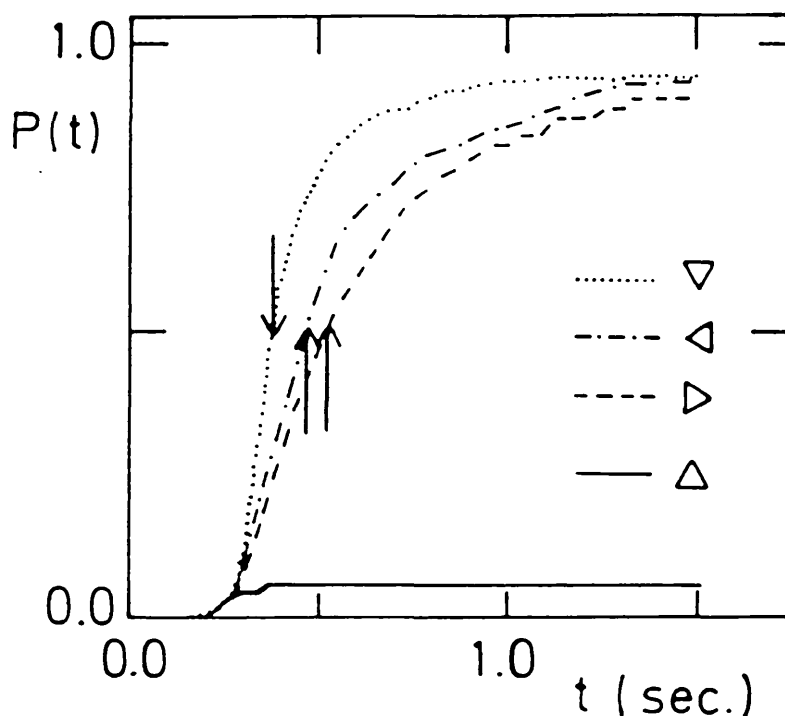


Figure 2.28 Typical graph showing the probability of detection of the target at a particular time. The background element is $\triangle$ and the targets are ∇ , $\triangleright$, $\triangleleft$. The arrows point to $T_{\frac{1}{2}}$ values for the three target types.

The number of 'false positive' for the 'null targets' provided one measure of the subject's accuracy but a further measure is provided by the number of failures in detecting the targets. During an experiment a running total of the number of presentations for each target and the number of these detected by the observer is shown on the microcomputer's integral monitor and the number of targets that the observer failed to detect is noted by the experimenter at the end of an experiment.

This equipment was used for many of the experiments described in Chapter Five. For these experiments the observer was seated 1.9 m from the monitor, which at this distance subtended 8.5° horizontally by 6.3° vertically at

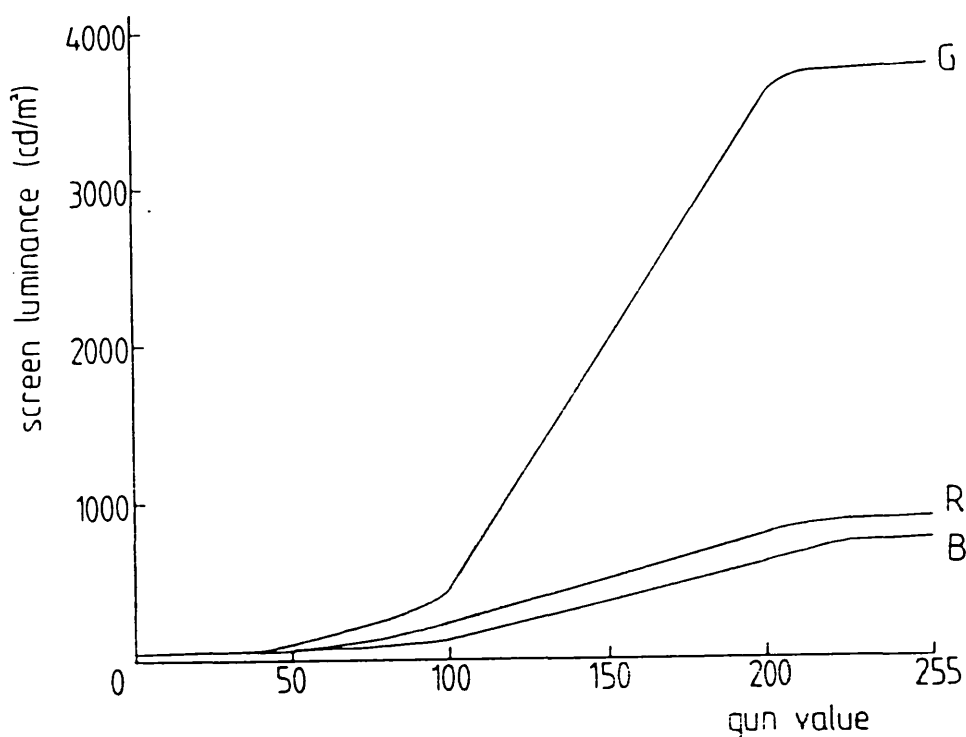


Figure 2.29 Luminance of the screen of the colour monitor versus gun value for each of the three electron guns – red (R), green (G) and blue (B).

the observer's eye. The screen colour was green with C.I.E. co-ordinates $x=0.310$, $y=0.485$. Before each experiment, the observer was instructed as to the nature of the pattern elements and the parameter by which the target could be distinguished and told to scan the field in order to detect the target. On detection of the target, the observer immediately pressed the appropriate reply button. Measurements were made under binocular viewing conditions or with each eye separately, as required by the experiment. In the latter case the 'unused' eye was covered with an eye-patch.

(a) Calibrations of the Apparatus for Luminance

The colour monitor was placed in a darkened room and its screen

calibrated by Dr. V.A. Barbur of Kodak Ltd. using a tele-spectro radiometer (Pritchard Model 1980B). The luminance from a 4 cm diameter circular area in the centre of the screen was measured as a function of the gun value for each of the three electron guns. Each gun could have any integer value between 0 and 255 inclusive and each on its own gave a red, green or blue coloured screen of brightness increasing with the number (from 0 to 255). The scan was done taking measurements at 5 nm steps from 380 to 780 nm. Figure 2.29 shows a graph of screen luminance versus gun value for red, green and blue guns. The green electron gun gave the greatest range of screen luminance and all the background and target elements used in the experiments were green in colour.

(b) 'Dead Time' for Response

One component of reaction time is the period it takes for an observer to spot the target, the other component is the amount of time taken from spotting the target to pressing the reply button. This 'dead-time' was measured for 2 normal observers by displaying a single stimulus and instructing them to press the 'yes' button as soon as they saw the stimulus appear on the screen. The target used was of high contrast and area 0.5 degree^2 and the resulting distribution of responses in time was a sharply tuned Gaussian with a mean of 190 ms, and standard deviation of 20 ms.

Each experiment was normally carried out twice, thus each target type was presented 50 times.

(c) Pattern Elements

The pattern elements used for the experiments of Chapter Five are illustrated in figures 2.30 and 2.31. The patterns used for the background are

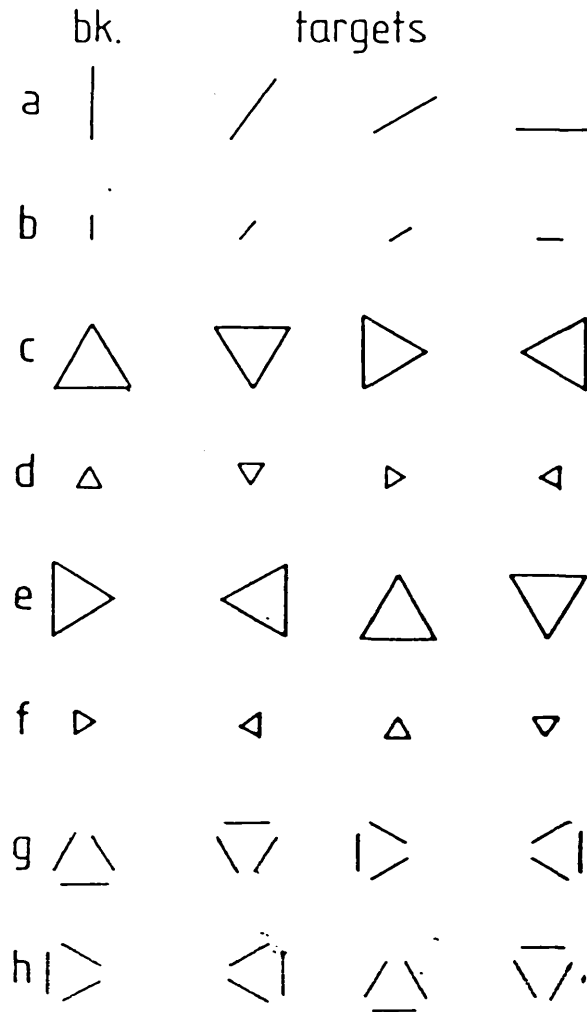


Figure 2.30 Pattern elements used in discrimination experiments on strabismic amblyopes reported in Chapter Five. The background element is the first of each set of four stimuli and the remaining three are the target elements. 40 background elements were used in the experiments.

the first of each row of four patterns, the other three are the targets. The patterns are constructed from point or line elements, except for a few cases in which a textured pattern has been used and they are all simple geometric shapes. The targets differ from their respective backgrounds in orientation, size, texture, brightness or shape.

The targets of figure 2.30 were used to measure the pattern

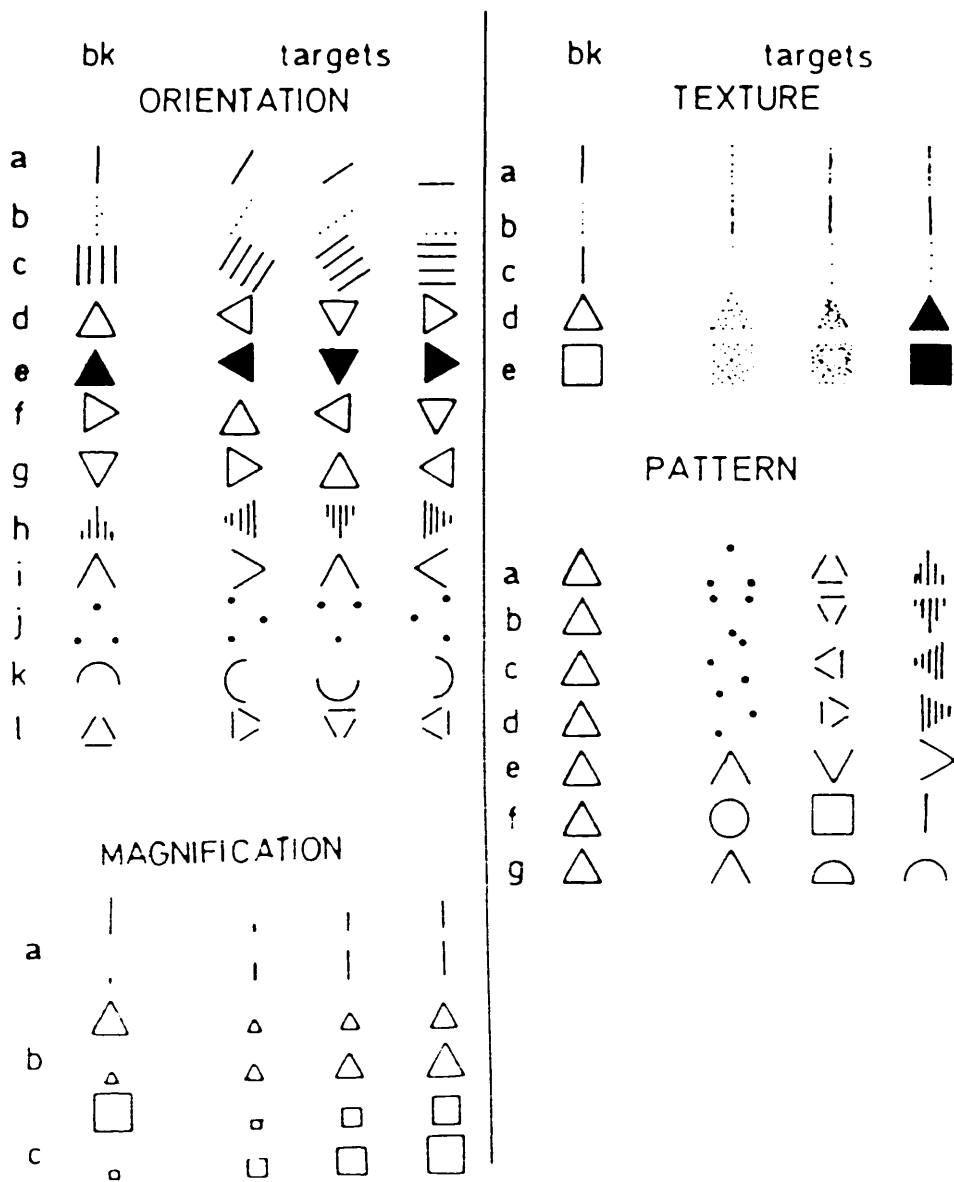


Figure 2.31 Pattern elements used in discrimination experiments on the visual agnosia subject reported in Chapter Five. The first elements of each set of four is the background pattern. The targets differ from the background by the parameters marked above.

discrimination of strabismic amblyopes who have reduced visual acuity which cannot be corrected by refraction. Lines are of width 0.03° . The length of the lines of the larger targets was 1.5° and those of the smaller targets 0.5° .

The targets of figure 2.31 were used to investigate pattern discrimination of a single subject with an unusual visual defect, called visual agnosia, which impairs visual recognition. This latter study required modifications of the standard procedure and these modifications are described in the following section.

2.4 Modification of the Apparatus for Experiments with a Subject Suffering from Visual Agnosia

(a) Timescale

This subject's (H.J.A.) ability to recognize visually displayed objects is very poor [Humphreys and Riddoch, 1984, 1987]. For example he is unable to differentiate between a table mat and a biscuit. His reaction times in the pattern discrimination experiments are much slower than for normal observers. For this reason the program 'Last' was amended to allow collection of data for response times up to 10 seconds as well as the original timescale of 1.5 seconds. Before carrying out an experiment the experimenter chose between the two possible timescales. For all of the experiments except those involving elements of figure 2.31 (a), (b), (c) the longer timescale was used. It was preferable to use the shorter timescale because it yielded better resolution but it did not extend sufficiently for most of H.J.A.'s responses.

(b) Variation of the Number of Background Elements

Using background elements of the size shown in figure 2.31 up to 40 non-overlapping elements can be fitted easily onto the screen. For the very simple single lines, pattern discrimination experiments with H.J.A. were carried out with 40 background elements but for the more complex shapes, he was very slow. In order not to tire the subject the experiments were kept fairly

short. This was done by using only 20 background elements. A set of experiments were carried out to determine the relation between the number of background elements and the response time. Separate experiments were performed with N , the number of background elements equal to 1, 2, 3, 4, 5, 7, 10, 15 and 20.

(c) Measurement of the Number of Errors and Reaction Times as a Function of the Separation of Two Elements

An experiment was carried out to measure H.J.A.'s response times and error rate with a background consisting of 1 element, as a function of the separation of this single background and the target elements (figure 2.31). After each reply, the observer kept the reply button depressed, allowing the experimenter time to measure the distance between the 2 elements, and to note the target type, reaction time and whether the response was correct or not.

All the experiments carried out by H.J.A. were also carried out by a number of normal subjects.

CHAPTER THREE EARLY SPATIAL FILTERING OF NEGATIVE CONTRAST TARGETS

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Using background modulation techniques and a light (positive) contrast target, previous authors [Barbur and Ruddock, 1980a; Holliday and Ruddock, 1983] have characterized fully the responses of two visual channels with two filters, ST1 and ST2, which describe the Spatial and Temporal transmission properties of the channels. A review of the characteristics of these two filters is presented in section 2.2(a). Holliday and Ruddock [1983] associated the ST1 and ST2 filters with pre-cortical neuronal mechanisms, ST1 with X-type neuronal mechanisms and ST2 with Y-type mechanisms. X- and Y-type ganglion cells exhibit 'on' and 'off' centre responses [Enroth-Cugell and Robson, 1966] and it is thought that the responses mentioned above, obtained with light contrast targets, reflect the activity of the 'on' centre cells. In this chapter, ST1 and ST2 responses are obtained with a dark (negative) contrast target with the aims of determining whether the results are similar to those obtained with light contrast targets and of testing for independent activity of filter responses obtained with a light target (called L/ST1, L/ST2) and of filter responses obtained with a dark target (called D/ST1 and D/ST2).

3.1 Experimental Procedure

Exactly the same equipment (the Maxwellian view system) and procedure was used as described in section 2.2(a) except that a dark contrast instead of a light contrast target was used. The experiments were performed monocularly by a number of normal observers with their other eye covered by an eye patch. Their heads were positioned carefully and steadied by biting on a dental impression mounted on a metal blank in a three-dimensional carriage.

The position, in channel 2, of the slide used to produce the background field, was adjusted in order to produce a sharp image on the subject's retina when their eye was relaxed, whatever their visual acuity.

3.2 Results

(a) ST1 Spatial Response

To obtain this spatial response the background used consisted of a one-dimensional, periodic, square-wave grating with bars of width d (i.e. with a fundamental spatial frequency of $(2d)^{-1}$) as depicted in figure 2.10. Figure 3.1 shows threshold illumination, I_t , for detection of a 3.5° diameter, circular target, plotted against the value of $(2d)^{-1}$. The target moved at 15 degrees/second across the central 8° of the 17° diameter background. The spatial average illumination of the background, $\log I_b$, was $1.4 \log td$. throughout, and the threshold illumination for detection of the target against a spatially uniform background of this illumination level corresponds to the value for an unresolved grating of spatial frequency 40 cycles/degree. The graph shows that the threshold for target detection by each of the four subjects is raised above its threshold on a uniform background by backgrounds of spatial frequencies in the range 1 to 10 cycles/degree, and for all four observers the maximum increase in threshold occurs for spatial frequencies between 4 and 5 cycles/degree. The amplitude of the effect, defined as the difference between the maximum value of $\log I_t$ and its value for a uniform field, is about 0.5 log units. A similar amplitude and peak position was found by Barbur and Ruddock [1980a] using a light contrast target and a typical ST1 response found by them for $\log I_b = 1.4 \log td$. is illustrated in figure 2.14.

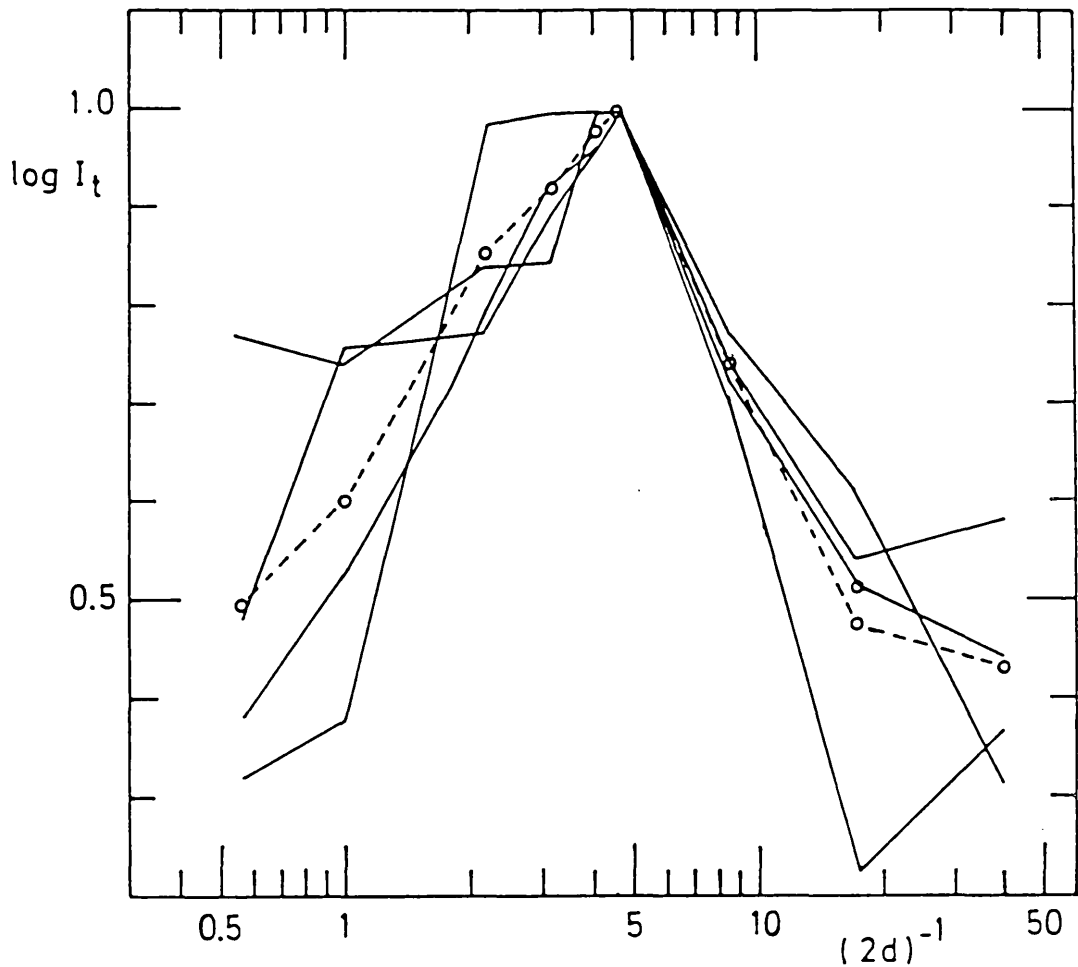


Figure 3.1 The ST1 spatial response obtained with a 3.5° diameter, circular, dark target moving at 15 degrees/second across the central 8° of a 17° diameter, 100%, spatially modulated, grating background of mean illumination 1.4 log td. (the field of view is illustrated in figure 2.10). Data for four observers and their average data ($\circ$ --- $\circ$ data points) are shown normalized to a peak value of $\log I_t = 1$. The standard deviation for the mean data is between 0 and 0.2 log units.

The effect of background illumination

The ST1 response was measured for one observer with the same target and background configuration as above (figure 3.1) but for a range of

background illuminations, I_b , between 1.1 log td. and 2.6 log td., and the data plotted in figure 3.2. For each of the background illuminations the ST1 response peaks around a spatial frequency of 3 to 5 cycles/degree and the amplitude (i.e. the difference in log I_t values between the peak and that at 40 cycles/degree) is of the order of 0.5 log units. A similar result was found by Barbur and Ruddock [1980] using a light contrast target, and in that case the peak amplitude was around 0.4 log units for all backgrounds brighter than 1 log td. They also found a second spatial response with a peak at 8 to 10 cycles/degree rather than 4 to 5 cycles/degree for mean background illuminations above 2 log td., and this is not observed with the dark contrast target. The reason for this difference is uncertain, but it cannot be concluded that there is a difference between the responses with light and dark contrast targets. In subsequent experiments the high frequency response has not been found for all subjects and in any case, the present experiments were restricted to $I_b \leq 2.6$ log td. The responses (figure 3.2) show broader, flatter peaks for $\log I_b > 2$ log td. as though both 'high' and 'low' spatial frequency functions are influencing them.

At higher illumination levels (greater than 2 log td.) the low frequency wing has lower threshold illumination values, log I_t , than the uniform field, for detection of the dark target. This was also found by Barbur and Ruddock [1980a] who suggested that with high contrast, spatially coarse gratings, uniform adaptation is not achieved over all the visual field so that, in this case, the dark target is detected when moving over the wide light bars.

The effect of retinal position

The ST1 spatial response was determined at non-foveal positions in the field. The same target and background configuration as that shown in figure

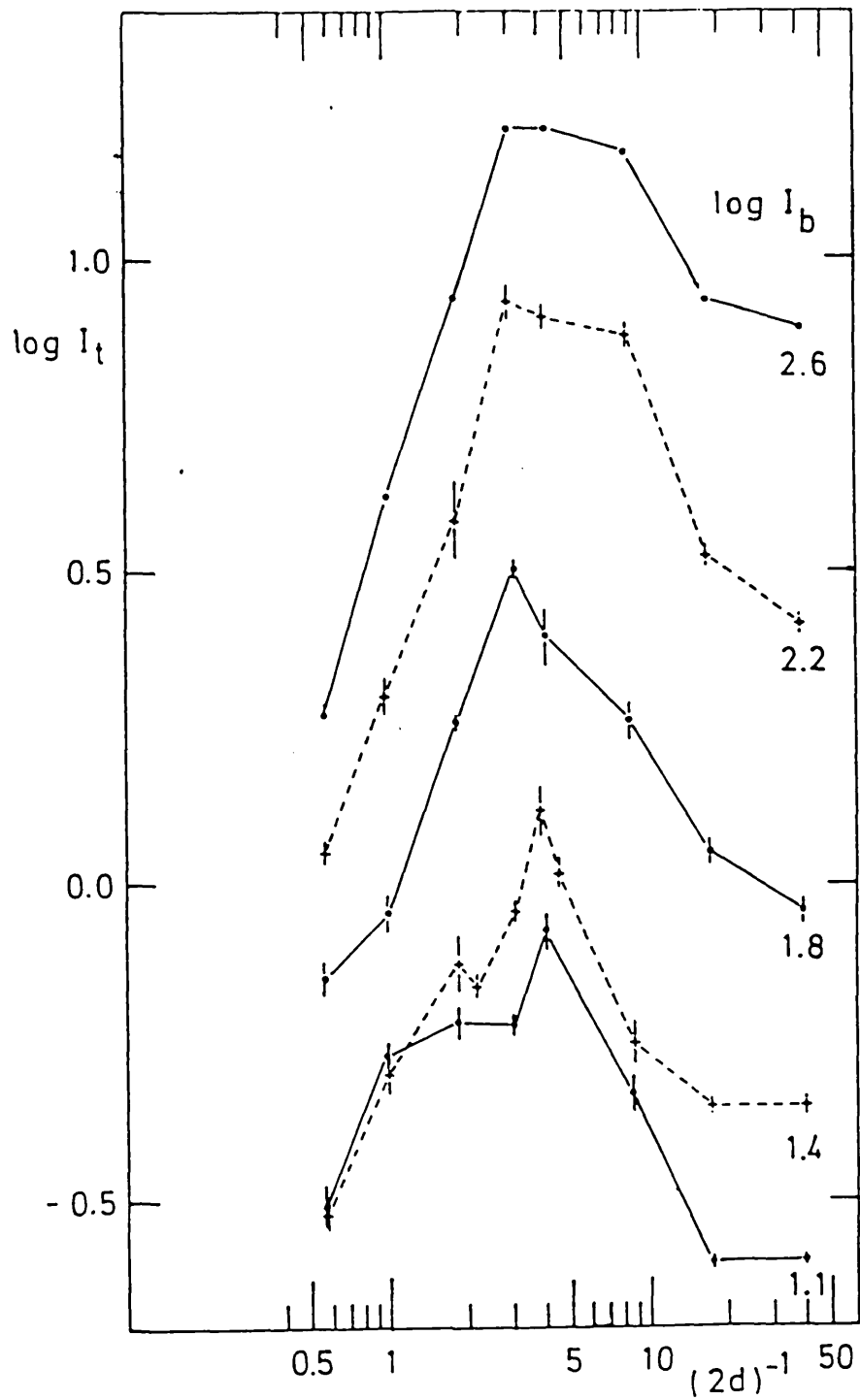


Figure 3.2 ST1 spatial responses obtained for one observer with the same target and background configuration as figure 3.1 but for a range of background illuminations. The background illumination is marked beside each curve and standard errors are plotted for each point.

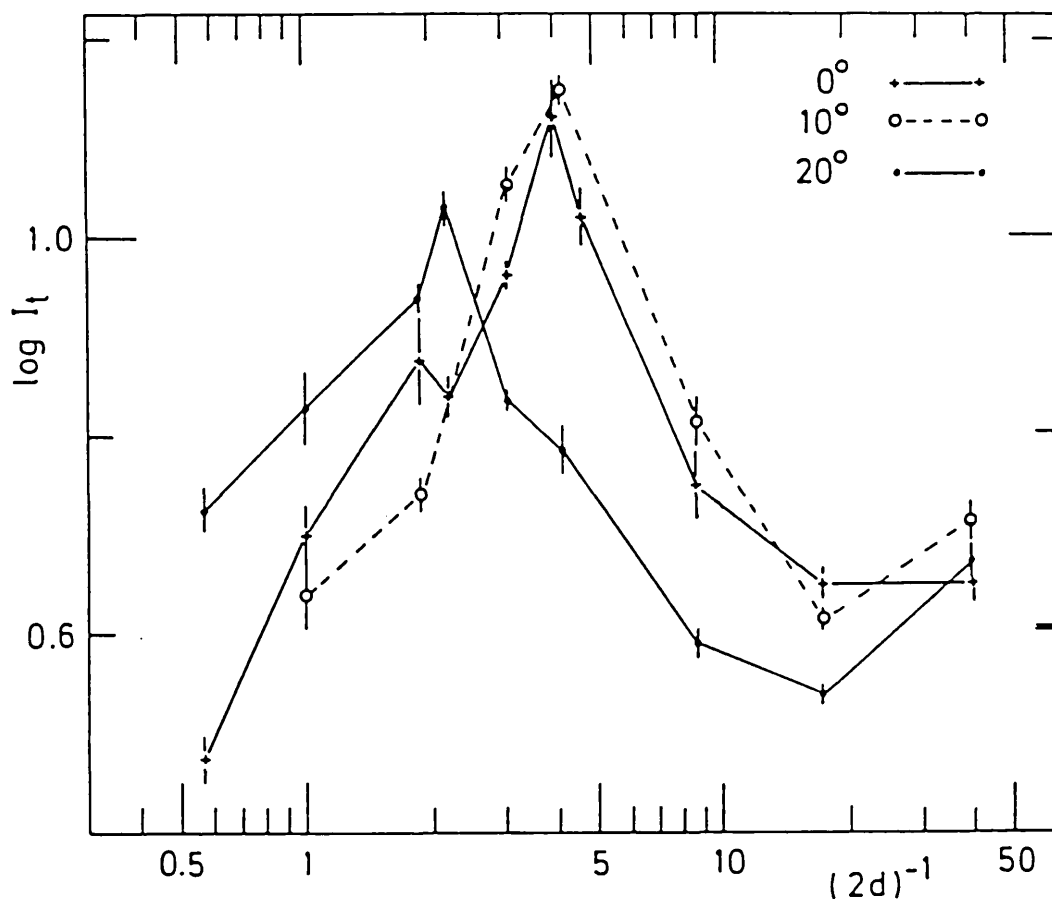


Figure 3.3 The variation of the ST1 spatial response with eccentricity. The same target/background configuration as described in figure 3.1 was used except a small, red fixation point was provided and mean background illumination was 1.3 log td. + data points for foveal presentation; o for target/background stimulus presentation 10° temporally and • for stimulus presentation 20° nasally. Standard errors are plotted at each data point. Subject J.B.

3.1 was used except that a red light emitting diode (LED) was used to provide a small fixation point for the observer throughout the experiment. The visual angle between the fixation point and centre of the background field is taken as a measure of the eccentricity of presentation of the target, and data were obtained at 0°, 10° on the nasal retina and 20° on the temporal retina (temporal retina to avoid the blindspot). Figure 3.3 shows data for observer J.B.. The curves all have a similar shape and the position of maximum

target threshold for presentation at 0° and 10° eccentricity is at 4 cycles/degree and the amplitude of the effect is 0.45 log units whilst that for presentation at 20° eccentricity peaks at 2 cycles/degree and its amplitude is slightly smaller, 0.4 log units. Barbur and Ruddock [1980a] also found a shift in the peak of the response for a light contrast target to lower spatial frequencies with increasing retinal eccentricity tested and at 30° eccentricity the peak was at 1 to 2 cycles/degree.

The orientation of the background grating

All the experiments reported so far were obtained with vertically orientated gratings with the target moving horizontally across the bars. Measurements were also made with the gratings orientated horizontally and the target moving parallel to the bars. Data obtained for observer J.B. with an identical target/background configuration to that described in figure 3.1, except that the grating was orientated horizontally, are plotted in figure 3.4. There is no significant difference in the ST1 spatial responses for the two background grating orientations indicating that the response mechanism which mediates this response for the dark contrast target has non-orientated, circularly symmetric, receptive fields. Barbur and Ruddock [1980a] found a similar result for the mechanism detecting a light contrast target and also obtained the ST1 spatial response with non-orientated backgrounds such as matrices of spots and chequer-board patterns demonstrating further the absence of orientation selectivity in the response.

No study was made of the effect of varying target parameters since they had little effect on the ST1 spatial response obtained with a light target. Barbur and Ruddock [1980a] found that the amplitude of the effect increased linearly with increasing background contrast and this enabled them to use

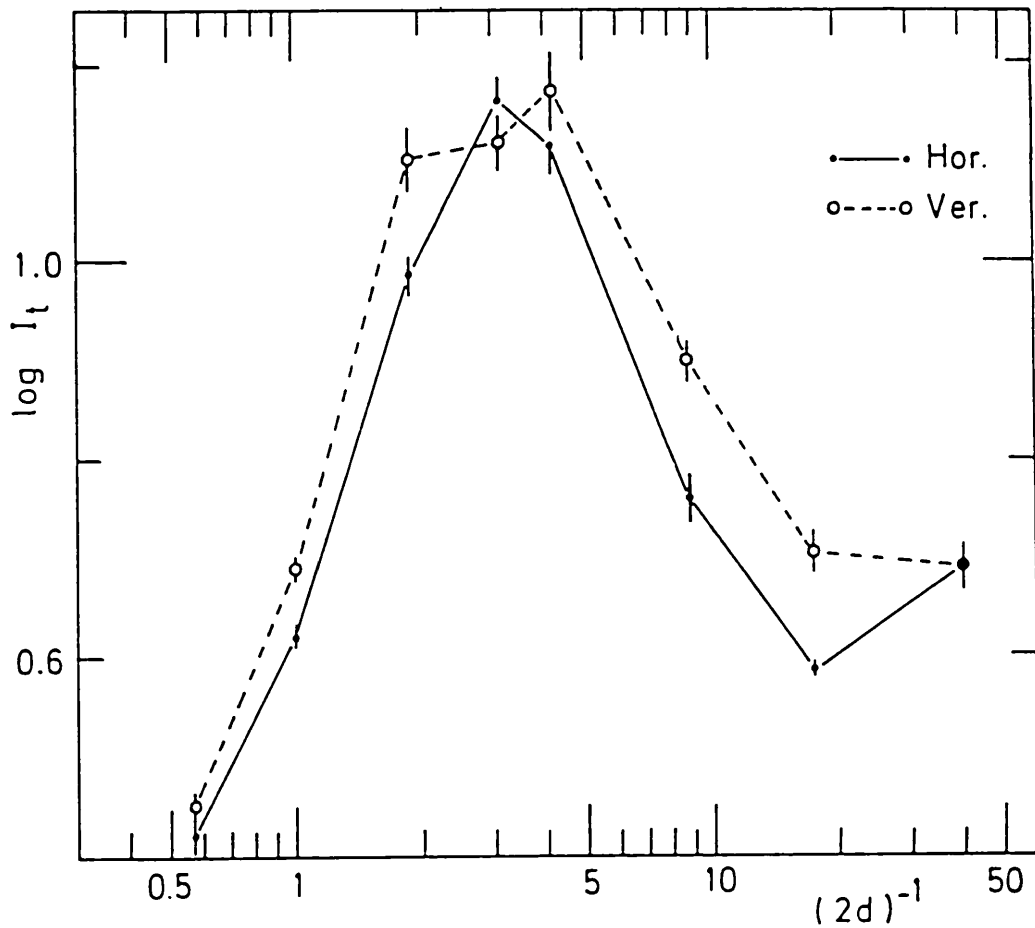


Figure 3.4 ST1 spatial responses obtained with the grating bars parallel (● data points) and perpendicular (○ data points) to the direction of the target movement. The target/background configuration was the same as that described in figure 3.1 and the mean background illumination, $\log I_b$, 1.4 log td. Standard errors are shown with each data point.

transform methods to calculate the receptive field distribution for the ST1 mechanism. The new experiments described above (figures 3.1 to 3.4) used background fields of 100% contrast and they all had amplitudes similar to those obtained with a light contrast target and 100% contrast background. The new results (figures 3.1 to 3.4) are sufficient to establish that the spatial filter obtained with a dark contrast target has the same response characteristics as for a light contrast target [Barbur and Ruddock, 1980a]. The mechanism

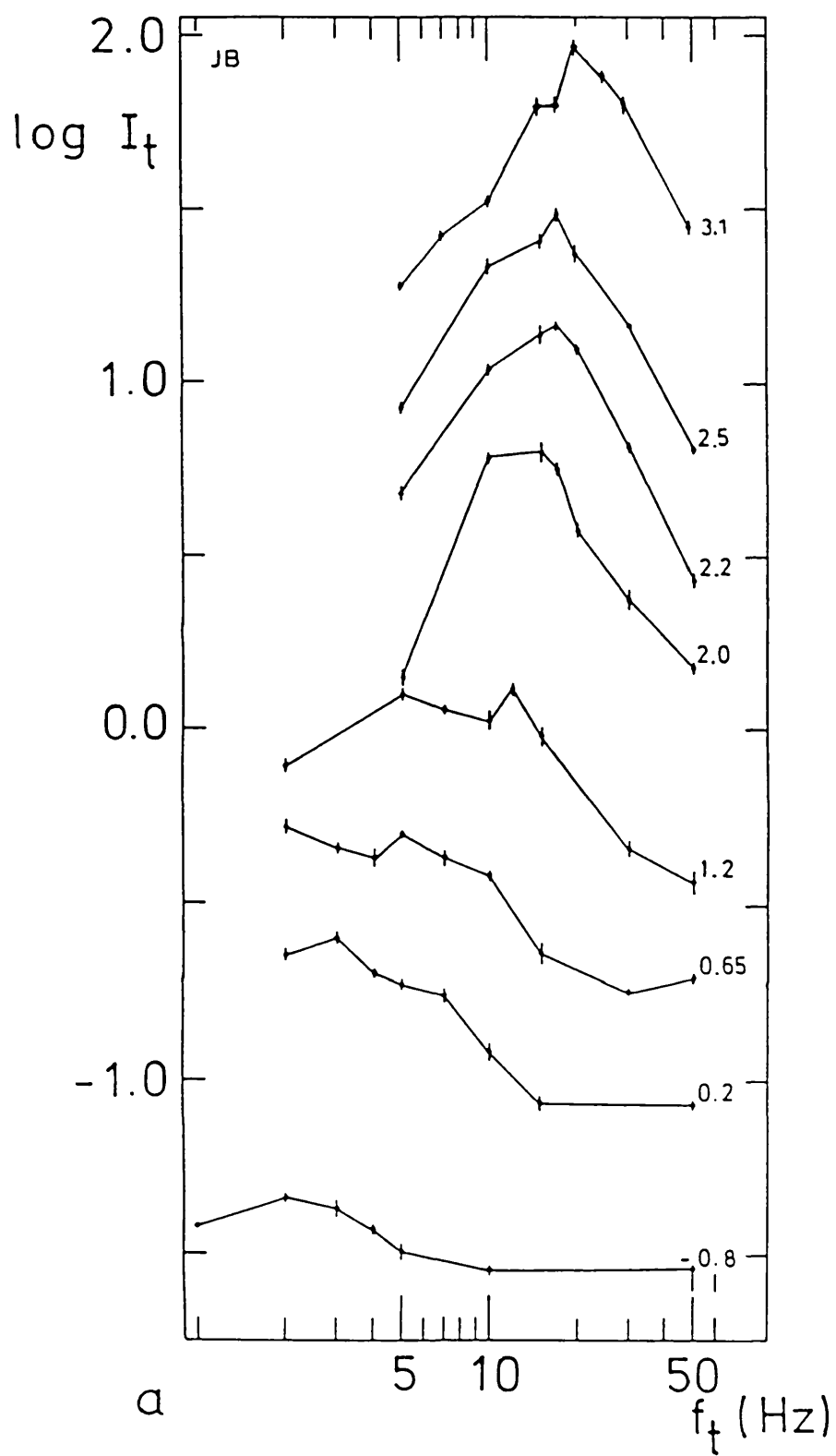
which mediates the response is non-orientation selective, and the spatial organisation computed for light contrast target is centre-surround antagonistic, as illustrated in figure 2.18.

(b) ST1 Temporal Response

The ST1 temporal response was not determined for dark contrast targets. It is experimentally difficult to produce the alternating grating background (figure 2.11) especially when using fine gratings. Experimentally, this response is closely related to the ST2 temporal response, the ST2 temporal response being obtained by subtracting pairs of inputs from ST1 temporal units with a time delay between them or preferably, by introduction of low frequency filtering of the negative component. These two methods of deriving the ST2 responses are represented, respectively, by the filter networks of Holliday and Ruddock [1983] and Skinner, Ruddock and Wilson [1985]. The ST2 temporal response can be determined much more easily than the ST1 response, and because the two are closely related, it was considered sufficient to measure only the former.

(c) ST2 Temporal Response

To obtain the ST2 temporal response a 17° diameter, temporally modulated, but spatially uniform background is required (figure 2.13) and threshold illumination, $\log I_t$, for detection of a 3.5° diameter, dark contrast target moving at 15 degrees/second across the central 8° , was measured as a function of the temporal modulation frequency, f_t . Data for four observers are plotted in figure 3.5, and refer to a range of background illuminations. The results yield band pass tuning curves for background illuminations down to 1 log td. Thresholds for the target presented on backgrounds flickering at low



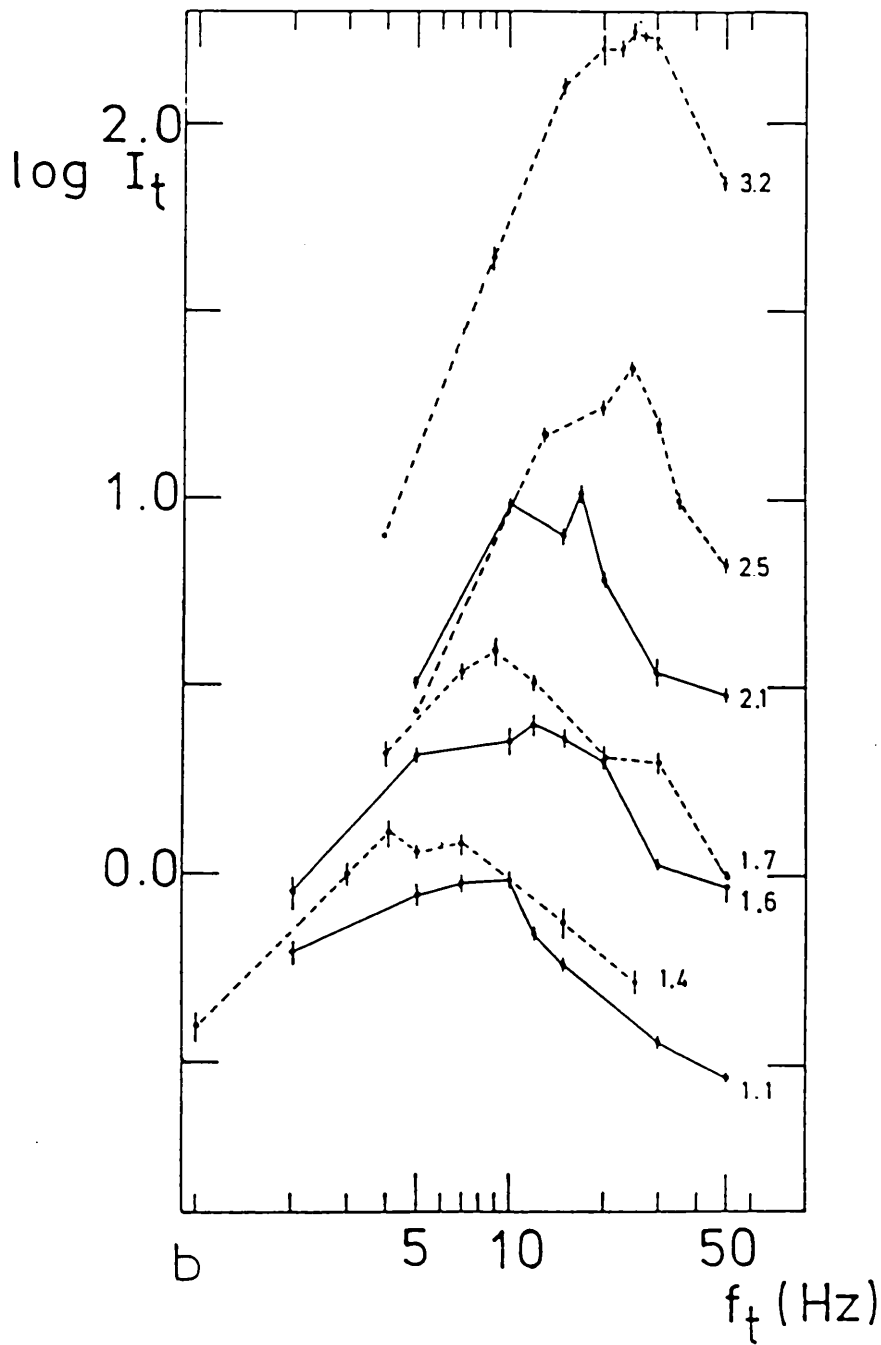


Figure 3.5 The ST2 temporal response obtained with a 3.5° diameter, circular, dark contrast target moving at 15 degrees/second across the central 8° of a 17° diameter, 100% temporally modulated background field. Threshold illumination, $\log I_t$, for the target is plotted as a function of the flicker frequency for a number of different background illumination levels, $\log I_b$. (a) Data for one observer, $\log I_b$ is marked by each graph. (b) Data for three observers; W.A., S.H.W. and J.M. $\log I_b$ is marked by each graph. The standard error is plotted for each point.

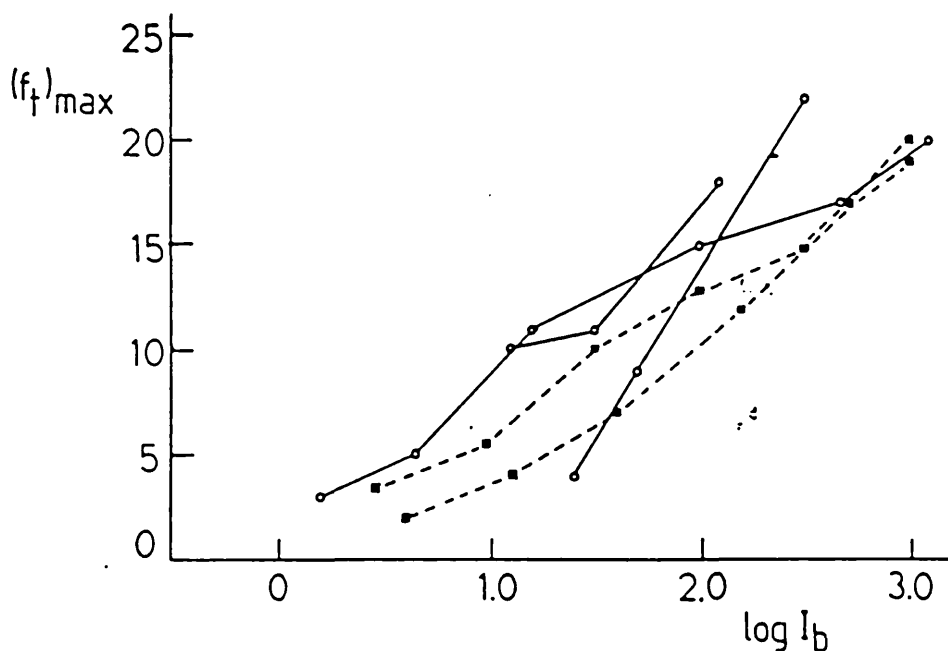


Figure 3.6 The frequency, $(f_t)_{\max}$, at which the ST2 temporal curves peak, plotted against the value, $\log I_b$, at which the curve was obtained. $\circ-\circ$ data points for a dark contrast target for three observers from figure 3.5; $\blacksquare-\blacksquare$ data points for a light contrast target for two observers, data taken from the paper by Holliday and Ruddock [1983].

temporal frequencies or frequencies approaching and greater than the flicker fusion frequency are unchanged from that obtained when the target is presented on a uniform field of the same mean luminance, but for intermediate flicker frequencies the target threshold is raised. The peak value of $\log I_t$ shifts progressively to higher frequencies as the background illumination increases while the amplitude of the effect, defined as the difference between the maximum value of $\log I_t$ and that obtained with an unmodulated uniform field, is constant, around 0.6 log units, at least for background illuminations greater than 1 log td. For background illumination levels below 1 log td. (figure 3.5(a)) the tuning curves are not so clearly band-pass in shape and have smaller amplitudes. Curves similar to those

shown in figure 3.5 were obtained for a light contrast target [Holliday and Ruddock, 1983]. Figure 2.16 shows one of a set of typical curves obtained with a light contrast target which peaks at a frequency and an amplitude similar to those obtained with a dark target at the same background illumination. The similar responses obtained with either target contrast is further demonstrated by figure 3.6 where the temporal frequency, $(f_t)_{\max}$ at which $\log I_t$ peaks is plotted against the background illumination. The variation with background illumination of $(f_t)_{\max}$ is similar for both contrast polarities.

Figures 3.5 and 3.6 demonstrate that similar ST2 temporal responses are obtained with light or dark contrast targets and as explained above, it is inferred that this also applies to the ST1 temporal response.

(d) The ST2 Spatial Response

This is obtained by measuring threshold illumination for detection of a 3.5° diameter, dark contrast target moving across the central 8.0° of a 17° diameter background field consisting of bars which are alternately steady and flickering with constant time average illumination over the whole field (see figure 2.12). The spatial modulation therefore occurs only because of the temporal flicker. The results for observer J.B. are shown in figure 3.7, and were obtained with flickering bars of modulation frequency 17Hz corresponding to the frequency $(f_t)_{\max}$ for maximum threshold elevation at that background illumination level ($2.5 \log \text{td.}$) (see figure 3.5(a)). The band-pass response has a maximum value of $\log I_t$ at a background spatial frequency of 1 cycle/degree. A similar result was obtained by Holliday and Ruddock [1983] (see figure 2.17), for light contrast targets, and their data were essentially independent of background illuminations in the range -0.5 to $2.7 \log \text{td.}$ The amplitude of the response is about 0.5 log units for either target contrast

[Holliday and Ruddock, 1983].

The responses described above (figures 3.1 to 3.7) show that the characteristics of the ST1 and ST2 filters determined with dark contrast target are closely similar to those obtained with a light contrast target [Barbur and Ruddock, 1980a; Holliday and Ruddock, 1983]

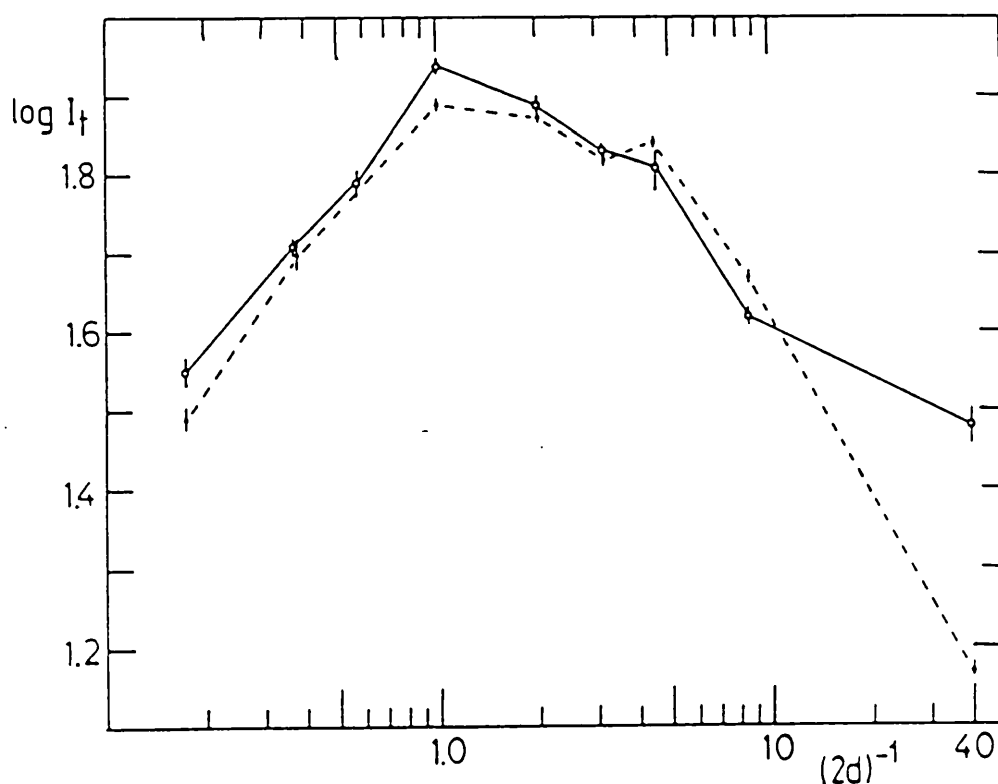


Figure 3.7 ST2 spatial response obtained with a 3.5° diameter dark contrast target moving at 15 degrees/second across the central 8° of a 17° diameter background of the type illustrated in figure 2.12. The mean background illumination was 2.5 log td. and alternate bars flickered at 17 Hz, the frequency which gave maximum elevation of threshold for the observer J.B. for this value of I_b in figure 3.5. O data points, J.B. and • data points, H.A. Standard errors are plotted at each point.

3.3 Experiments with New Background Stimuli

The experiments based on threshold perturbation techniques and described in the previous section show that the mechanisms which mediate

detection of dark contrast targets have characteristics very similar to those of the mechanisms which mediate detection of light contrast targets. The question raised by these experiments is – " Is it the same ST1 and ST2 mechanisms which mediate detection of both light and dark contrast targets, or are there two independent sets of mechanisms one for detection of each target polarity? If the second is correct, do the two mechanisms act independently?" Electrophysiology suggests that dark and light contrast targets are handled by separate 'on' and 'off' centre mechanisms, which act independently of each other and it is tempting to associate the ST1 and ST2 responses obtained with a dark contrast target and those obtained with a light contrast target with 'on' and 'off' centre ganglion cells respectively.

(a) Experimental Procedure

The experiments to be described were designed to test for independent action of the ST1 mechanisms sensitive to dark and light targets. To do this, new background stimuli were constructed which still provided a spatially modulated background field, but with the light and dark bars no longer of equal width. If the two mechanisms act independently, the responses of that detecting light contrast targets (called the L/ST1 mechanism) should be affected only by the variations of the widths of the light bars and not that of the dark bars, and vice versa for the mechanism detecting dark contrast targets (called D/ST1).

Two sets of differently spatially modulated backgrounds were used in these experiments, A and B.

Background Type A. The background field had constant periodicity of 4 cycles/degree, chosen because the peak of the ST1 spatial response occurs at this frequency, and the width, l , of the light bars and that, d , of the dark

bars were varied (figure 3.8). Thus $(l+d)$ is constant and the periodicity of the gratings is $(l+d)^{-1}$ and the ratio $R = l/d$ varied for each grating from 0.1 to 7.0 with the narrowest bar width subtending 0.02° and the broadest 0.21°

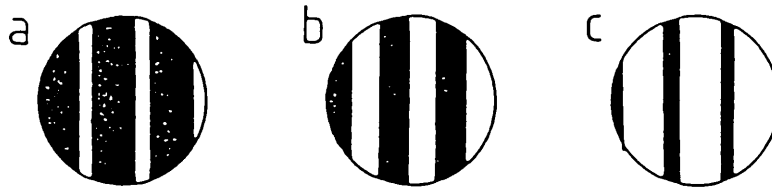


Figure 3.8 Diagram showing three typical fields of view of background type A where $l+d=\text{constant}$ but $l/d = R$ varies. All three have the same mean illumination level.

- (a) $l/d < \text{one}$; light bars are brighter than in (b)
- (b) $l/d = \text{one}$
- (c) $l/d > \text{one}$; light bars are dimmer than in (b).

The background fields were 100% spatially modulated and they were all of the same mean illumination level. This was achieved by varying the illumination of the light bars and keeping the dark bars at 0 log td. For the background field shown in figure 3.8 the light bars are brightest for (a) and dimmest for (c).

Background Type B. In this case one component e.g. the dark bars of the background were of constant width, whilst the other e.g. the light bars, were varied for different measurements. This yields two sets of grating structures, one in which the widths of light bars are varied whilst those of the dark bars are constant, and another in which the dark bars' width is varied whilst the light bars' width is constant. Typical fields of view provided by these two sets are illustrated in figure 3.9. All the background fields were 100% spatially

modulated and of the same mean illumination level. This was achieved by varying the illumination of the light bars whilst keeping that of the dark bars as 0 log td. When the light bars of a particular field were narrower than the dark bars (figure 3.9(a) first picture and (b) last picture) their illumination was greater than the light bars of a background field where the bars were of equal width (figure 3.9(a) and (b) middle pictures). When the light bars of a particular background were wider than the dark bars (figure 3.9(a) last picture and (b) first picture) their illumination was correspondingly lower.

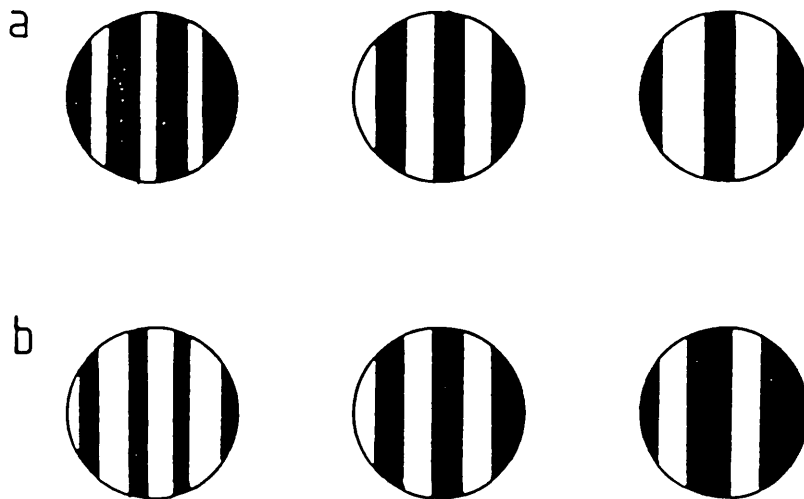


Figure 3.9 Spatially modulated background fields provided by gratings of type B with one bar width constant and the other bar width varying.

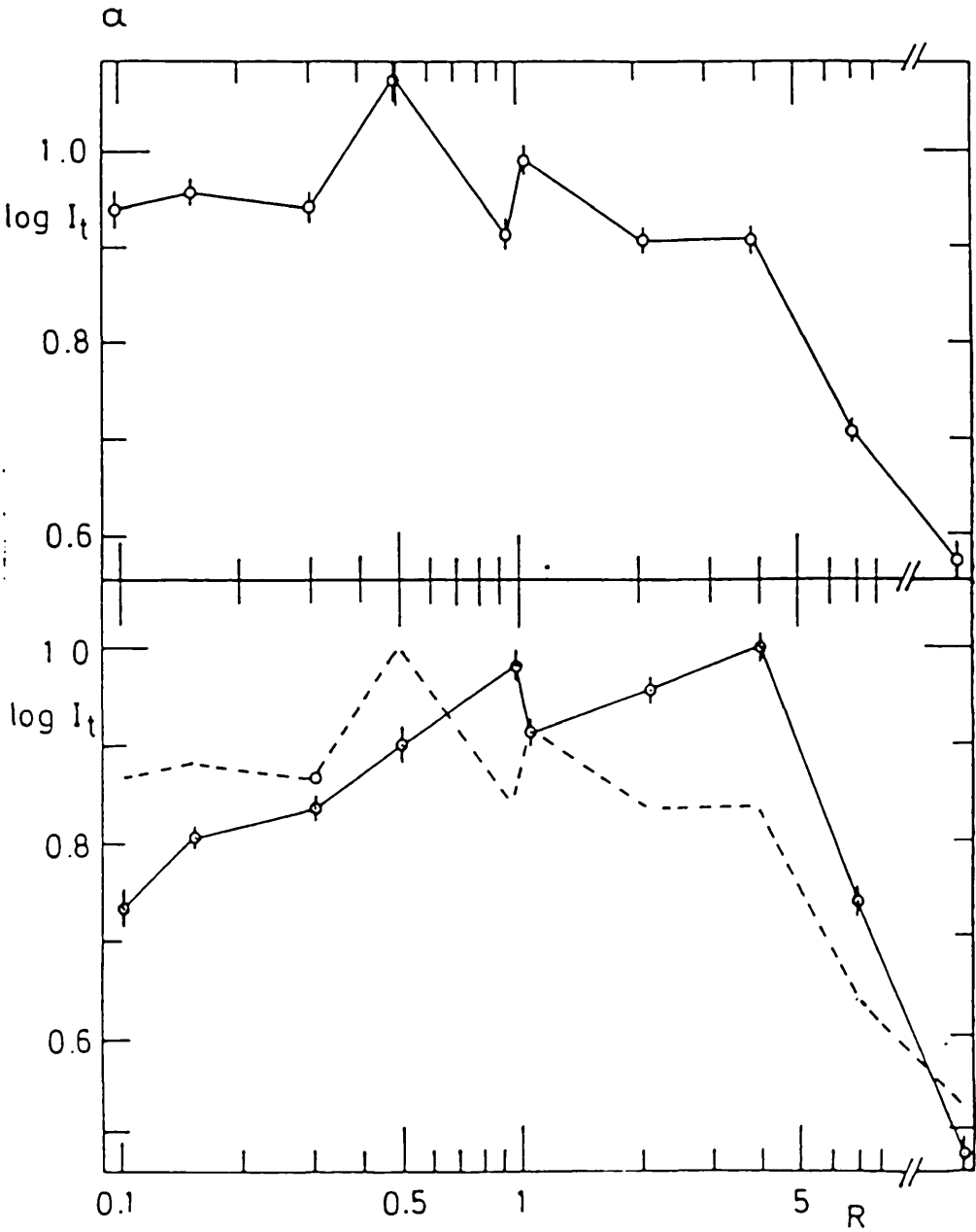
- (a) light bar width varying, dark bar width constant.
- (b) dark bar width varying, light bar width constant.

Threshold illuminations were determined for detection of both light and dark targets moving across these spatially modulated backgrounds.

(a) Experiments for Background Type A

The data obtained with these backgrounds are plotted in figure 3.10.

For each of the observers separate graphs are plotted for the light and dark targets and on each graph the threshold illumination, $\log I_t$, is plotted as a function of the ratio, R , of light bar width to dark bar width. The graphs obtained are broad and have no clear peak, in contrast to those normally



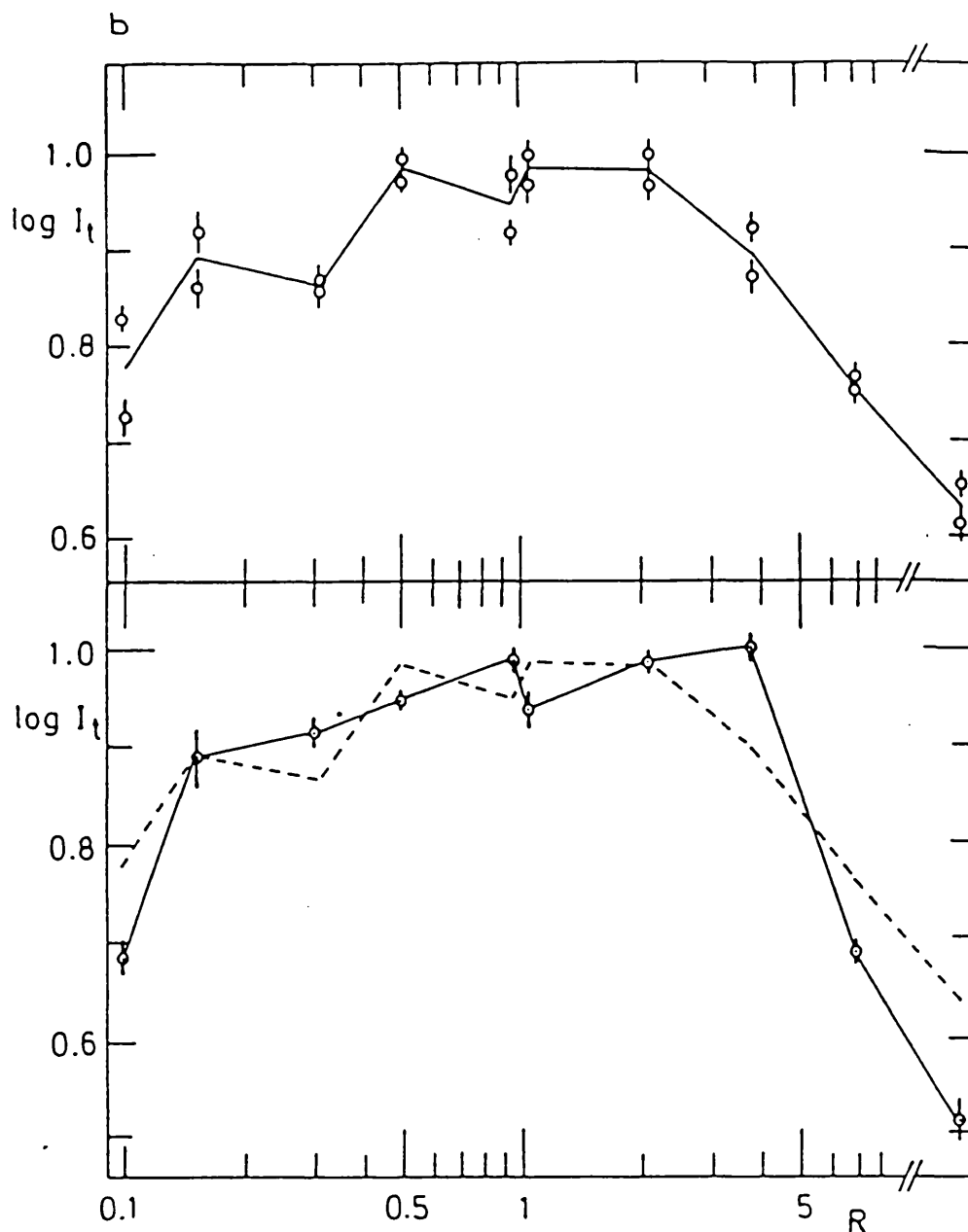
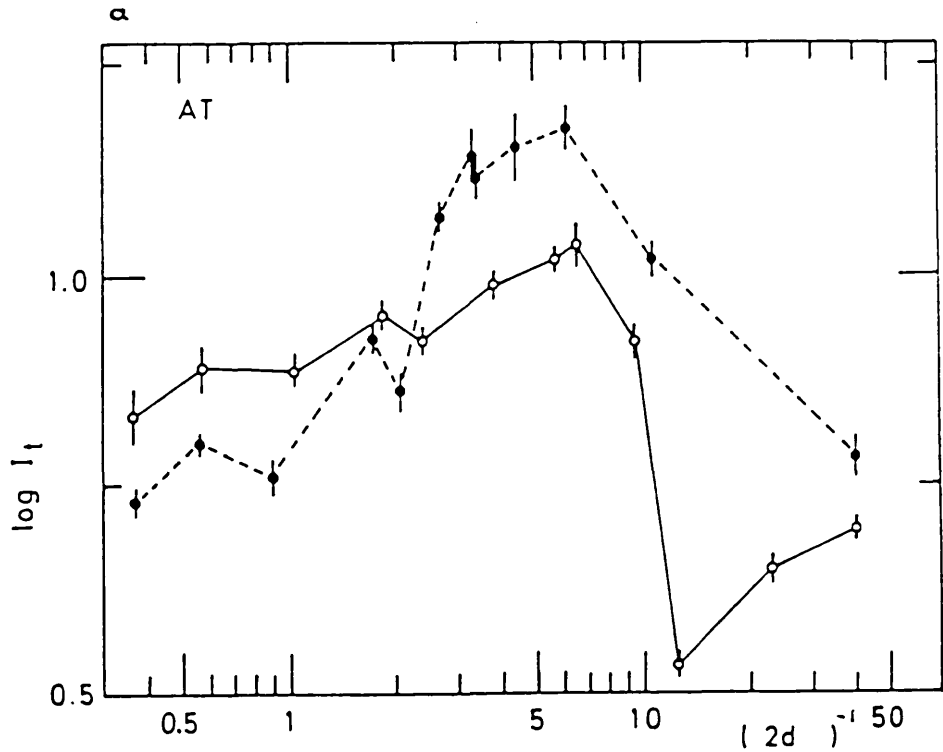


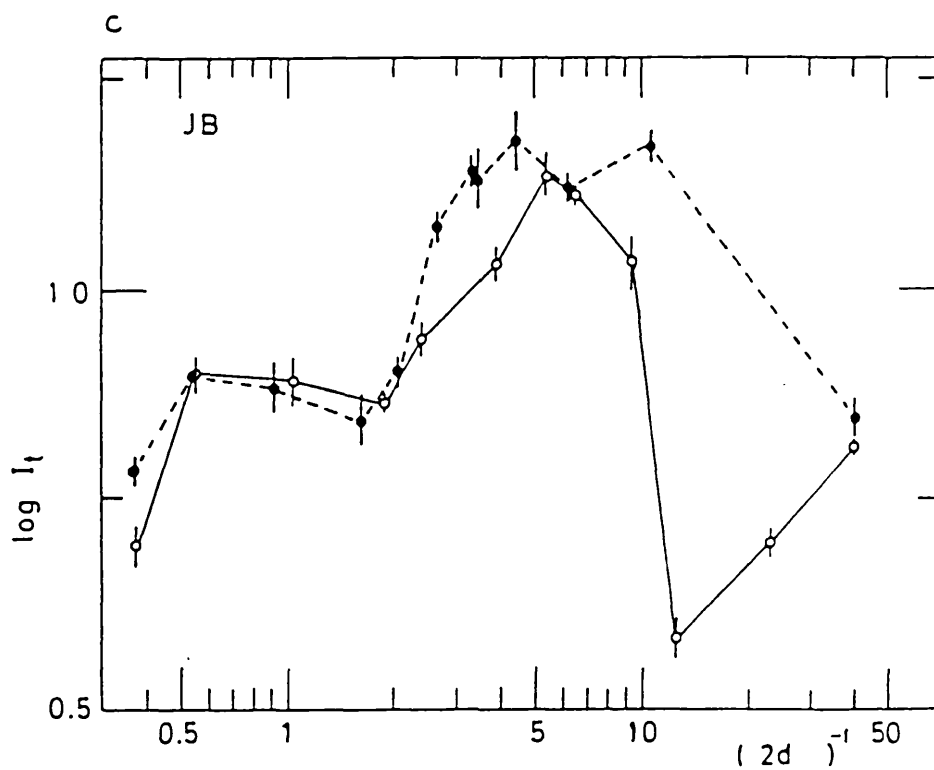
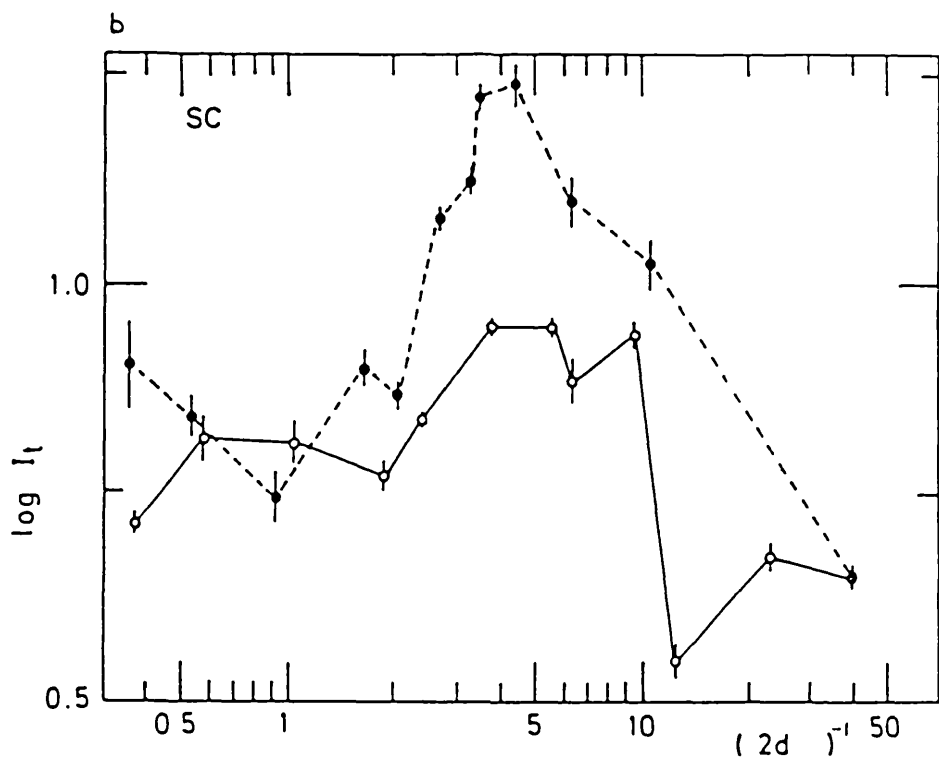
Figure 3.10 The threshold illumination, $\log I_t$, for detection of a 3.5° diameter target moving at 15 degrees/second across the central 8° of a 17° diameter, spatially modulated background field of type A (figure 3.8), plotted as function of the ratio, $R = l/d$. $\log I_b = 1.4 \log t_d$. (a) Data obtained for observer A.J.; the top graph was obtained using a light target and the bottom one using a dark target (the data obtained with the light target is also plotted, with a broken line, on the bottom graph). (b) as for (a) but data obtained for observer JB. Each data point is the mean of 16 determinations of $\log I_t$. Standard errors are of the order of 0.01 for each point.

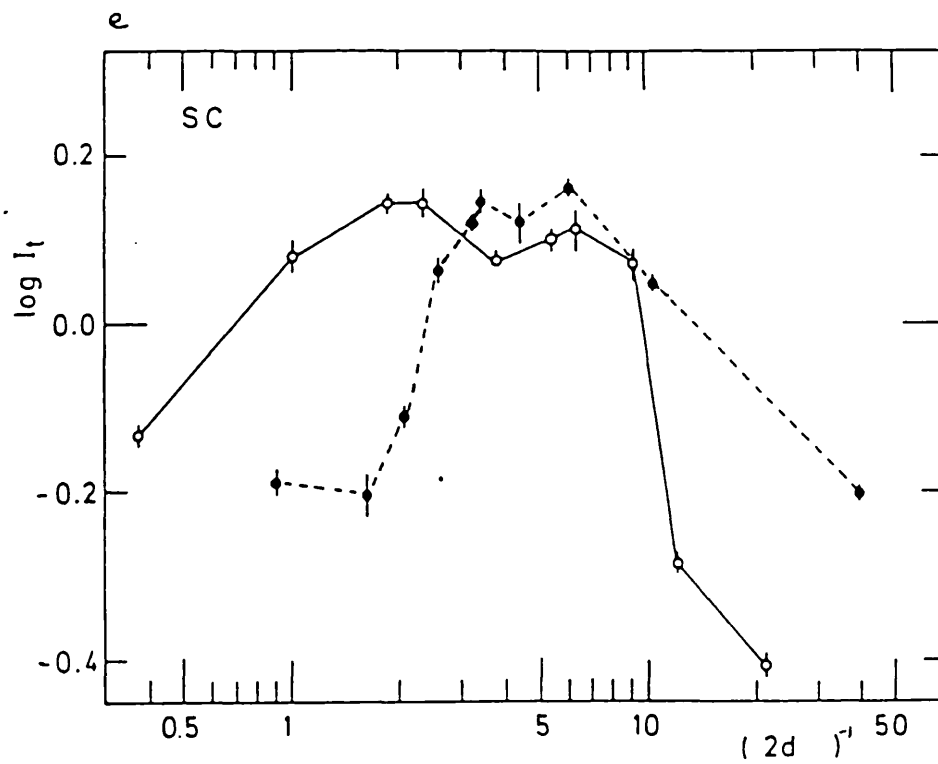
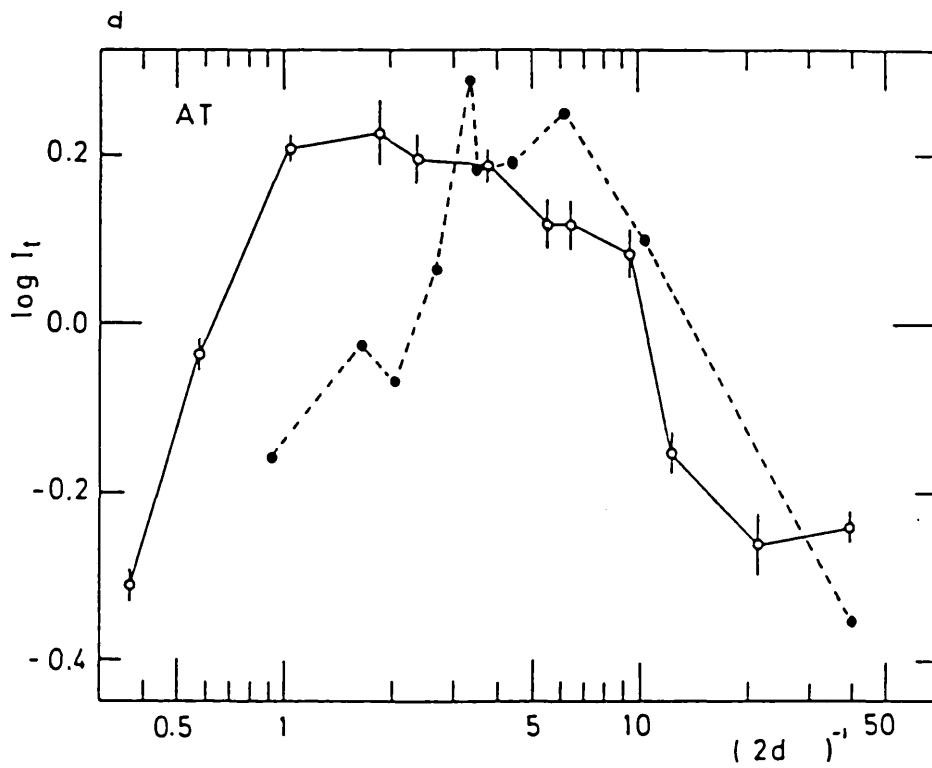
associated with the ST1 mechanism (figure 2.14 and figure 3.1) which peaks around 4 cycles/degree (equivalent to $R=1$ on figure 3.10). The graphs obtained with the light and with the dark targets are similar in shape to each other.

(c) Experiments for Background Structure B

Data were obtained for three observers with these backgrounds (figure 3.9) and they are plotted in figure 3.11. As there were two sets of background structure, (one with light bar width varying and dark bar width constant, and the other with light bar width constant and dark bar width varying) and two different targets, there are four curves for each observer. $\log I_t$ is plotted against $(2d)^{-1}$, where d is the width of the variable bar component. In figure 3.12 the average data for all three observers for the light and dark targets separately are plotted, this time as a function of the periodicity of the background grating i.e $(1+d)^{-1}$







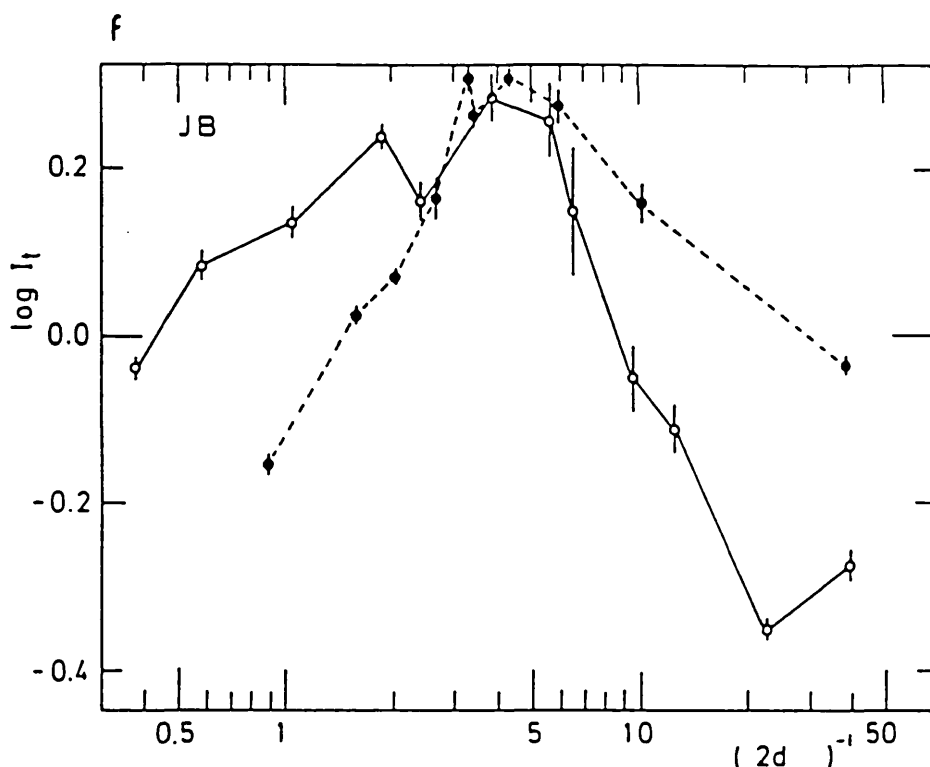


Figure 3.11 The threshold illumination, $\log I_t$, for detection of a 3.5° diameter target moving at 15 degrees/second across the central 8° of a 17° diameter spatially modulated background field of type B (figure 3.9). $\log I_t$ is plotted as a function of $(2 \times \text{variable bar width})^{-1}$; the spatial frequency of a grating consisting of bars of the variable width only. $\log I_b = 1.2 \log t_d$. (a), (b) and (c) Data for three observers obtained with a light target. (d), (e) and (f) Data for three observers obtained with a dark target. $\circ$ Data points for gratings with variable light bar width, constant dark bar width. $\bullet$ Data points for gratings with variable dark bar width, constant light bar width.

These graphs (figures 3.11 and 3.12) are narrower and more obviously peaked than those obtained with background structure type A (figure 3.10), but once again, curves obtained with light or dark targets are similar. The two background structures, one with the dark bars varying and the other with the light bars varying do, however, yield different results (figure 3.12). When the dark bar width varies but the light bar width is constant (dashed line), a peak is obtained around 5 cycles/degree whilst for the light bar width varying and dark bar width constant background (full line), a peak at lower spatial frequencies, around 3 cycles/degree, is obtained. In order to compare the

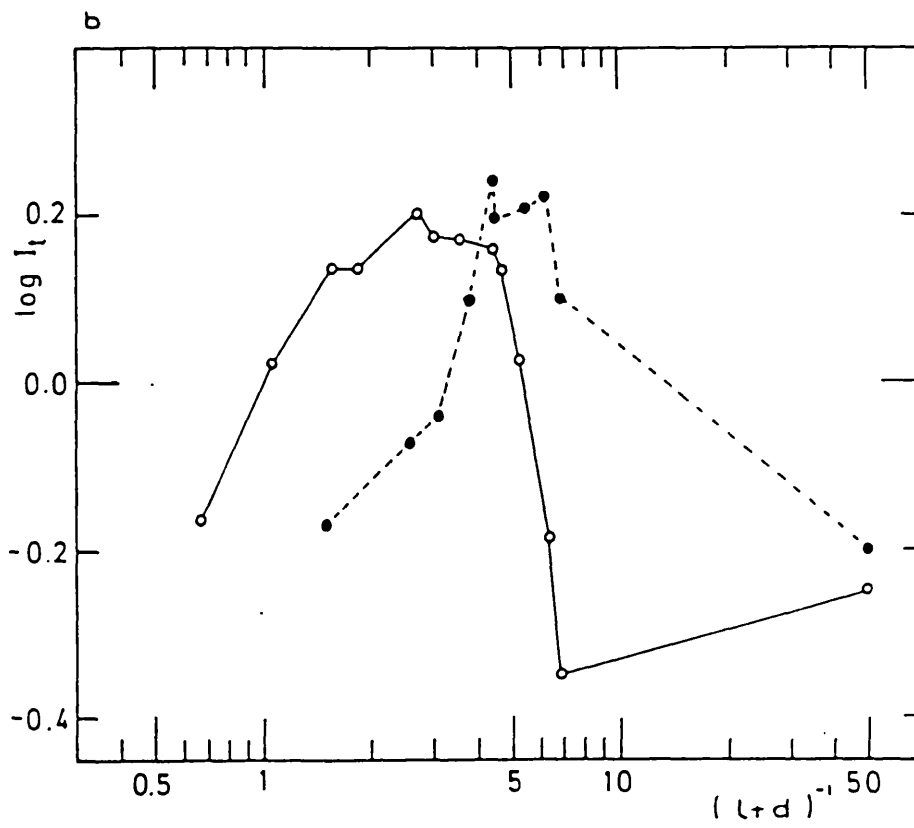
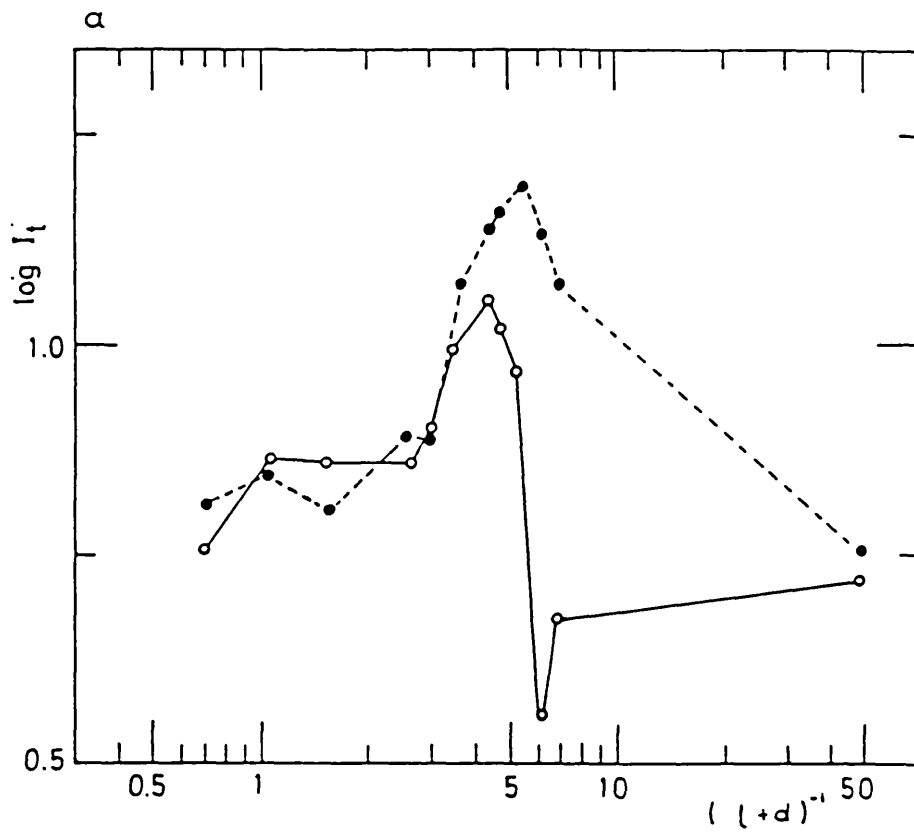


Figure 3.12 As for figure 3.11 except that $\log I_t$ is plotted as a function of $(1+d)^{-1}$, the periodicity of the background structure. (a) Mean data for three observers obtained with a light target. (b) Mean data for three observers obtained with a dark target. $\circ$ data points for gratings with variable light bar width, constant dark bar width. $\bullet$ data points for gratings with variable dark bar width, constant light bar width.

curves obtained with dark and light targets the difference between $\log I_t$ obtained with a grating from the light bar width varying set and $\log I_t$ obtained with a grating from the dark bar varying set, defined as Δ , is plotted against $(1+d)^{-1}$ (figure 3.13). There is some evidence of a difference between the two target types at lower spatial frequencies where the values for the dark and light targets, plotted respectively as circles and crosses, diverge.

3.4 Discussion

The experimental results obtained with different light:dark ratios in the background field do not clearly differentiate thresholds for detection of the dark and light targets. There is some indication of such a difference in the data of figure 3.13, but it is a second order effect. Thus although the mechanisms for detection of dark and light contrast targets have similar properties, the experiments fail to establish that there are two independent mechanisms. This contrasts with the evidence of adaptation data describing the properties of orientation and width selective mechanisms located centrally in the system [Gilinsky, 1968; Pantle and Sekuler, 1968; Blakemore and Campbell, 1969; Blakemore and Sutton, 1969]. In this case, a number of studies undertaken to test the independence of the mechanisms sensitive to bars of dark and light contrast have yielded clear differentiation between the two. Both Burton, Naghshineh and Ruddock [1977] and de Valois [1977] showed that apparent changes in bar width induced by pre-adaptation occur independently for either the light or the dark bars. In the case of the

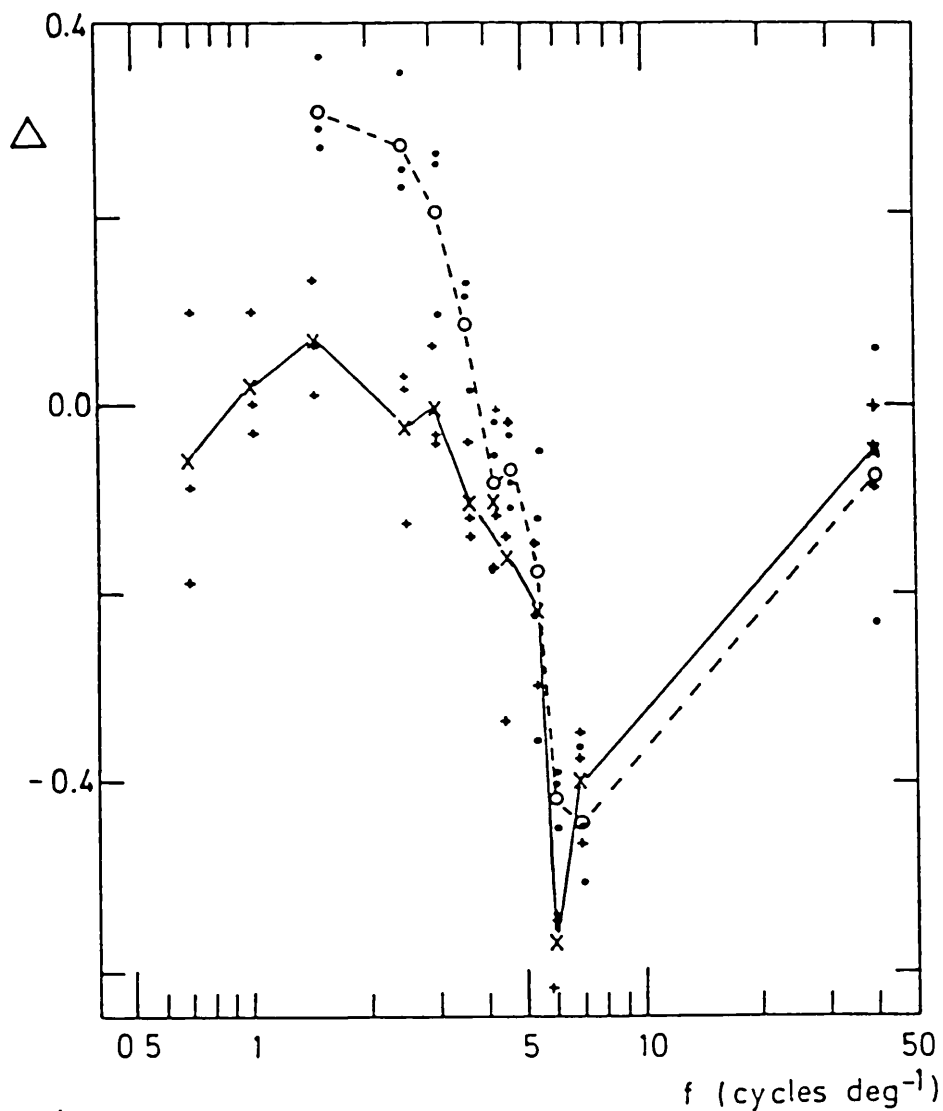


Figure 3.13 The difference, Δ , between $\log I_t$ obtained with a grating from the varying l , constant d set and $\log I_t$ obtained with a grating from the varying d , constant l set. Data is taken from figure 3.11. $+$ and $\times$ data points refer to data for the three observers and the mean of the three observers, respectively, for the light target; $\bullet$ and $\circ$ data points refer to data for the three observers and the mean of the three observers, respectively, for the dark target.

contrast threshold elevation effect, Naghshineh and Ruddock [1978] showed effects specific only to the positive contrast component, but subsequently Georgeson and Reddin [1981] demonstrated effects specific to the positive and

the negative contrast bars. The failure to demonstrate independent activity in the ST1 system may be due either to inadequate methodology or to the fact that both mechanisms are involved in the detection of moving targets, as was suggested by Barlow and Levick [1965] and by Marr and Ullman [1978]. Positive and negative contrast targets gave the same ST1 and ST2 responses and this symmetry between 'on' and 'off' mechanisms was also found by Roufs and Blommaert [1981] using incremental and decremental flashes. It seems unlikely, in view of the physiological evidence, that there is only a single response mechanism involved in detection of both contrasts.

CHAPTER FOUR SPATIAL PATHWAYS FOR THE SPECTRAL
RESPONSE MECHANISMS

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4.1 Introduction

The rods and cones in the retina are the neurones with which the visual system detects light. Microspectrophotometric measurement on these photoreceptors in primates provides evidence for the existence of three cone types and one rod type, each containing a single pigment. Dartnall, Bowmaker and Mollon [1983] using 7 enucleated human eyes made 173 records of different photoreceptors. On averaging their results they found absorption spectra with peaks at 496.3 ± 2.3 nm for the rods and 558.4 ± 5.2 nm, 530.8 ± 3.5 nm and 419.0 ± 3.6 nm for the three different cone types (known as red-sensitive, green-sensitive and blue-sensitive cones). The absorption spectra of the four different photopigments are broad and overlapping and they all have a similar shape when plotted on a wavelength abscissa, but their bandwidth increases as the peak frequency increases. [Bowmaker, Dartnall and Mollon, 1980]. When light is incident on the photoreceptors it is differentially absorbed in the three cone types, the amount of light absorbed by each cone type depending on the wavelength of the light. Comparison of the differential rate of absorption in the three cone types by post-receptoral neurones enables the visual system to discriminate stimuli by their spectral composition.

The greatest density of cones is at the fovea and this density decreases rapidly into the periphery, but there are no blue-sensitive cones or rods in the fovea. The blue-sensitive cones are the least numerous photoreceptors in the retina and the rods are the most numerous. Rod density increases from zero to a maximum at 10° to 15° from the fovea and then decreases on moving further out. The rods mediate low light level (scotopic) vision and make no

contribution to colour vision whilst the cones mediate normal vision at medium and high illumination levels. The red- and green-sensitive cones at the fovea mediate high acuity processes in the visual system.

As mentioned above, spectral sensitivity curves for the photoreceptors have been found by microspectrophotometry. Psychophysical methods have also been used to obtain these curves. W.S. Stiles [1949,1959] developed a method, called the two-colour increment threshold technique, to obtain spectral sensitivity curves for individual photoreceptor types by suppressing the responses of the others, section 1.2 (b).

Stiles' technique not only reveals spectral sensitivities similar to those of the different classes of photoreceptors but also provides a method of studying in isolation the response characteristics of the mechanisms which generate them. Stiles, himself, found that the spatial responses of the blue-sensitive mechanism (π_3) were significantly coarser than those of the red- (π_2) and green- (π_4) sensitive mechanisms. [Stiles 1939, 1959, 1978]. That is, the spatial summation for the blue-sensitive mechanism is greater than that of the red- and green-sensitive mechanisms [Stiles 1949]. Brindly [1954] found that the blue-sensitive mechanism's summation extended over some 8' compared with a value of around 1' to 2' for the red- and green-sensitive mechanisms.

The response characteristics of the blue-sensitive mechanism have been found to differ in a number of ways from those of the red- and green-sensitive mechanisms. The low spatial resolution mentioned above is associated with low contrast sensitivity throughout the spatial frequency domain [Green, 1968; Kelly, 1973; Cavonius and Estévez, 1975] and the Fechner fraction for detection of flashed increments is correspondingly high [Stiles 1946]. There has been speculation that at post-receptoral levels, signals from blue-sensitive cones are carried by colour-opponent but not by luminance

channels [Guth, Alexander, Chumbly, Gillman and Patterson, 1968; Mollon and Krauskopf, 1973; Foster and Snelgar, 1983] and this hypothesis has been confirmed by some direct investigations [Whittle, 1974; Tansley and Boynton, 1978; Eisner and Macleod, 1980] but not by Marks [1974].

I have used the two-colour increment threshold technique in order to study the way in which signals from π_3 are transmitted along the visual pathways. I have studied the contribution of the π_3 and π_5 to the adaptation mechanism which gives rise to the contrast threshold elevation effect.

4.2 Experimental Procedure

The Maxwellian view optical apparatus, described in Chapter Two was used to carry out the adaptation experiments. It was set up to provide binocular viewing, see figure 2.2 of Chapter Two, with the adaptation and test gratings presented to different eyes as there is some evidence of wavelength selectivity in the monoptic case. In the experiments to be described detection of the grating target was mediated by π_3 or π_5 , and the effect of contrast elevation on target detection was determined. A yellow conditioning background was used to isolate π_3 and a blue-green conditioning background to isolate π_5 . The wavelengths of the fields were produced by inserting appropriate interference filters in the three channels and these gave near monochromatic stimuli. The grating patterned visual fields were formed by placing high contrast photographic slides, with one-dimensional bar patterns on them, in the appropriate beams. The two observers who took part in the experiments were emmetropic and the slides were positioned at the first focal point of the viewing lens i.e. at OP1 and OP3 shown in figure 2.2, so that their eyes did not accommodate. The observers dark adapted for at least ten minutes before any experiments were carried out. During an experiment the

observer controlled the setting of the neutral density wedge which determined the test illumination and after each threshold setting the wedge was re-set by the experimenter to an arbitrary, suprathreshold setting. The wedge had been calibrated separately for each wavelength used in the measurements.

4.3 Results

(a) Isolation of the π -mechanisms

It was necessary, first of all, to check that the combination of wavelengths for the target gratings and conditioning, background fields did isolate the π -mechanisms. A 9° diameter, circular field of wavelength μ provided the conditioning background on which was flashed, centrally, a circular target (diameter 6°) of wavelength λ , for one second every two seconds (Figure 4.1). The target was spatially modulated in the form of a square wave grating, with periodicity 2.9 cycles/degree. This was the spatial frequency f_t of the test grating to be used in the adaptation experiments and was sufficiently coarse to be resolved by the π_3 mechanism [Brindley, 1954].

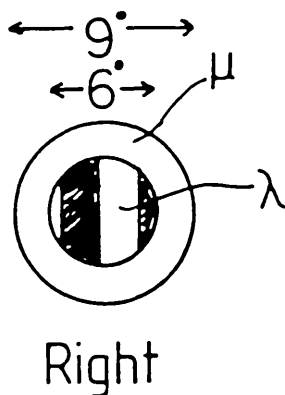


Figure 4.1 The visual field configuration used to measure relative spectral sensitivity for detection of the test grating of variable wavelength λ in the presence of a conditioning field of wavelength, μ .

The conditioning background field to isolate π_3 was yellow, wavelength $\mu = 582$ nm and its illumination level was 3.45 log td., whereas for isolation of π_5 it was blue-green, wavelength $\mu = 495$ nm and of illumination level 3.23 log td. In order to check on the the effectiveness of these background wavelengths in isolating the appropriate π -mechanisms the energy E_λ , required for detection of the target grating was measured as a function of, the test wavelength, λ . The corresponding detection sensitivities defined as E_λ^{-1} are plotted in Figure 4.2. Plotted on the graphs, as dotted lines, are the π_3 (Figure 4.2a) and π_5 (Figure 4.2b) spectral responses for detection of a uniform target [Wyszecki and Stiles, 1982].

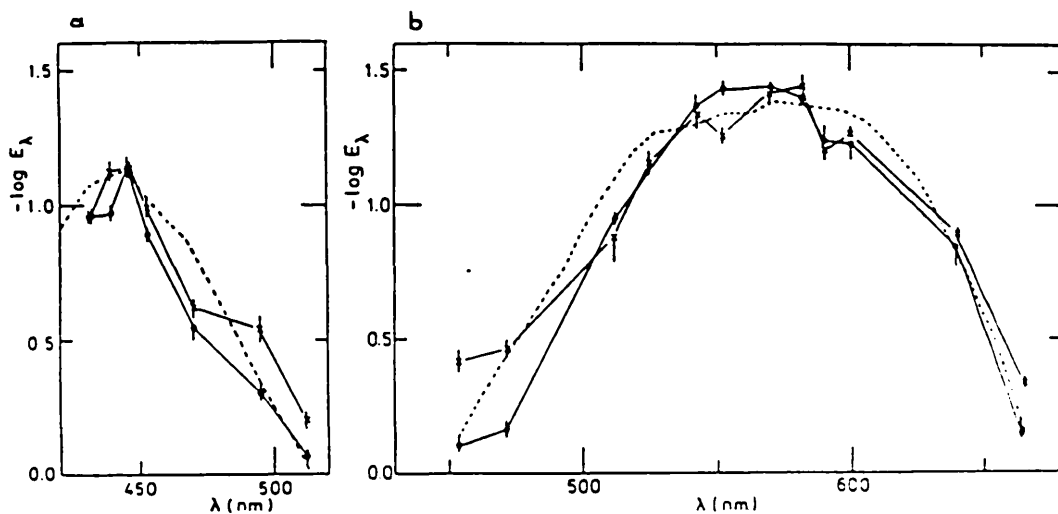


Figure 4.2 Relative spectral sensitivity for detection of a grating of wavelength λ presented on a uniform background of wavelength μ . The inverse of the energy E_λ required for detection of the grating which was of periodicity 2.9 cycles/degree is plotted against λ . Data for 2 observers, IB $\times$ and JB $\bullet$. (a) Values for a background of wavelength $\mu = 582$ nm and 3.45 log td. illumination. The broken line shows the π_3 spectral response (after Wyszecki and Stiles, 1982). (b) Values for a background of wavelength $\mu = 495$ nm and of 3.23 log td. illumination. The broken line shows the π_5 spectral response (after Wyszecki and Stiles, 1982). Each data point is the mean of four readings and the standard error is plotted with each data point.

The data show that for $\mu = 582$ nm, threshold sensitivity follows the normal π_3 response for $\lambda < 500$ nm (figure 4.2a) and for $\mu = 495$ nm it is mediated by π_5 for $\lambda > 500$ nm (figure 4.2b). In the experiments that follow the π_3 mechanism was isolated using a test grating of wavelength $\lambda = 446$ nm on a background of $\mu = 582$ nm and the π_5 mechanism with a combination of $\lambda = 640$ nm on $\mu = 495$ nm.

(b) Spatial Tuning Curves for π_3 and π_5

The procedure used to carry out the adaptation experiments is described below.

1. The observer adapted for two minutes with the left eye to a bright, 100% modulated grating, of 9° diameter. The grating periodicity was f_a cycles/degree and its wavelength was similar to that of the test grating.
2. The test stimulus and the conditioning field were then presented to the right eye. The circular, 6° diameter test stimulus, had grating structure of 2.9 cycles/degree and the uniform background field was of 9° diameter and wavelength μ .
3. The test and adaptation patterns were then presented alternately for 2 seconds and 20 seconds until the test grating illumination had been set to threshold. Figure 4.3 shows the visual fields seen by the left and right eyes. Both eyes look straight at their respective fields so that corresponding retinal areas are illuminated.
4. The threshold illumination level of the test stimulus, I_t , was determined four times for each adaptation grating and the average value found.
5. The threshold value for the test stimulus following adaptation to a uniform field was found. The uniform field was of the same wavelength, illumination level and size as the grating adaptation field. The threshold value

found was called I_0 . This was usually determined 20 times per session and all of these values were averaged.

6. These two threshold values, I_t and I_0 obtained with a grating adaptation field and a uniform adaptation field respectively, were used to determine the grating adaptation effect Δ , defined as

$$\Delta = \log I_t - \log I_0 \quad \text{equation 4.1}$$

In plotting the data I_0 is adjusted to zero, thus $\Delta = \log I_t$.

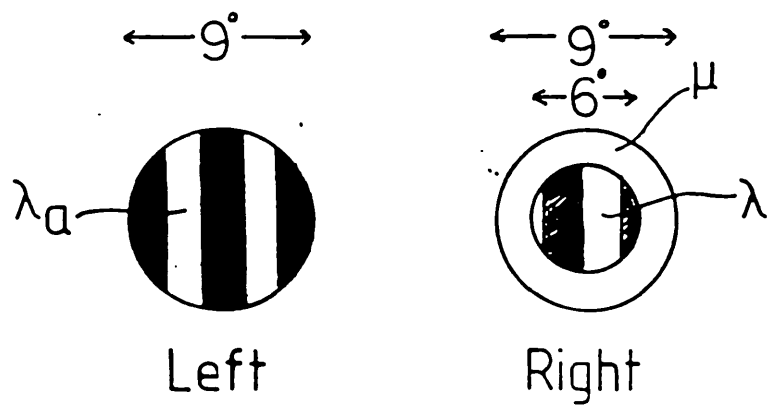


Figure 4.3 Visual field configuration used in adaptation experiments. After preliminary viewing of the adaptation grating with the left eye for two minutes, the test grating on the conditioning field and the adaption grating were viewed alternately for 2 seconds and 20 seconds.

In the first adaptation experiment performed the grating adaptation effect Δ was measured as a function of the periodicity of the adaptation grating. Its value was determined four times for each adaptation grating. In measurements for π_3 the adaptation grating wavelength, λ_a , was 470 nm and its illumination level 3.6 log td. The test grating viewed by the right eye was of $\lambda = 446$ nm and it was presented on a conditioning background with $\mu = 582$ nm and of 3.2 log td. illumination level. For measurements on π_5 , the adaptation grating wavelength was $\lambda_a = 635$ nm and of 3.6 log td., the test

wavelength, λ , was 640 nm and the conditioning field of wavelength $\mu = 495$ nm and 3.2 log td. illumination level. Figure 4.4 shows the tuning curves obtained under these conditions.

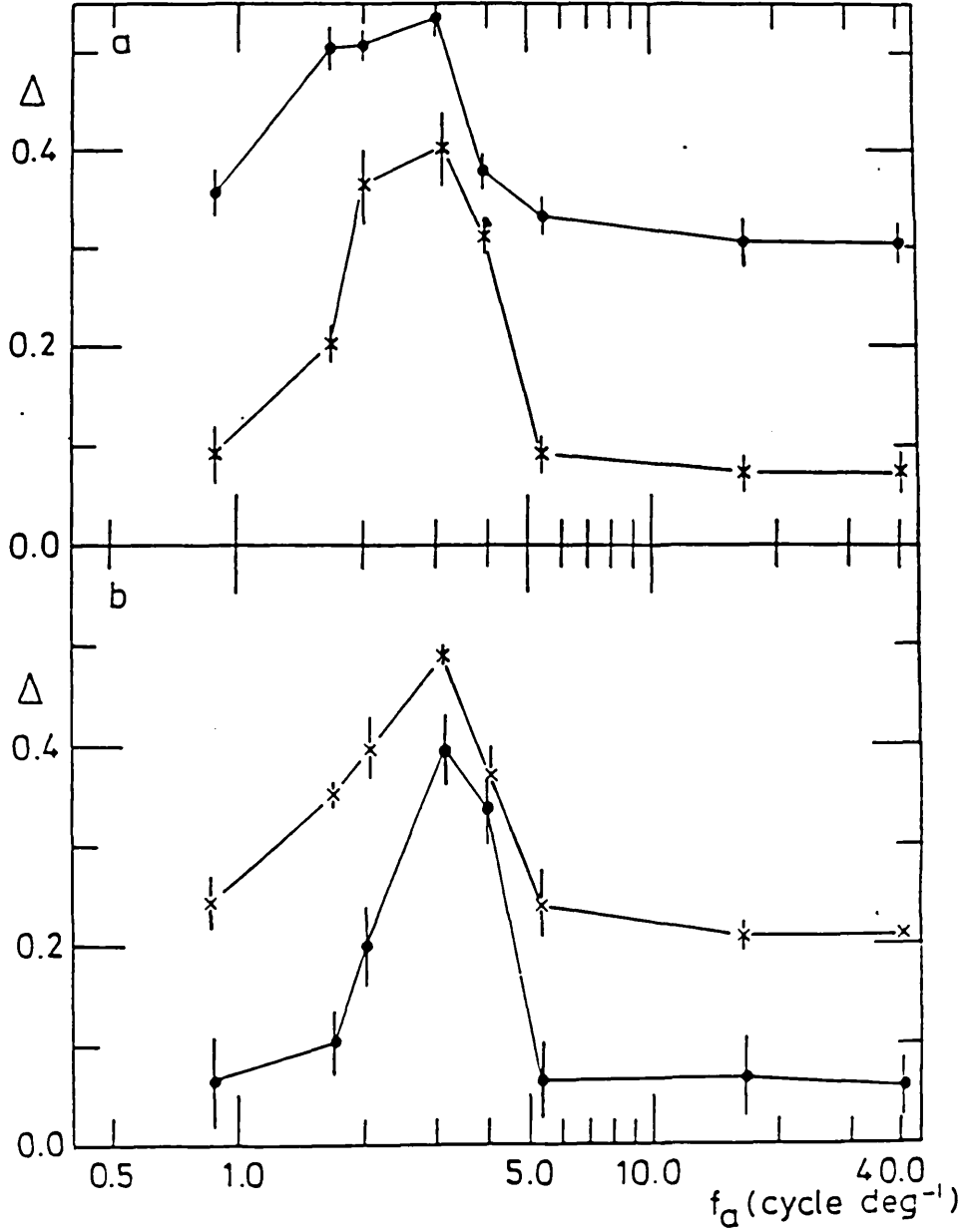


Figure 4.4 Spatial tuning curves for threshold values Δ (see equation 4.1) measured in detection of a test grating following adaptation to a matched grating presented to the contralateral eye (see figure 4.3). The test grating was of periodicity 2.9 cycles/degree and the adaptation f_a cycles/degree. (a) Detection of the test grating mediated by π_3 -mechanism. The test grating ($\lambda = 446$ nm) was superimposed on a uniform field ($\mu = 582$ nm, illumination 3.2 log td.) and the adaptation grating was of wavelength 470 nm and mean illumination 3.6 log troland. Data for I.B. ($\times$) and J.B. ($\bullet$). Data points for J.B. have been displaced upwards along the Δ axis by 0.3 log units and for I.B. by 0.07 log units. (b) Detection of the test grating mediated by π_5 . The test grating ($\lambda = 640$ nm) was superimposed on a uniform field ($\mu = 495$ nm illumination 3.2 log td.) and the adaptation grating was of wavelength 635 nm and mean illumination 3.6 log td. Data points for I.B. ($\times$) have been displaced upwards along the Δ axis by 0.21 log units and for J.B. ($\bullet$) by 0.06 log units. All values are the mean of 4 readings and standard errors are shown with data points. The threshold value for the uniform field is plotted at 40 cycles/degree.

The spatial responses for both π -mechanisms peak sharply at an adaptation grating spatial frequency of 2.9 cycles/degree, which matches the test spatial frequency. The threshold values are raised relative to the uniform field level (plotted at 40 cycles/degree) only within the frequency range 0.9 to 5.4 cycles/degree. The features of these responses are similar to those obtained under both monoptic and dichoptic presentation of test and adaptation gratings by Blakemore and Campbell [1969] and Maudarbocus and Ruddock [1973 a,b]

(c) The Effect of Adaptation Wavelength on the Grating Adaptation Effect, Δ

Δ was measured as a function of adaption grating wavelength, λ_a , with the grating periodicity maintained at 2.9 cycles/degree in order to give maximum adaptation effect. The pattern viewed by the right eye remained exactly as in the first experiment. Threshold values obtained for different wavelengths of the adaptation grating are shown in figure 4.5.

All adaptation wavelengths produce similar threshold elevation for both π_3 and π_5 with no systematic differences in spectral distribution between data for the two mechanisms.

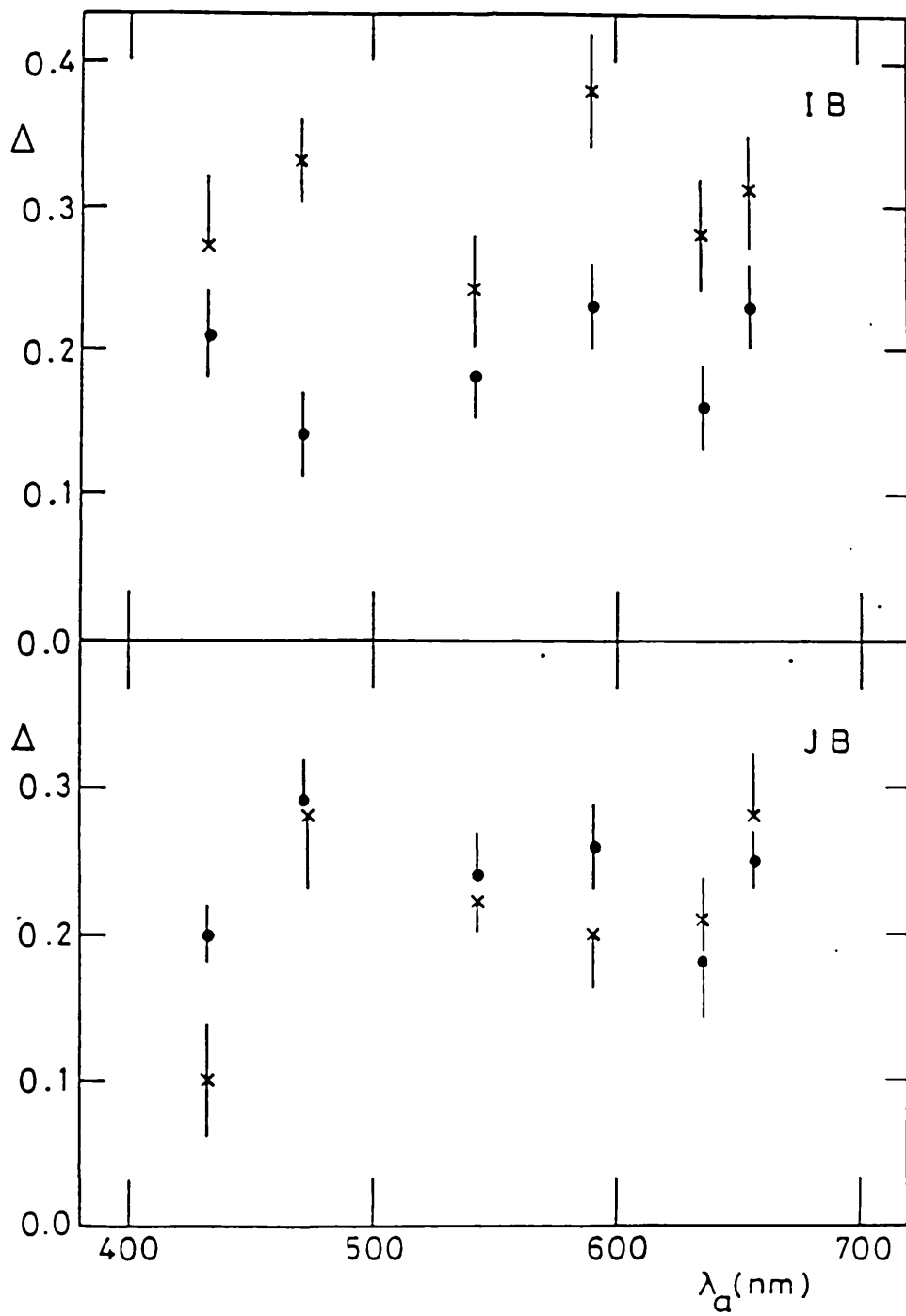


Figure 4.5 Spectral variations in the values of Δ obtained after adaptation to a grating of wavelength λ_a . The periodicity of both the test and adaptation gratings was equal to 2.9 cycles/degree and the illumination level of the adaptation grating for each value of λ_a was in log td: 2.77 (432nm), 3.63 (471nm), 3.85 (542nm), 4.19 (590nm), 3.98 (635nm) and 2.67 (655nm). Values for detection mediated by π_3 and by π_5 were obtained with the stimulus parameters as defined in the caption to figure 4.4. (a) Data for subject I.B., $\times$ refer to π_3 and $\bullet$ to π_5 . (b) Data for subject J.B., $\times$ refer to π_3 and $\bullet$ to π_5 . Each value is the mean of four readings and standard errors are shown with the data points.

4.4 Discussion

The spatial responses of figure 4.4 have an overall bandwidth of 2 to 3 octaves for both π_3 and π_5 , much as is observed in all the adaptation studies cited in the section 2.2(b). There is some variation in the amplitudes of the different responses, with subject I.B. giving a larger peak response for π_3 and J.B. a larger response for π_5 . When different wavelengths were used for the adaptation grating (figure 4.5) the mean values of Δ for observer I.B., when averaged over all the adaptation wavelengths used were 0.30 ± 0.02 for π_3 and 0.19 ± 0.02 for π_5 . The corresponding averaged Δ values for J.B. were 0.22 ± 0.03 and 0.24 ± 0.02 . These values for Δ are of similar size to the variations in amplitude in the spatial tuning curves. In order to get as large an adaptation effect as possible the largest adaptation illumination levels obtainable with the apparatus were used. The value depended on the interference filter used (actual illumination levels are listed in the caption to figure 4.5) so the illumination level of the adaptation grating varied with its wavelength. In this second experiment the aim was to compare the two Δ values obtained for each adaptation grating, one when detection of the test grating was mediated by π_3 the other when it was mediated by π_5 . For both values the same adaptation illumination level was used.

As discussed in the section on the adaptation mechanism, under

binocular viewing the adaptation effects for different adaptation wavelengths are equivalent when they are set to the same suprathreshold value, however Δ values only change slowly as $\log I_a$ increases [Maudarbocus and Ruddock, 1973b]. So, despite using different $\log I_a$, values of Δ for different adaptation grating were not expected to vary greatly.

The lack of spectral sensitivity in the data of figure 4.5 is demonstrated by taking the ratio of the mean Δ for $\lambda_a < 480$ nm, in which region the blue-sensitive cone mechanism has significant sensitivity, to those for $\lambda_a > 540$ nm, in which region its sensitivity is very low. The ratios of the two sets of data (Table 4.1) show that for neither π -mechanisms do the ratios differ greatly from unity, thus there is no indication of an opponent response involving the π_3 mechanism. Also, contributions from a red-green opponent system can be ruled out by the large value of Δ at 540nm, which is a neutral wavelength for the red-green opponent system measured both psychophysically and electrophysiologically [Wiesel and Hubel, 1966; Gouras, 1974; de Monasterio, 1978a].

Subject	π_3	π_5
I.B.	1.01 $\pm$ 0.07	1.17 $\pm$ 0.10
J.B.	1.55 $\pm$ 0.28	0.97 $\pm$ 0.08

Table 4.1 The average values for the ratios of $\Delta_{\lambda_a > 540\text{nm}} / \Delta_{\lambda_a < 540\text{nm}}$. Eight values were obtained by taking $\Delta_{\lambda_a > 540\text{nm}} / \Delta_{\lambda_a = 432\text{nm}}$ and $\Delta_{\lambda_a > 540\text{nm}} / \Delta_{\lambda_a = 471\text{nm}}$ (four values each) from the data of figure 4.5 and the mean was then found. The standard errors are given with the means.

In these experiments we have shown that signals generated in the blue-sensitive cones are transmitted to a central mechanism with broad-band spectral responses. Their contribution to the total signal in a luminance

channel may be relatively small, but our experiments provide no evidence on this point.

**CHAPTER FIVE SPATIAL FILTERING AND PATTERN DETECTION IN
AMBLYOPIA AND VISUAL AGNOSIA**

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5.1 Introduction

The neuronal processing of spectral content in the visual image following transduction by the photoreceptors, can be conveniently divided into two stages. The first, corresponding to the retina, optic nerve, LGN and striate cortex, can be considered as the 'filtering' stage, and involves the activities of cells with circular, centre-surround antagonistic receptive fields (e.g. ganglion cell) and those with orientation specific responses (simple and complex cells of the striate cortex). The second can be described as the 'computational' stage, in which the filtered image is processed to generate the perceived response. The filtering process in the human system can be studied by the background modulation method, which yields circularly symmetric centre-surround antagonistic responses (Chapter Three) and by adaptation methods, which establish the activity of orientation sensitive response mechanisms (Chapter Four). The experimental study of 'computational' processes has proved more difficult, but data pertaining to discrimination of geometric patterns has been derived from measurements on 'multi-element' stimuli [Ike, Ruddock and Skinner, 1987]

In this Chapter, I describe data obtained for two classes of abnormality of the visual pathways which disrupt the processing of spatial patterns. The first, amblyopia, involves blurring of the retinal image with corresponding loss of visual resolution which is neural in origin and cannot, therefore, be corrected by refraction. Grounds, Holliday and Ruddock [1983] showed that for such subjects, certain spatial responses determined by the background modulation method are abnormal and I have extended the study to the case of

targets with negative contrast. The other abnormality, visual form agnosia, is a study on a single subject who lacks the ability to recognise everyday objects. In this case, I have measured discrimination for geometric targets with multi-element stimuli. This method has also been applied in the study of the amblyopes.

5.2 Examination of Spatial Processing in Amblyopia

(a) Experimental Procedure

Both the Maxwellian view apparatus and the computer controlled, pattern discrimination apparatus (described in Chapter Two) were used in the investigation of the spatial vision in amblyopes. The experiment carried out with the Maxwellian view apparatus measured the spatial properties of the ST1 filter for each of the amblyopes' eyes separately, with both dark and light contrast targets. In section 2.2(a), I described the characteristics of the ST1 filter found using a light contrast target and Chapter Three contains the results of the measurements of its characteristics in normal subjects using a dark contrast target. The field configuration was that illustrated in figure 2.10 and threshold illuminations for detection of circular 3.5° diameter target moving across the central 8° of a 17° diameter, circular grating background were found as a function of the spatial frequency, f_s , of the background grating. The non-localised nature of the target eliminates the influence of the amblyopes' eccentric fixation in the determination of detection thresholds, the 8° traverse of the moving target being significantly greater than the angles of eccentric fixation in all but one of the amblyopic subjects (table 5.1). Grounds, Holliday and Ruddock [1983] considered in detail and rejected the possible contribution of eccentric fixation to the threshold values. Measurements were made for both dark (negative) contrast and bright (positive)

contrast targets.

In the pattern discrimination experiments the monitor was viewed from 1.9m, at which distance it subtended $8.5^\circ \times 6.3^\circ$ visual angle. The pattern elements used in the discrimination experiments are shown in figure 2.30 with the background pattern the first of each set of four elements. The other three elements are the targets and differ from the background by their orientation. The pattern elements are of two different sizes one being three times the size of the others. The large targets are the lines (a) which are 1.5° long, the triangles (c), (e), (g) and (h) which have sides of 1.5° . The gap on the cornerless triangles is 0.12° from line end to apex. The small targets are the lines (b) which are 0.5° long and the triangles (d) and (f) whose sides are 0.5° in length. All line widths are 0.03° .

All the experiments were carried out with 40 background elements and figure 2.27 shows a typical screen with triangular elements. 200 presentations were made for each set of pattern elements (a) to (h) to each eye separately and then to both eyes together of the amblyopes. The normal observers, whose data were required for comparison purposes, carried out the same experiments as well, except that they used only one of their eyes on its own and then both eyes together. Each target type appeared on 50 occasions and a background element appeared as a 'null' target in the remaining 50 occasions. The subject's response was measured in terms of $T_{\frac{1}{2}}$ the time required for 50% probability of detecting the target and the subject's accuracy was determined by the number of times that they mistakenly pressed the 'target present' button when the 'null' target was presented. The rate of false positive replies to the 'null' target was not more than 5% for all observers.

(b) Subjects

Five strabismic amblyopic subjects, whose details are given in table 5.1 and seven normal subjects, all aged between nineteen and twenty-four years, took part in the experiments. Six of the normal subjects and all amblyopes were naive psychophysical observers. One of the amblyopic subjects, P.D., reported that when young, he alternated fixation freely between the two eyes, but ophthalmic examination failed to confirm that this is currently the case and, as with all the other amblyopic subjects, results for his normal eye are presented separately (Grounds, Holliday and Ruddock [1983] showed that the visual responses were similar for each eye of a subject with alternating fixation).

Subject	Sex	Age	Class	Fixation Angle	V.A 'normal' eye	V.A 'abnormal' eye
M.G.	M	22	Con.	1.5°w	6/5	6/18
AM.N.	F	20	Con.	0.0°	6/5	6/6
J.P.	M	19	Div.	8.0°t	6/4	6/12
P.D.	M	19	Con.	0.5°n	6/4	6/5
D.G.	M	24	Div.	1.5°t	6/6	6/12

Table 5.1 Details of the five strabismic amblyopes. The fourth column gives the classification as convergent (Con.) or divergent (Div.). The fifth column gives the angle of eccentric fixation in the amblyopic eye, either nasal (n), temporal (t) or wandering (w), determined with the Linksz star graticule. Visual acuity (V.A.) was measured with the Snellen test chart, with refractive correction. All subjects had normal fundi and none was able to perceive images in random dot stereograms.

(c) Results

ST1 Spatial Response

The ST1 spatial responses were measured for four normal subjects using

both positive and negative contrast targets. The mean data is plotted in figure 5.1 and the curves, with peaks at 4 to 5 cycles/degree, are the same for both target types and similar to previous data published for the light target [Barbur and Ruddock, 1980a; Holliday and Ruddock, 1983] and for the dark target (see Chapter Three).

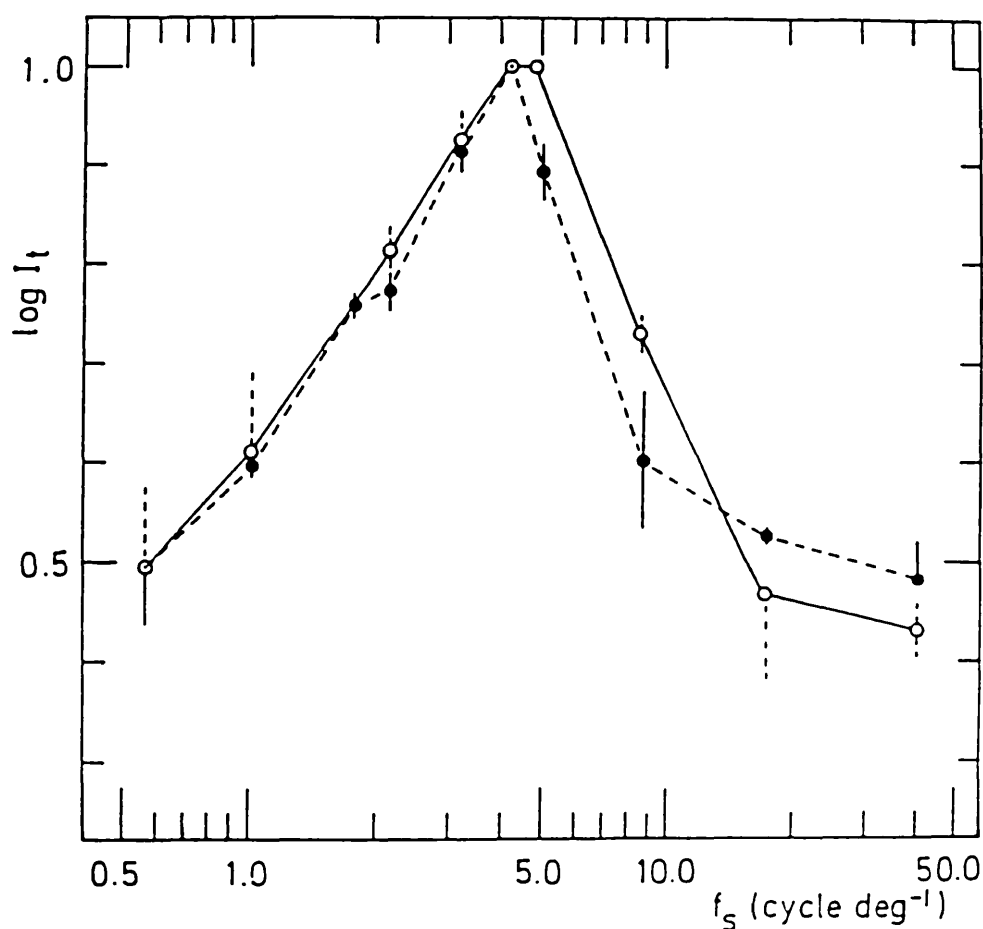


Figure 5.1 Threshold illumination, I_t , for detection of a 3.5° diameter target moving across the central 8° of a 17° diameter circular grating background of periodicity, f_s . Mean background illumination, $\log I_b = 1.4 \log \text{td}$. Average values for four subjects with normal vision; dark circles refer to dark (negative) contrast targets and light circles to light (positive) contrast targets. The data is normalized to a peak value of $\log I_t$ equal to one. Error bars denote the standard errors amongst the subjects.

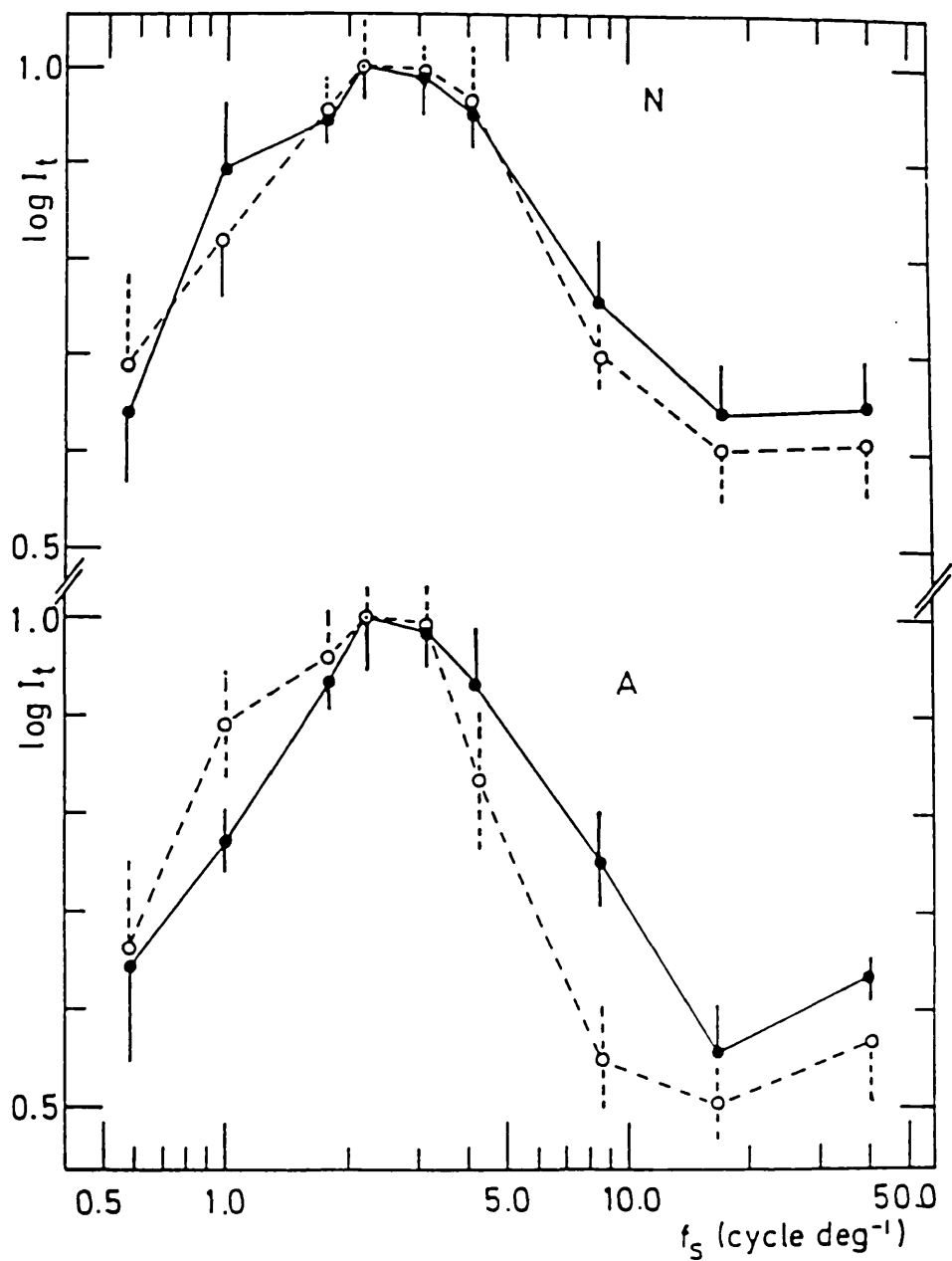


Figure 5.2 As figure 5.1, but mean values are for five subjects with strabismic amblyopia. Average data for the 'normal' eyes, N, and the 'abnormal' eyes, A.

The ST1 spatial response was measured for each eye separately of the five amblyopes and for both light and dark contrast targets. The mean data for the normal eyes and the means for the abnormal eyes are plotted separately in figure 5.2. The response curves, which peak at a spatial frequency of 2 to 3 cycles/degree for both eyes and both target types, are displaced to low frequencies relative to the normal responses and are similar to those found for light (positive) contrast targets for each eye of a large group of amblyopes [Grounds, Holliday and Ruddock, 1983].

Pattern Discrimination

Values of $T_{\frac{1}{2}}$ for detection of the target are shown in figures 5.3 to 5.7 where T for the single eye (abnormal or normal) is plotted against T_b , the time taken for both eyes together, for each of the eight sets of pattern elements shown in figures 2.30 (a) to (h) respectively. The mean data for normal subjects are denoted $+$ and those for the amblyopic subjects are denoted $\circ$ and $\bullet$ for the abnormal and normal eyes respectively. The reaction times for the different targets are not distinguished in each group as it is the overall response time, and not the discrimination of the different target orientations which is important. The dotted line on each graph shows the line $T = T_b$.

For a background consisting of vertically orientated straight lines (figure 5.3) the T values for either eye are similar to those obtained for both eyes, for both sizes of the line elements. Figures 5.4 and 5.5, which refer to background elements $\triangle$ and $\triangleright$, show that response times are mostly greater than for single line elements. With the small targets (figures 5.4 (a) and 5.5 (a)) T values for the 'abnormal' eyes are greater than those for the 'normal' eyes, and for the binocular response, the three latter values being similar.

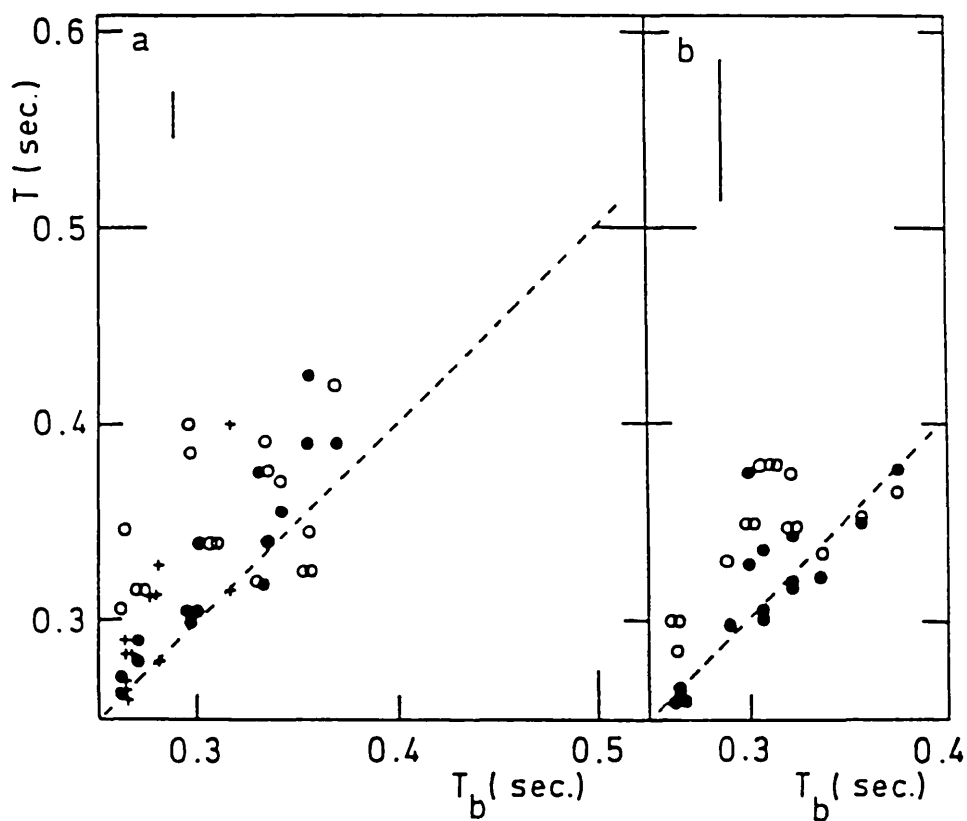


Figure 5.3 The time, T , for the target to be detected using one eye on 50% of occasions, plotted against the equivalent time, T_b , obtained with binocular viewing. The background elements were vertically orientated straight lines. $\circ$, data for the 'abnormal' eye of amblyopic subjects; $\bullet$, data for the 'normal' eye of amblyopic subjects; $+$, data for either the right or left eyes of the normal subjects. Data set (a) refer to lines of length 0.5° and (b) to lines of length 1.5° .

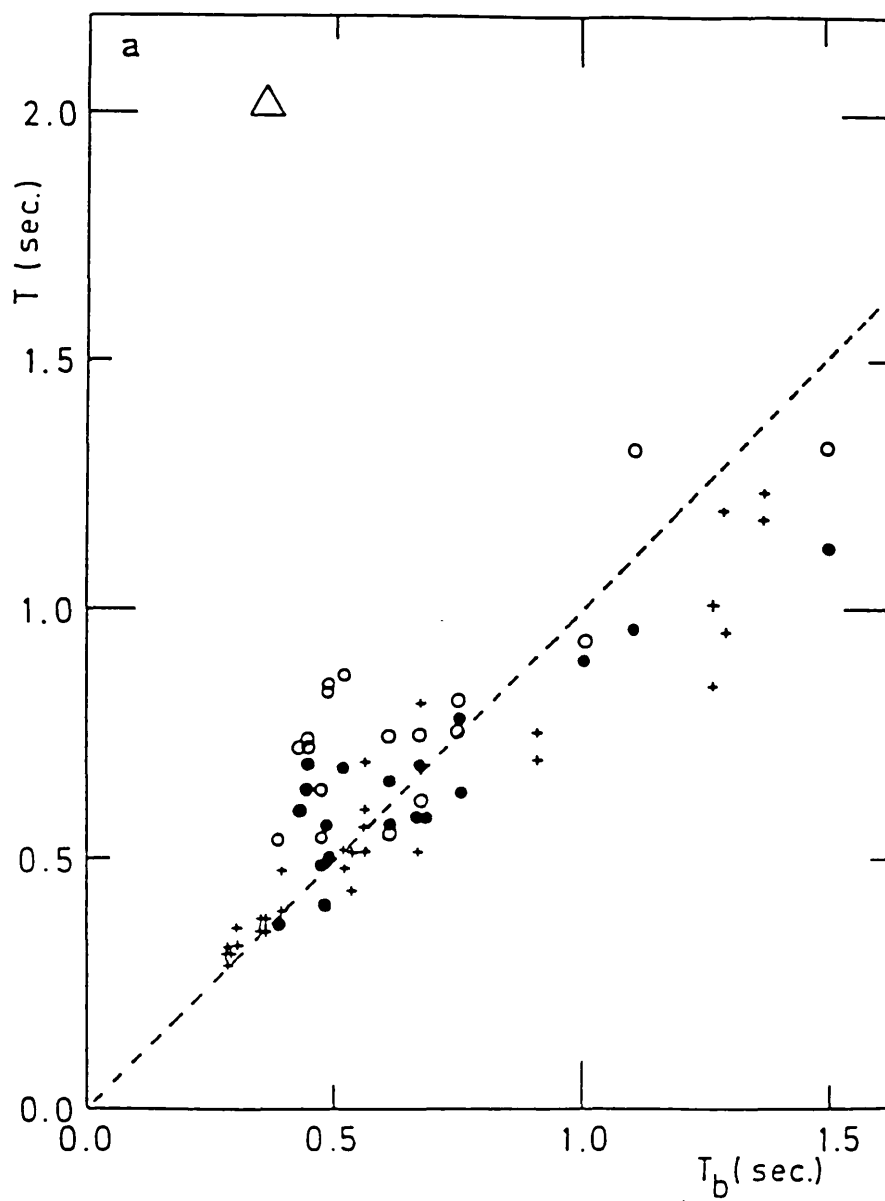


Figure 5.4 As for figure 5.3, but for background elements Δ . Data set (a) refer to elements constructed from lines of length 0.5° and (b) to elements constructed from lines of length 1.5° .

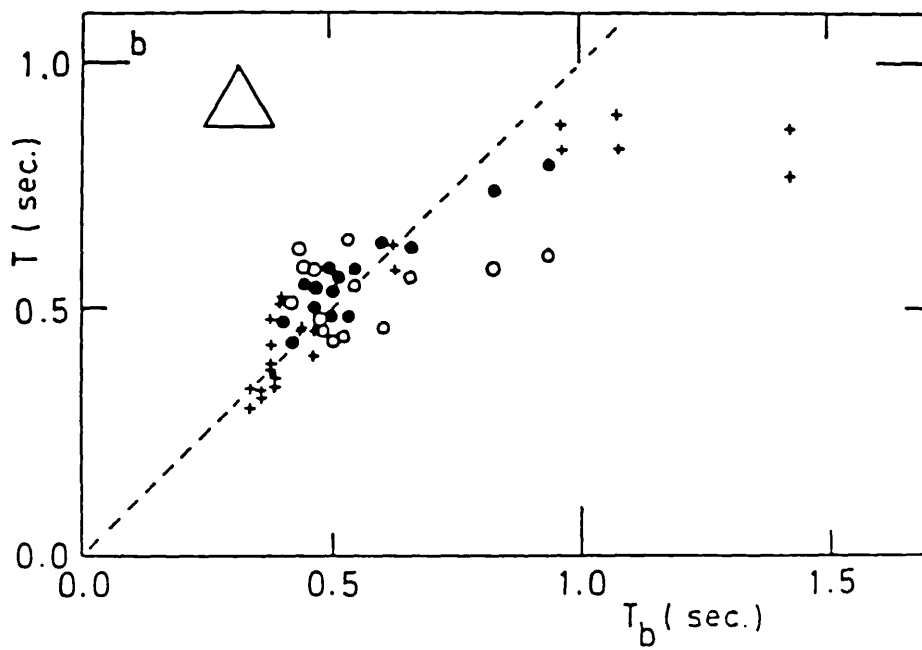


Figure 5.4 (cont.)

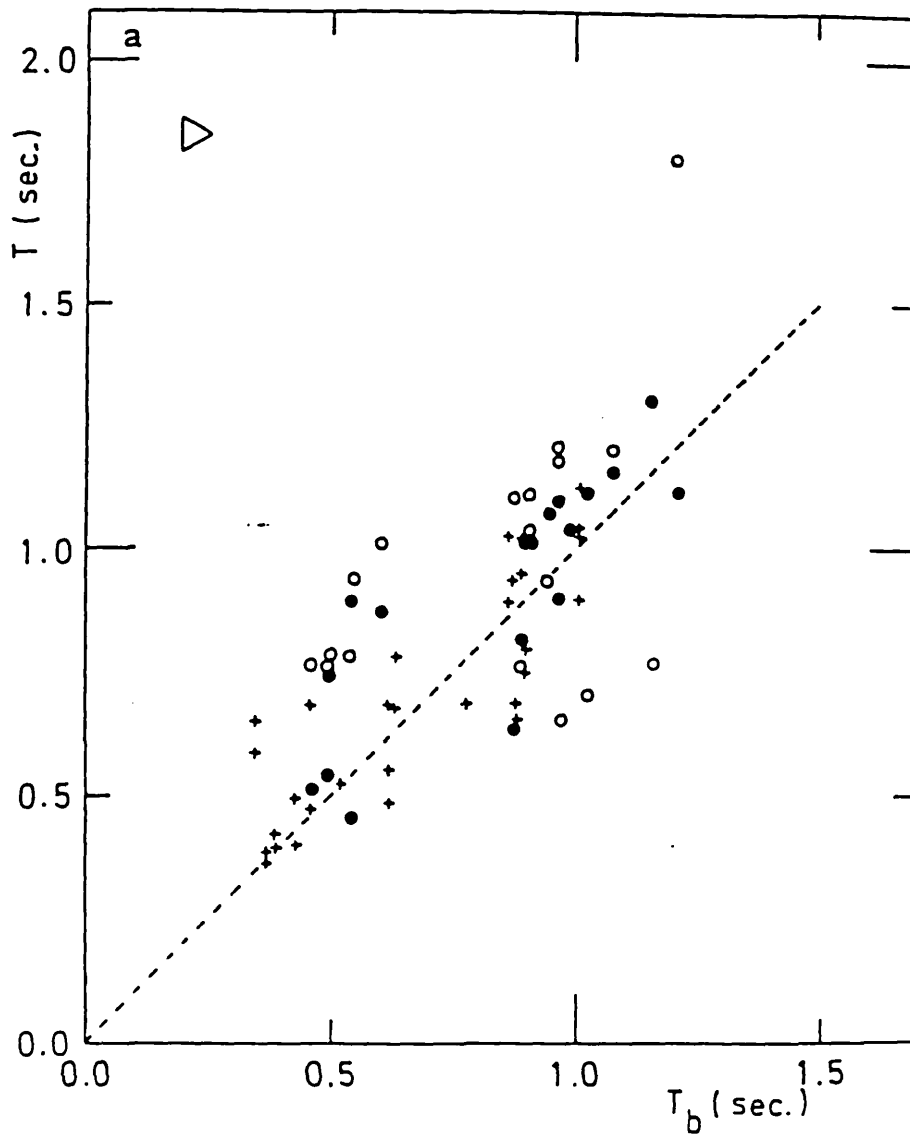
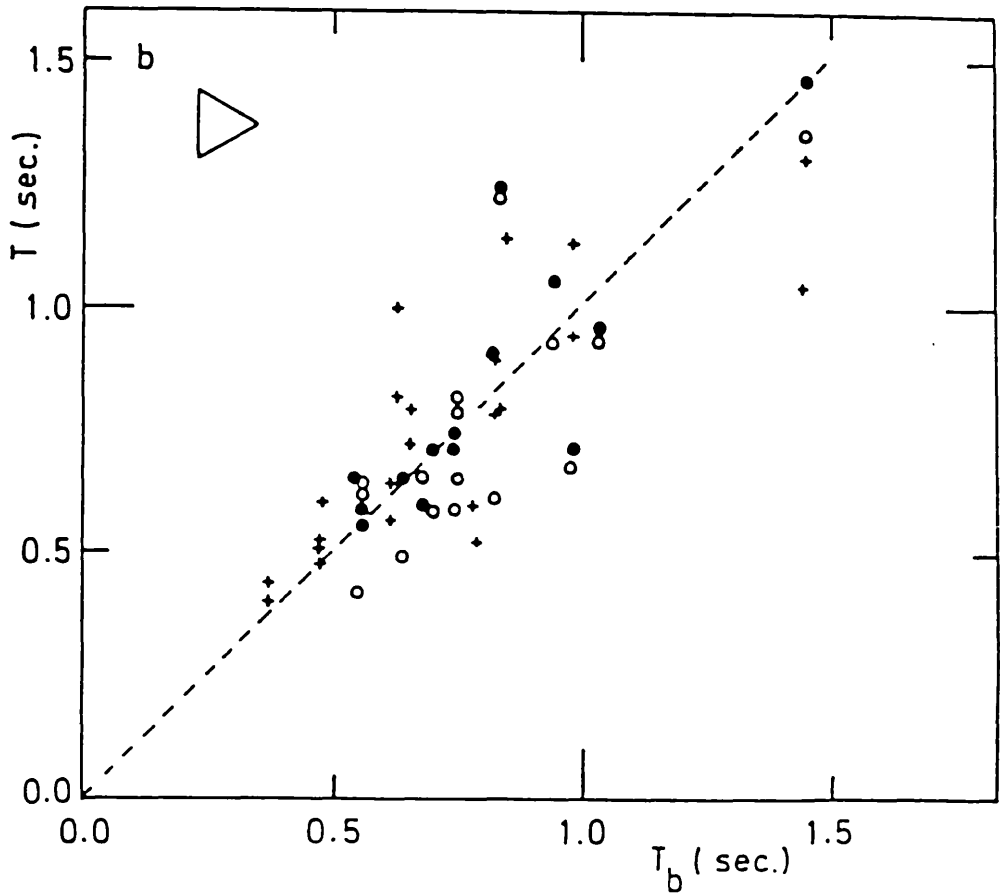


Figure 5.5 As figure 5.3, but for background elements $\triangleright$. Data set (a) refer to line length 0.5° and (b) to line length 1.5° .

Figure 5.5 (cont.)



For large targets (figures 5.4 (b) and 5.5 (b)), however the data for the 'abnormal' eyes are similar to those for the 'normal' eyes and to the binocular values, and are therefore clustered around the line $T = T_b$. The data for the background elements $\triangleleft$ and $\triangleright$ are plotted in figures 5.6 and 5.7 where only the small elements (0.5° side length) were used. Discrimination times for these targets are significantly greater than those for ordinary triangles and the values for the 'abnormal' eyes of the amblyopes are greater than those for their 'normal' eyes, and for those obtained with both eyes.

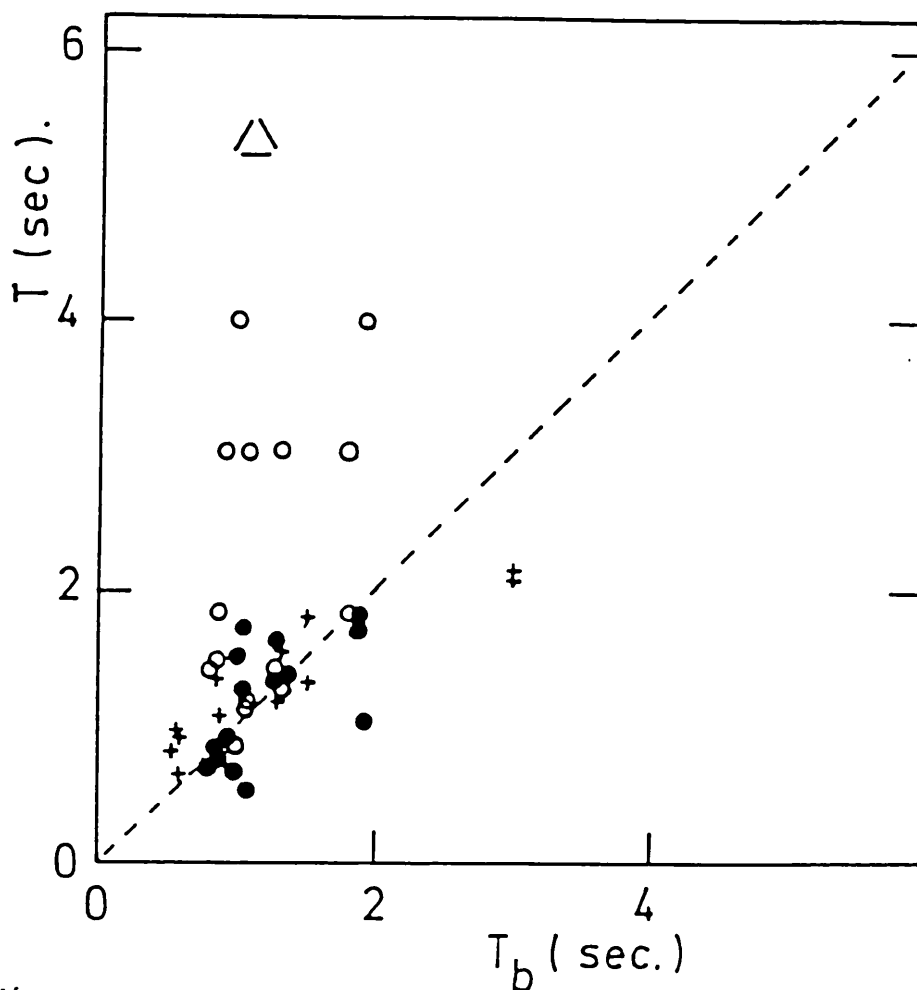


Figure 5.6 As for figure 5.3, but for background elements, $\triangle$. The line lengths were 0.5°.

The data for the normal subjects' eyes show similar reaction times for the single eye and both eyes together and are clustered along the $T = T_b$ line, but they show an increase in T values from elements 1 to $\triangle$ and $\triangleright$ to $\triangleleft$ and $1 \triangleright$.

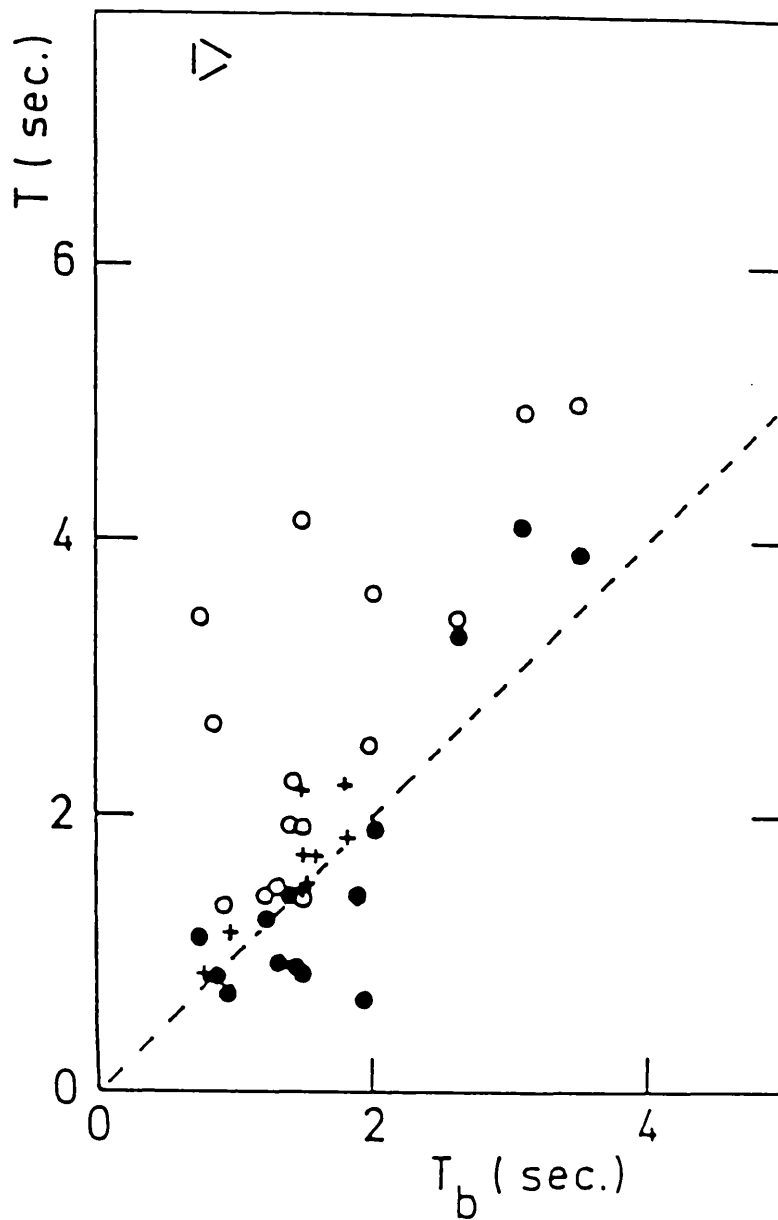


Figure 5.7 As for figure 5.3, but for background elements, $\triangle$. The line lengths were 0.5° .

(d) Discussion

These experiments measured two characteristics of spatial vision in amblyopia, the spatial response of the ST1 filter and the discrimination of pattern orientation. ST1 spatial responses for normal subjects peak at a spatial

frequency around 4 cycles/degree whereas those for the amblyopes peak at lower spatial frequencies for both 'normal' and 'abnormal' eyes. A similar result was found by Grounds, Holliday and Ruddock [1983] who suggested that the low spatial frequency shift which occurred for the 'normal' eye was due to the patching treatment for the squint given during childhood. All the amblyopes who took part in the experiments had patching treatment except J.P. and, in agreement with the suggestion of Grounds, Holliday and Ruddock [1983], this subject's 'normal' eye gave a normal ST1 spatial response with no shift in the peak frequency.

It has been suggested that the ST1 filter, with its small spatial extent and low-pass temporal response, corresponds to the X-type cells found pre-cortically in primate pathways (see section 2.2 (a) and the discussion section of Holliday and Ruddock, 1983). In Chapter Three it was also suggested that the light and dark contrast targets, which give similar ST1 filter responses, reflect the activity of 'on' and 'off' centre electrophysiological mechanisms. The amblyopic subjects show similar low frequency shifts of the ST1 spatial curve for both dark or light contrast targets and this implies that both their 'on' and 'off' centre X-type mechanisms are affected, and have larger receptive field sizes than normal. In experiments on strabismic amblyopia, induced by surgical manipulation during the critical period of the kitten eye, it was found [Ikeda and Tremain, 1978, 1979; Ikeda, Tremain and Einon, 1978; Ikeda, 1980] that both 'on' and 'off' centre X-type ganglion and geniculate cells had increased receptive field sizes compared with normal cats.

As the data of figure 5.3 shows the strabismic amblyopes perform as well as normal subjects at the discrimination of rotated single lines with either their 'normal' or 'abnormal' eyes. For the small (0.5° side length) triangular elements, however, responses for the amblyopes 'abnormal' eye are much

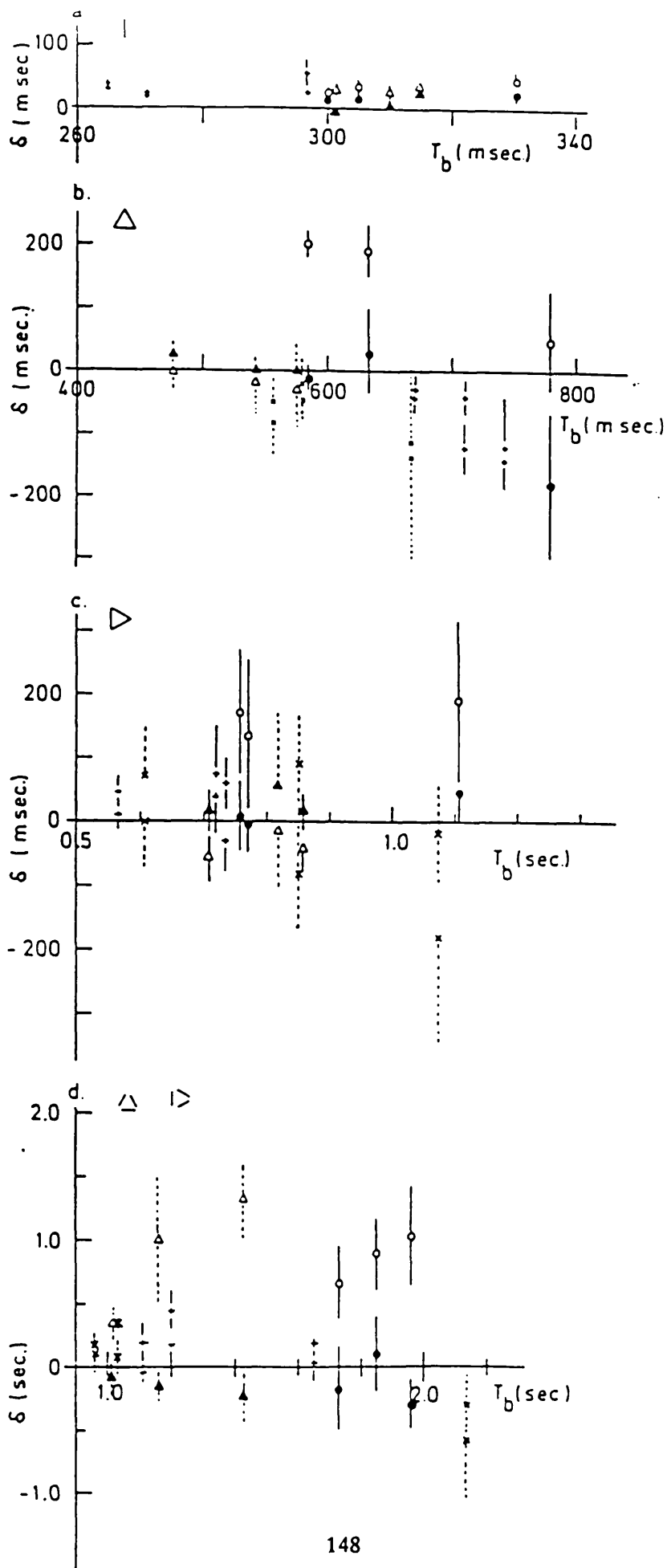


Figure 5.8 Value of δ , equal to $T - T_b$, plotted against T_b . Data taken from figures 5.3 to 5.7. (a) For background elements $\mid$ (figure 5.3). Data for the 'abnormal' eyes of the amblyopes are denoted by $\circ$ (0.5° line length) and Δ (1.5° line length); those for the 'normal' eyes are denoted by $\bullet$ (0.5° line length) and $\blacktriangle$ (1.5° line length); and for the normal subjects by $+$ (0.5° line length) and $\times$ (1.5° line length). (b) For background elements $\triangle$ (figure 5.4), symbols as for (a). (c) For background elements $\triangleright$ (figure 5.5), symbols as for (a). (d) For background elements $\triangleleft$ (figure 5.6) and $\triangleright$ (figure 5.7). Data for 'abnormal' eyes of amblyopes denoted by $\circ$ (elements $\triangleleft$) and Δ (elements $\triangleright$); data for 'normal' eyes of the amblyopes denoted by $\bullet$ (elements $\triangleleft$) and $\blacktriangle$ (elements $\triangleright$); data for normal subjects denoted by $+$ (elements $\triangleleft$) and $\times$ (elements $\triangleright$).

longer than for their 'normal' eye and for the eyes of normal subjects. The delayed responses for the 'abnormal' eye observed with some pattern elements is demonstrated in figure 5.8, where the average values of the difference, δ , between T obtained with a single eye and T_b obtained with both eyes (i.e. $T - T_b$), is plotted against T_b , the values being taken from the data in figures 5.3 to 5.7. With the small triangular elements δ values for the 'abnormal' eyes (data points $\circ$ and in figure 5.8(d) only, Δ) are large while those for the 'normal eyes' ($\bullet$ and $\blacktriangle$) and those for the normal subjects ($+$ and $\times$) are generally smaller corresponding to the result $T = T_b$. For the larger triangular elements (data points Δ in figures 5.8 (b) and (c)) and for the single lines (data points $\circ$ and Δ) δ values for the 'abnormal' eyes are similar to those for the 'normal' eyes, thus their performance is similar for each eye.

The amblyopes' poor discrimination performance for small triangular elements cannot be explained solely by a loss in spatial resolution associated with the low frequency ST1 spatial response because there is no correlation between discrimination performance and amount of shift of the ST1 curve peak. For example, subject D.G. showed the biggest difference between T values for the 'normal' and 'abnormal' eyes, whereas his ST1 curves, plotted in figure 5.9, peak to the high frequency side of the mean for the amblyopes.

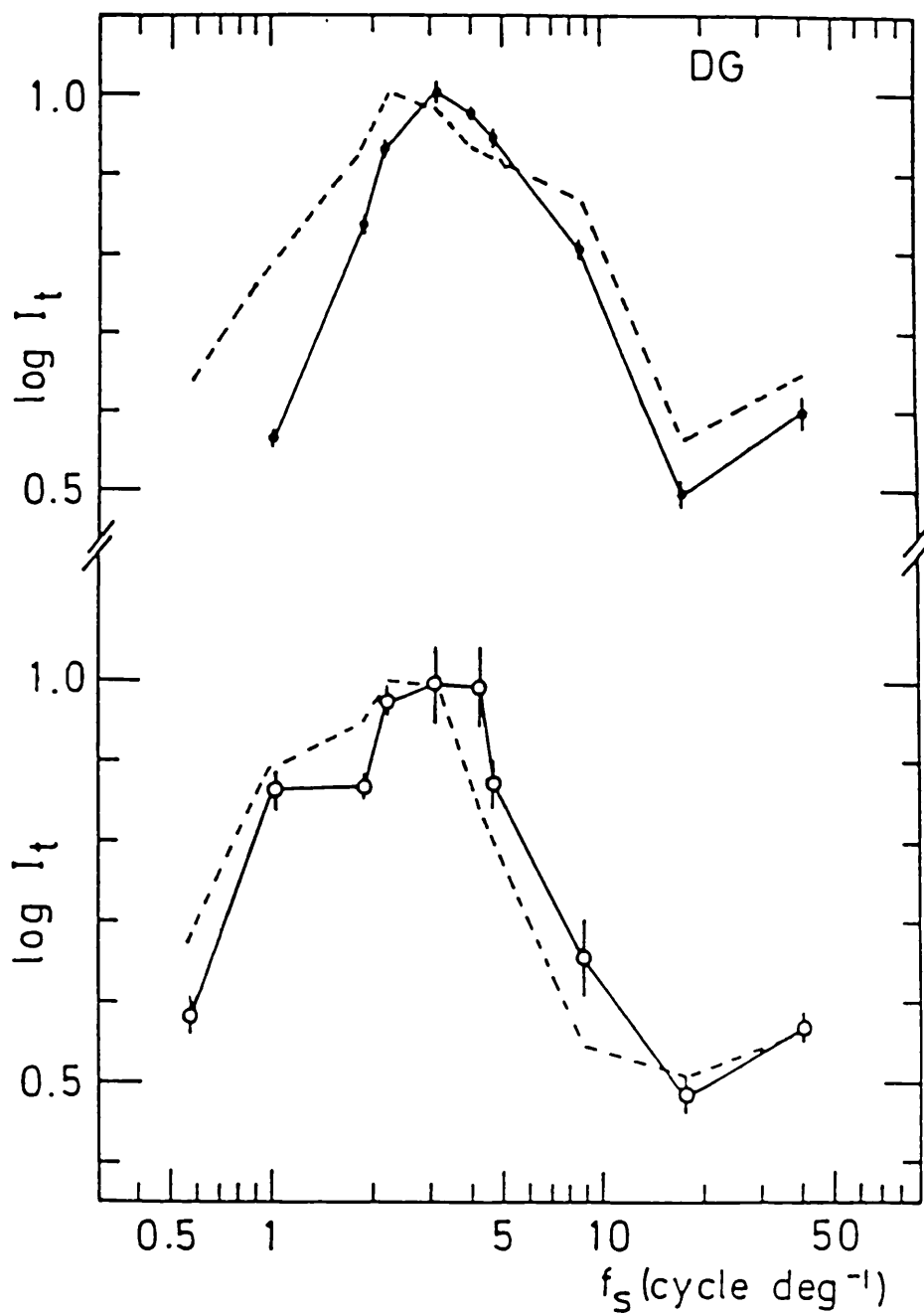


Figure 5.9 Data for the 'abnormal' eye of subject D.G. (full lines with symbols), plotted with the mean data for the 'abnormal' eyes of the five amblyopes taken from figure 5.2. Upper data sets refer to a dark target and lower data sets to a light target. Error bars give standard errors of D.G.'s data

It should also be noted that similar ST1 responses were obtained with both the 'normal' and 'abnormal' eyes of the amblyopic subjects but only their 'abnormal' eyes showed poor pattern discrimination ability. A corresponding result was obtained by Grounds, Holliday and Ruddock [1983], who found no correlation between the ST1 spatial response and Snellen acuity. It would be expected, however, that since the discrimination task performed in the present experiments involving high contrast targets is similar to the Snellen test, a correlation between performance on the two tests would be found. In order to examine this, the difference between T values, T_a (abnormal) and T_n (normal), for each eye of the amblyopes, averaged over all measurements with the small triangular elements, was plotted against Snellen acuity in figure 5.10. There is a strong correlation between the two variables with $(\overline{T_a - T_n})$ increasing as acuity falls. Subject D.G., however, has the largest value for $(\overline{T_a - T_n})$, despite having an intermediate value for Snellen acuity. This subject has a severe refractive error in his amblyopic eye ($3/60$ without correction and $6/12$ with correction) which was corrected for these experiments, but generally he does not wear refractive correction. His strabismic deficit is therefore compounded by a refractive deficit and this may contribute to the large T values for his 'abnormal' eye.

The results of these experiments can be compared with those of other studies on amblyopia. It is noteworthy that despite having severe loss in Snellen acuity, the amblyopic subjects are unimpaired at orientation discrimination for a background of single lines and Vogels, Orban and Vandenbussche [1984] using a different method of measuring discrimination of line orientation concluded that this response is unimpaired in amblyopia. Levi and Klein [1982] found that for strabismic amblyopes, vernier acuity is related to Snellen acuity but that performance at neither of these could be predicted

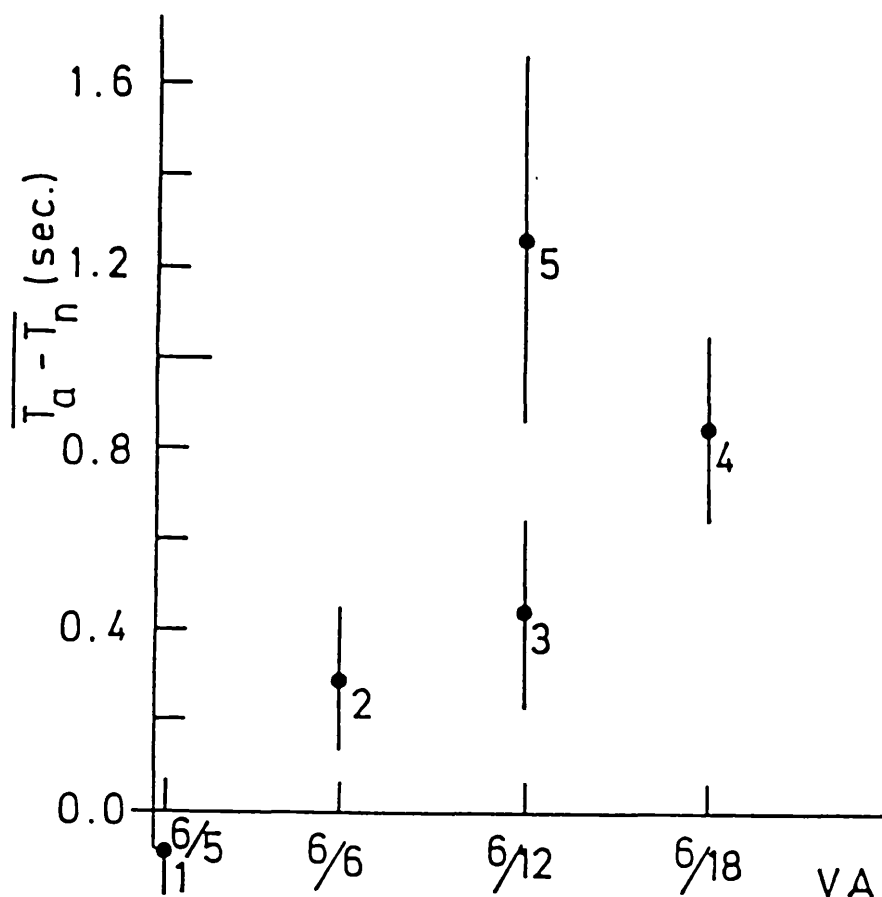


Figure 5.10 The difference between the characteristic response times recorded for the 'abnormal' and 'normal' eye of each amblyope, $\overline{T_a} - \overline{T_n}$, plotted against the Snellen acuity recorded for the 'abnormal' eye. Data are averaged for elements of line length 0.5° , taken from figures 5.4 (a), 5.5 (a), 5.6 and 5.7, and error bars denote standard errors of the means. Subjects P.D. (1), AM.N. (2), J.P. (3), M.G. (4) and D.G. (5).

from their resolution for simple gratings. The triangular elements used in the experiments described above, for which the amblyopes suffer loss of orientation discrimination (figure 5.4 to 5.7), are similar to the Snellen acuity targets, therefore the correlation between these experiments and visual acuity (figure 5.10) is to be expected. The ST1 responses (see figure 2.14) obtained with gratings probably arise at an early stage of visual processing [Holliday and Ruddock, 1983] and the lack of correlation in the amblyopic data between this

response and the orientation data for triangular elements is, therefore, consistent with Levi and Klein's [1982] conclusions.

Barbur and Ruddock [1980] found that for normal subjects the ST1 spatial response when measured non-foveally, shows a shift in its peak position to lower spatial frequencies similar to that obtained by the amblyopes. Levi and Klein [1986] concluded that both normal peripheral vision and central vision in strabismic amblyopia are characterized by sparse sampling in the spatial domain, and the low frequency ST1 spatial characteristics imply precisely such a mechanism.

The amblyopic discrimination responses were simulated in normal subjects by degrading or demagnifying the images. Thus a defocusing +4 diopters lens caused a five-fold increase in T values for J.M.B (background elements Δ). Decreasing the elements to half their previous minimum size (sides of length 0.25°) increases T by a factor of 1.5 (subject J.M.B.) and 1.6 (subject A.J.) with background elements Δ and by a factor of 1.25 (subject J.M.B.) and 1.7 (subject A.J.) with background elements $\triangleright$. Thus degradation of image quality or reduction of stimulus size both lead to increase in the response time T, and therefore the amblyopic data for the 'abnormal' eye are consistent with responses of a system with reduced spatial resolution.

Strabismic amblyopes have a deficit in first stage processing of spatial information, as is shown by the shift to lower spatial frequency of their ST1 spatial mechanism. Their visual problems cannot be attributed solely to this change in ST1, however, as their poor performance at orientation discrimination observed for some targets, occurs only for their 'abnormal' eye and not for their 'normal' eye, despite the fact that ST1 responses are similar for the two eyes. It is concluded that other factors, arising centrally with respect to the ST1 filter, must contribute to the loss of visual resolution and reduced discrimination in amblyopia.

5.3 Examination of Spatial Processing in Visual Agnosia

(a) Experimental Procedure

The majority of the experiments to investigate spatial processing in visual agnosia were carried out using the computer controlled, colour monitor and involved the measurement of pattern discrimination ability. The stimulus patterns used are shown in figure 2.31, the background element being the first of each set of four, followed by the three targets. A background element provides a fourth, or 'null' target, and the number of errors for this target gives a measure of an observer's accuracy. The pattern stimuli are arranged in groups according to the parameter by which targets are differentiated from the background – orientation, magnification, texture, lightness and distortion. Reaction times to find targets were measured and the results are characterized by the time, $T_{1/2}$, at which a target is detected on 50% of occasions. A single experiment consists of twenty-five presentations of each target i.e. for each set of elements in figure 2.31 a hundred presentations are made, and at each presentation, any one of the targets may appear. For many of the patterns the experiment was repeated and a total of two hundred presentations were made for each group of four elements.

In the majority of the experiments to be described there were 20 background elements, as a greater number than this made the experiments excessively difficult and tiring for the visual agnosic subject. However, in the orientation discrimination experiments, a background of 40 elements was used for the discrimination of straight lines and parallel lines. A background of 40 elements was also used in the magnification discrimination of straight lines.

Two other experiments, in which the background parameters were varied, were carried out. One measured the effect of the number of

background elements, N , on response times and error rates, for which values of $N=1, 2, 3, 4, 5, 7, 10, 15$ and 20 were used with pattern stimuli $\triangle$     and $N=1, 5, 10$ and 20 with the pattern stimuli $\triangle$ ∇ $\triangleright$ $\triangleleft$. The other investigated the influence of target separation, s , on response times and error rates when one background and one target drawn from the pattern stimuli $\triangle$     were used. The procedure for this experiment is described in section 2.4 (c).

Where possible, timing was carried out using the short time scale, with timing of responses up to 1500ms, in order to obtain the best resolution, but for most of the experiments involving the visual agnostic subject the larger timescale (described in section 2.4 (a)) was necessary, and this extended the timescale to 10 seconds. At the end of each experiment the number of errors made for each target type was recorded. The screen was viewed with both eyes and it was of dimensions $9.5^\circ \times 7.1^\circ$ while the single line targets, the sides of the triangular and square elements and the diameter of the circular and half-circular targets were all of 30 minutes of arc length and of width 2 minutes of arc. These dimensions were varied only in experiments involving change in magnification.

The Maxwellian view optical system (figure 2.2) was used to determine increment threshold for detection of a circular, 3.5° diameter, light target flashed, for 0.1 seconds, on the centre of a 30° diameter, uniform background, the method of measurement being described in section 2.2 (d). Threshold illumination for the target was determined as a function of background illumination, I_b , using the threshold program (section 2.2 (a)). The Wright tristimulus colorimeter which provides near monochromatic stimuli [Wright, 1927-28, 1946] was used to check the visual agnostic subject's wavelength discrimination and brightness matching. Contrast threshold sensitivity was

determined with photographic plates designed by Barbur [1986], and stereoscopy with two-colour anaglyphs [Julesz,1971].

(b) The Visual Agnosic Subject

H.J.A. is a sixty-seven year old man who until 1981 had normal vision. In April 1981 he suffered a 'stroke' after a surgical operation and following this he has had problems with recognizing even familiar objects. The deficit is restricted to vision, as other senses appear to function normally. He cannot recognize friends and relatives by their faces, although he can see their eyes, noses etc., but as soon as they speak or make any gesture peculiar to themselves he can identify them. He can recognize some objects by using contextual information, but he finds pictures of objects particularly difficult to recognize although he can copy them (but in a slavish line-by-line fashion). Because of his visual agnosia he also has difficulty finding his way around (topographical agnosia) and difficulty with reading. Immediately after the stroke, he could not read at all but with practice he has improved and can read typed script in a letter-by-letter fashion. He has considerable difficulty with cursive handwriting and although he can write he cannot easily read back what he has written. He also has no colour discrimination (achromatopsia), as one of the tests carried out shows, and he describes everything he sees as being in shades of grey.

The basic features of his spatial vision have been described elsewhere [Humphreys and Riddoch, 1984, 1987]. He has a bilateral scotoma in the upper half visual fields but with appropriate refractive correction he has $6/6$ Snellen visual acuity in the intact field. The scotoma did not extend completely to the fovea and under the conditions used in the experiments he was still able to see the whole screen when he fixated on the lower edge.

A CT X-ray scan (figure 5.11) shows extensive brain damage in both occipital lobes, in the area supplied by the posterior cerebral artery. His condition is stable and he is a good subject, being very keen and interested in the experiments he performs. The stroke caused no impairment of intellectual ability or memory and none of his other senses is affected.

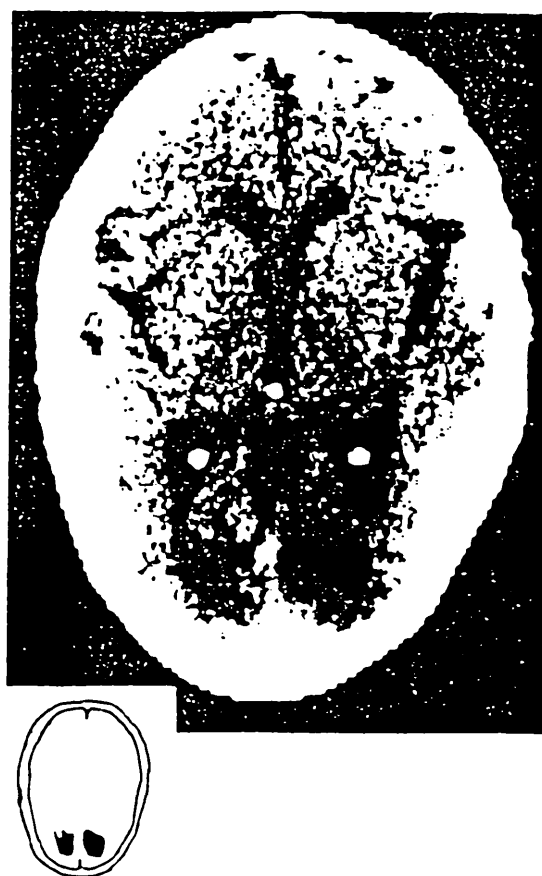


Figure 5.11 CT X-ray scan of H.J.A. The marked areas on the inset diagram show a bilateral lesion in the region supplied by the posterior cerebral artery.

In order to provide comparison data for normal performance, a large number of naive subjects carried out the same experiments as H.J.A., under the same conditions.

(c) Results

Orientation discrimination

Orientation discrimination was measured for linear and two dimensional elements (figure 2.31) and both $T_{1/2}$ and error rates recorded and plotted in figure 5.12 (a) to (l). Data points $\circ$ are for H.J.A. and data points $\bullet$ are for the averaged data of three normal subjects. All the error scores both for normal subjects and H.J.A. were, in the case of single line elements, less than 5% and are not plotted.

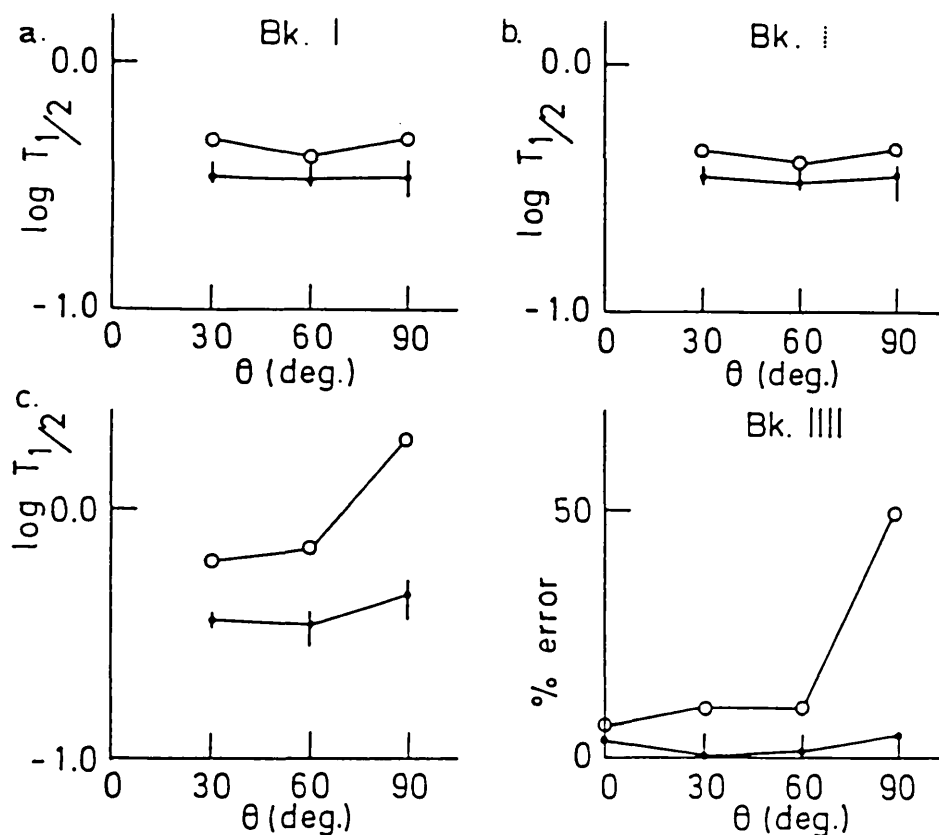
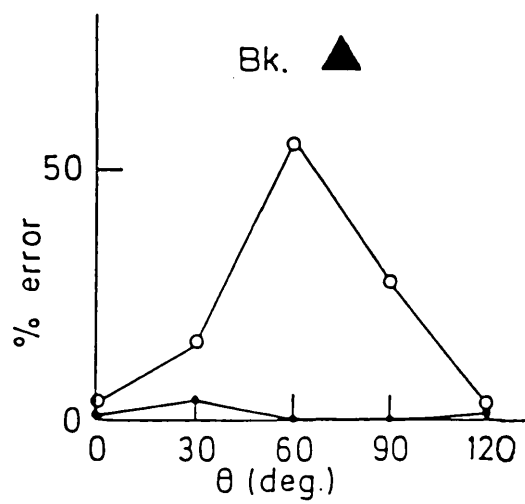
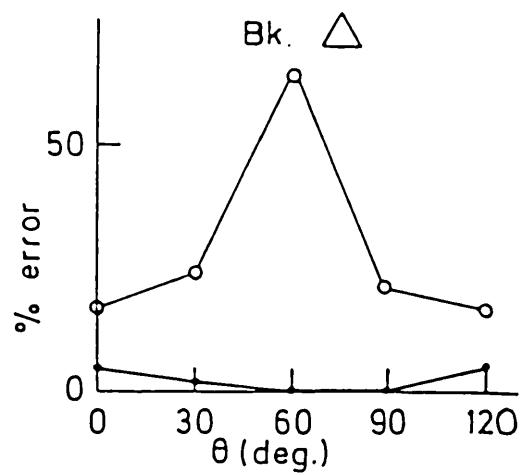
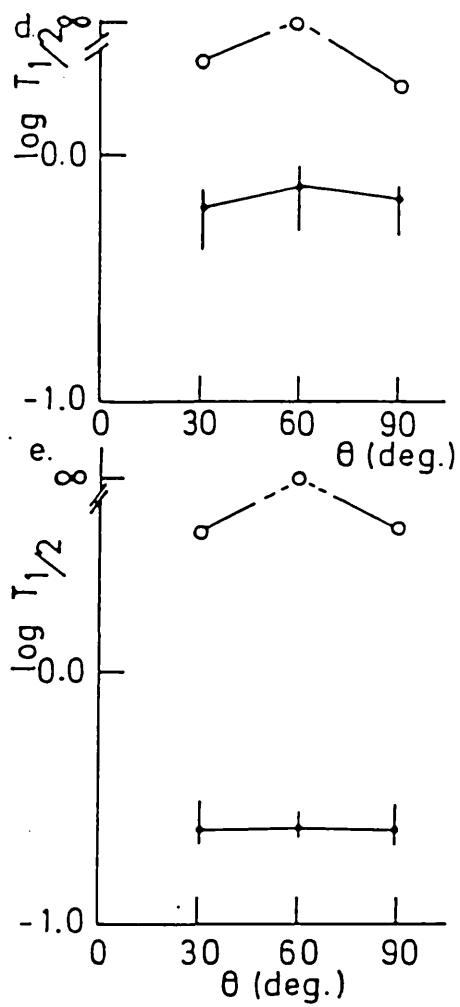


Figure 5.12 Orientation discrimination for subject H.J.A. (open circles) and mean data for three normal subjects (full circles). Values of the time $T_{1/2}$, for the target to be detected on 50% of occasions are plotted against target orientation θ for (a) straight line elements, I (b) dotted line elements, II and (c) elements consisting of four parallel lines IIII. Error scores for elements I, II were not more than 5%. Error bars on the normal data denote the spread between the three subjects.



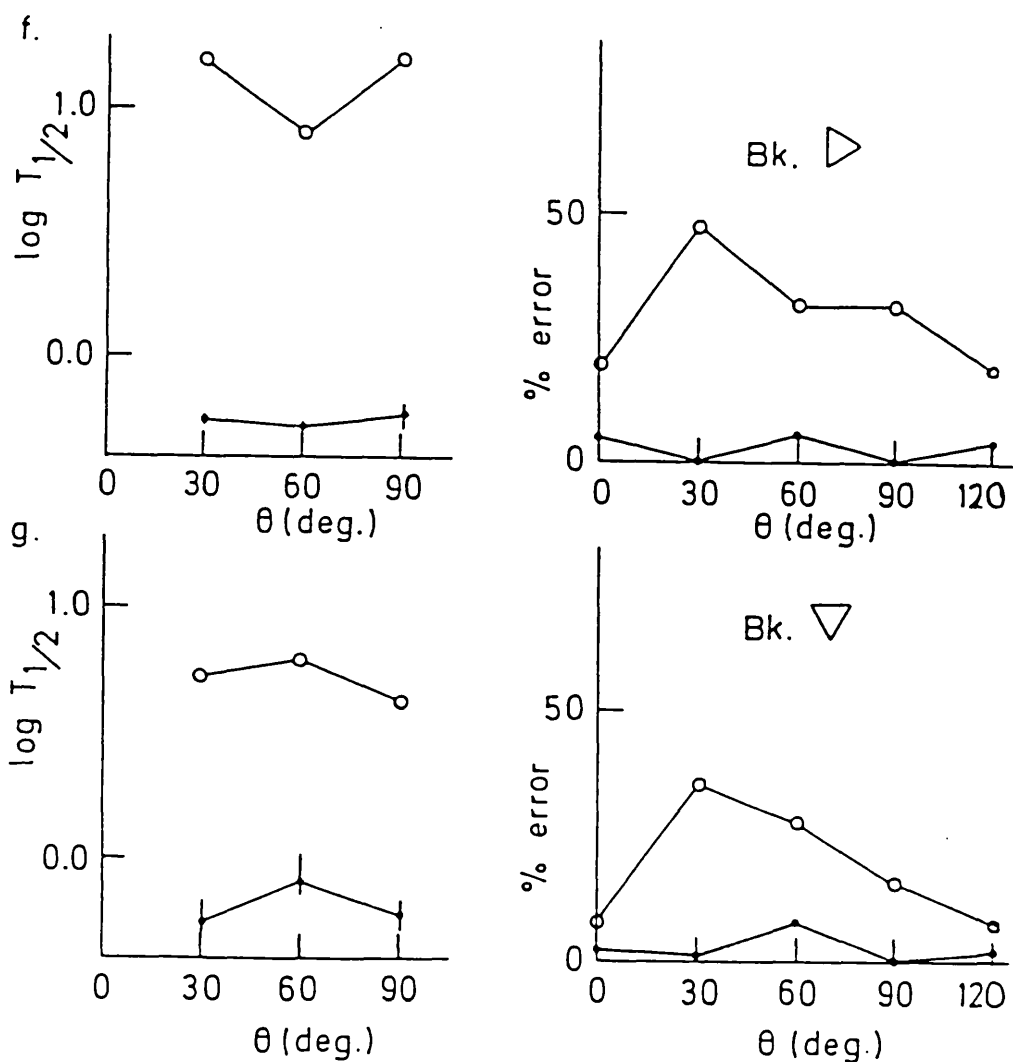
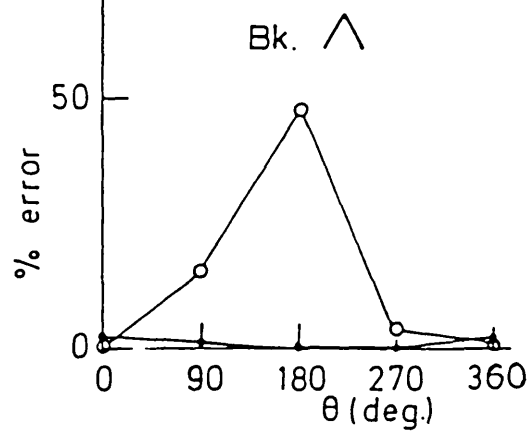
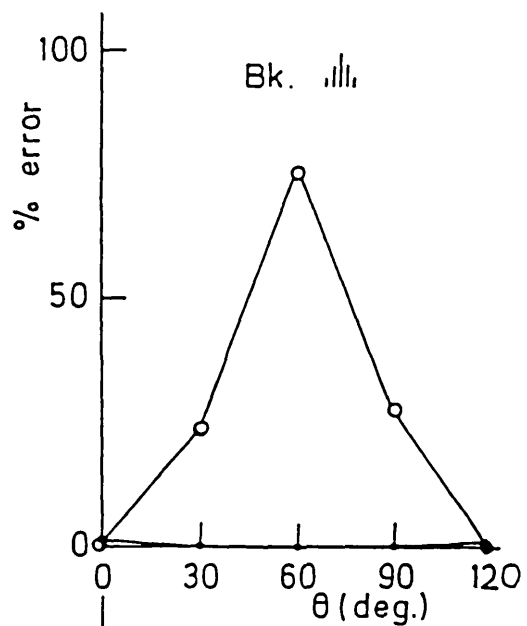
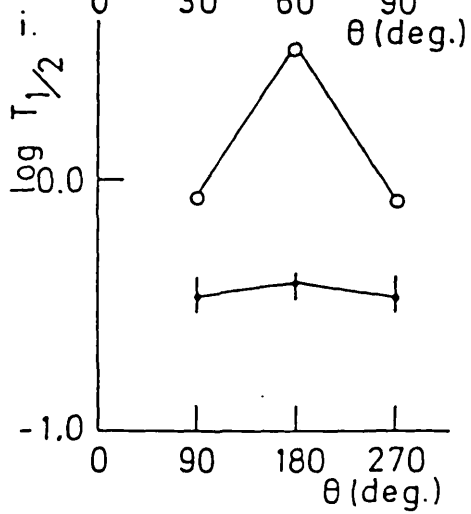
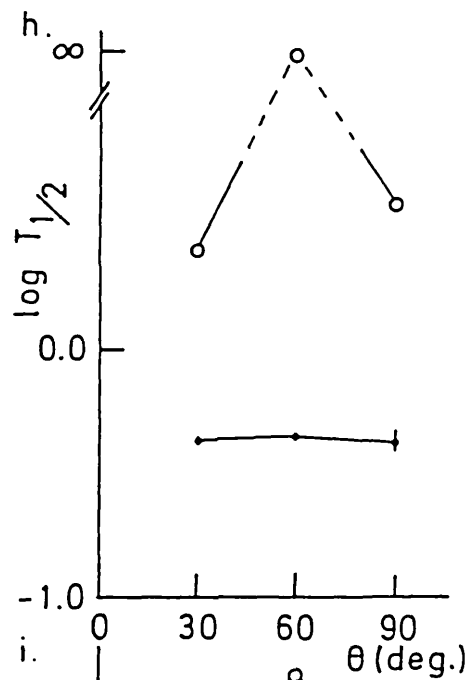
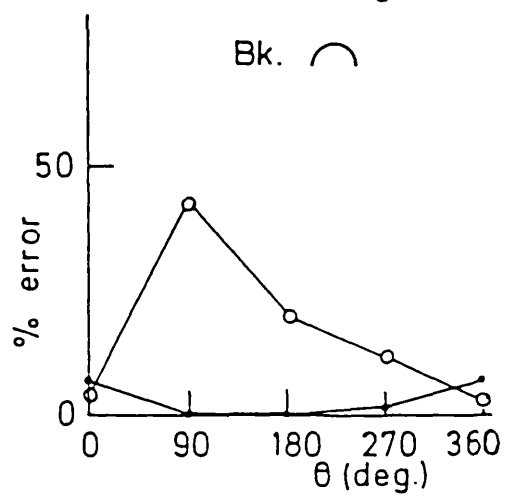
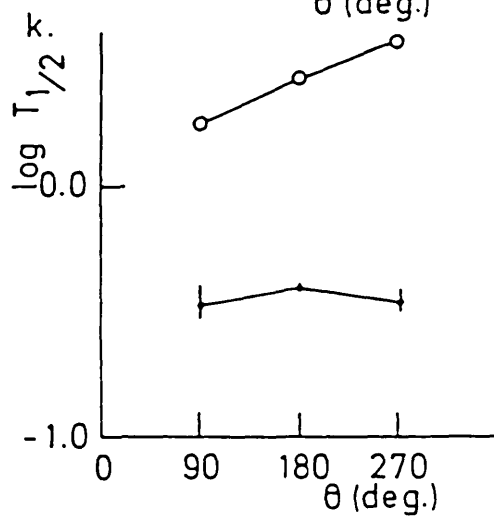
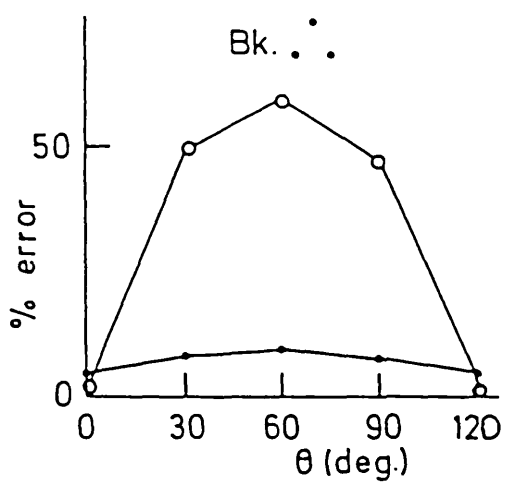
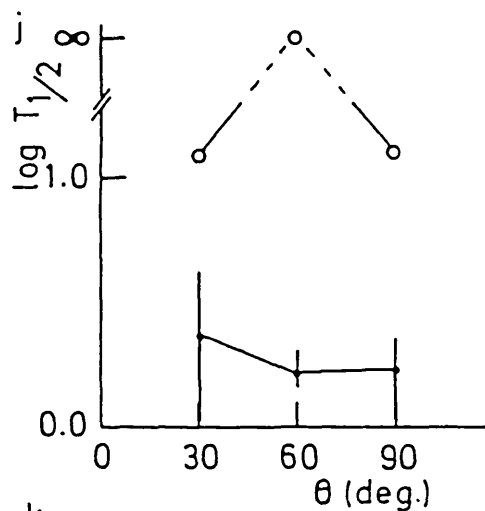


Figure 5.12 cont. $\log T_{1/2}$ and percentage error plotted against target orientation. (d) Elements $\triangle$, (e) elements $\blacktriangle$, (f) elements $\triangleright$ and (g) elements ∇ . Data points $\circ$ for H.J.A. and $\bullet$ for the averaged data of normal subjects.





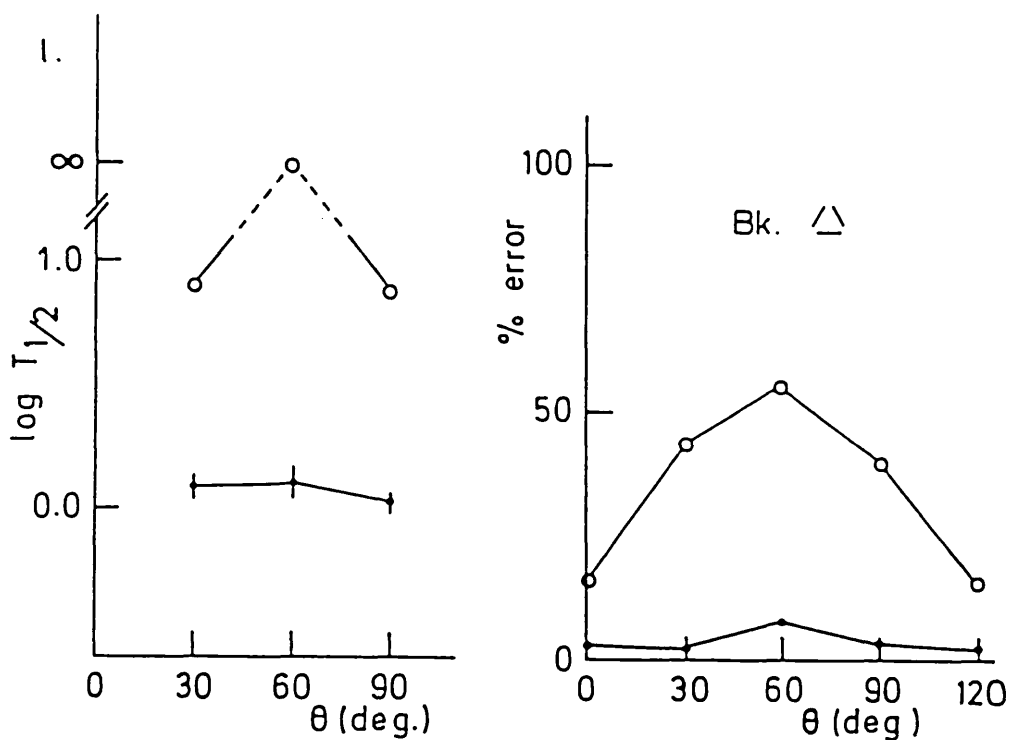


Figure 5.12 cont. As for (d) (h) elements $\parallel$, (i) elements $\wedge$, (j) elements $\cdot\cdot$ (k) elements $\cap$, (l) elements $\triangle$.

H.J.A.'s $T_{1/2}$ values vary enormously from near normal for $|$ and $:$ elements to very poor for many of the two dimensional elements. For some of the triangular elements he does not manage to detect the mirror image target e.g. $\triangle \rightarrow \nabla$ on 50% of occasions. The difference between H.J.A.'s response times and those of the normal subjects is illustrated further by figure 5.13. For the null target, H.J.A.'s error score is as low or lower than that of the normal subjects, but for the other targets he has larger error scores, the largest occurring in conjunction with the largest values of $T_{1/2}$.

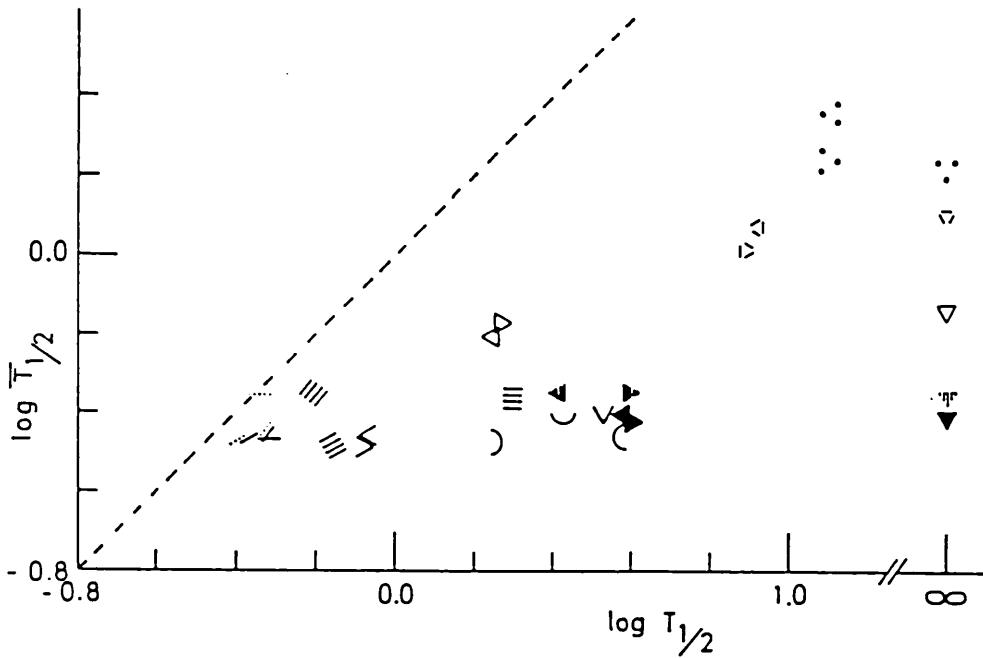


Figure 5.13 The mean values of $T_{1/2}$ for the three normal subjects for each target type are plotted against the $T_{1/2}$ values obtained by H.J.A. The target type is plotted as the data point and the data are from figure 5.12.

Magnification Discrimination

In figure 5.14 $T_{1/2}$ values and error scores for magnification discrimination are plotted against the magnification of the target, expressed as δl , the difference between the line length of the elements from which the different patterns ($\mid$, Δ and $\square$) are constructed. On the positive δ axes the target is bigger than the background and on the negative δ axes it is smaller than the background. H.J.A.'s $T_{1/2}$ values (data points $\circ$) are greater than normal (data points $\bullet$) and similarly to the orientation discrimination data, his error scores are largest when his $T_{1/2}$ values are slowest, although in all cases except one, his error score for the null target is as low as that of the normal subjects.

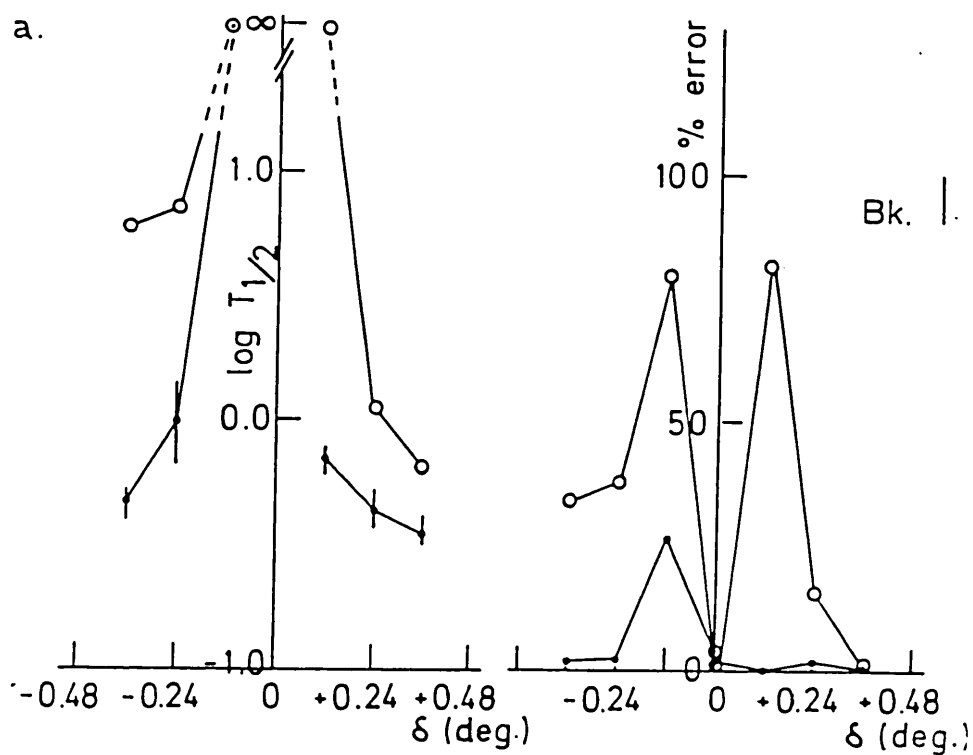


Figure 5.14 Magnification discrimination for subject H.J.A. (open circles) and the means for three normal subjects (full circles). $T_{1/2}$ values and error scores for discrimination of magnified and reduced targets. δ is the difference between the line lengths of the background element and target, positive values correspond to magnified targets and negative values to reduced ones. (a) elements I, (b) elements Δ and (c) elements $\square$.

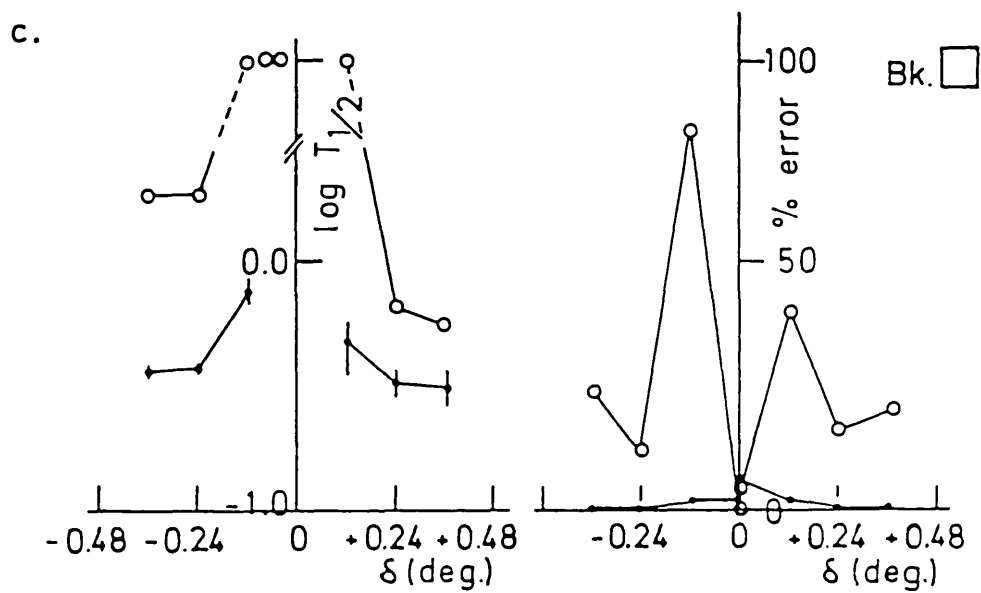
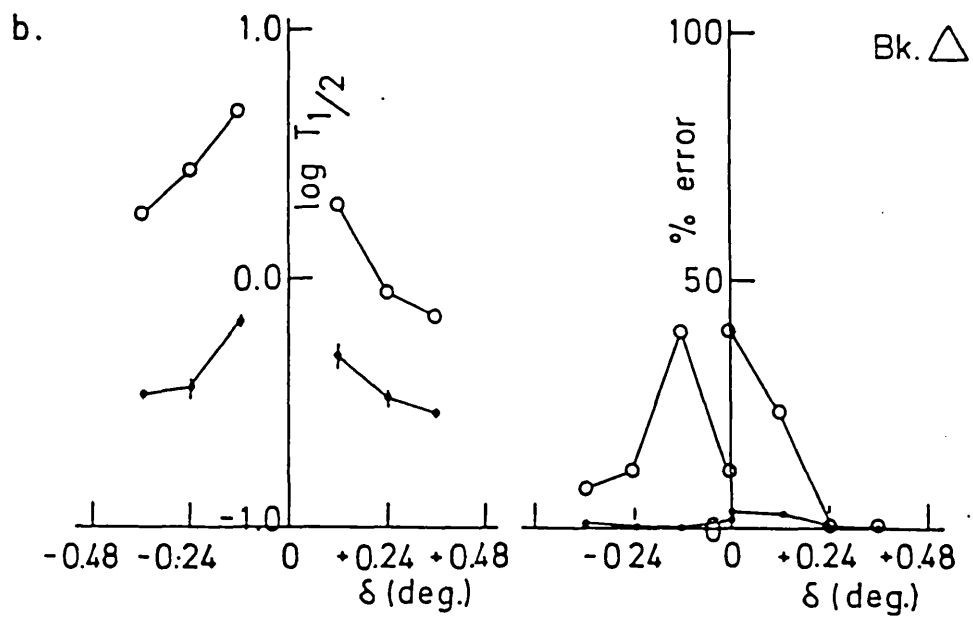
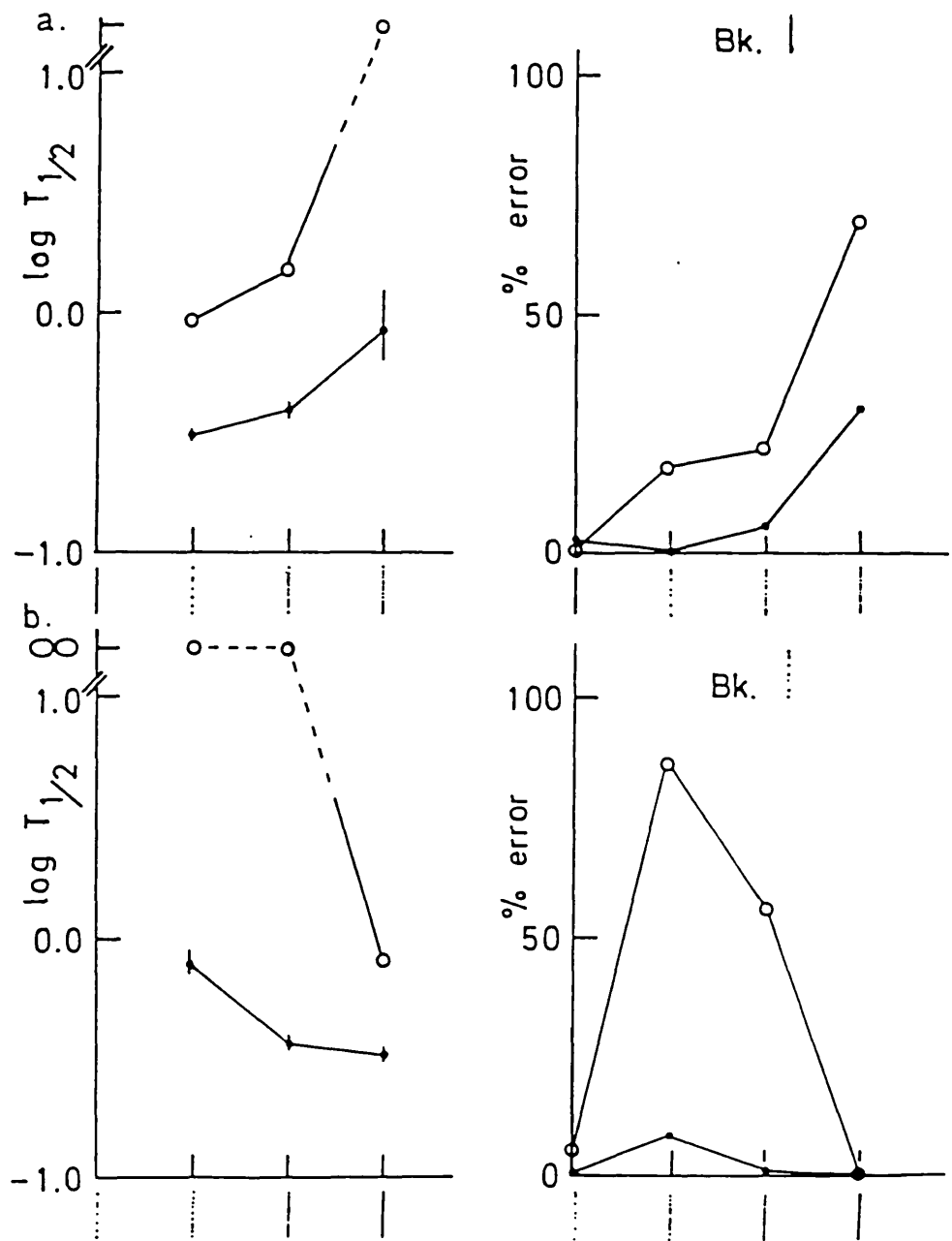


fig 5

Texture Discrimination

The pattern elements used for texture discrimination are shown in figure 2.31 and the different targets are identified on the graphs of figure 5.15. H.J.A.'s $T_{1/2}$ and error scores are once again larger than the normals for linear and two dimensional pattern elements except for the null target, where his error scores are as small as those of the normals.



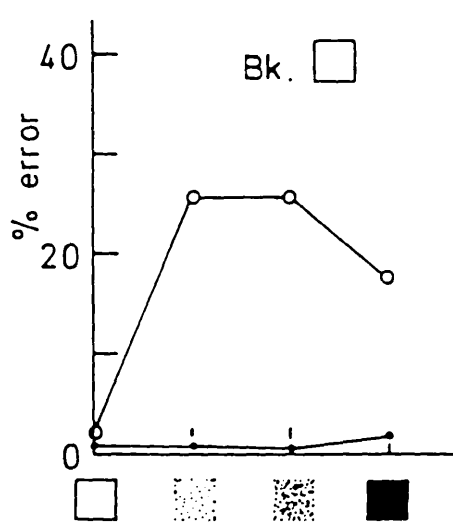
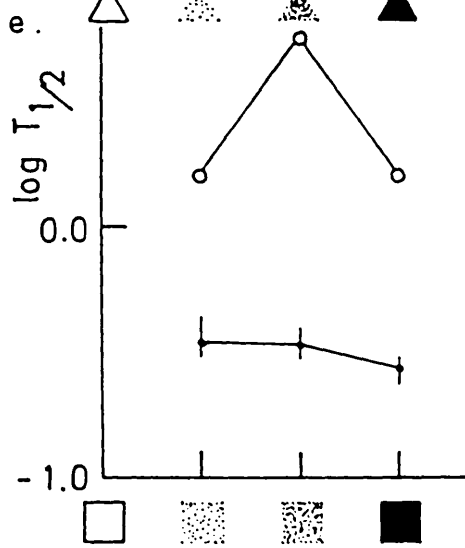
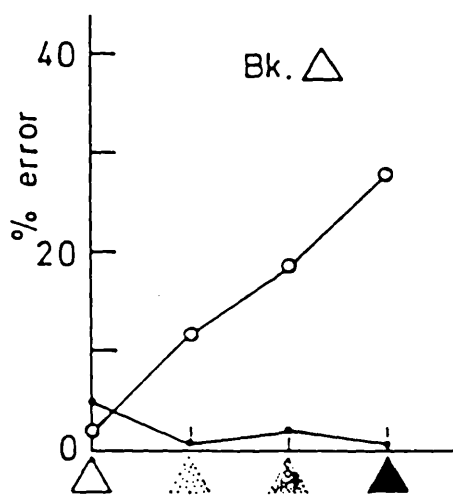
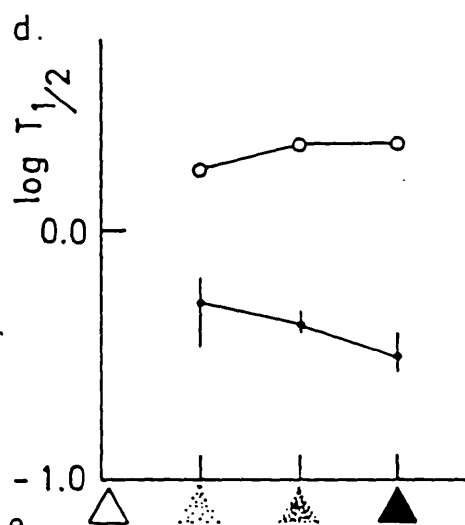
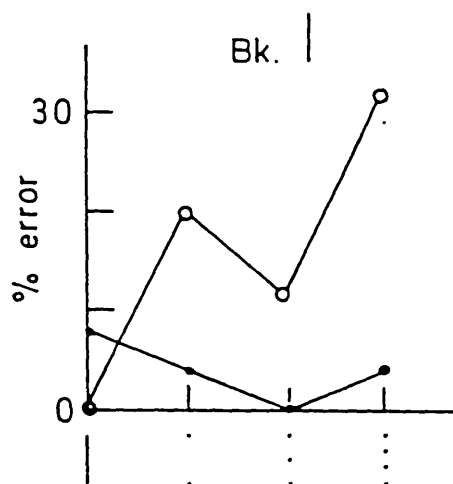
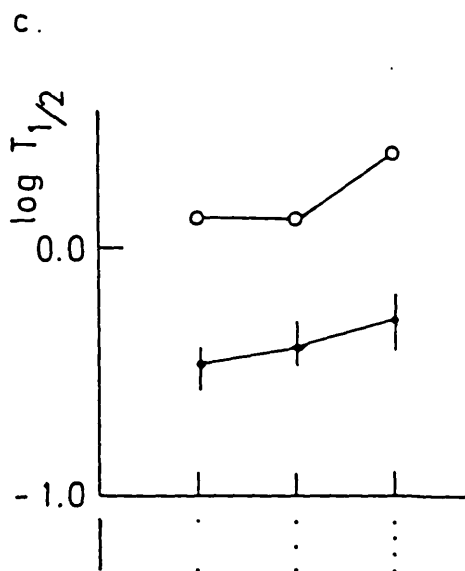


Figure 5.15 Texture discrimination for subject H.J.A. (open circles) and the mean for three normal subjects (filled circles). $T_{1/2}$ values and error scores plotted against target texture. The different targets are drawn on the abscissa and the background elements at the top right of each data set.

Lightness/Darkness Discrimination

In figure 5.16 $T_{1/2}$ and error scores for lightness/darkness discrimination with single line and triangular elements are plotted. The lightness/darkness of a target is denoted by a reference number. H.J.A.'s $T_{1/2}$ values and error scores are greater than the normal values showing that he has poor discrimination of patterns by difference in lightness/darkness.

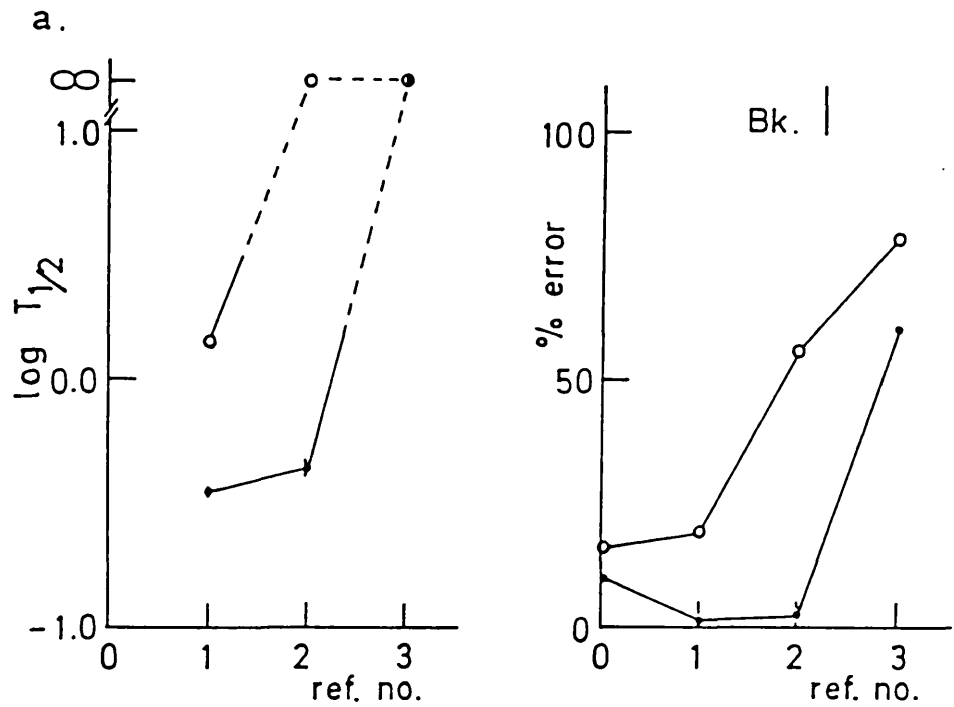


Figure 5.16 Lightness discrimination for H.J.A. (open circles) and mean data for three normal subjects (full circles). $T_{1/2}$ values and error scores plotted against the lightness/darkness of the targets denoted by a reference number. The reference numbers denote the following relative luminances of the targets: (a) 125 : 1 : 32 : 72. (b) 1 : 32 : 72 : 125. (c) 125 : 1 : 32 : 72.

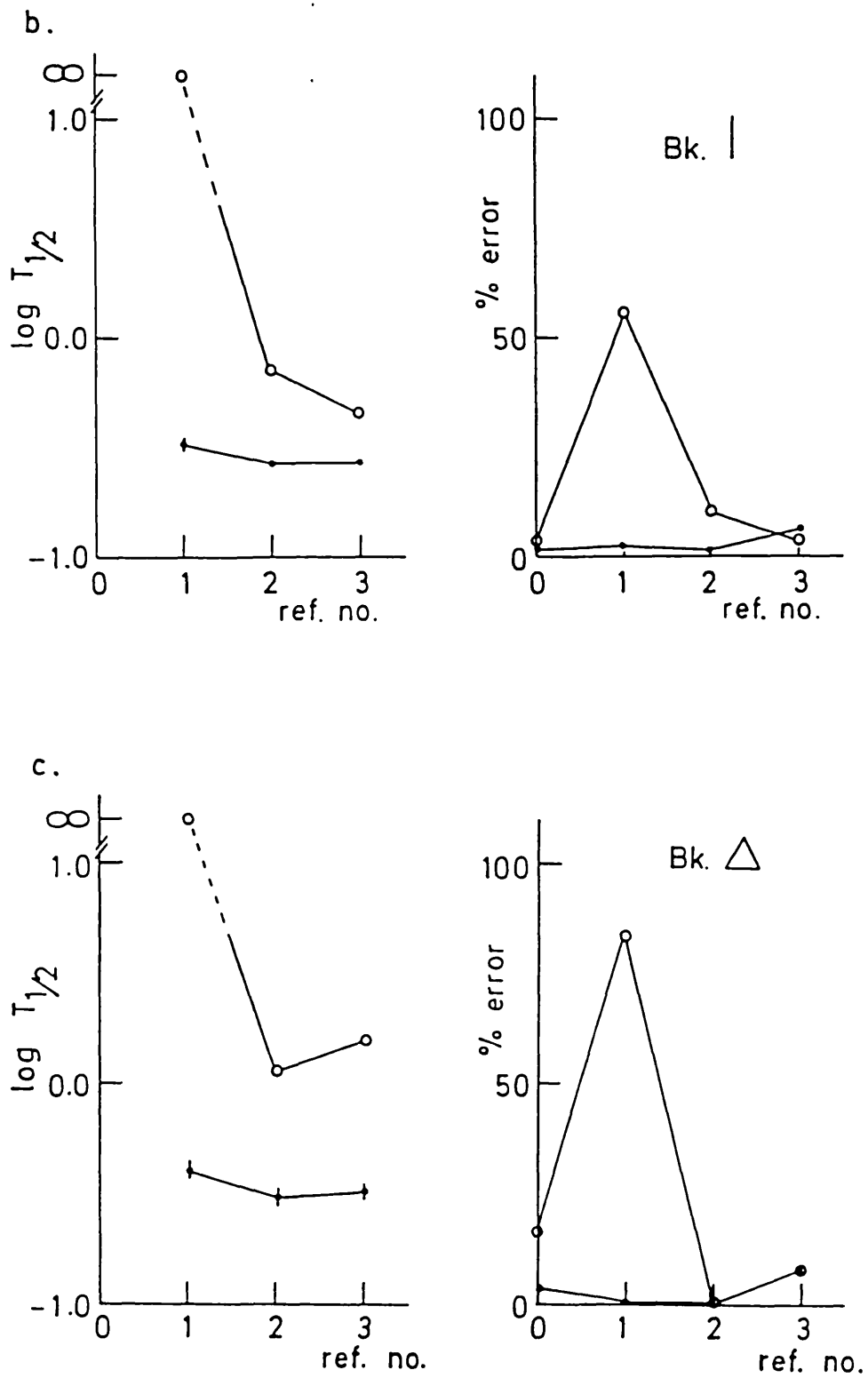


Figure 5.16 (cont.)

Distortion Discrimination

In these experiments the background element was always a triangle Δ and targets differed from it in their spatial structure. They are illustrated on the horizontal axes of figure 5.17 where both $T_{1/2}$ values and the error rates are plotted. H.J.A.'s $T_{1/2}$ values and error scores, except in the case of the null target, are larger than those of the normal subjects. His performance is least bad for the targets made up of three dots, e.g. $\cdot\cdot\cdot$, followed by parallel lines, e.g. $\parallel\parallel$ and the single line, $|$. When given another clue to use in discrimination e.g. orientation $\cdot\cdot^{\cdot}$, his values are lower again.

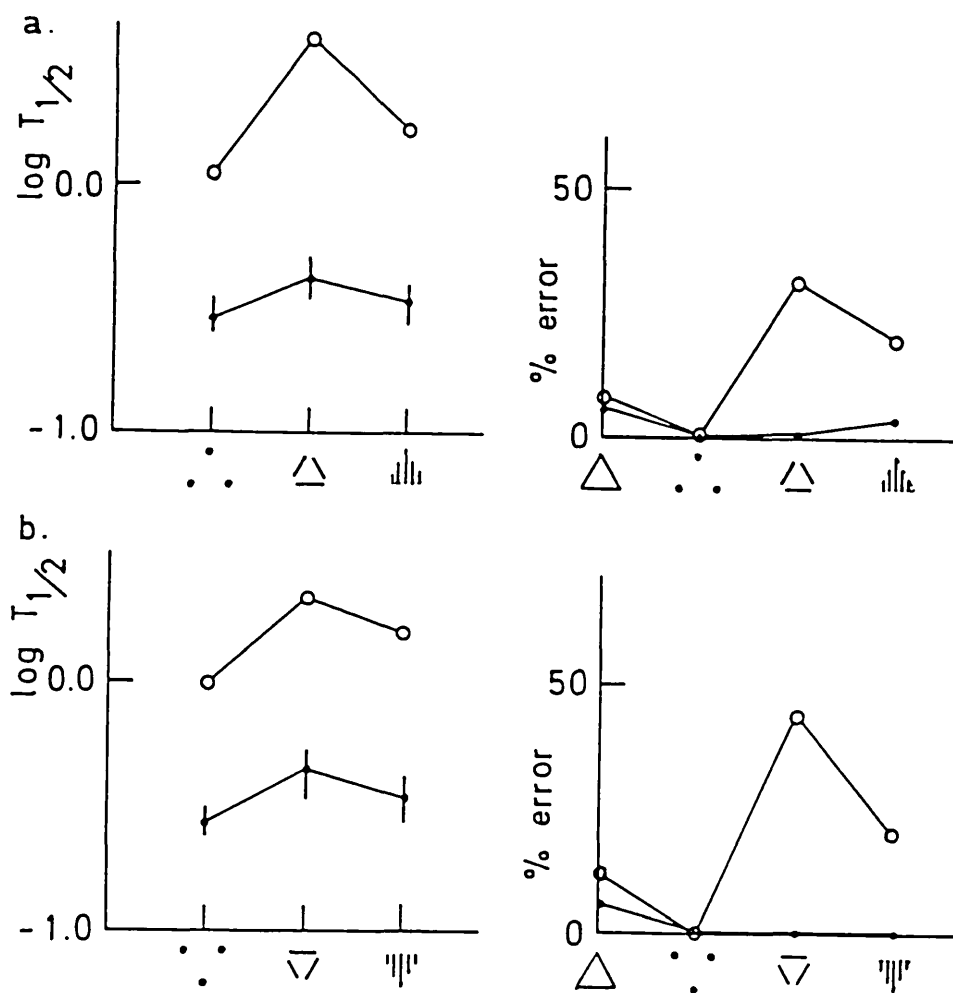


Figure 5.17 Pattern discrimination for H.J.A. (open circles) and mean data for three normal subjects (full circles). $T_{1/2}$ values and error scores plotted against the target pattern. In all experiments the background element was Δ .

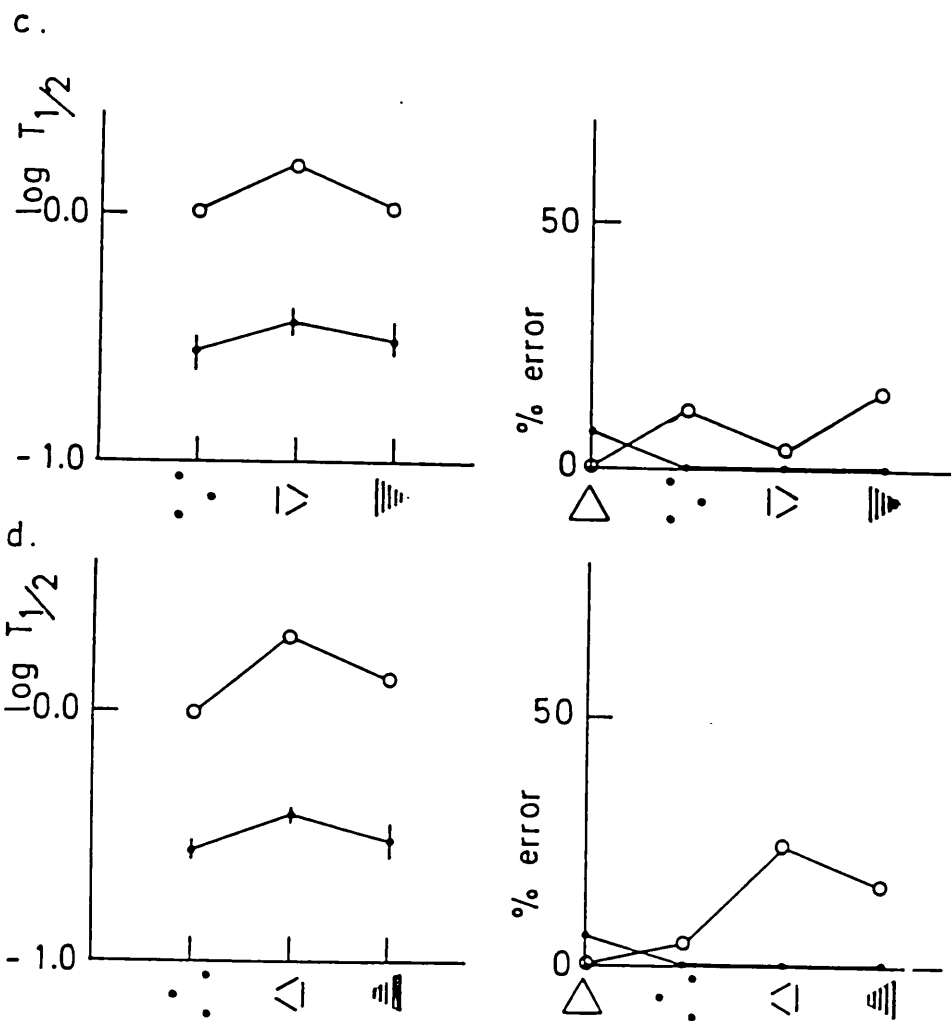


Figure 5.17 (cont.)

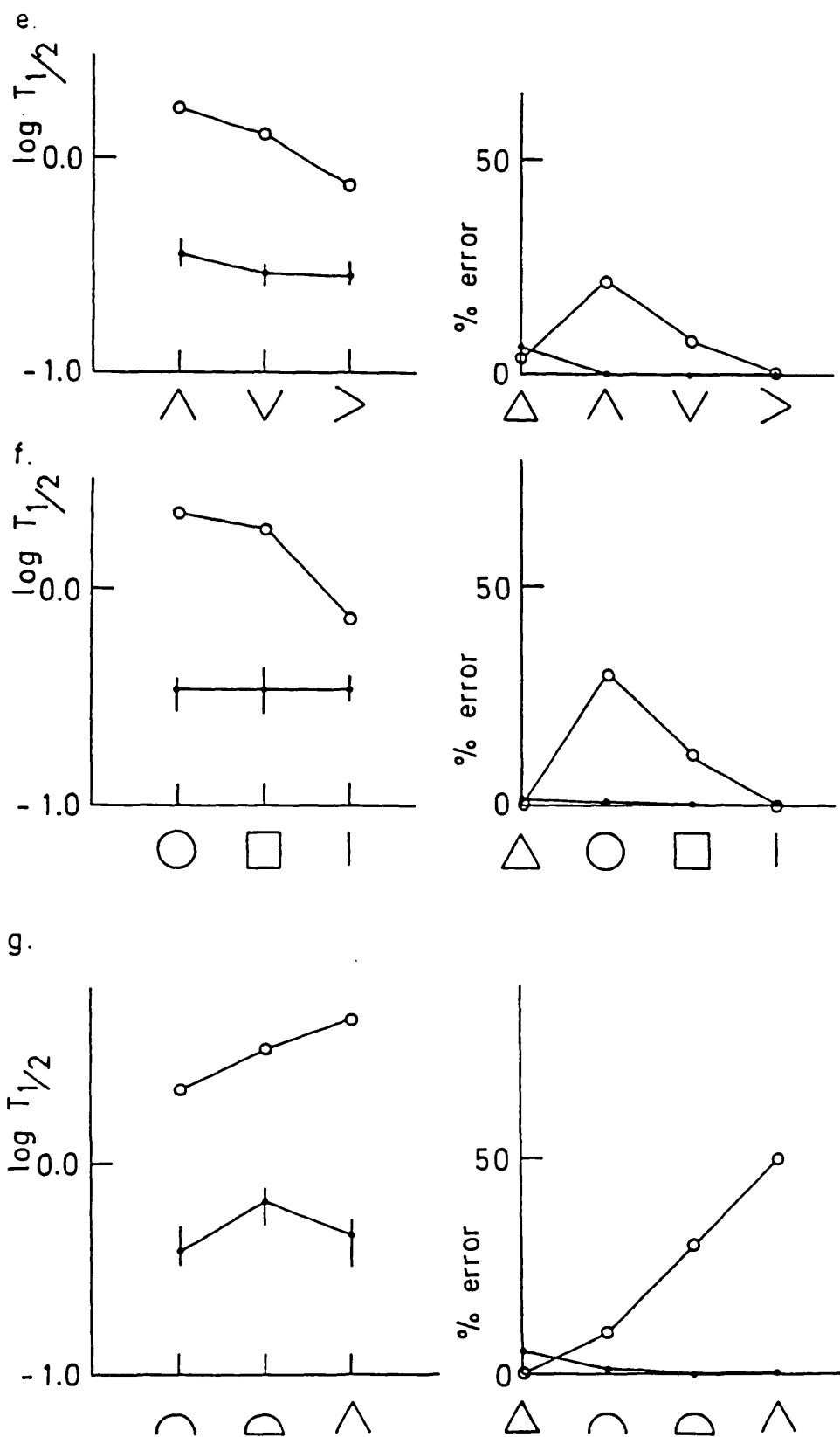


Figure 5.17

Variation of the Number of Background Elements

The influence of N , the number of background elements, on H.J.A.'s $T_{1/2}$ values and error scores are plotted in figure 5.18 (a). The background element was a triangle, $\triangle$, and the different targets are illustrated on the graph. $T_{1/2}$ values for two normal observers are plotted in figure 5.18 (b). For H.J.A. there is a strong correlation between $T_{1/2}$ and N for all the targets investigated, whereas, for the normal subjects there is very little variation of $T_{1/2}$ with N . However, results similar to those of H.J.A. can be produced in normal subjects by using appropriate targets. This is illustrated in figure 5.18(c) for target elements $\cdot \cdot \cdot$.

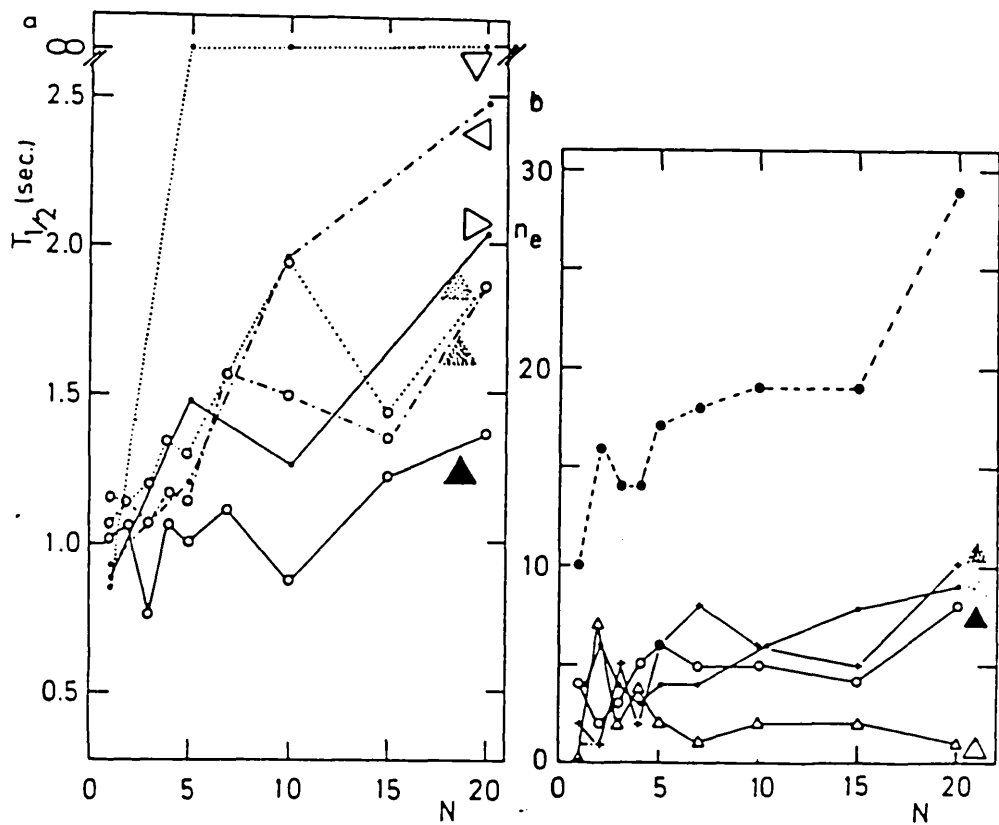
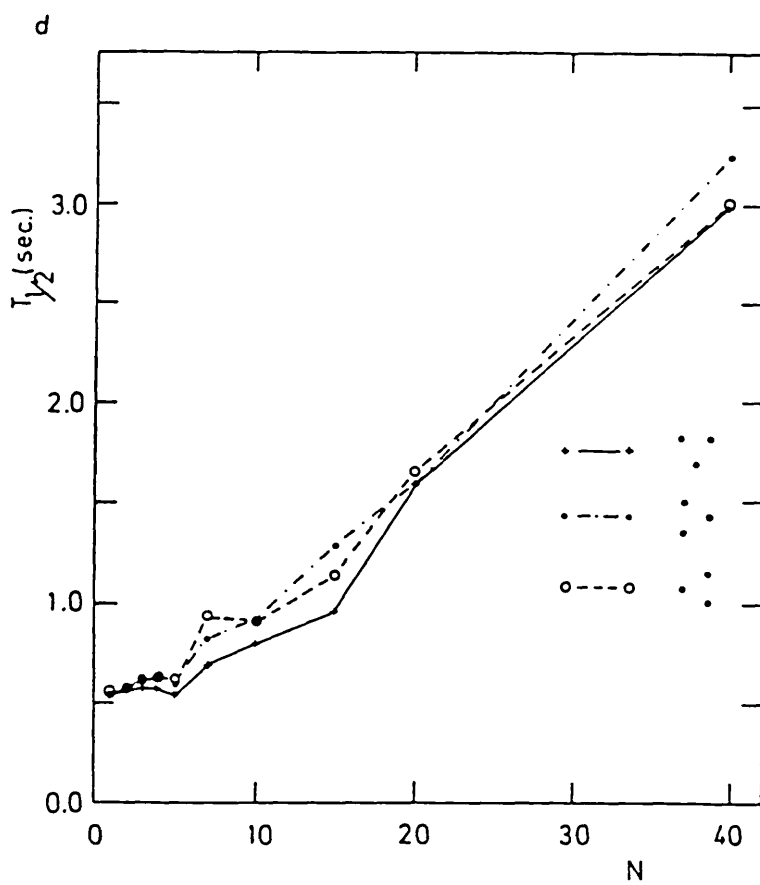
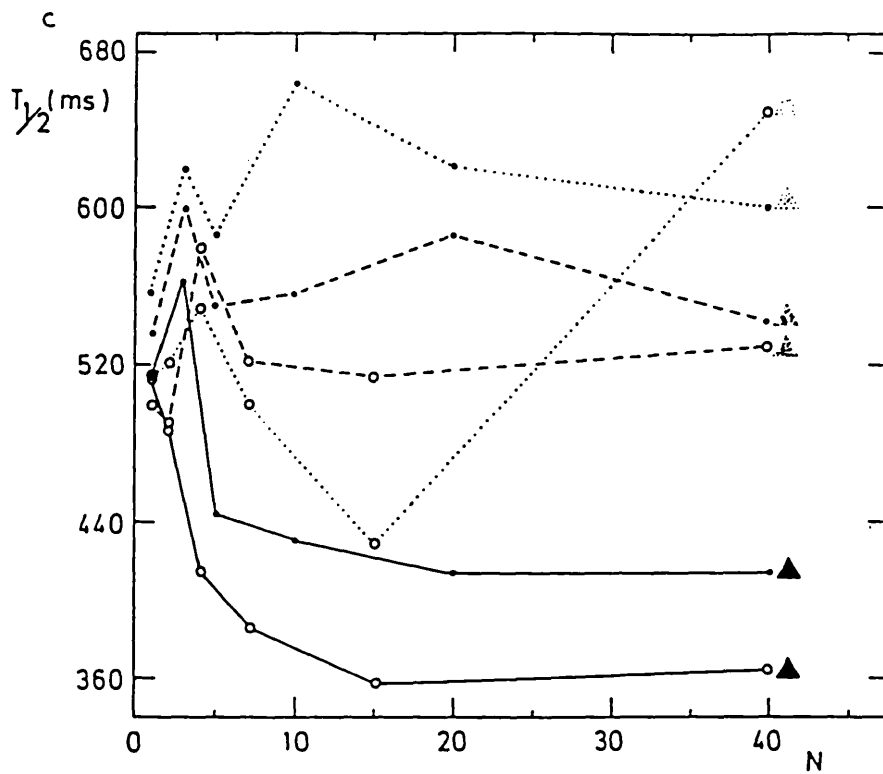


Figure 5.18 $T_{1/2}$ values and error scores plotted against N , the number of background elements. $\circ$ refer to one set of experiments with targets $\triangle \nabla \blacktriangle$ and $\bullet$ to another set of experiments with targets $\nabla \triangleright \triangle$. (a) Data for H.J.A. (b) Number of errors recorded for 50 presentations of each target from the set $\triangle \nabla \blacktriangle$. Also shown are the accumulated errors for all three target types (full circles). (c) Comparison data for two normal subjects. (d) Data for normal subject V.I. with elements $\cdot \cdot \cdot$.



The Effect of Target Separation

With just one background element and one target element the discrimination task reduces to that of identifying 'same' or 'different' and the effect of the separation, s , of the two elements on detection time has been determined. The same background and target elements as in the previous experiment of varying N were employed. Both H.J.A. and the normal subjects take slightly longer for discrimination at larger values of s .

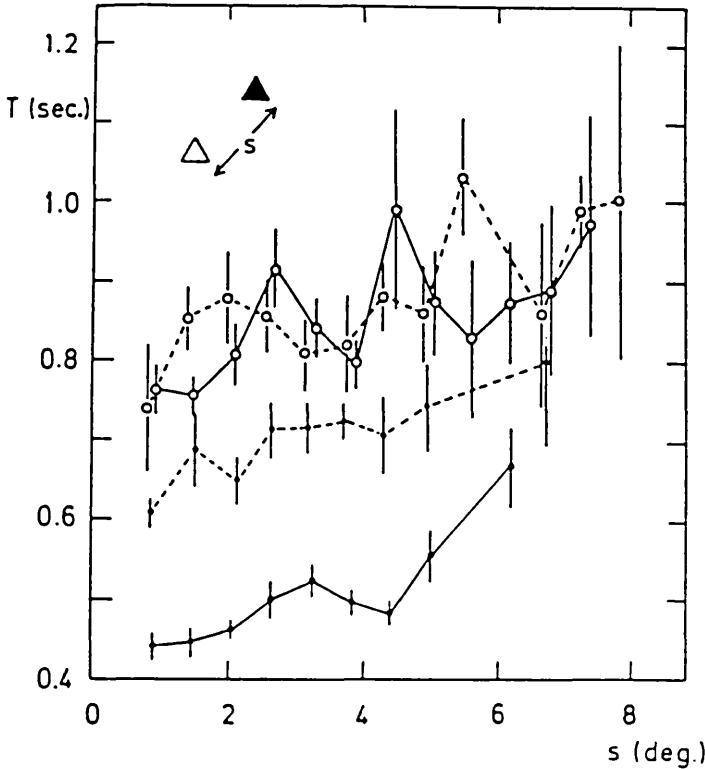


Figure 5.19 $T_{1/2}$ values plotted against target/background separation s , in degrees. $\circ-\circ$ refer to $\cdot\cdot\cdot$ $\cdot\cdot\cdot$ $\blacktriangle$ targets and $\circ-\circ$ refer to ∇ $\triangleright$ $\triangleleft$ targets for H.J.A. $\bullet-\bullet$ refer to normal data with $\cdot\cdot\cdot$ $\cdot\cdot\cdot$ $\blacktriangle$ targets and $\bullet-\bullet$ to normal data with $\odot$ $\odot$ $\odot$ targets. Error bars denote standard errors for each separation. There were generally 20 readings for each point, but this drops to about 5 for the largest values of s .

Standard Visual Tests

H.J.A.'s contrast sensitivity for gratings was measured with test charts developed by Barbur [1986] and his sensitivity was found to be significantly below normal (compared with two twenty-one year old subjects and his wife who is a similar age to him) over most of the spatial frequency range (figure 5.20). This may result from lack of appreciation of multi-element images, but it could none the less contribute to his poor discrimination performance. To check the effect of poor contrast sensitivity on the pattern discrimination experiments the contrast between the elements and the screen background was decreased and the experiments repeated by two normal subjects. Only when the elements were near contrast threshold and only just discernable did their $T_{\frac{1}{2}}$ values increase significantly. H.J.A. reported that during experiments the targets were clear and 'stood out' so it seems unlikely that his reduced sensitivity was a significant factor in his large $T_{\frac{1}{2}}$ values.

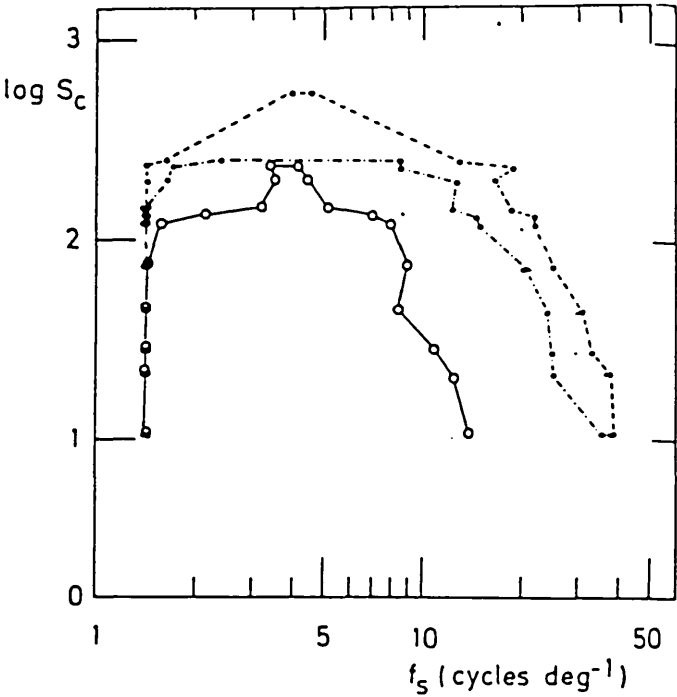


Figure 5.20 Contrast sensitivity S_c , defined as $(\text{contrast})^{-1}$ for detection of a grating, plotted against the spatial frequency, f_s , of the grating. Data for H.J.A. (open circles) and for two normal subjects (full circles).

Figure 5.21 shows increment thresholds for H.J.A. ($\circ$ data points) and two normal observers ($\bullet$ and $+$ data points) for detection of a target flashed on a uniform background. H.J.A.'s graph has a form similar to that of the normals but is raised by about 0.75 log units relative to theirs. This indicates a decreased contrast sensitivity, as was found with the contrast sensitivity test charts. The targets on the colour monitor, used for the discrimination experiment, are 3.5 log units above threshold but his increment threshold is only 0.75 log units above normal, which again suggests that his reduced contrast sensitivity is not a major factor in his performance on the discrimination tests.

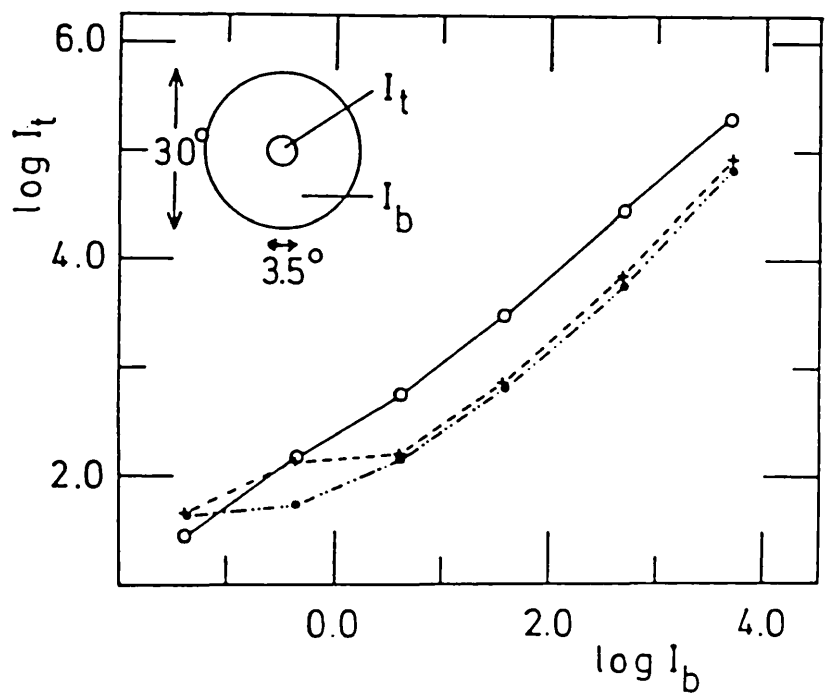


Figure 5.21 Increment threshold for a 3.5° diameter, circular target flashed at the centre of a 30° diameter, circular, uniform background of illumination I_b . $\circ$ data points for H.J.A.; $\bullet$ and $+$ data points for two normal observers.

H.J.A. gave normal responses for the visual illusions named after Ehrenstein, Kanizsa, Müller-Lyer, Poggendorf, Ponzo and Zollner [Gregory, 1970]. He detected changes in apparent orientation of parallel bars following adaptation to a mis-aligned grating, as do normal subjects [Gibson, 1933], but did not notice changes in their apparent width following adaptation to a grating mis-matched in bar width (called the frequency shift effect, Blakemore and Sutton, 1969). H.J.A. had normal orientation discrimination for single lines, I figure 5.12(a) but reduced ability at detecting the magnification of single lines figure 5.14(a) and the results of the adaptation experiments are consistent with this.

H.J.A.'s brightness matching was normal but in the matching experiment with monochromatic stimuli H.J.A. showed no colour vision. Stereoscopic depth perception, observed with random dot stereograms [Julesz, 1971] was normal and he made normal eye movements in tracking moving targets and identifying the direction of movement.

(d) Discussion

As figures 5.12 to 5.17 show, H.J.A.'s response times, $T_{\frac{1}{2}}$, for discrimination of a target differentiated from the background elements by a single parameter is, except in one case, much larger than normal response times for all the target parameters tested. His response times are near normal in the case of orientation discrimination of single straight lines, figure 5.12(a), and, therefore, his problem is not simply one of failure in parallel (simultaneous) processing [Kinsbourne and Warrington, 1962] since at some level of visual organisation he can still process multi-element stimuli. Other discriminations at which he is relatively unimpaired are the orientation of parallel lines, IIII (figure 5.12(c)) and magnification involving large target

elements (figure 5.14). Whilst he is particularly poor at spotting the mirror image target in some orientation discrimination experiments, e.g. $\triangle \rightarrow \nabla$ (figure 5.12(d)) and at some texture discriminations, e.g. $\triangle \rightarrow \blacktriangle$ (figure 5.15(d)).

For the cases where H.J.A. has large $T_{1/2}$ values, he also has large error scores. This is not due to the lack of concentration or care as his error scores for the null target are similar to or lower than normal but is due to his being unable to discriminate, or detect, the target. Figure 5.22 clearly shows this correlation of error score with discrimination time, $T_{1/2}$.

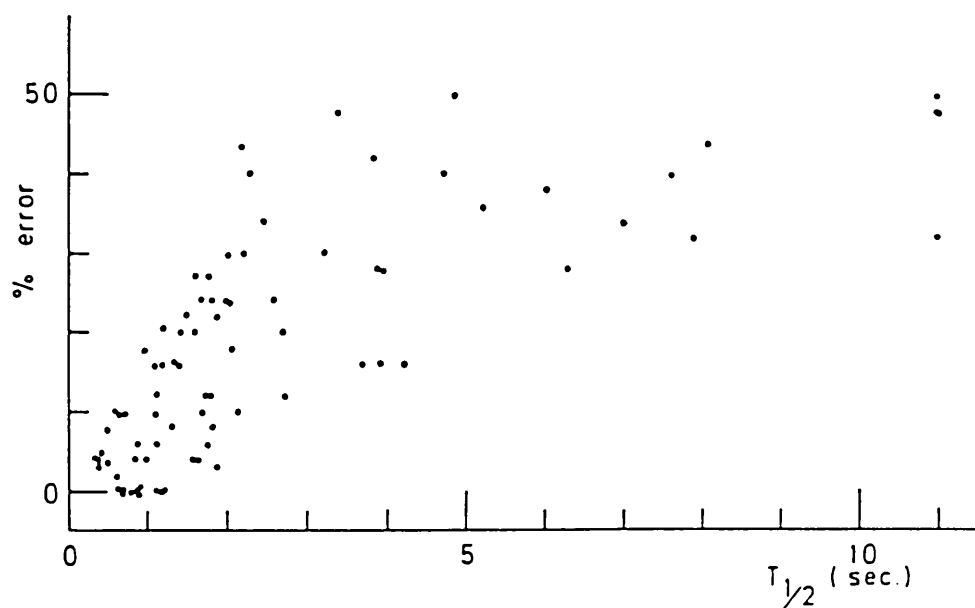


Figure 5.22 H.J.A.s error scores plotted against his $T_{1/2}$ values showing the correlation between them. The correlation coefficient between the two variables is 0.749 (81 pairs of variables).

H.J.A. is able to discriminate most of the targets but requires much longer than normal and has higher error scores because he fails to find targets more often than normal. If in making discrimination he utilizes a mechanism with properties similar to that which mediates normal discrimination, his $T_{1/2}$

values for the different targets should correlate with those of normals. The average response time, $\bar{T}_{1/2}$, for normal subjects, plotted against H.J.A.'s response time, $T_{1/2}$, (figure 5.23) demonstrates just this, but it also shows that H.J.A. takes about ten times longer to respond than normal. The range of $\bar{T}_{1/2}$ values is restricted but Ike, Ruddock and Skinner [1987] found that putting a circle around the pattern elements e.g. ①, ②, ③ extends considerably the response time. Normal subjects' data were, therefore, collected for such stimuli, thereby extending the normal response times, $T_{1/2}$, showing more clearly the correlation between the two variables. H.J.A.'s discrimination mechanisms therefore give subnormal levels of discrimination but have the same characteristics as those in normal subjects and there is no evidence of selective loss or retention of discrimination for any particular parameter.

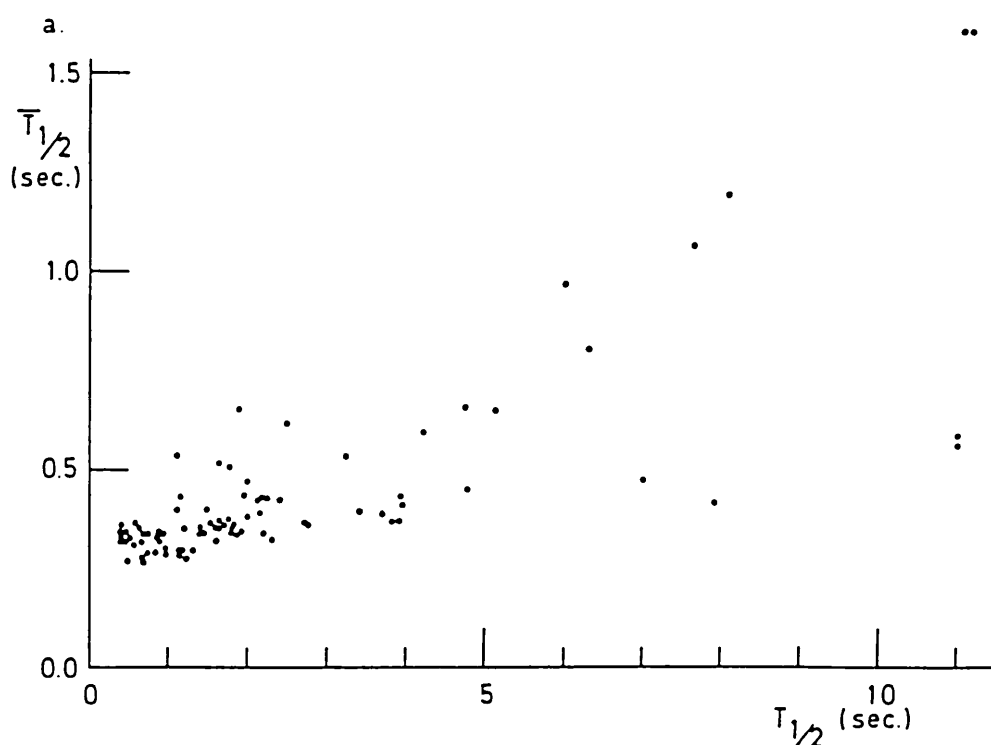


Figure 5.23 Average values of the response time, $T_{1/2}$, for normal subjects plotted against response time, $T_{1/2}$ of H.J.A. (a) Data from figures 5.12 to 5.17. (b) Same as (a) but for the normal subject all the values were determined for pattern elements in circles e.g. ① ② ③ to slow their response time down. The correlation coefficient for the two variables is 0.752 (33 pairs of values)

Figure 5.23 (cont.)

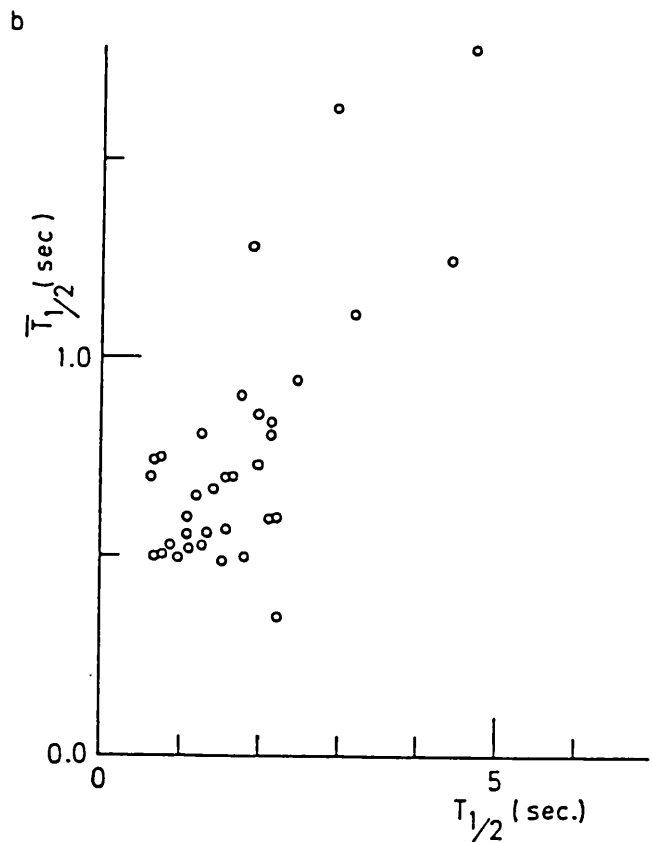


Figure 5.19 shows that H.J.A.'s discrimination of two dimensional patterns is not restricted to a local region of the visual field and that his discrimination ability is maintained at normal levels as the separation, s , of the target and background element increases. There is, therefore, no evidence that his mechanism of discrimination operates only over a restricted area [Bay, 1953]. However, H.J.A. has an intrinsic reduction in the rate of discriminating two dimensional elements even in the simplest case of two elements located next to each other (figure 5.19). Figure 5.18(a) and (b) show that as the number of background elements, N , increase, H.J.A.'s $T_{1/2}$ values and error scores also increase whilst normal subjects show very little variation in $T_{1/2}$ as N increases. This result is in agreement with H.J.A.'s report that he scans the pattern elements sequentially to find the target and is

confused by large numbers of elements whilst, for normal subjects, the target just 'pops out' from the background. Figure 5.18(c) shows that for certain pattern elements $T_{\frac{1}{2}}$ values for normal subjects also increase with N , and in these cases normal subjects are also reduced to sequential scanning in order to find the target.

H.J.A. recognizes objects in outline, but once features are put into the outline, he is unable to discriminate between related objects, such as faces [Humphreys and Riddoch, 1987]. Discrimination between closely related objects such as faces requires the simultaneous assessment of multiple features, but the experiments described above demonstrate that H.J.A. cannot perform simultaneous discrimination even with simple geometrical shapes. For example, increasing the number of background elements from one to five changes the value of $T_{\frac{1}{2}}$ from 0.84s to infinity for the discrimination of ∇ from Δ (figure 5.12 (d)).

The experimental data establish that H.J.A. has normal discrimination of orientation for single lines (figure 5.12(a)), but once two or more lines are joined together his performance becomes much worse. Orientation sensitive responses for single bars were found in recordings from single cells of the striate cortex [Hubel and Wiesel, 1962, 1968] thus this level of visual processing appears to be undisturbed, but the mechanism for the association of lines to form shapes is impaired. The location of such a cortical mechanism is unknown but some part of the V2-V3 complex may be involved in such processing as is suggested by some of the neuronal responses to e.g corners, originally reported by Hubel and Wiesel [1965, 1968]. H.J.A.'s stereoscopic depth perception, as measured by the Julesz [1971] random dot stereograms, remains intact, and electrophysiological evidence suggests that this is generated in area 18 [Hubel and Wiesel, 1970] which corresponds to V2 and V3 [Zeki,

1978]. At least some pre-striate function is therefore normal, but the complete absence of colour discrimination indicates malfunction in the pre-striate complex V4 or its afferent projections [Zeki, 1978, 1980]. More anterior mechanisms such as those located in the inferior temporal sulcus, which respond to specific stimuli such as faces and hands [Perret, Smith, Potter, Mistlin, Head, Milner and Jeeves, 1985] may also be impaired. The CT X-ray scans of H.J.A.'s brain (see figure 5.11) show extensive damage in the occipital lobe which suggests impairment at a relatively early stage of the cortical visual pathway and loss of discrimination of simple geometric patterns is consistent with this.

The first stage of neuronal processing of spatial content in the visual image, the 'filtering' stage described at the beginning of this chapter, is unaffected in H.J.A. and he can discriminate normally the orientation of single lines. It is at the later stage, where the filtered image is processed to generate the perceived response, that H.J.A.'s responses are impaired.

CHAPTER SIX RESPONSE CHARACTERISTICS IN A CASE OF VISUAL PERSEVERATION

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6.1 Introduction

The spatial vision defects described in Chapter Five were caused by abnormal development of the visual system and by brain lesion. They resulted in reduced visual acuity and reduced shape recognition. In this chapter, data are presented for a subject who has a rare spatial vision defect which results in long lasting after-images. Her visual defect fits into a class of similar defects, described as visual perseveration and discussed in Chapter One (1.3(d)).

F.B. experiences prolonged after-images which persist for tens of seconds following stimulation by light which is insufficiently intense to produce after-images in normal subjects. The after-images she sees have similar spatial structure to that of the stimuli which elicit them. F.B.'s visual problems started in July 1984 when for a few seconds several times a day she saw white spots like fireflies throughout her visual fields. This effect could be brought on by sudden head movements or by walking into an area of bright light e.g. by going out of a shop into daylight. Also, white objects appeared brighter than before and she experienced discomfort when she looked at her babies' white nappies. She noticed that she had prolonged after-images when she looked at bright lights and that as they faded they became green in colour. Before these visual problems had developed F.B. had experienced a variety of episodic symptoms such as slurred speech, heaviness and numbness in her right hand and leg and in her left hand. These were initiated during her first pregnancy in 1982.

F.B. was referred to the Vision Group at Imperial College by Dr. Chris

Kennard, consultant neurologist at The London Hospital, who had been unable to reach a definitive clinical diagnosis [Blythe, Bromley, Ruddock, Kennard and Traub, 1986]. At this time she suffered from bad headaches and numbness and weakness of her left hand. The measurements made on F.B. were carried out from November 1984 to June 1985. At the end of this time F.B. was treated with the anticonvulsant drug, carbamazepine, as an electroencephalogram (EEG) carried out at The London Hospital had shown a minor, left temporal abnormality consisting of theta activity with occasional sharp waves, indicative of epilepsy. Six weeks after treatment, measurements were made of the duration of the after-image and a 30% decrease was found. F.B. also reported that bright white objects were slightly less intense. However, when the after-image duration was measured three months later there had been no further decrease in its duration.

The psychophysical tests carried out at Imperial College were designed to investigate the stimulus-response relationship for the after-image and to provide evidence regarding the pathway(s) involved in its generation. They also, as noted above, made it possible to quantify the effectiveness of the medical treatment given to F.B.

6.2 Experimental Procedure

The majority of the experiments were carried out using the Maxwellian view system to measure increment threshold, critical fusion frequency and to measure the duration of the after-image by means of the procedures described in 2.2 (d), (e), and (f). Timing of the after-image duration could, in principal, have been done by the computer but for many of the long time periods a stop clock was used. Most of the experiments were carried out using white light stimuli but monochromatic stimuli were also used, and these

were produced with narrow-band interference filters.

One experiment required pairs of grating stimuli which differed in spatial frequency, one located in the upper and the other in the lower half of the visual field. This was achieved by inserting photographic negatives with grating structure covering a $12^\circ \times 12^\circ$ square at OP2 and OP3 (figure 2.2), positioning them in the two halves of the visual field and providing a fixation point between the two stimuli. Another experiment required a grating of alternate red and green bars. This was obtained by placing matching gratings at OP2 and OP3, positioning them in spatial antiphase with a red interference filter (630nm peak) in one beam and a green interference filter (531nm peak) in the other. The two sets of bars were matched for subjective brightness by inserting neutral density filters in the beams.

An experiment to measure decremental threshold was carried out using the computer controlled colour monitor. The observer sat one meter from the screen and a program written by Robin Morris (an undergraduate at Imperial College) presented, on a $16^\circ \times 12^\circ$, green background a dimmer green, rectangular target $2.5^\circ \times 2.2^\circ$ flashed for 0.4seconds every 0.8seconds with the 'off' brightness the same as the background. By moving the joy stick on the reply box the observer could vary the brightness of the flashing target to threshold.

6.3 Investigation of F.B.'s Vision

(a) Basic Measurements

Basic visual properties were measured. F.B.'s foveal colour vision was examined using the tristimulus colorimeter and methods of measurement described by Wright [1946]. Tristimulus colour matches for spectral test stimuli were normal and the relative spectral sensitivity function (V_λ)

determined by flicker photometry was also normal. Her foveal acuity was $\frac{6}{4}$ in each eye without correction, stereoscopic depth perception for random dot stereograms [Julesz, 1971] and dark adaptation for a circular target (diameter 3.5° , wavelength 495nm) located 10° off-axis, were also normal.

(b) Verbal Description of the After-Image

At each session F.B. viewed for 5 seconds a 30° diameter circular patch of white light of retinal illumination 2.8 log td. Her description of the after-image was consistent from session to session. In darkness it appeared to be the same size as the white light patch, but appeared khaki in colour and matched approximately to a surface colour with C.I.E. coordinates $x = 0.411$; $y = 0.476$ and $Y = 42.5$ although this surface colour appeared rather brighter than the after-image. F.B. could tell when the white light stimulus was turned off because of the change in colour from the white stimulus to the coloured after-image. For about 20 seconds after the white light was turned off the after-image remained the same brightness, it then began to fade from the middle outwards, becoming ring shaped and finally disappearing after 30 seconds or longer. When viewed against a white surface, the after-image was similar to that seen when the subject was in darkness, but it faded more rapidly and appeared like a 'dark shadow' before finally disappearing. The after-image moved as F.B. moved her eyes in both light or darkness, it occurred following stimulation of either eye and she could still see it if she closed the stimulated eye. She could detect the after-image in all quadrants of the visual field and over the range of eccentricities tested (up to 40°) and its duration of about 30s was effectively independent of location.

The following experiments were carried out in order to measure the characteristics of the after-image. Measurements were made in darkness and with the after-image perceived foveally. After a measurement F.B. sat in darkness and the next measurement was proceeded to only when the after-image had faded away. The light used to elicit the after-image will be referred to as the primary stimulus.

(c) Time Course for the Detection of a Test Flash

After 5 seconds viewing of the circular, white light patch F.B.'s threshold for detection of a target flashed on the after-image was found to be raised for 10s to 15s. In order to measure the time course for F.B.'s recovery of sensitivity the following experiment was carried out.

A small, circular target of 3.5° diameter was flashed for 0.1 second every 1second at the centre of the primary stimulus — a 30° diameter, circular patch of white light. Threshold illumination, I_0 , for detection of the target was found using the threshold program (2.2(d)). The target illumination level was then set at various levels below I_0 and the time at which the flashing stimulus was detected following 5 seconds viewing of the primary stimulus was signalled by pressing the reply button. Thus post-stimulus changes in sensitivity were determined. They are displayed in figure 6.1.

The experiment was repeated using a primary stimulus of the same illumination but of monochromatic light (531nm). The experiment was also performed under dichoptic conditions with the white light primary stimulus presented to the left eye and the flashing target to the right. The results from these experiments are also shown in figure 6.1 as + and × data points respectively. The graph shows that sensitivity rapidly recovers some 15 seconds after cessation of the primary stimulus for all three experiments. For

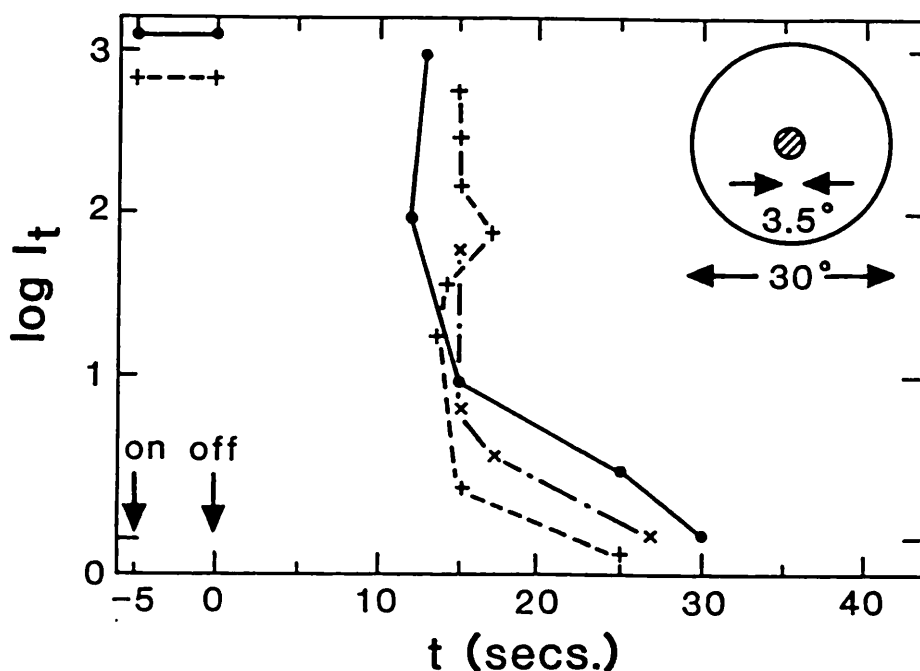


Figure 6.1 Graph showing the time at which a white light, circular target (diameter 3.5°) of illumination I_t flashed for 0.1 seconds every 1 second at the centre of the circular primary stimulus (diameter 30°) becomes visible following 5 seconds viewing of the primary stimulus which was turned off at $t = 0$. Filled circles denote data obtained with a white light primary stimulus of illumination 2.9 log td.; crosses + denote data obtained with a primary stimulus of 531nm wavelength and 2.9 log td.; crosses x denote data obtained with dichoptic presentation of the test and white light primary stimuli.

normal observers carrying out this experiment threshold sensitivity returns to normal level within 100ms of the primary stimulus being turned off.

Measurements were also made with F.B. for four different illumination levels of the white light primary stimulus (figure 6.2) and it appears that the threshold illumination level remains approximately the same after stimulation as before, although there is in some cases evidence of a transient increase following stimulus offset. F.B. observed a 'darkening' of the after-image at about the same time that she was able to detect the target (i.e. about 15s after offset of the primary stimulus), but she could still detect the after-images

for one to two minutes later.

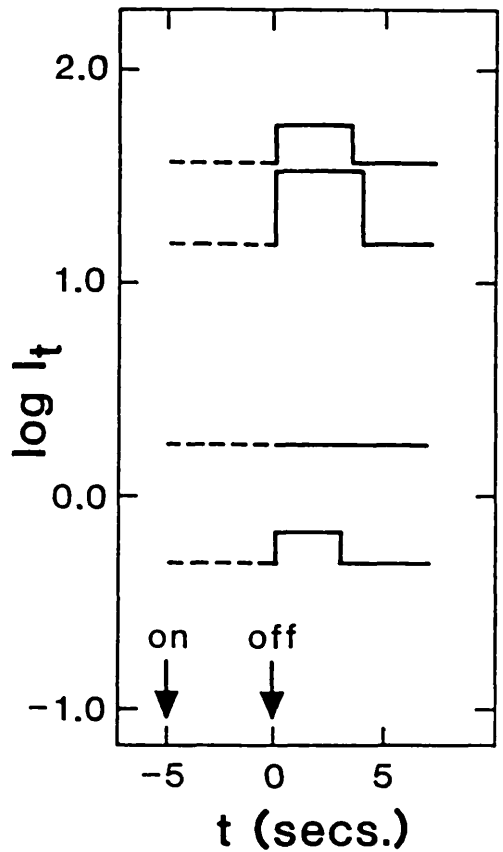


Figure 6.2 As for figure 6.1, but values of $\log I_t$ are plotted for four different illumination levels of the white light primary stimulus.

(d) Duration of the After-Image as a function of the Brightness of the Primary Stimulus and Period of Viewing

Since the primary stimulus caused extended loss of threshold sensitivity, measurements could be made to find the effect of different primary stimuli in terms of $T_{\frac{1}{2}}$, the time following offset of the primary stimulus at which illumination for detection of the target fell to half the value it had during presentation of the primary stimulus. The threshold program (section 2.2(a)) was used to find threshold illumination $\log I_t$ for detection of the target

flashed on the particular primary stimulus. Then the target was set at half this illumination level and flashed at the centre of the primary stimulus, as described in section 6.3(c). The time, $T_{1/2}$, from primary stimulus offset until the target became visible was recorded following 5 seconds viewing of the primary stimulus.

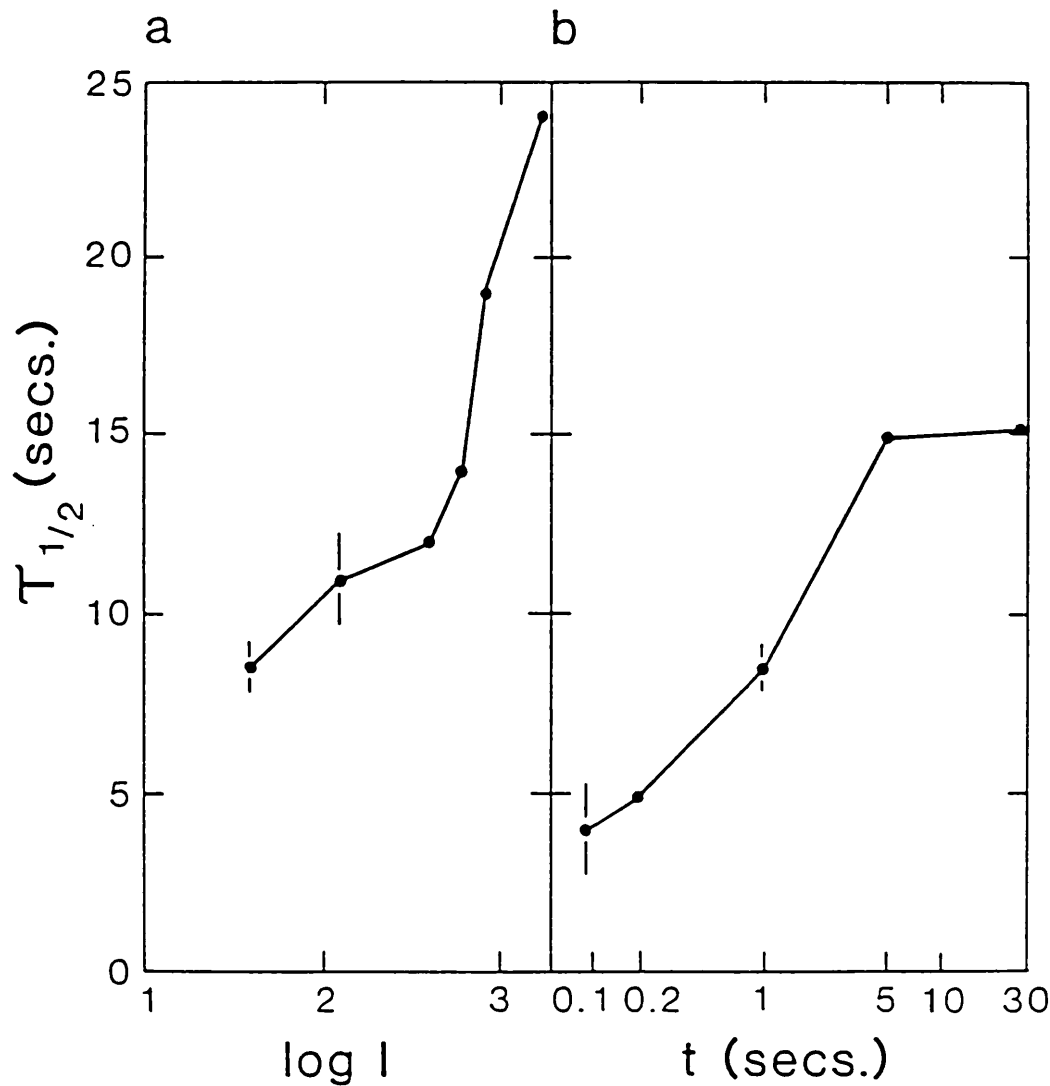


Figure 6.3 (a) $T_{1/2}$ plotted against the log of the illumination of the primary stimulus. The visual field was as for figure 6.1, both target and primary stimuli were white light and the primary stimulus was presented for 5 seconds. (b) $T_{1/2}$ plotted against t , the time for which F.B. viewed the primary stimulus. Visual field as for figure 6.1 and the primary stimulus was 2.8 log td.

$T_{\frac{1}{2}}$ increases rapidly as the illumination level of the white light primary stimulus increases to the maximum available with the Maxwellian view apparatus (figure 6.3). One of the clinical tests carried out on F.B. was flash photography of the retina for a fluorescein angiogram and the after-image caused by this had lasted for tens of minutes, which indicates that the steep increase in $T_{\frac{1}{2}}$ continues beyond the range covered by our measurements.

$T_{\frac{1}{2}}$ also increases with the time for which F.B. views the primary stimulus increases (figure 6.3(b)) and in this case, the restricted range of measurements was determined by the fact that the subject found prolonged viewing of the primary stimulus unpleasant and disturbing.

(e) Duration of the After-Image caused by different Wavelength Primary

Stimuli and for Monochromatic Gratings

The technique described in (d) above was used to measure $T_{\frac{1}{2}}$ for a number of different wavelengths, λ , of the primary stimulus. Each primary stimulus was viewed for 5 seconds and before measuring $T_{\frac{1}{2}}$ its illumination level was adjusted so that threshold illumination for detection of the white test flash against it was the same for all wavelengths. The data (figure 6.4, filled circles) establish that $T_{\frac{1}{2}}$ varies with λ , being longer for the green (531nm) and yellow (576nm) than for the red (630nm) and blue (453nm) primary stimuli.

In order to confirm the difference in the persistence of after-images induced by red and green lights, a grating was constructed from equally spaced bars, alternately red (630nm) and green (531nm). The red and green bars were matched so as to be of the same apparent brightness to F.B., they also appeared matched in brightness to other observers and both sets of bars were at a luminance level of 2.8 log td. F.B. viewed this grating for 5 seconds

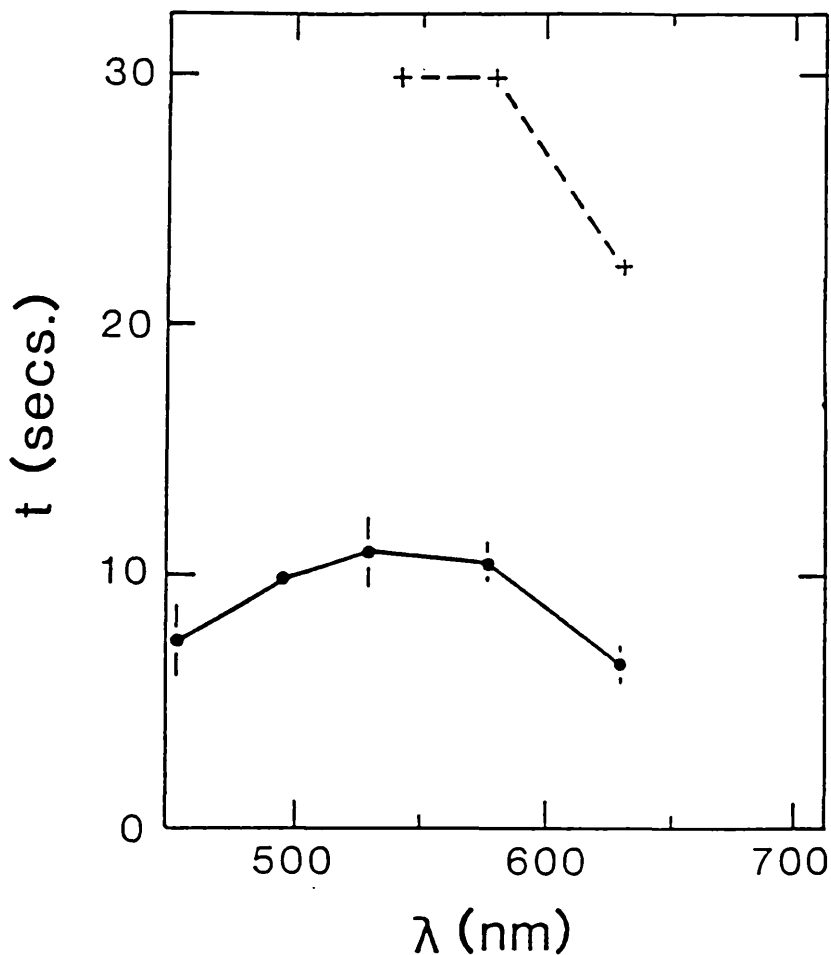


Figure 6.4 Filled circles (•). Values of $T_{\frac{1}{2}}$ plotted against the wavelength, λ , of the primary stimulus. The illumination levels of the different monochromatic stimuli were adjusted to give the same illumination for threshold detection of the superimposed white light target. Visual field configuration as for figure 6.1. Crosses (+), the total time for detection of the after-image following 5 seconds viewing of a grating of wavelength λ , and bar width 2 cycles/degree. The grating illuminations were 2.1 log td. (630nm and 542nm) and 2.5 log td. (576nm).

and on its offset described the after-image. For a few seconds it appeared similar in colour to the primary stimulus grating, but the red bars faded rapidly, leaving an after-image consisting of alternately green and black bars, which was detected for 75 seconds. When each grating was used on its own

to provide the primary stimulus, the after-image for the green grating was detected for 100 seconds and appeared 'mustardy-green' in colour whereas the after-image of the red grating was detected for 50 seconds, initially appearing as pink stripes but changing colour after a few seconds to look similar to the after-image of the green grating.

The total duration of the after-image was measured for three monochromatic gratings and these values are also shown on figure 6.4 (crosses). The after-image of the yellow (576nm) and green (542nm) gratings were more prolonged than that of the red (630nm) grating, but it should be noted that the illumination level of the yellow grating was somewhat greater than that of the other two. F.B. described the colour appearance of the after-image induced by the 576nm grating as 'mustard yellow' and black, whereas those elicited by other monochromatic gratings appeared green and black.

(f) After-Image Duration as a function of Primary Stimulus Structure

The experiments in (e) show that the after-images produced with coloured gratings have well defined structure. The effect on the after-image of the spatial structure in the primary stimulus was investigated by measuring the total duration, T , for which this spatial structure was perceived in the after-image. The gratings used were all of white light, 100% modulated, circular of 4° diameter and presented for 0.1 seconds. T reaches a peak for grating spatial frequencies of 1 to 2 cycles/degree and falls to zero for spatial frequencies above 15 cycles/degree (figure 6.5). Vertically and horizontally orientated gratings were equally effective. F.B. reported that for the primary stimulus of spatial frequency 2 cycles/degree, the lines in the after-image persisted after the circular outer limit of the after-image disappeared, whereas

with finer bar-widths (higher spatial frequencies), the image of the circular limit persisted after the grating disappeared.

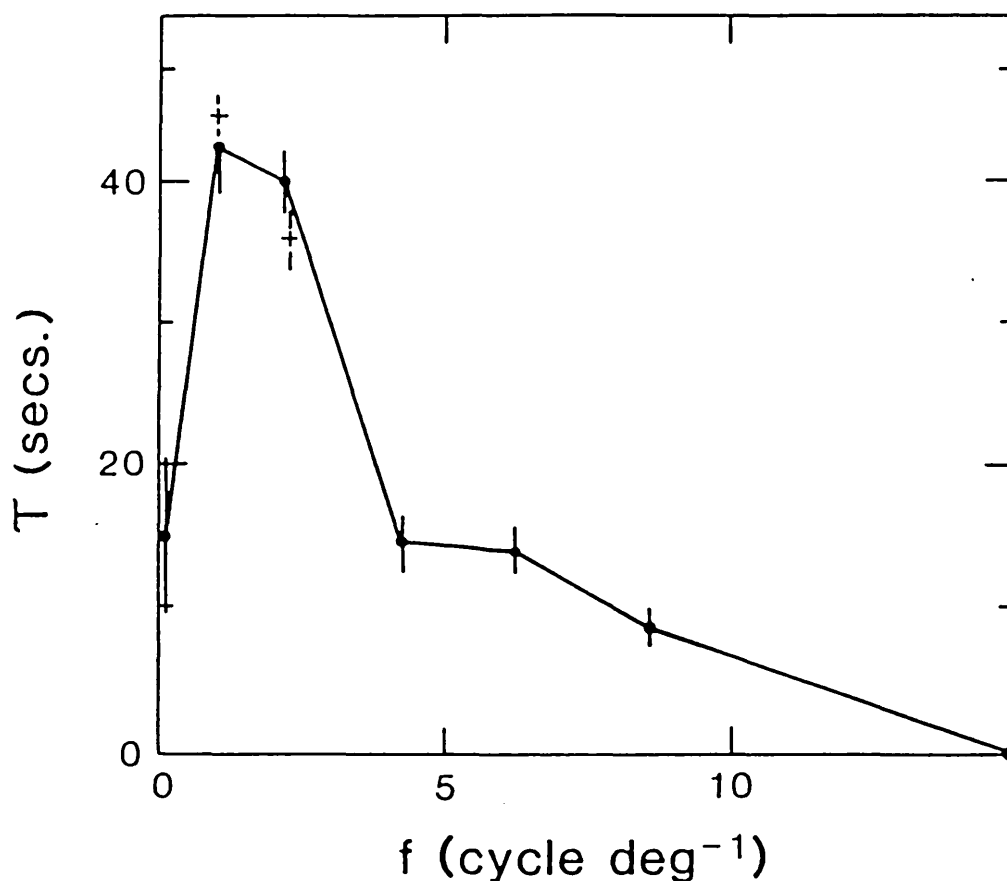


Figure 6.5 The duration, T , of the after-image induced by a grating stimulus plotted against the spatial frequency of the grating. The gratings were presented for 0.1 seconds. • data points correspond to vertically orientated gratings, + data points to horizontally orientated gratings.

Measurements were also made for the duration, T , of the after-images elicited by a circular spot (diameter 1°) and by a grating of spatial frequency 2 cycles/degree, and for given presentation time of the primary stimulus, the duration, T , for the grating exceeds that for the uniform circular spot (figure 6.6).

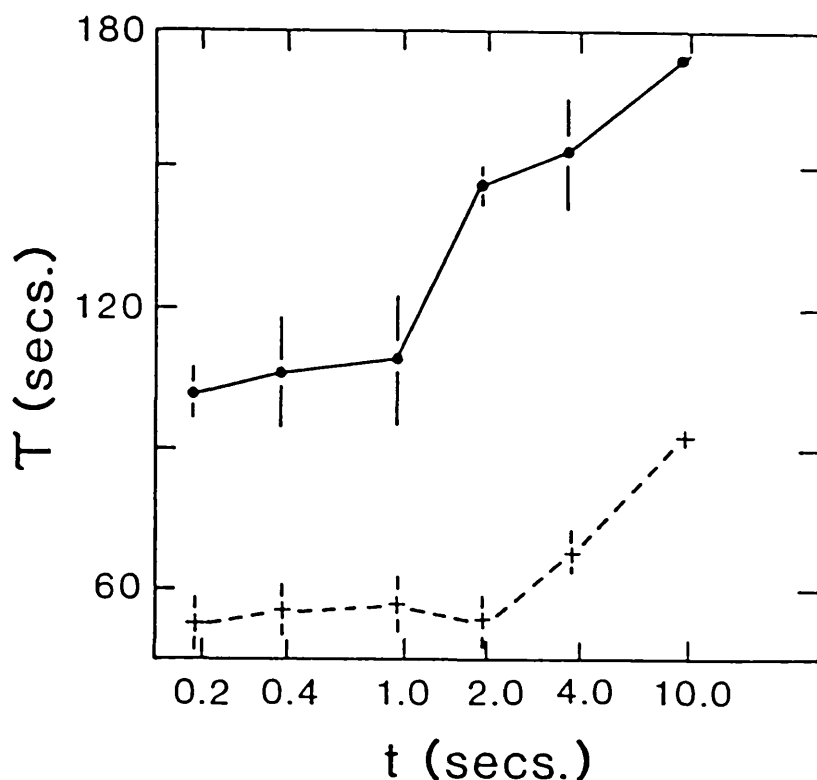


Figure 6.6 The duration, T , of the after-image plotted against the time of viewing the white light primary stimulus. $+$ data points correspond to the circular uniform primary stimulus (diameter 1°) and $\bullet$ data points correspond to the vertical grating stimulus (spatial frequency 2 cycles/degree).

(g) Spatial Content of the After-Image caused by a Spatially Modulated Primary Stimulus

Primary stimuli in the form of a grating elicit a grating after-image and the relationship between the primary and after-image was determined in a matching experiment. F.B. viewed a fixation point and the primary stimulus was presented in the upper half field for 5 seconds. She continued to view the fixation point and was asked to match the bar widths of the after-image to those of one of a series of gratings in the lower half-field (figure 6.7), bar-widths increasing by 15% between successive members of the series of matching gratings.

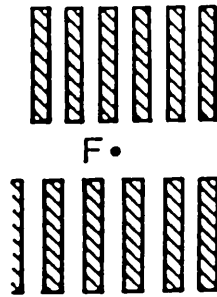


Figure 6.7 Matching configuration for a grating after-image (upper half-field), which is compared with one of a series of gratings presented in the lower half-field; F is the fixation point, provided by a small, red LED. The after-image was induced by 5 seconds viewing of a 1.1 cycle/degree square waveform grating, a square of size 12° , and measurements were made for 2.0 log td. and 3.0 log td. illuminations.

Matches were performed twice, following viewing of the primary stimulus at 2.0 and 3.0 log td. F.B. could perform matches for up to 2 minutes after viewing for 5 seconds the primary stimulus grating of illumination 3.0 log td. and in each trial the grating after-image matched to a comparison grating of spatial frequency identical to that which caused the after-image. Thus the after-image of the grating has the same spatial frequency content as the grating primary stimulus and there is no distortion or spreading of the after-image with time.

(h) After-Images caused by other Types of Primary Stimulus

Moving and flickering primary stimuli were used, but in neither case was any sensation of movement or flicker observed in the after-image. A circular target of 3.5° diameter and illumination level 2.6 log td. was presented moving across a dark background at either 15 degrees/second or 55 degrees/second. The target moving at 15 degrees/second produced an after-image of a 'spot with a streak behind it' and the target moving at 55

degrees/second produced a 'long oblong-shaped' after-image. Both after-images lasted for 15 seconds. A circular 12° diameter target 100% modulated at 8 Hz with a mean illumination of 2.6 log td., giving a strong sensation of flicker, produced an after-image identical in appearance to that elicited by a steady, circular target.

In addition to the measurements on F.B.'s after-images a number of standard responses were determined in order to characterize her temporal responses.

(i) Increment Threshold

Using the procedure of 2.2(d), a circular, 3.5° diameter, white light target was presented cyclically for 0.1 second every 1 second on the centre of a 30° diameter, white light background of illumination I_b . F.B.'s sensitivity for detection of the target was normal over most of the range of background field illumination, I_b , but her threshold values were raised for low I_b (0.8 log td. and below) (figure 6.8)

F.B.'s sensitivity to decremental change in illumination was measured using the computer controlled colour monitor as such measurements are difficult to make using the Maxwellian view apparatus. A flashing, decremental target was presented against a uniform background field and her sensitivity to the target was found to be the same as for normal subjects.

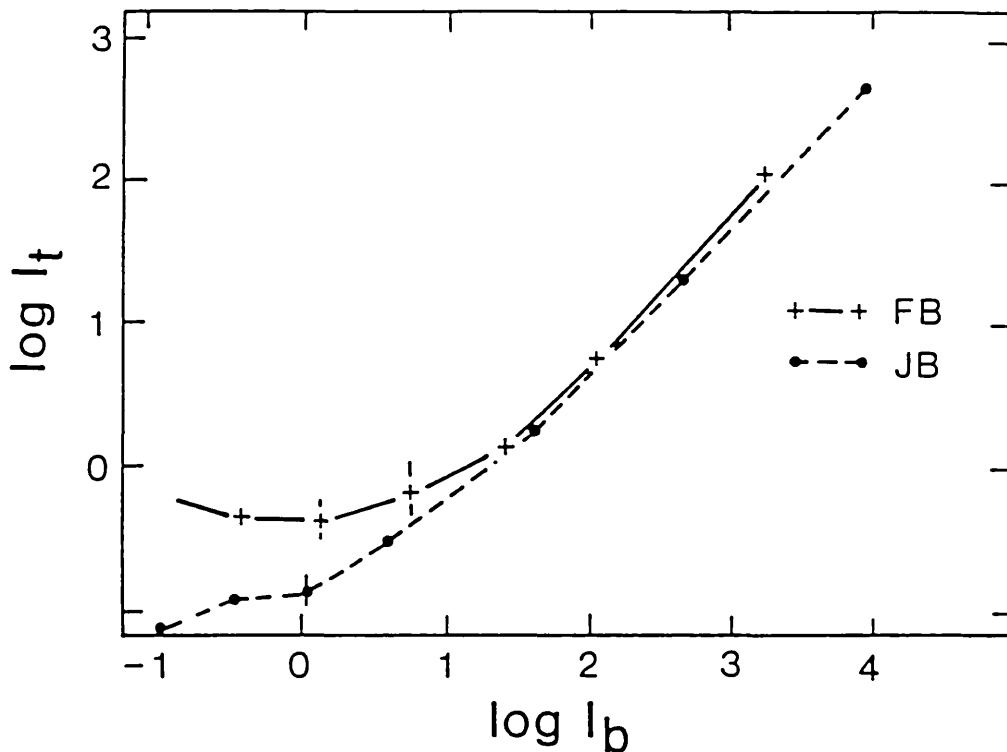


Figure 6.8 Log illumination, $\log I_t$, required for threshold detection of a circular target (white light, 3.5° diameter), superimposed centrally on a circular background (white light, 30° diameter) of illumination $\log I_b$. The target was presented cyclically for 0.1 second every 1 second. + data points correspond to data for F.B. and • data points correspond to data for a normal subject, J.B.

(j) Threshold for a Moving Target

F.B.'s sensitivity to a 3.5° diameter target moving at v degrees/second through the central 8.5° of the 30° diameter background field, illumination level 2.6 log td. was measured (figure 6.9). Her threshold sensitivity for detection of the moving target is normal, despite the extended tail she perceives behind the target.

Threshold illumination for detection of the bars of a grating moving across a uniform background was also measured for different grating velocities. The grating was in the form of a circular field of 4° diameter and of spatial

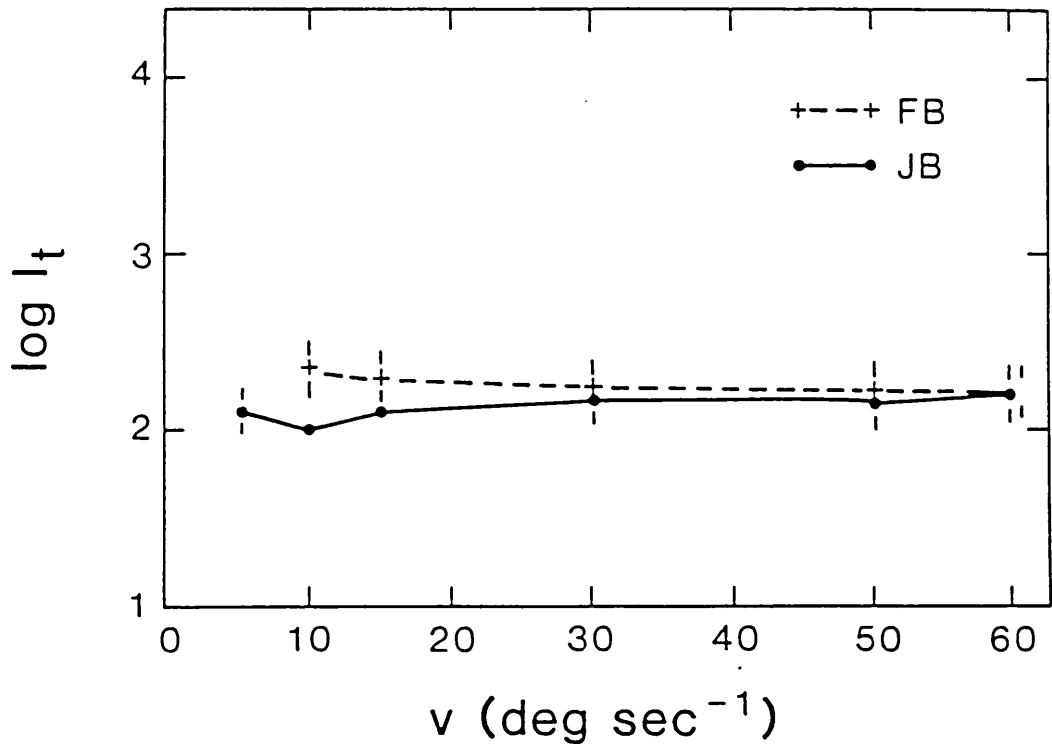


Figure 6.9 Illumination, $\log I_t$, for threshold detection of a circular target (3.5° diameter) moving at velocity v degree/second through the central 8.5° of the background field (30° diameter, illumination level $2.6 \log \text{td.}$). Both stimuli were white light. + data points correspond to data for F.B.; • data points correspond to data for a normal subject, J.B.

frequency 1 cycle/degree. It was orientated vertically and moved at velocity v degree/second along the horizontal meridian through the central 8.5° of a 30° diameter, $2.5 \log \text{td.}$ illumination background. Again F.B.'s thresholds are essentially normal (figure 6.10).

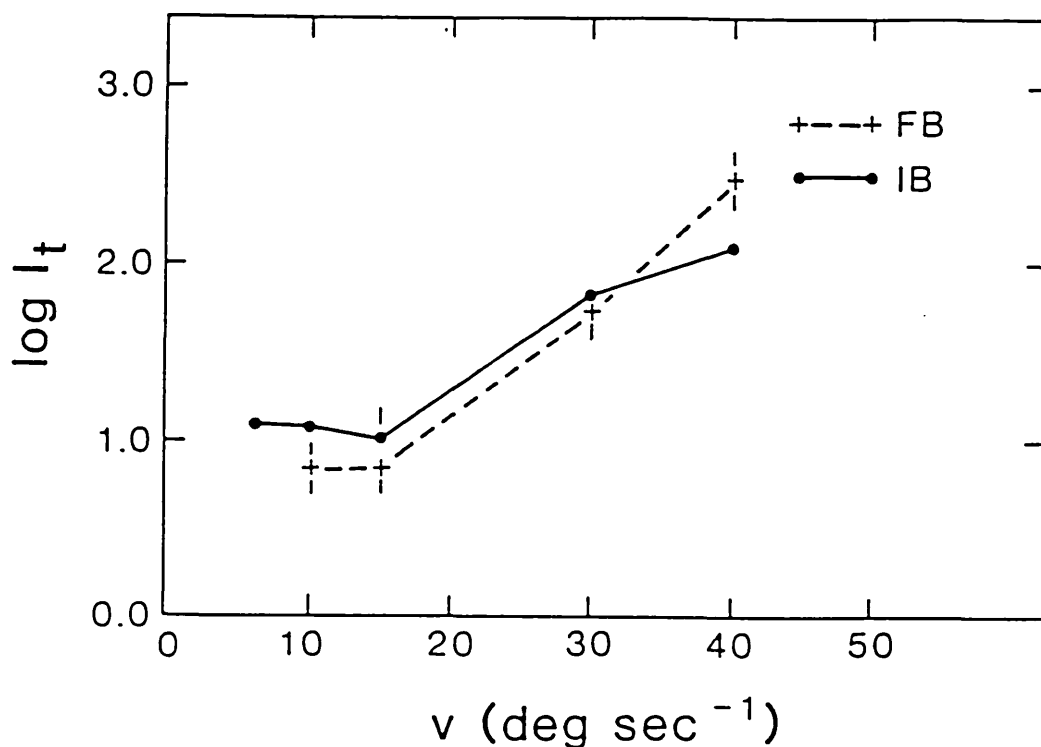


Figure 6.10 Illumination, $\log I_t$, for detection of a grating (1 cycle/degree spatial frequency in the form of a circular field of 4° diameter) moving at velocity v degree/second. The grating was orientated vertically, and moved along the horizontal meridian, through the central 8.5° of a 30° background (illumination 2.5 log td.). White light stimuli. The subject F.B. (+) and the normal subject I.B. (•) were instructed to find threshold for detection of the grating structure.

(k) Critical Fusion Frequency

The critical fusion frequency for 100% square waveform modulation was measured, using the method of 2.2(f), as a function of the 4° diameter circular stimulus illumination level, $\log I_b$. F.B.'s responses are similar to those of the normal subject J.B. (figure 6.11).

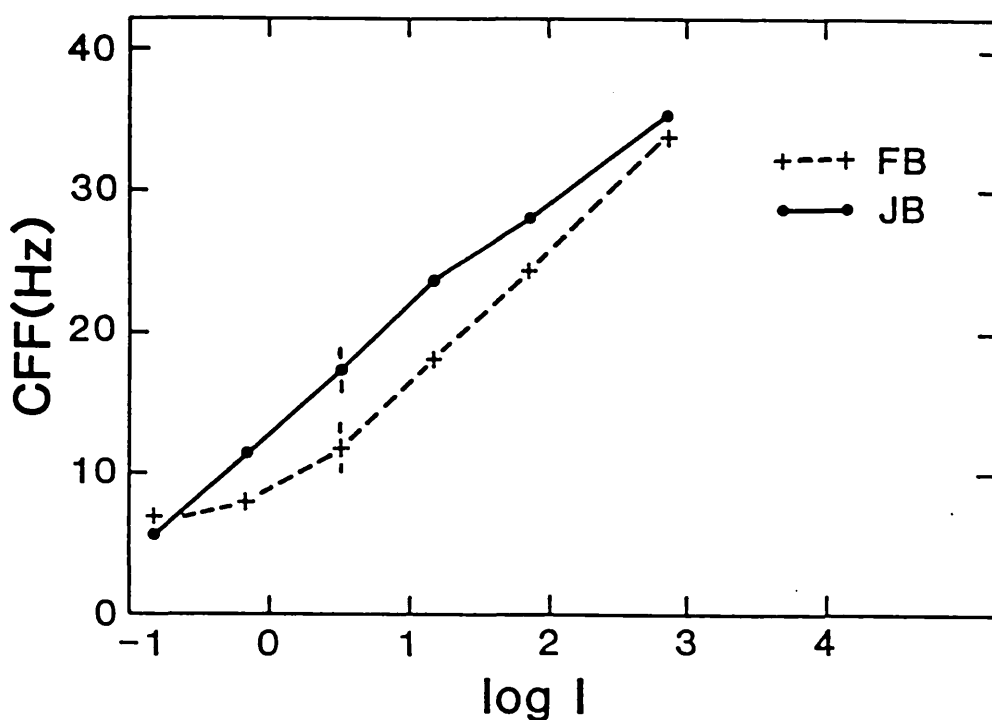


Figure 6.11 Critical fusion frequency (CFF) plotted against the mean illumination level, I , of the flickering stimulus (white light and circular of diameter 4°). + data points correspond to the data for F.B.; • data points correspond to data for J.B.

(1) Visual Illusions

F.B.'s responses to a number of illusory patterns including Poggendorf, Craik-Cornsweet, Kanizsa triangle, Ehrenstein and Hermangrid illusory figures [Gregory, 1970] were checked and in every case she described the normal illusory appearance.

6.4 Discussion

F.B. had suffered from a relapsing and remitting neurological disorder for three years prior to the period of testing at Imperial College. The major visual symptom of this disorder is the prolonged after-images caused by lights too dim to produce after-images in subjects with normal vision.

The after-images appear as soon as the light (called the primary stimulus) is turned off, and are observed at all locations in the visual field. They are of positive contrast and yellow-green in colour although they may have the same colour as the primary stimulus for the first few seconds, and they match the primary stimulus in size and spatial structure (figure 6.7). The after-image is accompanied by an increase in threshold sensitivity for detection of a test flash to about the same level of threshold sensitivity as that when the primary stimulus is present (figure 6.1). The threshold sensitivity returns to normal much before the after-image has faded away completely however.

After-images were produced with primary stimuli as dim as 0 log td., and the duration of their detection increases as the illumination of the primary stimulus increases (figure 6.3(a)). As mentioned in section 6.3(d), the very bright light used during a clinical examination to take flash photographs of F.B.'s retinæ caused an after-image which lasted for over half an hour. The after-image duration also depends on the exposure time of the primary stimulus, increasing as primary stimulus exposure time increases (figure 6.3(b)). The most extended after-images occurred after viewing gratings of 1 to 2 cycles/degree spatial frequency and the duration of these after-images were always longer than for spatially uniform fields of the same duration and illumination (figure 6.5). After-images were themselves gratings of the same bar size as the primary stimuli. For monochromatic spatially uniform primary stimuli, yellow and green wavelengths produced longer lasting after-images than red or blue wavelengths (figure 6.4).

The after-images moved as F.B. moved her eyes but moving or flickering primary stimuli did not produce any movement or flicker in the after-image. A streak-shaped after-image was produced by a moving light target and a flickering primary stimulus produced exactly the same after-image

as a uniform primary stimulus, thus F.B.'s after-images are specifically spatial in nature.

After-images are normally associated with photopigment bleaching but in the case of F.B. this explanation of her after-images is unlikely; after-images can be produced in F.B. with light of low illumination levels. Further, threshold for a target is raised under dichoptic presentation of the test flash and primary stimulus (figure 6.1) whereas bleaching lights do not influence increment threshold sensitivity under dichoptic conditions [Crawford, 1940; Mitchell and Liaudansky, 1955]. These observations suggest that the after-images are produced centrally. Despite the prolonged sensations produced by light stimulation F.B. has normal threshold sensitivity for detection of target flicker (figure 6.10), movement of a target (figure 6.9) and decrement of target illumination, so the perseveration of visual images cannot be due to a lack of temporal resolution or the failure of the mechanism signalling stimulus offset. Increment threshold, I_t , is normal except at low background illuminations, where I_t is raised. This implies an abnormally high Fechner fraction for threshold detection, which in turn implies large 'dark' or intrinsic noise in F.B.'s visual responses [Stiles, 1946]. The significance of this in relation to after-images is not known although, as both involve internally generated 'noise', they may be related phenomena. The duration of F.B.'s after-images, of the order of tens of seconds, is similar to the duration of raised contrast threshold observed following adaptation of orientation sensitive, binocularly controlled neural mechanisms [Gilinsky, 1968; Pantle and Sekuler, 1968; Blakemore and Campbell, 1969 and Chapter Four]. The contrast threshold elevation effect is subject to inhibitory binocular control, via a pathway with a well-defined, low spatial frequency response [Ruddock and Wigley, 1976; Ruddock, Waterfield and Wigley, 1979] and the spatial frequency

response of this binocular inhibition is in some respects similar to that found for F.B.'s after-images, although the amplitudes of the two responses are measured in terms of different variables and are, therefore, not directly comparable. The spectral response of the inhibitory mechanism is broad-band, as is that of the after-images (figure 6.4) but the former is closer to the photopic spectral sensitivity response. The build-up and decay of the inhibitory interaction takes 10 to 20 seconds, which is comparable with the duration of F.B.'s after-images (see figure 6.1). Thus the inhibitory, binocular controlled mechanism, which inhibits the contrast threshold elevation effect, has certain response properties similar to those associated with F.B.'s after-images and may be involved in their generation.

F.B. suffers from palinopsia of the 'after-image' as opposed to the 'episodic type' (section 1.3(d)), that is, it occurs systematically following retinal stimulation. Unlike many of the patients studied by other authors F.B. does not have a localised cortical lesion, although it has been suggested that she could have a systemic disorder such as vasculitis which can produce diffuse microscopic damage. This would remain unresolved by the imaging techniques applied (NMR and CT X-ray scan), and would not lead to field loss or epilepsy. There was a focal abnormality evident on the EEG record, but there was only a minor improvement in her symptoms following anticonvulsant treatment and this was not sustained. F.B.'s responses show some similarities to those described for other patients whose palinopsia is specifically of the after-image kind. A moving stimulus produces a continuous streak across the visual field for F.B. and for case 1 of Kinsbourne and Warrington [1963]. This type of after-image for a moving target is also reported by Le Beau, Wolinetz and Rosier [1952]. In other cases, a moving stimulus is described as providing a series of 'stills' at different points along the path of the moving

stimulus [Castaigne and Greveleau, 1953; Teuber, 1961; case 2 of Kinsbourne and Warrington, 1963] and in one unusual case the after-image appeared to be moving twice as fast as the moving object [Cleland, Saunders and Rosser, 1981]. Many authors report positive contrast after-images like those of F.B.'s [Critchley, 1951 case 6; Le Beau, Wolinetz and Rosier, 1952; Kinsbourne and Warrington, 1963] but F.B.'s after-images are monochrome green in colour, whereas these others were black and white. There is also a report of after-images which go through a sequence of colour changes [Bender, Feldman and Sobin, 1968]. The duration of F.B.'s after-images is dependent on the duration and illumination level of the eliciting stimulus (figure 6.3), as was reported by Kinsbourne and Warrington [1963]. The novel aspects of F.B.'s responses are the well-defined dependence on the spatial structure of the eliciting stimulus (figure 6.5), the selective dependence on the wavelength of the eliciting stimulus (figure 6.4), and the increase in threshold sensitivity associated with the after-image (figure 6.1). Of these observations, only low spatial frequency dependence has been reported previously, and then in cases of episodic palinopsia [Bodis-Wollner, Bender and Diamond, 1984].

Abnormal prolongation of visual images is expressed in a variety of response patterns. F.B.'s after-images are specifically spatial in nature, whereas other subjects exhibit after-images possessing temporal and chromatic properties, as is particularly clearly illustrated in the exaggerated movement of the after-images described by Cleland, Saunders and Rosser [1981]. It is proposed, therefore, that abnormal perseverance of visual sensation can arise in one or more of a number of neuronal mechanisms, each of which causes selective prolongation of responses to different parameters. The central representation of the retinal image in a series of field maps was described in section 1.1(d) and figure 1.3. The evidence is that each mapping represents a

different parameter of the retinal image e.g. colour in V4. Thus the organisation of the central pathways is capable of supporting activity specific to one aspect of the image, in this case spatial structure. F.B.'s perseveration may well reflect prolongation of activity in areas V2 and/or V3, which are specifically concerned with spatial pattern.

**CHAPTER SEVEN DISCRIMINATION OF STIMULUS DISPLACEMENT IN
RESIDUAL VISION ASSOCIATED WITH STRIATE LESIONS**

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7.1 Introduction

Damage to the striate cortex usually causes blindness in those regions of the visual field which map to the area of neural damage. However, as discussed in section 1.3(a) of Chapter One, some patients with such damage can detect flashed and moving targets located within the blind area (scotoma). In this chapter the results of measurements of target displacement discrimination in two such subjects, who have residual vision, are reported and the visual pathways by which this residual vision for target displacement could be mediated are discussed.

7.2 Subjects

G.Y. is a 28 year old male who is blind in his right half field of view for both eyes (right homonymous hemianopia) but with sparing of about 3° around the fovea and R.C. is a 27 year old male who is blind in the upper right quadrant field of view for both eyes (right homonymous quadrantanopia). G.Y. received brain damage in a motor car accident when he was eight years old and R.C. sustained a cortical infarct following an attack of migraine when aged twenty-three years. Computer tomography X-ray scans of the brains of the 2 subjects show lesions in the left striate cortex. Degeneration of the area is complete for G.Y. and partial for R.C. The only result of this brain damage is the visual field abnormality and neither of them show any neuropsychological disturbance such as aphasia or memory disturbance. Both subjects have residual vision rather than 'blindsight' [Weiskrantz, 1986] in that they experience a conscious visual sensation for flashed or moving targets

presented with their scotoma, the targets being perceived as 'dark shadows'.

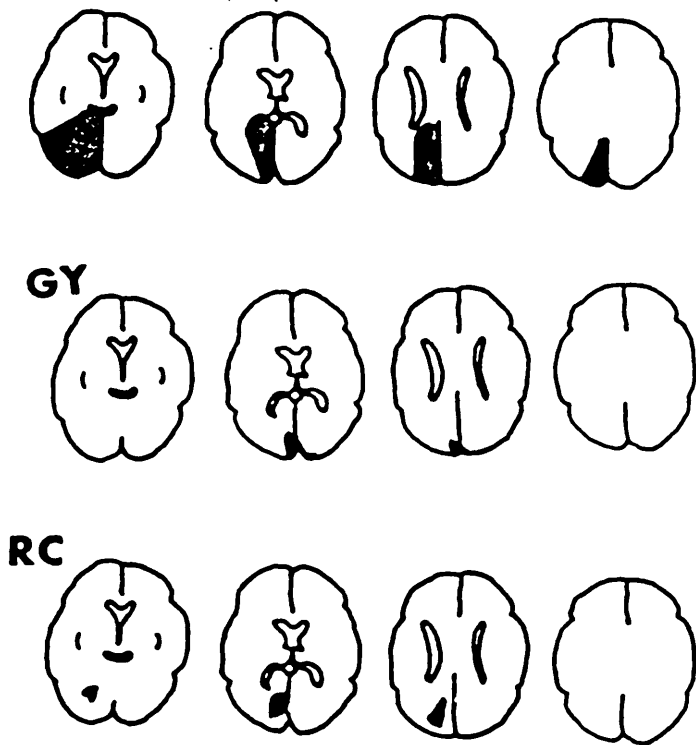


Figure 7.1 Outline tracings of the CAT brain scans from G.Y. and R.C. The upper set of templates show the area of the calcarine cortex (black) and the territory supplied by the posterior cerebral artery (grey).
(from Blythe, Kennard and Ruddock, 1987)

These two subjects, along with twenty-three others, took part in previous studies, [Barbur, Ruddock & Waterfield, 1980 ; Blythe, Kennard and Ruddock, 1987] in which visual fields were mapped using a Goldmann perimeter and two different sized targets. Their visual field plots are shown in figure 7.2.

Neuro—ophthalmological examination failed to reveal any disturbance of eye fixation or saccadic eye movements (see figure 7.3). In the study they were both found to make accurate saccades to stimuli in their blindfield. They could detect a circular target moving at velocity v in either hemifield but their thresholds for movement within their blind field were higher than the

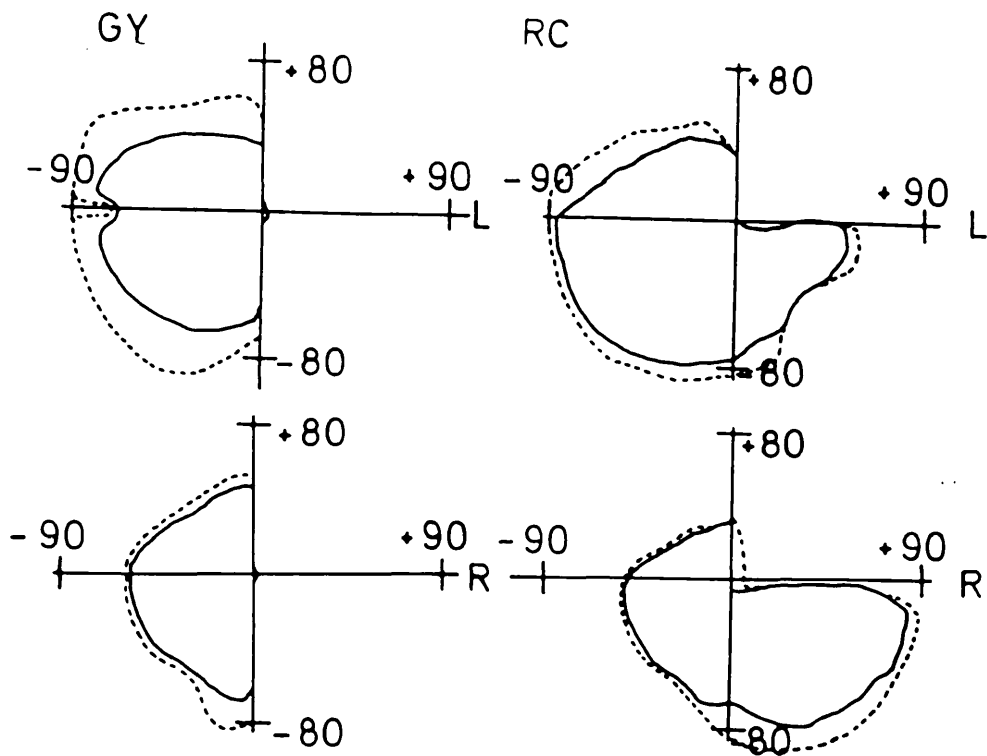


Figure 7.2 Receptive fields measured with a Goldmann perimeter for the left (top row) and right (bottom row) eyes of G.Y. & R.C. Each plot shows the vertical and horizontal meridian, positive angles denoting upper hemifield and right hemifield for the respective axes. The detection limits for a large target ($V=64\text{mm}^2$) are shown by the continuous line, and that for a small target ($II=1\text{mm}^2$) by a broken line. The target was moved at 2 to 3 degrees/second from the field periphery towards the centre and the limits denote positions of first detection. The targets were of luminance 320 cd/m^2 and the background 3.2 cd/m^2 .

(from Blythe, Kennard and Ruddock, 1987)

movement in their normal field, especially for low velocities where threshold was raised by about $3\log\text{td}$ (see figure 7.4). Their sensitivity for transient, non-moving stimuli measured in terms of their critical fusion frequency at different illumination levels was significantly lower in their blind areas than in their normal field (see figure 7.5) Neither of them showed any pattern recognition ability in their blind field and could not tell the difference between horizontally and vertically orientated gratings of 1 cycle/degree spatial

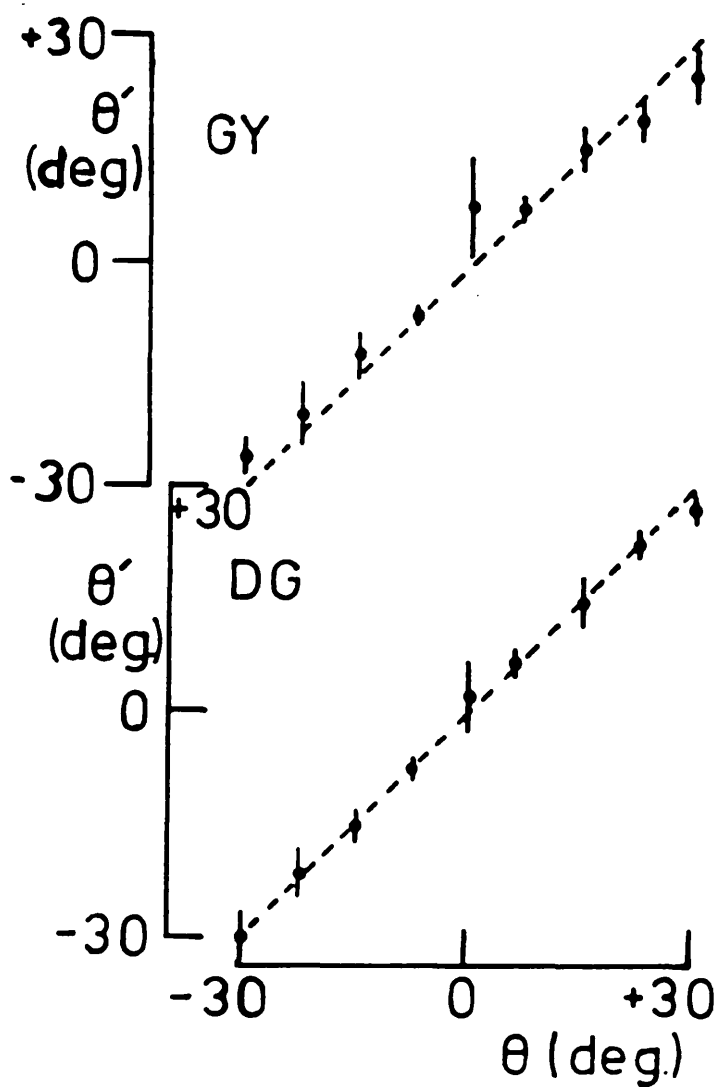


Figure 7.3 The angle, θ' through which the eyes were moved in order to detect a light flash located on the horizontal meridian at angular location θ from primary fixation (positive angles denote the right hemifield). The lights were of diameter 23 minutes, wavelength 565 nm, duration 100 mseconds and luminance 56.2 candela/m². Top graph, G.Y., bottom graph, a normal subject, D.G. Error bars define the standard errors around the mean of ten readings

(from Blythe, Kennard and Ruddock, 1987)

frequency, 4° square in size or between an equilateral triangle with sides of length 4° and a circle of 4° diameter, both of which are trivial discriminations to make in the normal field of view. Neither subject had any sensation of colour in their blindfields although another subject of the study by Blythe, Kennard and Ruddock, [1987] was able to tell the difference between red (635nm) and green (530nm) light flashes.

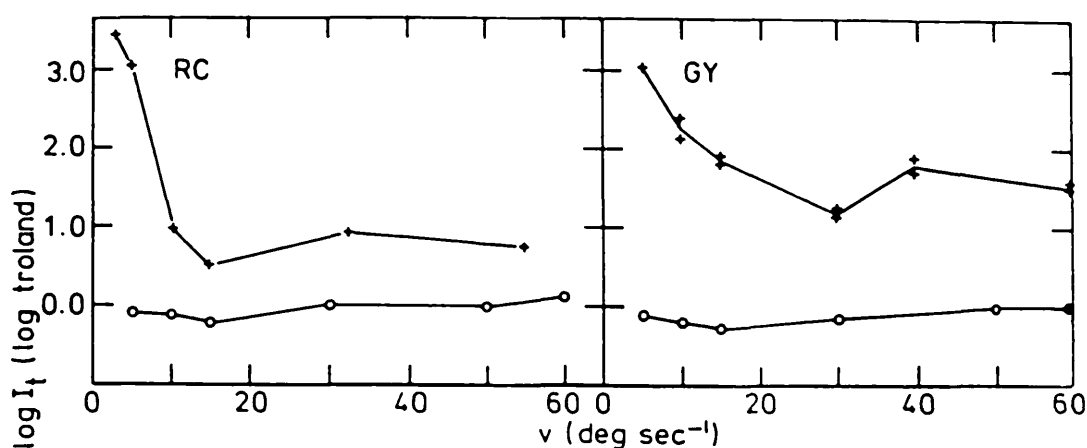


Figure 7.4 Threshold illumination, $\log I_t$, for detection of a circular target (diameter 3.5°) moving at v degrees/second along a direction parallel to the horizontal meridian, against a uniform background of illumination 1 log td. The target traversed 8° , and was located within the field scotoma (crosses) or in the corresponding position in the normal field (open circles). The target location for G.Y. was $\pm 30^\circ$ along the horizontal meridian and for R.C. $\pm 25^\circ$ from the horizontal and vertical meridians

(from Blythe, Kennard and Ruddock, 1987)

Thus the two subjects can perform accurate eye movements into their blindfield, their residual vision is transient in nature, with a low frequency temporal response, but neither can identify the colour, size or shape of a stimulus in their blindfield. The dissociation between shape discrimination and movement is illustrated by the observation that movement of the experimenter's hand can be detected and its direction identified, but it cannot be

differentiated from movement of a black, square card of much greater area.

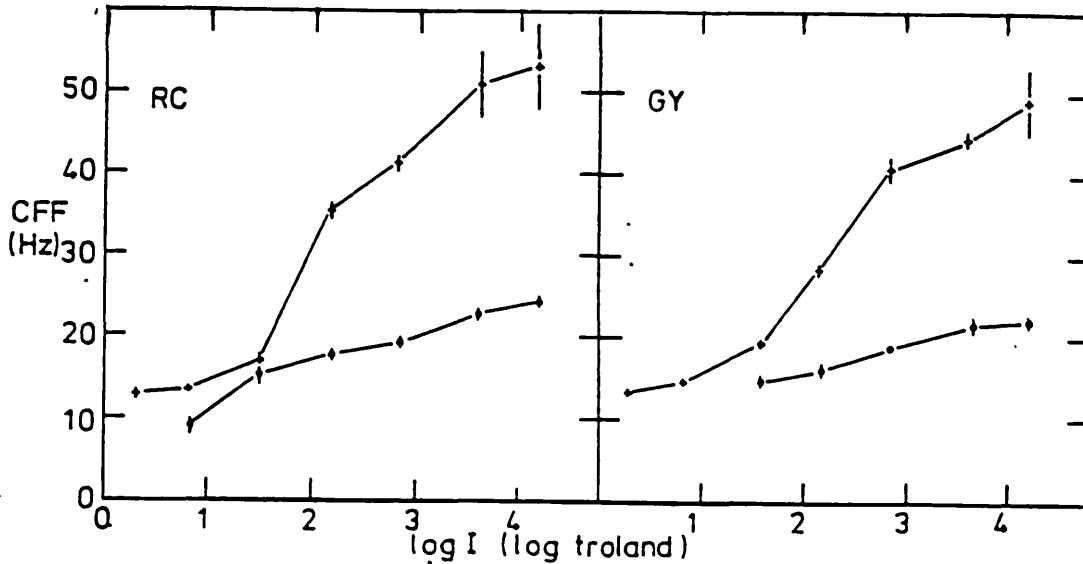


Figure 7.5 Values of critical fusion frequency (CFF) plotted against the logarithm of the target illumination ($\log I$). The sinusoidally modulated target (diameter 5.5°) was superimposed on a uniform background of illumination $0.75 \log \text{td}$. Circles refer to values for stimuli located within the scotoma and crosses to values for the corresponding location in the normal field. The stimulus locations were the same as in figure 7.4.

(from Blythe, Kennard and Ruddock, 1987)

7.3 Experimental Procedure

The Maxwellian view apparatus was used as explained in 2.2(g) in order to study the responses of the subjects to sequentially flashed targets. Such stimuli elicit, in normal subjects, a strong sensation of movement directed from the first to the second flash, and this sensation was reported by the two subjects for stimulus presentation within either the normal or 'blind' areas of the visual field. All measurements were made monoptically, with the right eye, and the observer's head was kept steady relative to the instrument's exit pupil by a dental clamp. The targets were small, circular patches of white light. The probability, P , of correctly identifying spot displacement to the left

or to the right was measured as a function of spot separation d and 10 presentations were made for each separation.

7.4 Results

(a) Direction Discrimination at Different Positions along the Horizontal Axis

The field of view is illustrated in figure 7.6(a) with two spots of 1° diameter and both at 3.2 log td. The change in direction discrimination ability was measured as the separation, d , of the two targets was varied for a number of different locations along the horizontal axis and the results are shown in figure 7.6. The data for G.Y. (figure 7.6(b)) is for positions 5, 10, 15, 20 and 30° off-axis along the horizontal meridian in the blind (right) hemifield and at 5° off-axis in the normal hemifield. Data for a normal subject for similar locations in their right hemifield are shown in figure 7.6(c). The data for both G.Y. and the normal subject, I.B., show that the probability for correct discrimination of apparent motion increases rapidly as the separation of the two targets increases and that it decreases as the distance of the stimulus from the fixation (its eccentricity) increases. G.Y.'s performance in his blindfield is worse than at a comparable points in his normal hemifield or than that at comparable points in the normal observer's field. In order to compare discrimination ability for normal and blindfields the values of d for a probability of correct direction discrimination of 90% at each retinal location are plotted in figure 7.7. This shows that up to 15° eccentricity the blindfield requires only slightly larger target separation for direction discrimination but that at higher eccentricities the difference between the two fields becomes more marked.

a.

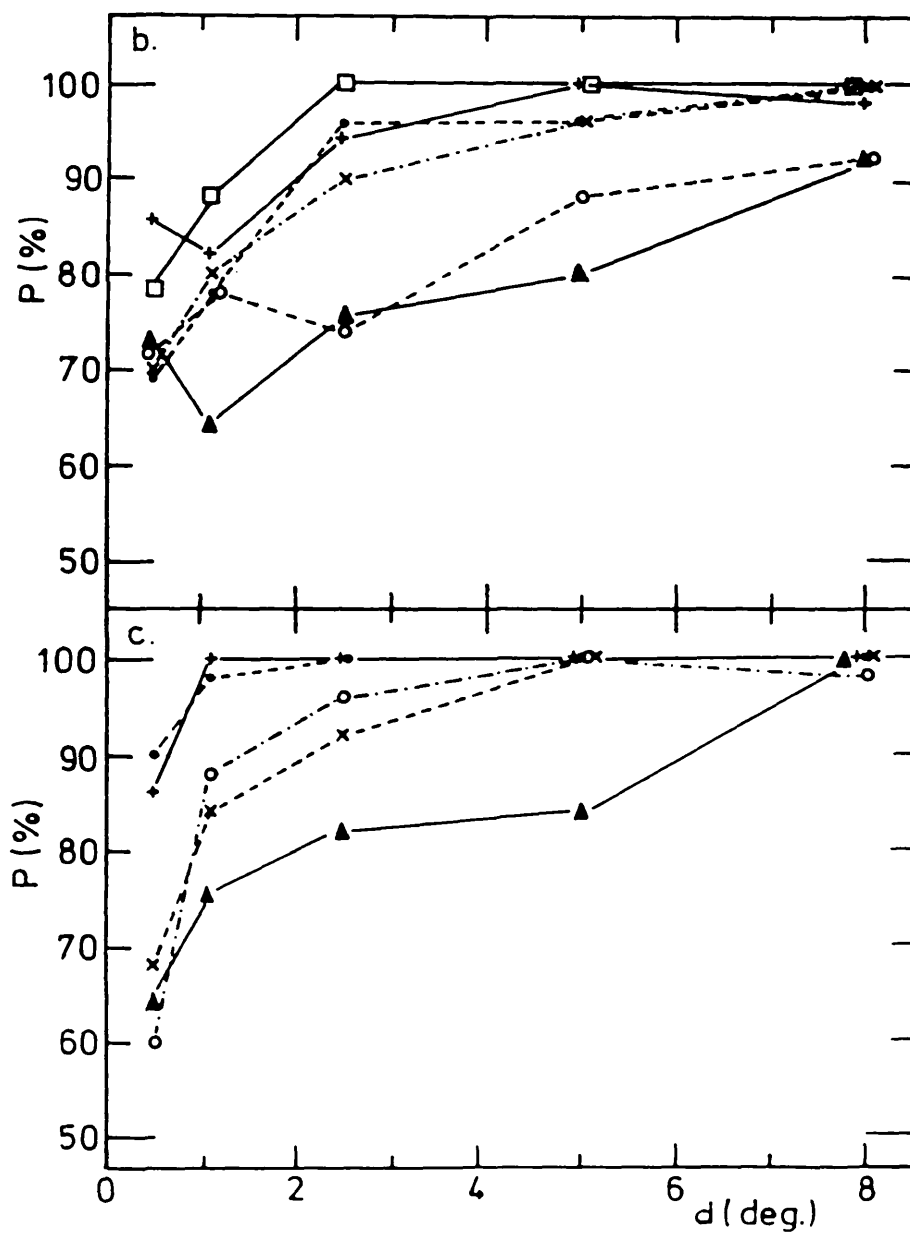
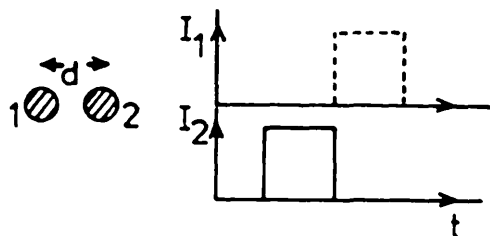


Figure 7.6 (a) The stimulus configuration used to elicit apparent movement. The two circular targets were displaced centre to centre by distance, d , which was the variable parameter of the measurements, and were presented successively for 800ms each. The value of d and the order of presentation of the two spots were varied randomly between presentations. Each stimulus configuration was repeated 10 times. I_1 and I_2 denote the (equal) illumination levels of the two targets.

(b) Data of subject G.Y.; probability for correct discrimination of the target, $P(\%)$, is plotted against d , the separation of the two spots, expressed in degrees. The spots were of 1° diameter and the illumination level was $3.2 \log td$. Measurements were made in the 'blind' hemifield, at 5° , $+$, 10° , $\bullet$, 15° , $\times$, 20° , $\circ$ and 30° $\blacktriangle$ off-axis along the horizontal meridian, and at 5° off-axis in the normal hemifield ($\square$).

(c) As for (b), but for the normal subject I.B.; symbols as for (b).

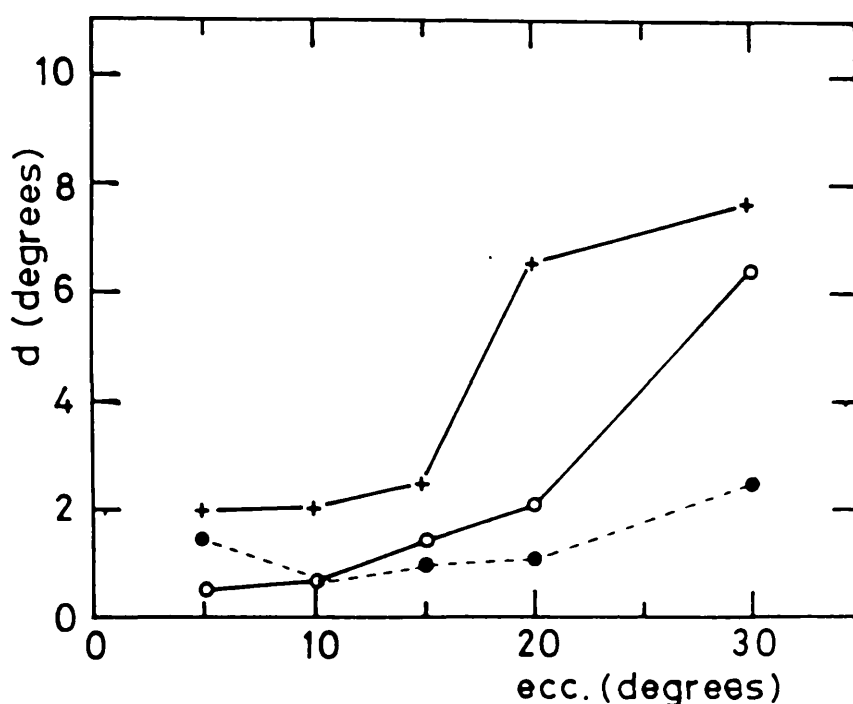


Figure 7.7 Values of d required for 90% probability of correct discrimination of the direction of target displacement from right to left, or vice versa. Data for subject G.Y.'s blind hemifield (+) and I.B. (o) plotted against stimulus eccentricity, are taken from figure 7.6. Data for G.Y.'s normal hemifield (•) were obtained by similar methods.

(b) Directional Discrimination for Different Spot Sizes

A single stimulus location was used and discrimination of direction was measured for different spot sizes as a function of spot separation. The experiment was performed by R.C., a quadrantinope, so in order to present

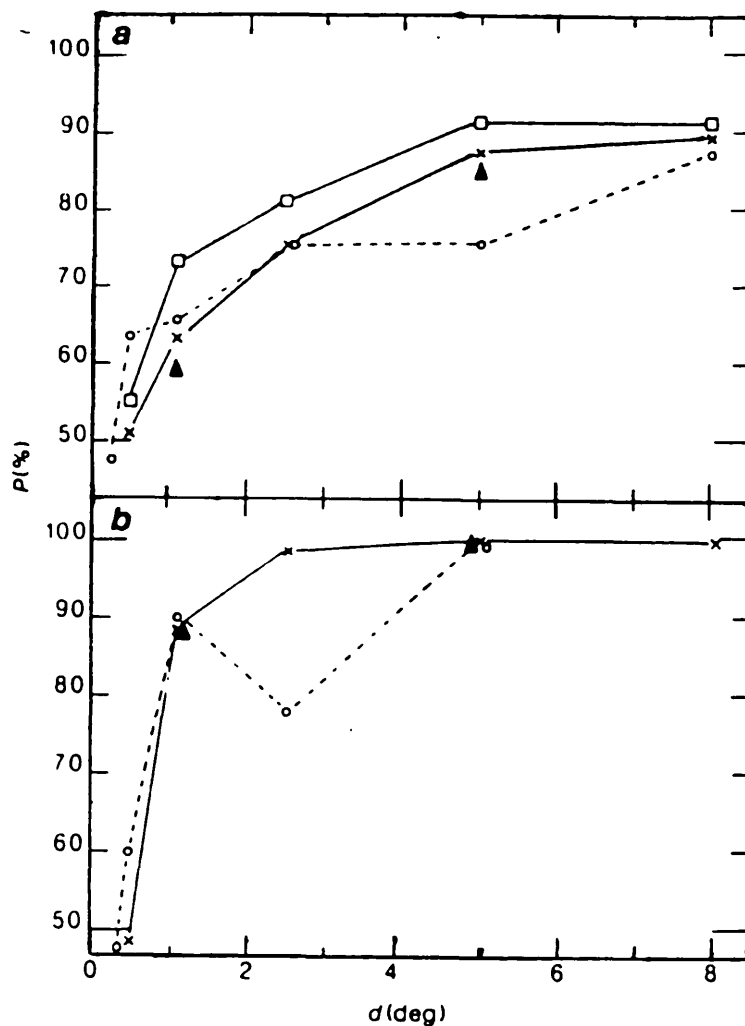


Figure 7.8 (a) As for figure 7.6, but measurements were made at a single location, 10° off-axis relative to both the vertical and horizontal meridians, placing the targets in the upper right quadrant, that is within R.C.'s blindfield area. The data for R.C. refer to circular targets of 0.2° (▲), 0.5° (○) and 1.0° (x) diameter. Comparison data are also given for an equivalent location in the normal left upper quadrant for targets of diameter 1.0° (□). (b) As for (a) but for upper right quadrant of the normal subject I.B. Symbols as for (a).

targets within his blind field they were situated in the upper right quadrant, 10° off-axis and at equal distances from the horizontal and vertical meridian. The targets were of 0.2 , 0.5 and 1° diameter and all of $3.2 \log \text{ td}$. illumination. The results in figure 7.8 show that the probability for correct

identification of the direction of apparent motion increases with separation, d , of the ~~two~~ targets and that it is essentially independent of spot size. Results for target presentation in the blind area are similar to those obtained in the normal field, figure 7.8(a), and in the normal observer, figure 7.8(b), although R.C.'s blindfield yields poorer discrimination performance for displacement than does I.B.'s normal field.

(c) Shape Discrimination

Shape discrimination was tested for a pair of stimuli, a 1.1° diameter circular target and two 1.1° diameter circular targets separated by 7° and presented at the same time. Both stimuli were centred 13.5° off-axis along the horizontal meridian and the single target illumination was equal to the illumination of the two targets together so the stimuli could not be differentiated by total flux. One hundred presentations were made, with the two stimuli presented in random sequence and before the experiment G.Y. was instructed as to the nature of the stimuli. For presentation in the blindfield he correctly identified the single target in 23 out of 50 presentations and the pair of targets in 26 out of 50 presentations, ie he performed at chance, whereas he was 100% correct for target presentation in his normal field.

7.5 Discussion

These experiments, carried out on two subjects with residual vision within scotomata caused by striate lesions, show that whilst they have no pattern recognition ability and perform at chance levels for discriminating stimuli in their blindfield, they have near normal ability to discriminate the displacement of two targets flashed sequentially in their blindfield (figure 7.6

and figure 7.8)

A number of authors, including Campion, Latt and Smith [1983], have suggested that residual vision is due to light scattered into the normal field. However this implies residual vision would be possible with scattered light in all cases of partial-field blindness but this is not the case and the study of Blythe, Kennard and Ruddock [1987] found that out of twenty-five subjects with retrogeniculate lesions only five had residual vision. In the experiments described above very fine discriminations were being made in the blindfield which, if scattered light was being used, would mean that it would have to be well localized. A number of other arguments against the scattered light explanation of residual vision have been given by Barbur, Ruddock and Waterfield [1980], Barbur and Ruddock [1983] and Blythe, Kennard and Ruddock [1987] (G.Y. was a subject in all of these studies.)

Computer tomography X-ray scans show damage of the striate cortex (and only of the striate cortex) in both subjects. Such damage has been reported in many other subjects and it results in blindness of the corresponding retinal area. Subjects exhibiting residual vision do not differ systematically from those who do not exhibit residual vision in the extent of damage to the striate cortex and blindsight has been reported for a subject in which a large part of the striate cortex was surgically ablated [Weiskrantz, Warrington, Sanders and Marshall, 1974]. Therefore, in our subjects, another brain area must be able to localize transients. Blythe, Kennard and Ruddock [1987] suggest that age of onset of the brain damage is an important factor and that recovery of function may occur in young subjects.

It has been argued that the characteristics of residual vision in one of these two subjects are similar to those of electrophysiological responses recorded from the superior colliculus [Barbur, Ruddock and Waterfield, 1980],

which itself projects via the pulvinar to the prestriate cortex. Subsequently however, a direct, albeit sparse, projection from the primate lateral geniculate nucleus to the prestriate cortex has been demonstrated [Fries, 1981; Yuki and Iwai, 1981]. Although the experiments do not identify the pathway which mediates residual vision, they do demonstrate a complete functional dissociation between visual localization of transients and pattern discrimination, as would be predicted by the 'two systems theory' of visual organization.

CHAPTER EIGHT CONCLUSIONS

The principal experimental findings and conclusions presented in this thesis can be summarised as follows.

8.1 Experiments with Spatially and Temporally Modulated Stimuli

(Chapter Three)

- (a) Visual detection of a dark contrast, moving target is influenced by spatial and/or temporal modulation of the background field. The spatial and temporal frequency response characteristics of the visual mechanisms, found by measurement of changes in threshold illumination caused by the background modulation, are similar to the response characteristics of the visual mechanisms found by Barbur and Ruddock [1980a] and Holliday and Ruddock [1983] using a light contrast target and the same background fields.
- (b) The spatial frequency response obtained with a dark contrast target and a background consisting of alternate light and dark bars (grating structure)(see figure 3.1) is band-pass, peaks between 3 and 5 cycles/degree and is similar to the ST1 spatial response (the IMG response of Barbur and Ruddock, 1980) for a light contrast target. No shift of the peak to higher spatial frequency was found with background illuminations greater than 2 log td., but the highest background illumination used only 2.6 log td. (figure 3.2). Experiments with light contrast targets carried out after the 1980 paper have not found such a shift for all subjects. The ST1 spatial response measured with a dark contrast target has other parametric properties similar to those obtained with a light

contrast target. Thus similar data are obtained with horizontally or vertically orientated background gratings (figure 3.4), establishing that the mechanism which mediates the response is non-orientation selective and the peak response is displaced to lower spatial frequencies for measurements made at greater retinal eccentricities (figure 3.3).

(c) The ST1 temporal response obtained with two matched gratings presented in spatial and temporal antiphase was not measured for a dark contrast target. But the ST2 temporal response, which is closely related to the ST1 temporal response, was measured for a negative contrast target by presenting the moving target on a spatially uniform, flickering background. This ST2 temporal frequency response is band-pass (figure 3.5) and the frequency for maximum response increases with mean background illumination, in a manner similar to that of the ST2 temporal response obtained with a light contrast target (figure 3.6). From this it is inferred that the ST1 temporal responses for dark and light contrast targets are similar.

(d) The spatial response obtained with a dark contrast target moving across a background field consisting of alternate steady and flickering bars of the same mean illumination is band-pass (figure 3.7), with a peak response at 1 cycle/degree and is similar to the ST2 spatial response obtained for a light contrast target.

(e) The use of two different sets of spatially structured backgrounds with light and dark bars of unequal width (figures 3.10 to 3.12) failed to show that there are separate ST1 mechanisms detecting light and dark contrast targets, respectively. This failure may be due to inadequate methodology and for one set of background stimuli (in which one bar polarity had a constant width whilst the other had varying width) (figure 3.13), there were some differences at low spatial frequencies between detection of light and dark contrast targets.

8.2 Experiments on the Contributions of Different Spectral Classes of Cone to Central Mechanisms. (Chapter Four)

- (a) The contrast threshold elevation effect was elicited with inputs derived from single cone types, using the two colour increment threshold technique of Stiles.
- (b) The responses obtained from the π_3 or π_5 (figure 4.4) mechanisms are similar to those obtained using white light under either monoptic or dichoptic presentation of test and adaptation gratings. In each case the maximum increase in contrast threshold occurs when the adaptation and test gratings are of the same spatial frequency.
- (c) All adaptation wavelengths tested produce contrast threshold elevation when either π_3 or π_5 mechanisms are isolated (figure 4.5).
- (d) It is concluded that signals generated in blue sensitive cones are transmitted to a central mechanism with broad-band spectral responses, contrary to the assertion that they are propagated solely in narrow-band 'opponent colour' channels.

8.3 Experiments on the Processing of Spatial Patterns in Subjects with Abnormalities of the Visual System (Chapter Five)

- (a) ST1 spatial responses obtained for both light and dark contrast targets are shifted to lower spatial frequencies in the 'amblyopic' eye of five strabismic amblyopes and in the 'normal' eye of those subjects who have undergone patching treatment for their squint (figure 5.2).
- (b) This result suggests that both 'on' and 'off' centre X-type physiological pathways are affected in strabismic amblyopia.
- (c) Discrimination ability for orientation (figures 5.3 to 5.7) is degraded

relative to normal, only for the 'amblyopic' and not for the 'normal' eyes of strabismic amblyopes and then only for small two-dimensional pattern elements (figures 5.4 to 5.7), not for single line elements (figure 5.3). The amblyopic eye's poor discrimination response can be simulated in normal subjects by defocusing or demagnifying the images.

(d) The amblyopes' poor discrimination performance cannot be explained solely by loss in spatial resolution as measured by the ST1 spatial response and it appears that other factors arising centrally in the pathways contribute to reduced discrimination performance. A correlation was found between discrimination of small, two-dimensional pattern elements and Snellen acuity (figure 5.8).

(e) Orientation discrimination for single lines is normal in amblyopes, a result found by other researchers [Vogels, Orban and Vandenbussche, 1984].

(f) Studies on a subject, H.J.A., with visual form agnosia establish that pattern discrimination for a target differentiated from background elements by a single parameter (either orientation, magnification, texture, lightness or distortion) is in all but one case abnormally slow (figures 5.12 to 5.17). The single exception is the discrimination of orientation for single lines (figure 5.12(a)).

(g) There is a clear correlation between the number of errors (failures) made by this subject in detection of a given target and the time taken for the discrimination of that target (figure 5.22).

(h) The characteristics of H.J.A.'s discrimination are similar to those of normal subjects but the time scale of his discriminations are of the order of ten times slower than normal (figure 5.23a).

(i) His discrimination between a pair of elements is not abnormally dependent on their separation over the central 10° or so of the field, but even

in the simplest case of two adjacent elements his responses are abnormally slow (figure 5.19).

(j) H.J.A.'s discrimination capacity for two dimensional elements deteriorates rapidly as the number of elements in the field increases, in contrast to normal subjects. Thus he appears unable to process two dimensional elements in parallel (figure 5.18).

(k) These results suggest that the problem with H.J.A.'s discrimination is not that it operates over only a restricted area (a theory proposed by Bay, 1953), but that it fails to perform simultaneous discrimination of geometric shapes except in the simplest case of single lines. This exception establishes that H.J.A.'s visual responses are intact at one level but that they are disturbed at the level where single lines are associated into two dimensional elements.

(l) H.J.A.'s normal stereoscopic depth perception indicates that some pre-striate function is normal, but the absence of colour vision and the extensive damage visible in a CT scan (figure 5.11), indicate impairment at an early stage of the cortical visual pathway.

(m) It is argued that the data obtained in the studies on two types of visual abnormality support the hypothesis that neuronal processing of spatial content of the visual image can be divided into a filtering stage and a computational stage.

8.4 Experiments on Temporal Disturbance of Vision — Visual Perserveration (Chapter Six)

(a) This subject, F.B., suffers from a relapsing and remitting neurological disturbance whose major visual symptom is prolonged after-images, caused by lights too dim to produce them in subjects with normal vision.

(b) The after-images are believed to be produced centrally. They occur throughout the visual field, are of positive contrast and yellow-green in colour. The duration of the after-images increases with the illumination and exposure time of the primary stimulus (figure 6.3) and it also depends on the spatial content (figure 6.5) and wavelength (figure 6.4) of the primary stimulus. The spatial content of the after-image is the same as that of the eliciting stimulus. Threshold sensitivity for detection of a test stimulus flashed on the after-image is increased for some 10 to 15 seconds, after extinction of the eliciting stimulus, although the after image can be detected for a longer period of time (figure 6.1).

(c) The after-images maintain the spatial structure of the eliciting stimulus but structures of spatial frequency of 1 to 2 cycles/degree persist longer than other structures and those with spatial frequency greater than 10 cycles/degree are not observed at all (figure 6.5).

(d) F.B.'s temporal resolution is normal (figures 6.9 to 6.11) but she has raised increment thresholds at low background illuminations (figure 6.8) which implies a large intrinsic or 'dark' noise in her visual system.

(e) The spatial frequency response of F.B.'s after-images is similar, in some respects, to that of the mechanism responsible for binocular inhibition of the contrast threshold effect [Ruddock and Wigley, 1976; Ruddock, Waterfield and Wigley, 1979].

(f) It is argued that these results, together with reports of other subjects [Cleland, Saunders and Rosser, 1981; Bender, Feldman and Sobin, 1968; Kinsbourne and Warrington, 1963], support the hypothesis that abnormal perseverance of visual sensation can arise in one or more of a number of neuronal mechanisms, each of which causes prolongation of response to different stimulus parameters. This subject's perseveration may well reflect

prolongation of activity in areas V2 and/or V3 which are specifically concerned with spatial pattern.

(g) Measurement of the subject's visual abnormality with psychophysical techniques makes it possible to quantify the effectiveness of medical treatment.

8.5 Experiments on the Residual Vision of Two Hemianopic Subjects (Chapter Seven)

(a) The residual visual properties of two hemianopic subjects are reviewed [Barbur, Ruddock and Waterfield, 1980; Blythe, Kennard and Ruddock, 1987] and direction and shape discrimination within their blind fields measured. Shape discrimination performance is at chance level, while the discrimination of the displacement of two spots flashed sequentially was near normal.

(b) The results of these experiments demonstrate a complete functional dissociation between visual localization of transients and pattern discrimination in hemianopic residual vision and are further evidence in support of the 'two systems theory' of visual organization.

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Pattern discrimination in a human subject suffering visual agnosia

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Since suffering a stroke some four years ago, H.J.A. has exhibited lack of visual pattern recognition, and CT scans show areas of neuronal damage localized bilaterally in the posterior cerebral cortex (Humphreys & Riddoch, 1984). His failure to recognize familiar objects, including faces, is particularly marked for line drawings (Humphreys & Riddoch, unpublished). We have measured the time required for detection of a target element which differs in orientation from multiple, identical

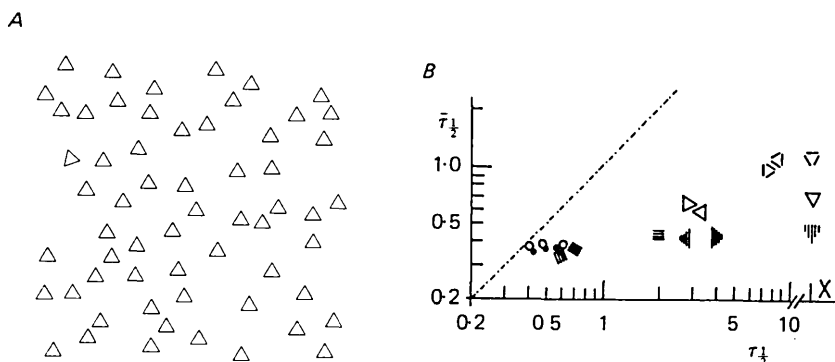


Fig. 1. *A*, typical stimulus pattern, of size 9.5 deg, 7.1 deg; locations of the non-overlapping elements were randomized between presentations. Four possible target orientations were presented 50 times each, in random sequence. Target elements were rotated 0 deg (null target), 30, 60 and 90 deg relative to the background elements. *B*, $\tau_{\frac{1}{2}}$ (seconds) for H.J.A. plotted against $\bar{\tau}_{\frac{1}{2}}$, average values for three normal, naive subjects. The different targets are illustrated on the figure, except for continuous lines and co-linear spots, denoted ● and ○ respectively, which give similar values for all orientations. Targets presented at time X were not detected on 50 % of presentations and the dot-dash line shows the locus $\tau_{\frac{1}{2}}$ equal to $\bar{\tau}_{\frac{1}{2}}$.

background elements (Fig. 1 *A*). Probability for detection of a given target, $P(t)$, was measured as a function of time, t , following its presentation, and $\tau_{\frac{1}{2}}$, the t value for 50 % probability of detection, provides a measure of discrimination performance. H.J.A.'s $\tau_{\frac{1}{2}}$ values for background elements | and : are essentially normal, but become increasingly abnormal for backgrounds |||, ||||, Δ and ∇ (Fig. 1 *B*). The data demonstrate that H.J.A.'s discrimination is disturbed for targets incorporating different line orientation, but not for single lines. Thus those mechanisms responsive to single lines function normally, whereas those which associate line elements into 2-D patterns are selectively disturbed.

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Abnormal prolongation of visual sensations in a human subject

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After a few seconds exposure to a high-contrast light stimulus, subject F.B. experiences an after-image of up to 3 min duration, with spatial structure similar to that of the stimulus. Psychophysical measurements establish that in association with the after-image, there is an increase in the illumination required for detection of a flashed target presented either dichoptically or monoptically with respect to the stimulus responsible for the after-image (Fig. 1). Stimuli spatially modulated at 1–2 c deg⁻¹ produce after-images of significantly longer duration than those elicited by uniform fields, but fine spatial structure (≥ 10 c deg⁻¹) is not perceived in the after-images. After-images of flickering or moving lights do not themselves exhibit temporal changes and all monochromatic lights yield after-images of similar colour appearance, with C.I.E. co-ordinates $x = 0.411$, $y = 0.476$; $Y \leq 42.5$. Increase in duration or illumination of the eliciting stimulus increases the duration of the after-image, as was found by Kinsbourne & Warrington (1963) for two similar cases. F.B. has normal sensitivity for detection of target movement and flicker. Her CT and NMR brain scans were both normal, but the EEG showed a minor irregularity, of a kind associated with epilepsy. The after-image duration was reduced by 30% following two months treatment with anti-convulsant drugs.

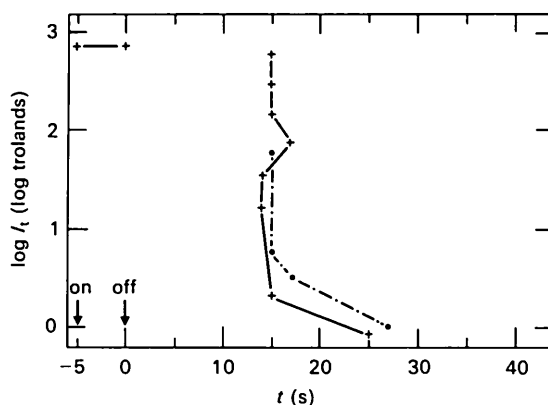


Fig. 1. Threshold illumination, I_t , for detection of a circular test flash (diameter 3.5 deg, 0.1 s presentation every 1 s), following 5 s exposure to a circular light stimulus (diameter 30 deg, illumination 2.9 log trolands). Data for presentation of the two light stimuli to the same (+—+) and to different (●—●) eyes. Subject F.B.; white-light stimuli. In normal vision, sensitivity to the test flash recovers within 0.1 s of stimulus offset.

REFERENCE

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A STUDY OF SYSTEMATIC VISUAL PERSEVERATION INVOLVING CENTRAL MECHANISMS

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SUMMARY

The subject of this investigation experiences vivid after-images which persist for tens of seconds following stimulation by light insufficiently intense to produce after-images in normal subjects. The after-images occur at all points in the visual field, and have spatial structure closely similar to that of the stimuli which elicit them, the only distortion being the absence of high (≥ 10 cycles $\cdot$ deg $^{-1}$) spatial frequencies. The duration of the after image is dependent on the spatial structure and spectral content of the eliciting stimulus, being maximum for low, nonzero spatial frequencies (1–2 cycles $\cdot$ deg $^{-1}$) and yellow or green wavelengths. The after-images appear 'khaki' or 'mustard-green' in colour, regardless of the spectral composition of the light stimulus, and those produced by flickering or moving targets do not themselves exhibit temporal fluctuations, although movement produces a streak along the path described by the moving object. After six weeks of treatment with the anticonvulsant drug, carbamazepine, the duration of the after-images fell by about 30%, but no further reduction occurred over the following three months. In spite of the prolonged after-images, the subject has normal sensitivity for detection of flicker and movement, but that for detection of a single flash is raised abnormally at low background illumination. Neither CT nor MRI brain scans revealed any abnormality. These responses are discussed in relation to those found in other subjects suffering visual perseveration or palinopsia, and we examine their possible causes.

INTRODUCTION

The term visual perseveration has been used to describe visual perceptions which exhibit either abnormal temporal persistence or abnormal spatial spread (Critchley, 1951). In this paper, we are concerned with abnormal prolongation of visual sensation, which is frequently termed palinopsia (or paliopsia) and variously described as continuation of visual sensation after cessation of the light stimulus or as episodic reappearance of images without immediate visual stimulation (Critchley, 1951; Bender *et al.*, 1968). Both kinds of subjective experience were described by Robinson and Watt (1947), and Critchley (1951) distinguished the former by the term 'palinopsia resembling an after-image'. Robinson and Watt

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(1947) regarded the prolongation of images after stimulation as the less common form of palinopsia, whereas Bender (1963) described it as relatively commonplace. We have studied visual function in a subject who systematically experiences particularly vivid and long lasting images following light stimulation, the spatial structure of the after-image being closely similar to that of the stimulus. We have made measurements on this phenomenon in order to establish the stimulus-response relationships for the after-image and to obtain evidence regarding the pathway(s) involved in its generation. In the course of the investigation, we found that thresholds for visual detection are raised during the poststimulus period and we have exploited this effect in measuring the parametric properties of the after-image and in examining the effect of treatment. Some aspects of the subject's responses are novel, whereas others correspond broadly to those noted for 1 of his 10 subjects by Critchley (1951), by Le Beau *et al.* (1952), and by Kinsbourne and Warrington (1963) for 2 subjects.

CASE REPORT

F.B., a 24-year-old woman, presented in July 1982, when 25 weeks pregnant, with sudden onset of drowsiness, slurred speech and heaviness and weakness of her right arm and leg. These symptoms rapidly resolved so that when admitted to hospital five days later the only abnormality found on clinical examination was a reduction in right arm swing when walking. Investigation during this admission revealed normal results for full blood count, urea, electrolytes, liver function tests, blood serology, autoantibody screen which included antinuclear factor, DNA binding, rheumatoid factor, C_{1q} binding and extractable nuclear antigen, serum complement (C_3 , C_4), CH_{50} , thyroid and parietal cell antibodies, quantitative immunoglobulin levels, EEG, CT scan, VEPs (pattern reversal), and echocardiogram. The only abnormality found was an erythrocyte sedimentation rate (ESR) of 70 mm at 1 h, which had fallen to 42 mm ten days later. Following delivery of a normal child she experienced recurrent episodes of numbness of her right hand and foot, each episode lasting about one week. Her ESR was then 25 mm at 1 h.

In May 1984, during the third trimester of her second pregnancy, she again experienced heaviness and clumsiness of her right hand, which persisted. At this time her ESR had again risen to 70 mm at 1 h but returned to normal after delivery. In August 1984 (two months post partum) she suddenly developed numbness and weakness of her left hand and complained of an increasingly poor memory.

She was readmitted in October 1984, when clinical examination revealed a slightly unsteady gait, a right-sided hemisensory impairment to light touch and pin prick, and mild pyramidal weakness of the right arm and leg without reflex changes. Both plantar reflexes were flexor. All the previous investigations were repeated and were all normal with two exceptions. There was now a polyclonal increase in serum IgM ($> 430\%$ of normal adult mean), and the EEG showed a minor left temporal abnormality consisting of theta activity with occasional sharp waves. Additional investigations included examination of her CSF which was normal, with absence of oligoclonal IgG bands. An ERG (single stimulus and flicker to 30 Hz), SEPs and BSAEPs, and a fluorescein retinal angiogram were normal, as also were CT and MRI brain scans. Formal psychometric testing revealed mild impairment of verbal memory, but perceptual and visuospatial skills remained unaffected.

Three months following this admission F.B. developed a polyarthralgia with morning stiffness but no objective synovitis. Investigations now revealed a raised ESR (30 mm at 1 h), a raised serum IgM and a normochromic microcytic anaemia (haemoglobin 10.0 g/dl).

A definitive clinical diagnosis was not reached (*see Discussion*).

Visual Symptoms

In July 1984, F.B. started to experience abnormal visual phenomena. Several times a day she noticed white spots 'like fireflies' of a few seconds duration throughout her visual fields. These could be brought on by sudden head movements or by walking into a bright light, for instance when she walked out of a shop into daylight. In addition, white objects appeared brighter than before and she experienced discomfort when looking at her babies' white nappies. She noticed that she had prolonged after-images when she looked at bright lights and that as they faded they became green in colour. Following flash photography of the retina, the after-image lasted for tens of minutes.

In view of the temporal lobe abnormality in the EEG it was decided to give her a trial of the anticonvulsant (carbamazepine, 300 mg/day). Following this she reported that bright white objects were slightly less intense.

Foveal colour vision was examined in detail, using the tristimulus colorimeter and methods of measurement described by Wright (1946). Tristimulus colour matches for spectral test stimuli and the relative spectral sensitivity (V_λ) function, the latter determined by flicker photometry, were both normal. Foveal acuity (6/4 without correction in either eye), stereoscopic depth perception for random dot stereograms (Julesz, 1971) and dark adaptation for a circular target (diameter 3.5 deg; wavelength 495 nm) located 10 deg off-axis, were also normal.

EXPERIMENTAL METHODS

Equipment

The majority of our measurements were made under controlled conditions with a three channel Maxwellian view optic system, fitted with a fixed artificial pupil (Barbur and Ruddock, 1980; Barbur *et al.*, 1980). The system, which can be adapted for binocular viewing, provides a large background field of up to 45 deg diameter, on which can be superimposed a target for threshold detection measurements and fixation points for positioning of the target at any chosen retinal location. The target can be presented either as a stationary flash or moving at constant velocity in the range 0 to 100 deg $\cdot$ s⁻¹ along the horizontal meridian, and its spatial structure is determined by the photographic negative which provides the target object. The target wavelength is set by placing interference filters (Balzer B40 with ± 5 mm transmission half-width) in the collimated beam, and target illumination is controlled by a neutral density wedge (Kodak), adjusted automatically via a microcomputer (Macsym 2), and threshold levels were determined by means of the random staircase method (Cornsweet, 1962). The stimuli used to elicit F.B.'s after-images were obtained by placing appropriate photographic negatives in the background beam. The subject's head was maintained in correct alignment by means of a dental clamp and a push button was provided with which to signal events such as onset or cessation of a visual sensation. Time differences could be measured to 10 ms accuracy by the Macsym, but the time course of F.B.'s after-image was of such duration that measurements were made with a stop clock. Certain measurements, particularly detection of decremental steps in the stimulus, were difficult to make with the Maxwellian view system, so a computer (Sharp MZ80B) controlled visual display unit (Microvitec) was used to present a flashing, decremental target against a uniform background field. The colour and illumination levels of the VDU screen were controlled by a Pluto colour graphics display controller (IO Research) which provided a 256 level grey scale, and up to 16 million hue settings. The VDU was viewed binocularly in a darkened room from a distance of 1 m. Some observations were made with stimuli projected onto a white screen with a Simda projector (Type 2200). Illumination calibrations were performed with a MACAM photometer and are given in trolands. Error bars denote the spread of mean settings.

RESULTS

All data were obtained before treatment with carbamazepine unless otherwise stated. F.B.'s verbal description of the image which occurred after viewing for 5 s a

circular patch of white light (diameter 30 deg; retinal illumination 2.8 log trolands) was consistent from session to session. In darkness, it appeared to be the same size as the white light patch, but was 'mustard-green', 'pale green' or 'khaki' in colour, and matched approximately to a surface colour with CIE coordinates $x = 0.411$; $y = 0.476$; $Y = 42.5$, although this surface colour appeared rather 'brighter' than the after-image. The image remained at a steady brightness for about 20 s after the white light was turned off, and then gradually faded from the centre of the field, adopting an annular form, without noticeable change in diameter, before finally disappearing after 30 s or longer. F.B. could identify accurately the time at which the light stimulus was removed because of the change in apparent colour between the light-evoked image and the 'after' image. The after-image moved with the eyes in light or darkness, was observed following stimulation of either eye and persisted during closure of the stimulated eye. It was detected in all quadrants of the visual field over the range of eccentricities examined (up to 40 deg) and its duration of about 30 s was effectively independent of location. Against a white background, the after-image was similar to that perceived in darkness, but it faded more rapidly, acquiring the appearance of a 'dark shadow' before finally disappearing. All quantitative measurements were made with the after-image perceived foveally, in darkness.

F.B.'s threshold for detection of a flashing target was raised for 10 to 15 s following 5 s viewing of the circular white light patch (which will be referred to as the 'primary stimulus'). In order to determine the time course for F.B.'s recovery of sensitivity, we measured threshold illumination, I_0 , for detection of the flashing target presented against the primary stimulus (fig. 1A). The target illumination level was then set at various levels below I_0 , and the time at which the target was detected following 5 s viewing of the primary stimulus was signalled by pressing a push button (*see Methods*). Thus poststimulus changes in sensitivity were determined and as can be seen (fig. 1A), rapid recovery occurs some 15 s after cessation of stimulation, whereas for normal vision, recovery occurs within 100 ms. We also measured threshold at fixed times following stimulus offset, with the target illumination either increased or decreased relative to I_0 , in order to determine the form of the changes in sensitivity immediately following stimulation. Measurements were made for four different illumination levels of the primary stimulus (fig. 1B) and it appears that the threshold illumination level remains approximately the same immediately after stimulation as before, although there is in some cases evidence of a transient increase following stimulus offset. The poststimulation elevation in F.B.'s threshold settings is also observed when the primary stimulus and the target are presented to different eyes, that is, the effect transfers from one eye to the other (fig. 1A). F.B. observed a 'darkening' of the after-image produced by the primary stimulus at about the time when she was able to detect the target (i.e., about 15 s after offset of the primary stimulus), but she could still detect the after-images for up to 1 to 2 min later.

The extended loss of threshold sensitivity induced by the primary stimulus enabled us to make objective measurements for different primary stimuli in terms of

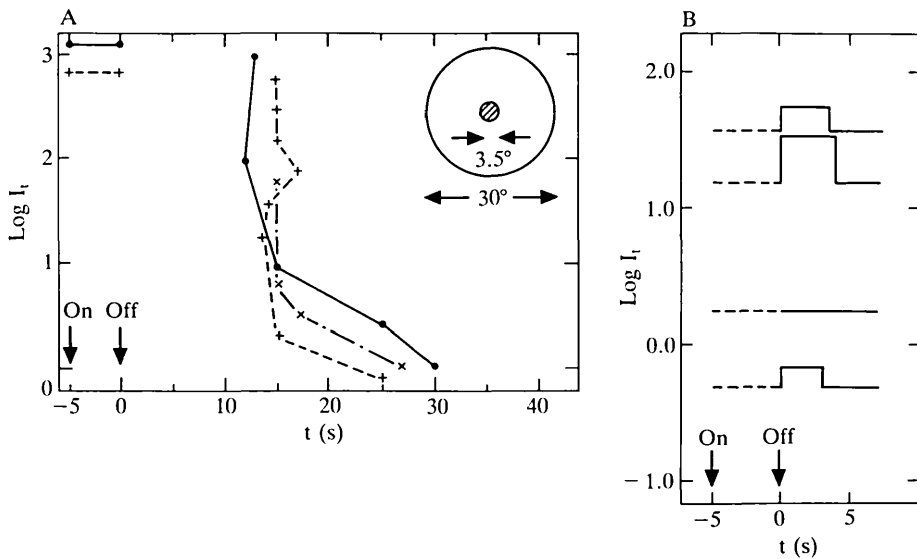


FIG. 1. Threshold illumination, I_t , for detection of a white light, circular target (diameter 3.5 deg) flashed for 0.1 s every 1 s, located centrally against the circular primary stimulus (diameter 30 deg). A, $\log I_t$ is plotted against time, t , following 5 s viewing of the primary stimulus, which was turned off at $t = 0$. Filled circles = white light primary stimulus of illumination 2.9 log trolands; crosses (+) = 531 nm primary stimulus (2.9 log trolands); crosses (x) = dichoptic presentation of the test and white light primary stimuli. B, as for fig. 1A, but values of $\log I_t$ are plotted for four different illumination levels of the white light primary stimulus.

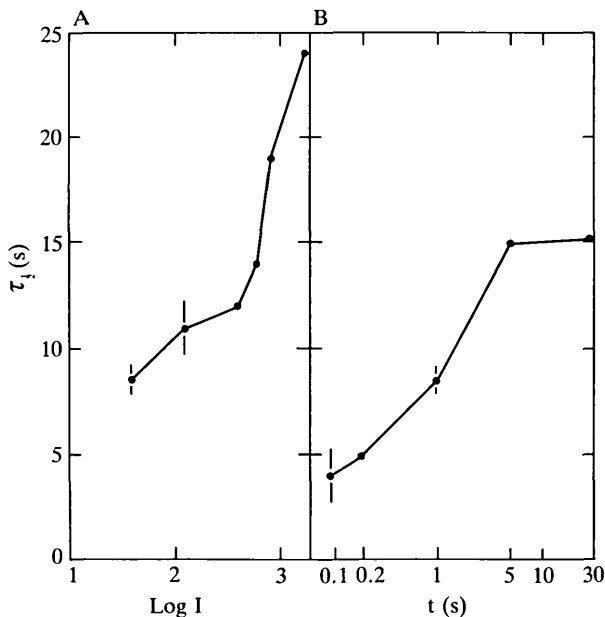


FIG. 2. A, τ_1 plotted against the logarithm of the illumination of the primary stimulus. The stimulus configuration was as for fig. 1A, both stimuli were white light, and the primary stimulus was presented for 5 s. B, τ_1 plotted against t , the time for which F.B. viewed the primary stimulus. Stimulus configuration was as for fig. 1A and the primary stimulus was of illumination 2.8 log trolands.

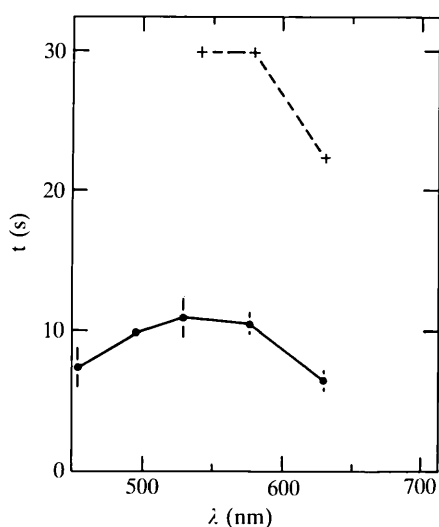


FIG. 3. Filled circles. Values of $\tau_{\frac{1}{2}}$ plotted against the wavelength, λ , of the primary stimulus. The illumination levels of the different monochromatic stimuli were adjusted to give the same illumination for threshold detection of the superimposed white light target. The stimulus configuration was as for fig. 1A. Crosses. The total time for detection of the after-image following 5 s viewing of a grating of wavelength λ , and bar-width 15 min. The grating illuminations were 2.1 log trolands (630 nm and 542 nm) and 2.5 log trolands (576 nm).

$\tau_{\frac{1}{2}}$, the time following offset of the primary stimulus at which illumination for detection of a target fell to half its value during presentation of the primary stimulus. $\tau_{\frac{1}{2}}$ increases rapidly as the illumination level of the stimulus increases to the maximum available with the Maxwellian view system (fig. 2A), and the prolonged after-image experienced by F.B. following retinal flash photography (*see Case Report section*) indicates that the steep increase in $\tau_{\frac{1}{2}}$ continues beyond the range covered by our measurements. $\tau_{\frac{1}{2}}$ also increases as the time for which F.B. views the primary stimulus increases (fig. 2B) and in this case, the restricted range of measurements was determined by the fact that the subject found prolonged viewing of the primary stimulus unpleasant and disturbing. Data showing that the total duration of the after-image increases with increase in the time for which F.B. views the primary stimulus are presented in fig. 4B. Measurements of $\tau_{\frac{1}{2}}$ were made for a number of wavelengths, λ , of the primary stimulus, the illumination levels of which were adjusted so that threshold illumination for detection of the white test flash against the different monochromatic primary stimuli was constant. The data (fig. 3) establish that $\tau_{\frac{1}{2}}$ varies with λ , being longer for the green (531 nm) and yellow (576 nm) than for the red (630 nm) and blue (453 nm) primary stimuli. In order to confirm the differences in the persistence of after-images induced by red and green lights, a grating was constructed from equally spaced bars, alternately red (630 nm) and green (531 nm), which were matched in apparent brightness by F.B. The match corresponded to a luminance level of 2.8 log trolands for both red and green bars, which appeared matched in brightness to the authors. After viewing this grating for

5 s, F.B. detected an after-image, which for a few seconds appeared similar in colour to the primary stimulus grating, but the red bars faded rapidly, leaving an after-image consisting of alternate green and black bars, which was detected for 75 s. Seen in isolation, the after-image for the green grating was detected for 100 s and appeared 'mustardy-green' in colour, whereas the after-image of the simple red grating was detected for 50 s, initially appearing as pink stripes but changing colour after a few seconds to look similar to the after-image of the green grating. The total duration of the after-image was measured for three monochromatic gratings, and these values are also shown in fig. 3 (crosses). The after-images of the yellow (576 nm) and green (542 nm) gratings were more prolonged than that of the red (630 nm) grating, but it should be noted that the illumination level of the yellow grating was somewhat greater than that of the other two. F.B. described the colour appearance of the after-image induced by the 576 nm grating as 'mustard yellow' and black, whereas those elicited by other monochromatic gratings appeared green and black.

The experiments with coloured gratings show that spatially structured primary stimuli induce after-images with well defined spatial structure, and we have examined the relationship between the spatial structures of the primary stimulus grating and those of the induced after-images. The total duration, τ , for which a 100% modulated grating was perceived in the after-image was measured as a function of the grating bar-width. τ reaches a peak for grating bars of width 30 to 15 min (spatial frequency 1–2 cycles·deg⁻¹), falling to zero for bar-widths less than 2 min (spatial frequency 15 cycles·deg⁻¹) (fig. 4A). The subject reported that with the bars of width 15 min, the lines in the after-image persisted after the circular outer limit of the after-image disappeared, whereas with finer bar-widths, the image of the circular limit of the field persisted after the grating disappeared. Measurements were also made for the durations, τ , of the after-images elicited by a circular spot (diameter 1 deg) and by a grating of bar width 15 min, and for a given presentation time of the stimulus, the duration, τ , for the grating exceeds that for the uniform circular spot (fig. 4B). Primary stimuli in the form of a grating elicit a grating after-image, and we determined the relationship between the two gratings in a matching experiment. Thus we produced an after-image of a grating in the upper half-field, and asked F.B. to match the bar-widths of this after-image to those of one of a series of gratings presented in the lower half-field (fig. 4C), bar-widths increasing by 15% between successive members of the series of matching gratings. Matches were performed up to 2 min after viewing for 5 s a primary stimulus grating of illumination 3.0 log trolands, and in each the after-image was successfully matched to a grating identical to that responsible for its generation. Thus there is no distortion or spreading of the after-image with time. After-images were also induced by moving and flickering stimuli, but in neither case was any sensation of movement or flicker observed in the after-image. A circular target (diameter 3.5 deg) of illumination level 2.6 log trolands and moving at either 15 deg·s⁻¹ or 55 deg·s⁻¹ gave an after-image of duration 15 s, which appeared as a 'spot with a streak behind it' in the first case and as a 'long oblong' in the second. A circular target, 100% modulated

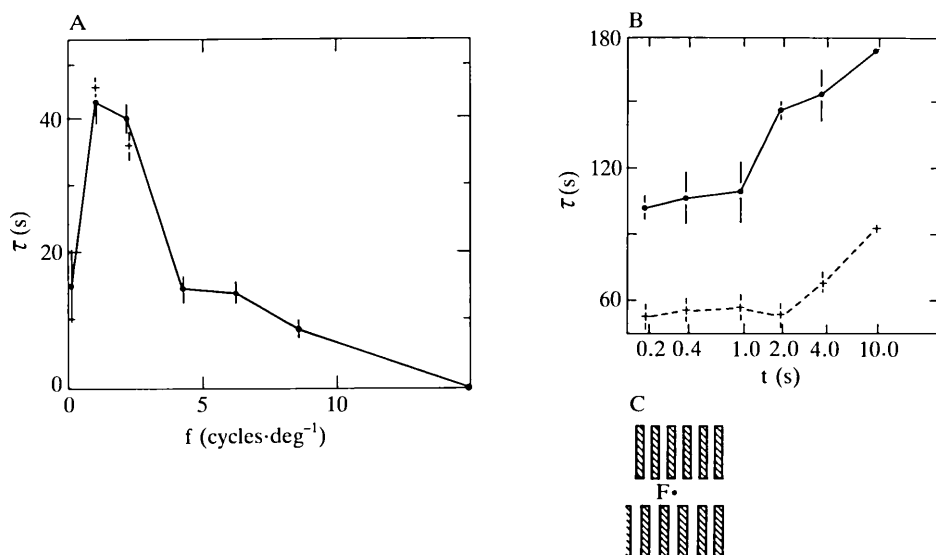


FIG. 4. A, the duration, τ , of the after-image induced by a grating stimulus plotted against the spatial frequency of the grating. The gratings were of square waveform, and the spatial frequency is defined as $(2d)^{-1}$, where d is the width of the grating bars. The grating stimuli were 12 deg square in size, white light and presented for 0.1 s. Filled circles correspond to vertically orientated gratings, crosses to horizontally orientated gratings. B, the duration, τ , of the after-image plotted against the time of viewing the primary stimulus. Crosses = circular stimulus (diameter 1 deg, white light); filled circles = vertical grating (spatial frequency 2 cycles $\cdot$ deg $^{-1}$, white light). C, matching configuration for a grating after-image (upper half-field), which is compared with one of the series of gratings, presented in the lower half-field; F = fixation point. The after image was induced by 10 s viewing of a 1.1 cycles $\cdot$ deg $^{-1}$ square waveform grating (12 deg $\times$ 12 deg), and measurements were made for 2 log troland and 3 log troland illuminations.

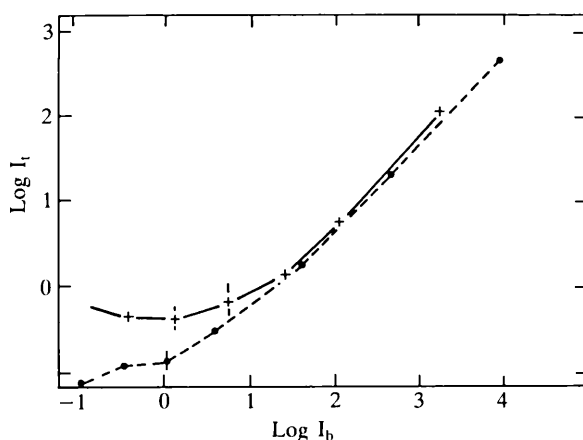


FIG. 5. Log illumination ($\text{log } I_t$) required for threshold detection of a circular target (white light, diameter 3.5 deg), superimposed centrally on a circular background (white light, 30 deg diameter) of illumination I_b . The target was presented cyclically for 0.1 s every 1 s. Crosses = data for F.B.; filled circles = data for normal subject J.B.

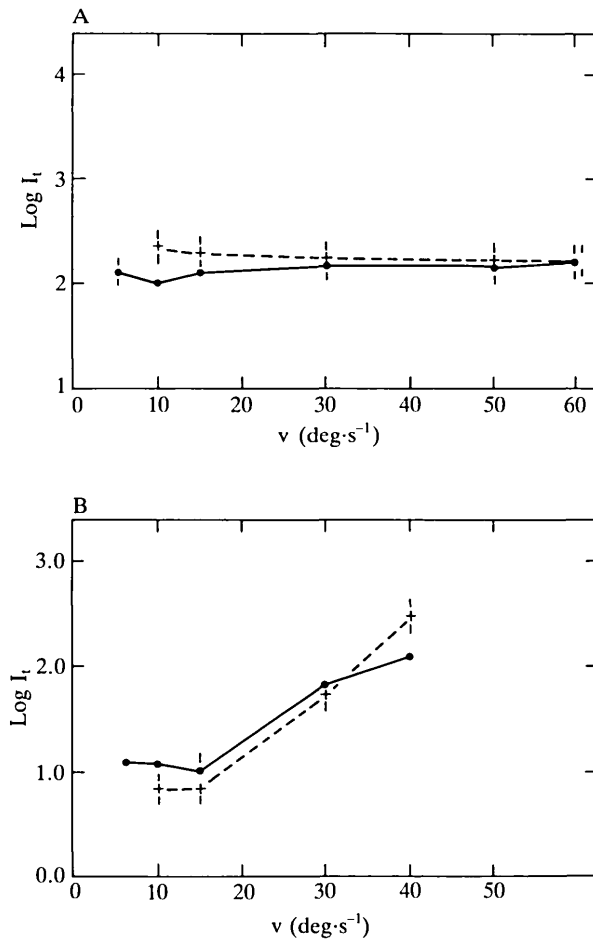


FIG. 6. A, illumination, I_t , for threshold detection of a circular target (diameter 3.5 deg) moving at velocity v degs.s⁻¹ through the central 8.5 deg of the background field (diameter 30 deg; illumination level 2.6 log trolands). Both stimuli were white light. Crosses = data for F.B.; filled circles = data for normal subject J.B. B, illumination, I_t , for detection of a grating (1 cycle.deg⁻¹ in the form of a circular field of diameter 4 deg), moving at velocity v . The grating was orientated vertically and moved along the horizontal meridian, through the central 8.5 deg of a 30 deg background (illumination 2.5 log trolands). White light stimuli. The subject F.B. (crosses) and the normal J.B. (full circles) were instructed to find threshold for detection of the grating structure.

at 8 Hz around a mean illumination level of 2.6 log trolands to give a strong sensation of flicker, produced an after-image identical in appearance to that elicited by a steady circular target.

In view of the prolonged and consistent after-image sensations experienced by F.B., we measured a number of her visual responses to conventional light stimuli. F.B.'s sensitivity to an incremental or decremental change in illumination is normal over most of the range of background field illumination, I_b , but increments are raised as I_b approaches zero (fig. 5). Her threshold sensitivity for detection of a

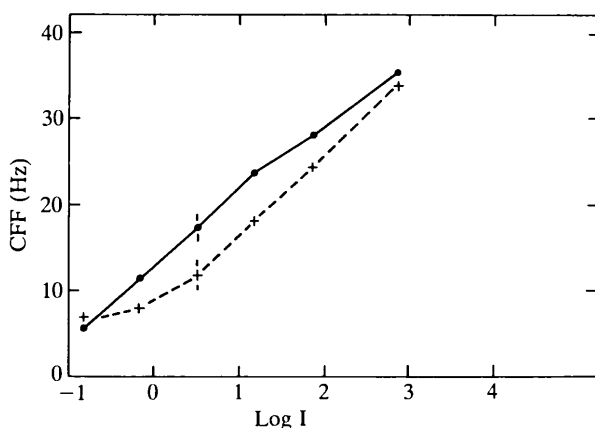


FIG. 7. Critical fusion frequency (CFF) plotted against the mean illumination, I , of the flickering stimulus (white light and circular of diameter 4 deg). The frequency values represent the fundamental of the square waveform flicker. Crosses = data for F.B.; filled circles = data for normal subject J.B.

circular spot moving at constant velocity, v , is effectively normal (fig. 6A), despite the extended tail she perceives behind such a target. Threshold illumination, I_t , was also measured for detection of the bars of a moving grating superimposed on a uniform field and again F.B.'s thresholds are essentially normal (fig. 6B). Critical fusion frequency for 100% square waveform modulation was measured as a function of stimulus illumination level and F.B.'s responses are again similar to those for the normal subject J.B. (fig. 7). Finally, we checked F.B.'s responses to a number of illusory stimulus patterns including the Poggendorf, Craik-Cornsweet, Kanizsa triangle, Ehrenstein and Hermann grid illusory figures (Gregory, 1970) and in every case she described the normal illusory appearance.

After completion of the experiments described above, F.B. was treated with carbamazepine and we remeasured the duration of her after-images 6 weeks and 18 weeks after commencement of this treatment. The value of $\tau_{\frac{1}{2}}$ measured after 6 weeks was 10 s, compared with a value of 15 s before treatment (fig. 1A), but no subsequent decrease was found after 18 weeks of treatment.

DISCUSSION

F.B. has suffered from a relapsing and remitting neurological disorder for three years. The possibility of multiple sclerosis was considered on a number of occasions but a variety of tests, including evoked potentials, isoelectric focusing of CSF immunoglobulins and MRI brain scanning, have always given normal results. There are, however, other features, for example arthralgia, raised immunoglobulins and ESR, suggestive of a systemic disorder such as a vasculitis. Extensive investigations so far have failed to confirm this possible diagnosis, although it is well recognized that diseases such as systemic lupus erythematosus can present with cerebral complications despite a normal autoimmune profile (Hughes, 1979).

The most prominent feature of F.B.'s visual responses are the prolonged images which she experiences after viewing suprathreshold lights. It should be noted that her threshold sensitivity for detection of flicker (fig. 7), target movement in a straight line (fig. 6) and decrements in illumination are normal. Thus the prolonged sensations following light stimulation cannot be attributed to a general lack of temporal resolution or to failure of the mechanisms responsible for signalling stimulus offset. The raised increment thresholds, I_t , for low background illuminations, I , (fig. 5A) imply an abnormally high Fechner fraction for threshold detection, which in turn implies large 'dark' or intrinsic noise in F.B.'s visual responses (Stiles, 1946). The significance of this in relation to perception of after-images is not known, although as both involve internally generated 'noise' they may be related phenomena.

F.B.'s abnormal responses differ significantly from those associated with the episodic form of palinopsia, in which reappearance of images sometimes occurs after a considerable time lapse following stimulation (Bodis-Wollner *et al.*, 1984). Thus Critchley (1951) describes palinopsia as intermittent, paroxysmal or episodic in nature, and in 9 of his 10 subjects the phenomenon was associated with lesions of the posterior cortex, usually parieto-occipital. In a study of 12 subjects, Bender *et al.* (1968) observed that palinopsia occurs early in the course of a progressive field defect or during resolution of a severe defect caused by parieto-occipital lesions with a preponderance of right-sided defects. Other authors have described cases of visual perseveration associated with lesions of the right posterior parietal region (Cleland *et al.*, 1981), of the right occipitotemporal region (Meadows and Munro, 1977), of the right parieto-occipital region (Cummings *et al.*, 1982), and of the occipital lobe (Michel and Troost, 1980). It has also been observed following temporal lobe surgery (Bynke, 1984). In our patient no focal parenchymal abnormality has been found, and if indeed she does have a vasculitis this may well produce diffuse microscopic damage which cannot be resolved by the imaging techniques used. Palinopsia sometimes appears to be associated with seizures and in these instances can be suppressed by treatment with anticonvulsant drugs (Jacobs *et al.*, 1972). In F.B.'s case there was no clinical evidence of epilepsy; indeed the visual phenomena were continuous rather than episodic. Although a focal abnormality was evident on the EEG, there was only a minor change in her symptoms following anticonvulsant treatment. Palinopic images are sometimes multiple, are subject to distortion and to changes in colour and magnification and are independent of the duration and intensity of the light stimulus (Robinson and Watt, 1947; Bender *et al.*, 1968). These descriptions of palinopsia differ in almost every respect from our observations on F.B.'s prolonged after-images, which occur throughout the visual field, in the absence of visual field loss or localized cortical lesions. Further, F.B. detects after-images only for high contrast images, whereas the episodic images are elicited by all contrast levels. Far from being episodic or hallucinatory, F.B.'s after-images are invariably associated with the primary light stimulus, are not subject to spatial distortion and except for a brief transition from the stimulus colour to green, do not vary in colour appearance. The duration of the after-image and its influence

on threshold sensitivity are directly related to the illumination level of the primary stimulus, and its duration is also dependent on the exposure time of the primary stimulus. Certain features of F.B.'s responses are, however, similar to those found in the after-image form of palinopsia, as described, for example, for 2 subjects by Kinsbourne and Warrington (1963), for Case 6 of Critchley (1951) and for the subject of Le Beau *et al.* (1952). As was discussed in the Introduction, the terms visual perseveration and palinopsia apply to a nonhomogeneous group of visual responses which can broadly be divided in two groups, one episodic and the other resembling an after-image. Despite the fact that the two types of defect can appear in association (Kinsbourne and Warrington, 1963), we believe that a clear distinction should be drawn between them. Some previous authors have also distinguished between the different manifestations of palinopsia (e.g., Bekény and Péter, 1961; Swash, 1979; Cummings *et al.*, 1982).

Only the spatial structure of the primary light stimulus is represented in F.B.'s after-images. She perceives no movement in the after-image elicited by a moving stimulus, the movement producing a continuous streak across the visual field, and flickering lights elicit a steady after-image indistinguishable from that caused by a steady light. It has been reported that in some cases of palinopsia, moving targets produce a continuous streak (Le Beau *et al.* 1952; Case 1 of Kinsbourne and Warrington, 1963), whereas in others, a series of 'stills' are perceived at different points along the path of the moving stimulus (Castaigne and Greveleau, 1953; Teuber, 1961; Case 2 of Kinsbourne and Warrington, 1963). In an unusual case, moving objects appeared to be moving twice as fast in the after-image (Cleland *et al.*, 1981). F.B.'s after-images are essentially positive in contrast and a monochrome green-yellow in appearance, although fleetingly, the colour of the primary stimulus is perceived in the after-image. Other reports refer to positive contrast, black and white after-images (Critchley, 1951, Case 6; Le Beau *et al.*, 1952; Kinsbourne and Warrington, 1963) or to a sequence of colour changes (e.g., Bender *et al.*, 1968). The duration of F.B.'s after-image is dependent on the duration and illumination level of the eliciting stimulus (fig. 2), as was reported by Kinsbourne and Warrington (1963). The novel aspects of F.B.'s responses are the well defined dependence on the spatial structure of the eliciting stimulus (fig. 4), the selective dependence on the wavelength of the eliciting stimulus (fig. 3), and the increase in threshold sensitivity associated with the after image (fig. 1). Of these observations, only low spatial frequency dependence has been reported previously, and then in cases of episodic palinopsia (Bodis-Wollner *et al.*, 1984).

F.B.'s after-images are associated with visual mechanisms characterized by the properties summarized in the previous paragraph. After-images generated by bleaching of the photopigments can be excluded because those in F.B. occur at such low illumination levels and their time course differs from that associated with recovery from bleaching. Further, increment threshold is raised under dichoptic presentation of the test flash and the primary stimulus (fig. 1), whereas bleaching lights do not influence increment threshold sensitivity under dichoptic conditions

(Crawford, 1940; Mitchell and Liaudansky, 1955). The duration of F.B.'s after-images, of the order of tens of seconds, is similar to that observed in the contrast threshold elevation effect associated with adaptation of orientation sensitive, binocularly controlled neural mechanisms (Gilinsky, 1968; Pantle and Sekuler, 1968; Blakemore and Campbell, 1969). The contrast threshold elevation effect is subject to inhibitory binocular control, via a pathway with a well-defined, low spatial frequency response (Ruddock and Wigley, 1976; Ruddock *et al.*, 1979), and the spatial frequency response of this binocular inhibition is similar to that found for F.B.'s after-images, although the amplitudes of the two responses are measured in terms of different variables and are, therefore, not directly comparable. The spectral response of the inhibitory mechanism is broad-band, as is that of the after-images (fig. 3), but the former is closer to the photopic spectral sensitivity response. The build-up and decay of the inhibitory interaction takes 10 to 20 s, which is comparable with the duration of F.B.'s after-image (*see* fig. 1). Thus the inhibitory binocularly controlled mechanism which inhibits the contrast threshold elevation effect has certain response properties similar to those associated with F.B.'s after-images and may be involved in their generation.

Four causes of palinopsia were considered by Bender *et al.* (1968), namely visual after-images, sensory seizures, psychogenic phenomena and hallucinations, and only the first explanation is consistent with F.B.'s responses. We have already argued against an explanation based on photopigment bleaching, and the time course of the after-images is similar to that of central adaptation phenomena, indicating a neuronal origin. Our review of the literature dealing with subjects suffering visual perseveration reveals that abnormal prolongation of visual images is expressed in a variety of response patterns. F.B.'s after-images are specifically spatial in nature, whereas other subjects exhibit after-images possessing temporal and chromatic properties, as is particularly clearly illustrated in the exaggerated movement of the after-images described by Cleland *et al.* (1981). We propose, therefore, that abnormal perseverance of visual sensation can arise in one or more of a number of neuronal mechanisms, each of which causes selective prolongation in response to different stimulus parameters.

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The contribution of blue-sensitive cones to spatial responses of post-receptoral visual channels in man

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Abstract—Psychophysical methods developed for the investigation of spatial and temporal pathways in human vision have been applied in combination with the two-colour increment threshold technique of W. S. Stiles to study the way in which signals from blue-sensitive cones are transmitted along the visual pathways. A flicker sensitive spatio-temporal filter, designated 'ST2', has been examined by background modulation methods, and spatial filters sensitive to bars of a specific width by grating adaptation methods employing dichoptic presentation of stimuli. It is shown that the blue-sensitive (π_3) spectral mechanism contributes to both classes of filter response, in a manner similar to that observed for the red-sensitive spectral mechanism. The binocularly driven, bar-sensitive filters have broad-band spectral response characteristics, thus the data demonstrate that signals arising in blue-sensitive cones converge onto a luminance channel. The results of this investigation, together with those previously published for a second (ST1) spatio-temporal filter, describe a variety of post-receptoral responses involving the π_3 spectral mechanism.

INTRODUCTION

The response characteristics of the blue-sensitive cone mechanism differ from those of the red- and green-sensitive mechanisms in a number of ways. Of particular concern to this study is the finding that spatial responses of the blue-sensitive mechanism, isolated by two-colour increment threshold methods (Stiles, 1939, 1959, 1978), are significantly coarser than those of the red- and green-sensitive mechanisms. Thus spatial summation for the blue-sensitive mechanism is greater than that of the red- and green-sensitive mechanisms (Stiles, 1949), extending over linear dimensions of some 8 min, compared with a value of around 1 to 2 min for the red- and green-sensitive mechanisms (Brindley, 1954). This low spatial resolution is associated with low contrast sensitivity throughout the spatial frequency domain (Green, 1968, Kelly, 1973, Cavonius and Estévez, 1975) and the Fechner fraction for detection of flashed increments is correspondingly high (Stiles, 1946).

Two-colour increment threshold measurements yield at least two, and in some subjects three blue-sensitive increment threshold responses designated π_1 , π_2 and π_3 (Stiles, 1978). There has been speculation that at post-receptoral levels, signals from blue-sensitive cones are carried by colour-opponent, but not by luminance channels (Guth *et al.*, 1968; Mollon and Krauskopf, 1973; Foster and Snelgar, 1983) and this hypothesis has been confirmed by some direct investigations (Whittle, 1974; Tansley and Boynton, 1978; Eisner and Macleod, 1980), but not by Marks (1974).

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We have applied two recently developed psychophysical techniques in order to examine the chromatic responses of those visual channels along which signals from the blue-sensitive cones are transmitted. The first of these, called the background modulation method, was developed by Barbur and Ruddock (1980a) and Holliday and Ruddock (1983) for the study of spatial and temporal characteristics of visual mechanisms which mediate detection of moving targets. The threshold illumination required for detection of a circular target is influenced by spatial and/or temporal modulation of the background over which it moves, and, with different forms of background modulation, two classes of spatio-temporal response are revealed. These are attributed to the activities of two visual channels, or filters, which contribute to the detection of the moving targets. The first, referred to by Holliday and Ruddock (1983) as the spatio-temporal (ST1) filter, has relatively high frequency spatial and sustained (low pass) temporal response. Barbur and Ruddock (1980a) described in detail the spatial characteristics of this filter and by choosing appropriately the wavelengths, λ and μ , of the target and background respectively, obtained ST1 spatial characteristics for detection by different (π) spectral mechanisms (Barbur and Ruddock, 1980b). Those for the red-sensitive (π_5) and green-sensitive (π_4) mechanisms were similar to the white light responses, whereas those for the blue-sensitive (π_3) mechanism were spatially much coarser. The difference between π_3 and the other mechanisms is consistent with the results obtained by other methods, as reviewed above. The second filter, designated ST2, has relatively low frequency spatial and transient (band-pass) temporal responses, measured for white light stimuli, and, in this paper, we examine the ST2 responses when detection of the moving target is mediated by the different π -mechanisms, and particularly π_3 . The choice of background filters required for the investigation of ST2 responses is described in the Methods section.

Both ST1 and ST2 spatial responses have radial symmetry and the filters are monocularly controlled, thus their responses are characteristic of pre-cortical neural mechanisms. In contrast, adaptation experiments employing bars of a given orientation and width, arranged as a 1-dimensional grating, yield responses characteristic of striate cortical neurones (Hubel and Wiesel, 1968). Following adaptation to a high contrast grating, contrast threshold for detection of a similar grating is raised transiently (Gilinsky, 1968; Pantle and Sekuler, 1968; Blakemore and Campbell, 1969). The effect is observed with dichoptic presentation of the test and adaptation gratings, under which conditions it is not wavelength selective (Maudarbocus and Ruddock, 1973a). In the experiments to be described, the test grating, of wavelength λ , is detected against a background, of wavelength μ , and with appropriate choice of λ and μ , detection is mediated by different π -mechanisms. The contributions of π_3 to responses of both the ST2 and the adaptation mechanisms have been determined and compared with those of other π -mechanisms. It is shown, thereby, that signals from π_3 are transmitted in visual channels which have broad-band (luminance) spectral characteristics.

METHODS

Experimental design

As explained in the Introduction, the background modulation experiments involve detection of a target moving across a modulated background. The background fields required for the isolation of the ST2 temporal and spatial responses are illustrated in

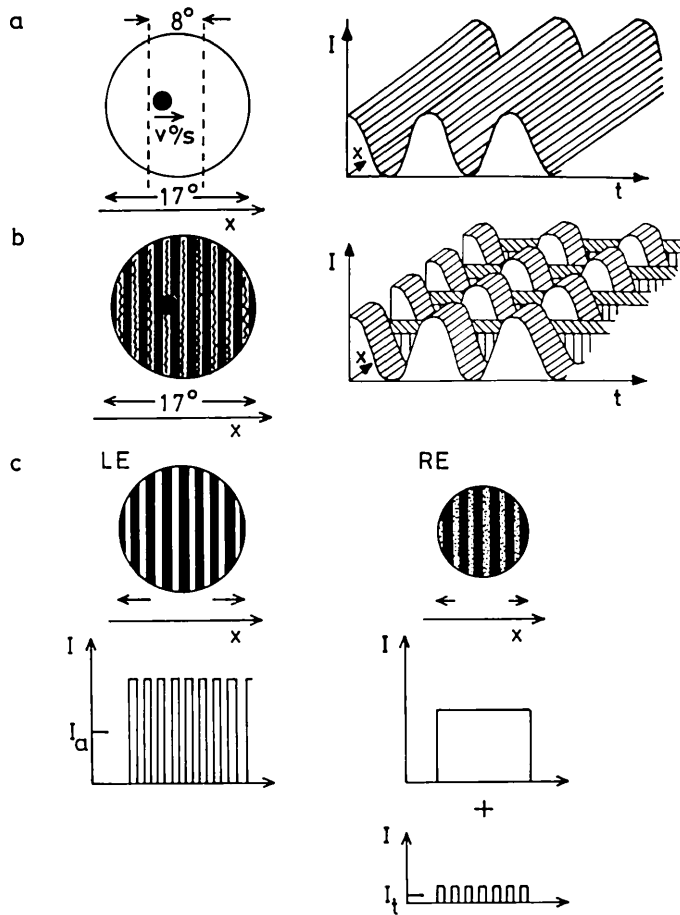


Figure 1. Stimulus configurations used in the experiments. (a) Measurement of ST2 temporal responses: The circular target (diameter 1.4 deg) moves along the horizontal meridian at 15 deg s^{-1} , across the central 8 deg of the 17 deg diameter background. The background field is spatially uniform but flickers sinusoidally at frequency f_i Hz. (b) Measurement of ST2 spatial responses: The test conditions are similar to those for (a), but the background consists of bars, alternately steady and flickering at fixed frequency. The time average illumination I_b of the background is uniform and all the bars have the same width, d . The periodicity of the background grating is expressed as the spatial frequency f_s , equal to $(2d)^{-1}$ cycles deg^{-1} . (c) Measurement of grating threshold illumination I_t , under dichoptic adaptation: The adaptation and test gratings, consisting of equally spaced dark and light bars, were presented to the left and right eyes respectively. The modulation of the adaptation grating was $> 98\%$, and its mean illumination, I_a , was held constant for each wavelength λ_a . The test grating, of wavelength λ , was superimposed on a uniform background of wavelength μ , and the mean illumination of the test grating was controlled by the subject, in order to set it to threshold for detection. The stimuli were presented alternately for 2 s and 20 s respectively. The spatial frequencies of the gratings are defined as $(2d)^{-1}$ cycles deg^{-1} , where d is the bar width.

Fig. 1a, b. The temporal response is measured for a target moving at constant velocity across a spatially uniform background modulated sinusoidally in time (Fig. 1a), the illumination required for detection of the target, I_t , being determined as a function of the background modulation frequency, f_t . The spatial response is measured for a background consisting of alternate steady and flickering bars, the two sets of bars being of the same width (Fig. 1b). The flicker frequency of the alternate flickering bars is constant and I_t is measured as a function of the periodicity of the background grating. [It should be noted that by changing the temporal frequency and keeping the spatial periodicity constant, this field configuration can be used for measurement of the ST2 temporal response. For white light stimuli, this yields the same results as are obtained with the spatially uniform background of Fig. 1a (Holliday and Ruddock, 1983), and as realisation of the latter is easier, it was chosen for the present study.] The different π -mechanisms were isolated with different combinations of wavelengths λ and μ of the test and background fields; π_3 was isolated with a violet ($\lambda = 445$ nm) target moving over a yellow ($\mu = 590$ nm) background and π_5 with an orange ($\lambda = 595$ nm) target moving over a blue-green ($\mu = 495$ nm) background. The extent to

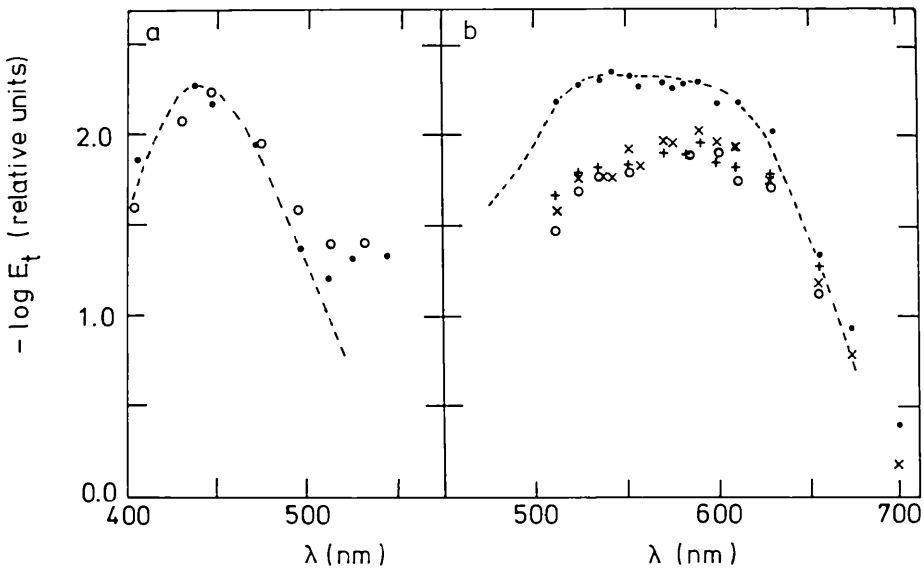


Figure 2. Relative spectral sensitivities for detection of a circular target, of wavelength λ , moving across a circular background field. The target configuration is illustrated in Fig. 1a, b, and threshold energy E_t was set for its detection against a background of fixed wavelength μ . (a) Measurements for a background field with μ equal to 590 nm and of 3.3 log troland illumination: Open circles refer to a square waveform grating of periodicity 1 cycle deg^{-1} , consisting of alternate steady bars and bars 100% modulated at 8 Hz (see Fig. 1b). Closed circles refer to a spatially uniform background, 100% modulated at 8 Hz (see Fig. 1a). The broken line shows the π_3 -spectral sensitivity function (taken from Wyszecki and Stiles, 1981, and adjusted to give energy units). Data for subject IH. (b) Measurements for a background with $\mu = 495$ nm and of 1.5 log troland illumination: Full circles give the values for a spatially uniform, non-flickering background (subject IH); crosses ($\times$) give the values for a spatially uniform background 25% modulated at 10 Hz (subject IH). Open circles and crosses (+) give the values for background grating (periodicity 1 cycle deg^{-1}) with alternate bars 100% modulated at 10 Hz. Data for IH ($\circ$) and PS (+). The broken line shows the π_3 spectral sensitivity data, taken from Wyszecki and Stiles (1982) and expressed in energy units.

All data points are the means of five readings, and standard errors were in the range ± 0.01 to ± 0.03 log units.

which these combinations of wavelengths isolate the required π -mechanisms was checked by measuring spectral sensitivities for different target wavelengths λ . Measurements were made with both uniform and with modulated backgrounds, in order to ensure that isolation was maintained for the different background conditions. For $\mu = 590$ nm and $\lambda < 500$ nm, the threshold responses follow the normal π_3 response (Fig. 2a) under all background conditions, and for $\mu = 495$ nm, they follow π_5 for a uniform background but not for the modulated backgrounds (Fig. 2b). In the latter case, however, the response remains clearly red-sensitive and the modification of the π_5 spectral sensitivity observed with flickering backgrounds requires further study.

The field configuration used for measurement of contrast threshold elevation is illustrated in Fig. 1c; dichoptic presentation of the test and adaptation grating serves both to avoid selective chromatic adaptation of the test eye by the adaptation grating and to ensure that the observed effects are localized to binocularly driven, central mechanisms. The high contrast ($\geq 98\%$) adaptation grating, of space-average illumination I , was presented to the left eye, and the target grating, also of $\sim 100\%$ modulation, but superimposed on a uniform background, was presented to the right eye. Both test and adaptation gratings were orientated vertically, and in some measurements, the adaptation grating was replaced by a uniform field of illumination I_a . Threshold illumination for detection of the target was determined after adaptation to either the grating or to the uniform field (see below for adaptation procedure). The value of the threshold illumination was recorded respectively as I_t and I_0 for the two adaptation stimuli, and the grating adaptation effect, expressed as

$$\Delta = \log I_t - \log I_0 \quad (1)$$

was measured both as a function of the periodicity of the adaptation grating, f_a , and as a function of adaptation wavelength λ_a . The test grating, of wavelength λ , is superimposed on a uniform background of wavelength μ (Fig. 1c); π_3 was isolated with a combination of $\lambda = 446$ nm and $\mu = 582$ nm, and π_5 with a combination of $\lambda = 640$ nm and $\mu = 495$ nm. In each case, the periodicity of the test grating was 2.9 cycles deg^{-1} , sufficiently coarse to ensure its resolution by π_3 . The isolation of the π_3 and π_5 mechanisms was again checked for both uniform and modulated backgrounds, by measuring spectral sensitivity for detection of the target against the fixed background wavelengths μ . The data show that for $\mu = 582$ nm, threshold sensitivity follows the normal π_3 response for $\lambda < 500$ nm (Fig. 3a), and for $\mu = 495$ nm, it is mediated by π_5 for $\lambda > 500$ nm (Fig. 3b), similar results being obtained for all background configurations.

Apparatus. Stimuli for both background modulation and adaptation experiments were presented under Maxwellian-view conditions. A different optical system was used for each type of measurement, but both were similar and based on high quality, multi-element camera lenses (Takumar) the design being described in detail by Barbur and Ruddock (1980a) and Holliday and Ruddock (1983). The background modulation method involves detection of a target moving at constant velocity across a background field modulated spatially and/or temporally, and the required stimulus configurations are provided by the optical systems described in the cited references. Target illumination was controlled by a neutral density wedge, which was calibrated separately for each wavelength used in the measurements. White light from a quartz tungsten-halogen lamp was filtered by narrow bandwidth (± 5 nm) interference filters

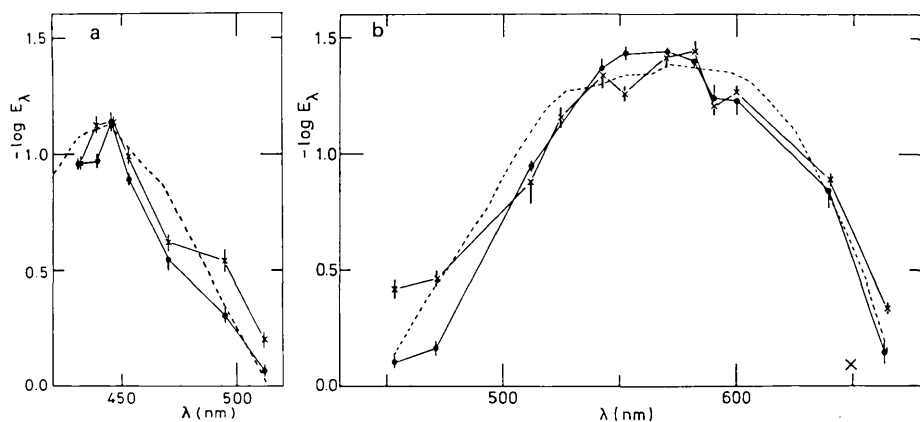


Figure 3. Relative spectral sensitivity for detection of a grating, of wavelength λ , presented on a uniform background, of wavelength μ . The inverse of the energy, E_λ , required for detection of the grating, which was of periodicity $2.9 \text{ cycles deg}^{-1}$, is plotted against λ . (a) Values for a background of wavelength μ equal to 582 nm and 3.45 log troland illumination: Data for IB ($\times$) and JB ($\bullet$); the broken line shows the π_3 spectral response (after Wyszecki and Stiles, 1982) (b) Values for a background of wavelength μ equal to 495 nm and of 3.23 log troland illumination. Data for IB ($\times$), and JB ($\bullet$); the broken line shows the π_5 spectral response (after Wyszecki and Stiles, 1982).

Each data point is the mean of four readings, and the standard error is plotted with each data point.

placed in the collimated light beams. Stimulus patterns were photographed onto Kodalith high contrast film and placed in the light beams, at the back focal plane of the exit lens. Exit pupils of 2 mm diameter were required because of the large convergence angle of the exit beam, but the effective beam diameter at the eye pupil is $\approx 0.6 \text{ mm}$. Eye alignment was maintained by the subject's biting on a dental clamp. Relative spectral energy for the different stimuli was measured by placing the detector element of a Macam spectroradiometer in the place of the subject's retina.

Subjects. All subjects had normal colour vision and were experienced in psychophysical measurements. No refractive correction was required as the locations of the stimulus patterns were adjusted in the beams to give a sharp focus for each subject.

Experimental procedures. Subjects were dark adapted for 10 min before each session. In measurements of the ST2 responses, thresholds for detection of the moving targets were determined by means of two randomly interleaved staircases (Cornsweet, 1962), the illumination settings of the target being obtained by driving the neutral density wedge by a microcomputer (Advanced Systems, Macsym 2). The direction of the target movement was reversed along the horizontal meridian between successive observations, and the subject was instructed to respond 'seen' if the target was detected, even without a sensation of movement. In practice, however, no threshold gap between detection and movement detection is found with the parameters used for this study. No effort was made to distinguish threshold settings made for the two opposite directions of movement, as no systematic differences between movement to the right or left had been found in previous studies. No fixation point was provided, but subjects were instructed to view the centre of the background field (Fig. 1a, b) and not to track the target (see Holliday and Ruddock, 1983, for a discussion of these points). Each

threshold setting was repeated five times and standard errors calculated from the values.

In the adaptation experiments, the left eye was initially adapted for 2 min to the grating (Fig. 1c), after which the test stimulus was presented for 2 s to the right eye. The adaptation and test patterns were then presented alternatively for 20 s and 2 s periods respectively, until the illumination of the test grating was set to threshold. The subject controlled the setting of the neutral density wedge which determined the test illumination, and after each threshold setting, the wedge was re-set by the experimenter to an arbitrary suprathreshold setting. The threshold value for each adaptation grating, $\log I_t$, was determined four times, and those for adaptation to a uniform field, $\log I_0$, were averaged over a single session, usually for about 20 settings. The errors in Δ are the combined standard errors of the difference values $\log I_t - \log I_0$.

RESULTS

Both temporal and spatial responses of the ST2 mechanism were determined, as described in the methods section. The temporal responses were measured at a series of

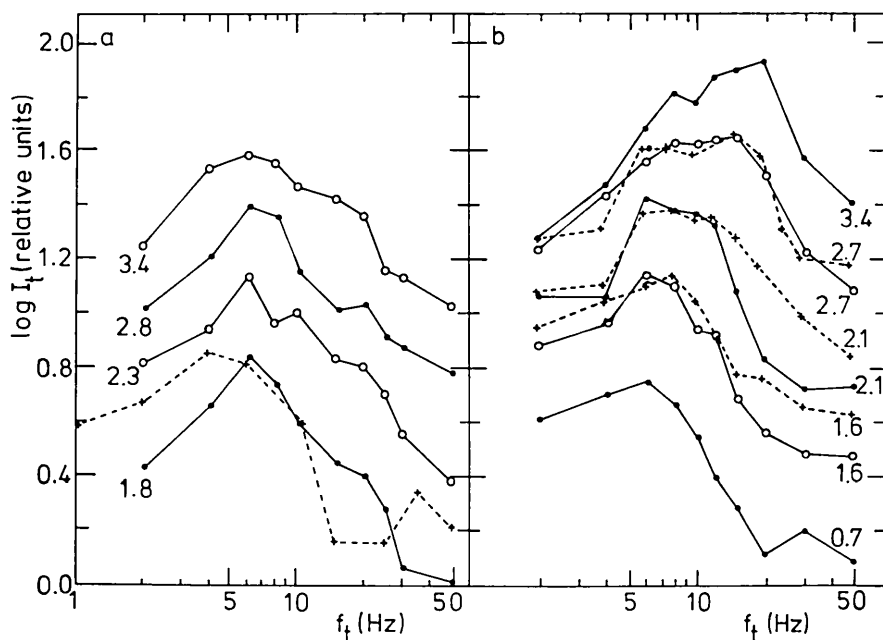


Figure 4. ST2 temporal responses. Threshold, I_t , for detection of the moving target is plotted against the flicker frequency of the 100% modulated background (see Fig. 1a). (a) Threshold detection mediated by π_3 , measured with target wavelength λ equal to 445 nm and background wavelength μ equal to 590 nm. Continuous lines refer to subject EI, and the illumination of the background field is noted against each set of data in log trolands. The broken line gives data for subject IH, at the single illumination level of 1.8 log trolands. The three upper curves for EI have been shifted upwards along the $\log F_t$ axis by 0.3, 0.6 and 0.5 log units for background illuminations 2.3, 2.8 and 3.4 log trolands respectively. (b) Threshold detection mediated by the π_5 related responses of Fig. 2b, measured with a target wavelength λ of 595 nm and a background wavelength μ of 495 nm: Data for EI (full lines) and IH (broken lines) were recorded for different background illuminations noted with each response curve, in log trolands. Data points were not shifted along the $\log I_t$ axis in this case.

Each data point is the mean of five readings, with standard errors in the range 0.01 to 0.04 log trolands.

background illuminations and data for both π_3 and π_5 are shown in Fig. 4. Both responses are band-pass in form, peaking at an intermediate frequency $(f_t)_{\max}$, and, for π_5 , $(f_t)_{\max}$ increases from 6 to 20 Hz as the background illumination increases, as is also observed for white light stimuli (Holliday and Ruddock, 1983). For π_3 , $(f_t)_{\max}$ is approximately constant at 6 Hz over the range of illuminations investigated, but as this was restricted due to shortage of energy in the test beam, it is not possible to say whether or not the π_3 temporal response differs from that for π_5 , as is found by other methods (see Introduction).

The ST2 spatial responses were measured for two subjects and data are given both for π_3 (Fig. 5a) and π_5 (Fig. 5b). The bandwidth and frequency for peak response at 0.75 to 1.0 cycle deg^{-1} are similar for both mechanisms and correspond to those found for white light stimuli (Holliday and Ruddock, 1983).

In the adaptation experiments, only spatial characteristics were determined, and were measured for detection of the test grating by either π_3 or π_5 . The tuning curves for π_3 and π_5 , obtained for different adaptation spatial frequencies, are shown in Fig. 6. The spatial responses for both π -mechanisms peak sharply at an adaptation frequency of 2.9 cycles deg^{-1} , which matches the test spatial frequency, and threshold values are raised relative to the uniform field level (at 40 cycles deg^{-1}) only within the frequency range 0.9 to 5.4 cycles deg^{-1} . The overall features of these responses are similar to those obtained under both monoptic and dichoptic presentation of test and adaptation gratings by Blakemore and Campbell (1969), and Maudarboocus and Ruddock (1973a, b). Threshold values obtained for different wavelengths of the adaptation

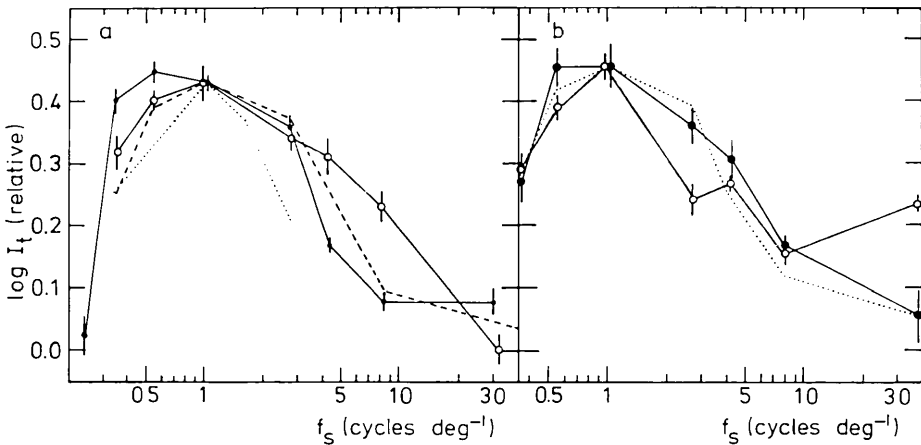


Figure 5. ST2 spatial responses. Threshold, I_t , for detection of the moving target is plotted against the periodicity, f_s , of the background grating, which consisted of alternate steady and flickering bars (see Fig. 1b). (a) Threshold mediated by π_3 measured for a target wavelength, λ , of 445 nm, and background wavelength, μ , of 590 nm. The mean background illumination was 2.7 log trolands and alternate bars were 100% modulated at 6 Hz: Values for IH (open circles) and MB (full circles). The broken and dotted lines define, respectively, the average ST2 spatial response for white light (Holliday and Ruddock 1983, Fig. 8b) and the ST1 spatial response mediated by π_1 (Barbur and Ruddock, 1980b, Fig. 4b). (b) Threshold detection mediated by the π_5 -related spectral mechanisms of Fig. 2b, measured for a target wavelength, λ , of 595 nm and a background wavelength, μ , of 495 nm. The mean background illumination was 1.5 log trolands, and alternate bars were 100% modulated at 8 Hz. Data for EI (open circles) and PS (full circles). The dotted line defines the average ST2 spatial response for white light (Holliday and Ruddock, 1983, Fig. 8b). Each value is the average of five recordings, with standard errors denoted with the data points.

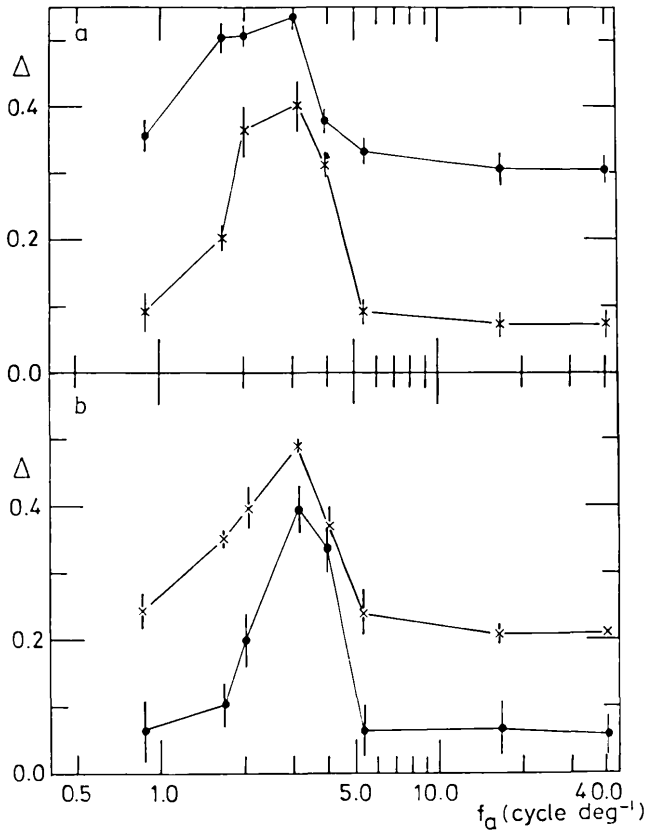


Figure 6. Spatial tuning curves for threshold values, Δ (see eq. 1), measured in detection of a test grating following adaptation to a matched grating presented to the contralateral eye (see Fig. 1c). The test grating was of periodicity $2.9 \text{ cycles deg}^{-1}$, and the adaptation f_s cycles deg^{-1} . (a) Detection of the test grating mediated by π_3 ; the test grating ($\lambda = 446 \text{ nm}$) was superimposed on a uniform field ($\mu = 583 \text{ nm}$; illumination $3.2 \log \text{ troland}$) and the adaptation grating was of wavelength 470 nm and mean illumination $3.6 \log \text{ troland}$. Data for IB (crosses) and JB (full circles). Data points for JB have been displaced upwards along the Δ axis by $0.3 \log$ units, and for IB by $0.07 \log$ units. (b) Detection of the test grating mediated by π_5 ; the test grating ($\lambda = 640 \text{ nm}$), was superimposed on a uniform field ($\mu = 495 \text{ nm}$, illumination $3.2 \log \text{ troland}$) and the adaptation grating was of wavelength 635 nm and mean illumination $3.6 \log \text{ troland}$. Data points for IB have been displaced upwards along the Δ axis by $0.21 \log$ units and for JB by $0.06 \log$ units.

All values are the mean of 4 readings and standard errors are shown with the data points.

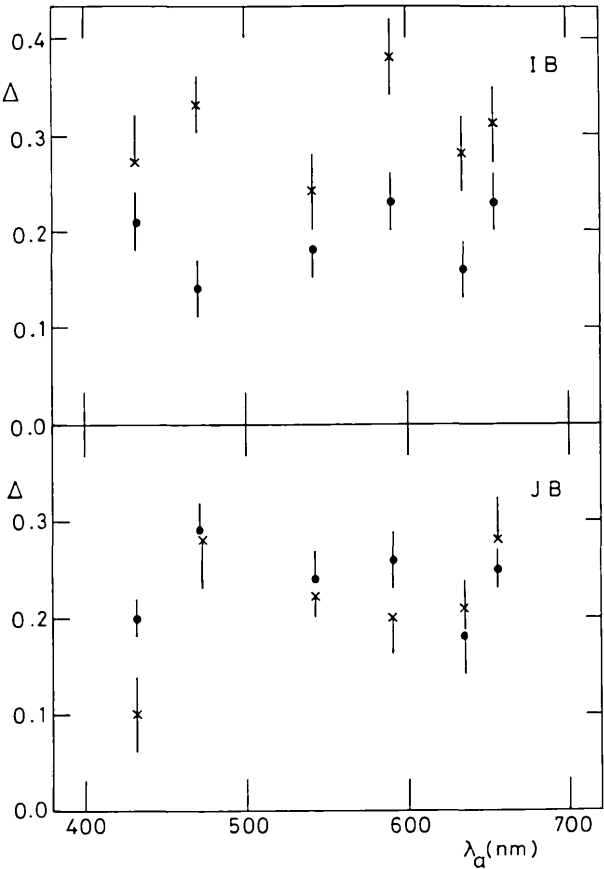


Figure 7. Spectral variations in the values of Δ obtained after adaptation to a grating of wavelength λ_a . The periodicity of both the test and adaptation gratings was equal to $2.9 \text{ cycles deg}^{-1}$, and the illumination level of the adaptation grating for each value of λ_a was, in log trolands, 2.77 (432 nm), 3.63 (471 nm), 3.85 (542 nm), 4.19 (590 nm), 3.98 (635 nm) and 2.67 (655 nm). Values for detection mediated by π_3 and by π_5 were obtained with the stimulus parameters defined in the caption to Fig. 6. (a) Data for subject IB; crosses refer to π_3 and circles to π_5 . (b) Data for subject JB, crosses refer to π_3 and circles to π_5 . Each value is the mean of 4 readings, with standard errors as shown with the data points.

gratings are shown in Fig. 7, for both π_3 and π_5 , and all adaptation wavelengths produce similar threshold elevation, with no systematic differences in spectral distribution between data for the two π -mechanisms.

DISCUSSION

The experiments were designed to examine the way in which signals from the blue-sensitive cone mechanism, isolated by the two-colour increment threshold technique, are transmitted along post-receptoral pathways. Both methods chosen for examination of this problem provide evidence of spatial responses with π_3 spectral characteristics, and we consider firstly the ST2 data obtained by background modulation methods. The ST2 spatial responses measured for detection by the blue (π_3) and red (π_5) sensitive mechanisms are similar to each other and to those for white light (Fig. 5). Other methods of assessing spatial vision, including that involving the ST1 spatial response, show that the spatial organisation of the blue-sensitive mechanism is coarser than that of the red- and green-sensitive mechanisms (see Introduction). ST2 is therefore exceptional in possessing a common spatial structure for the different π -mechanisms, and there are two alternative interpretations of this finding. One is that signals arising in the different π -mechanisms converge on to a single channel, and although this seems the likely explanation, it is not possible to rule out the alternative interpretation that there are a number of ST2 channels, with similar spatial organisation, but each receiving signals from a different π -mechanism. It has been argued that the ST2 channels correlate with Y-type electrophysiological mechanisms (Holliday and Ruddock, 1983) and Y-type ganglion cells are largely non-colour-opponent, with broad-band (luminance or L-type) spectral responses (de Monasterio, 1978). In particular, signals from blue-sensitive photoreceptors converge on to some class III Y-type ganglion cells with L-type spectral responses. The electrophysiological evidence therefore indicates that signals from different cone mechanisms converge on to a single ST2 channel, giving L-type spectral responses.

The spatial responses obtained by adaptation methods have an overall bandwidth of 2–3 octaves for both π_3 and π_5 (Fig. 6), much as is observed in all the adaptation studies cited in the Introduction. There is some variation in the amplitudes of the different responses, with subject IB giving larger peak response for π_3 and JB a larger response for π_5 . The measurements with different wavelengths, λ_a , of the adaptation grating show that there is no systematic spectral variation in the Δ values (Fig. 7). The mean Δ values averaged over all wavelengths were 0.30 ± 0.02 for π_3 and 0.19 ± 0.02 for π_5 (subject IB), and 0.22 ± 0.03 (π_3) and 0.24 ± 0.02 (π_5) (subject JB). These values reflect the variations in amplitude seen in the spatial tuning curves (Fig. 6). According to Maudarbocus and Ruddock (1973a), adaptation effects for different gratings are equivalent when they are set to the same suprathreshold illumination (I_a), and this method of equating the different adaptation gratings could have been adopted. The aim of the present experiments, however, was to compare Δ values for the same set of adaptation gratings but for different test gratings, and as Δ values change only slowly as $\log I_a$ increases (Maudarbocus and Ruddock, 1973b) it was decided to maximise the adaptation effects by using the highest values of I_a provided by the instrument. The lack of spectral selectivity in the data of Fig. 7 is demonstrated by taking the ratio of the mean Δ values for $\lambda_a < 480$ nm, at which the blue-sensitive cone mechanism has significant sensitivity, to those for $\lambda > 540$ nm, at which its sensitivity is very low. The

Table 1.

The average values for the ratios of $\Delta_{>540}/\Delta_{<540}$ for each subject and for π_3 and π_5 . The mean of eight values were obtained by taking $\Delta_{>540}/\Delta_{432}$ and $\Delta_{>540}/\Delta_{471}$ (four values each) from the data of Fig. 7 and the standard errors are given with the mean.

Subject	π_3	π_5
IB	1.01 ± 0.07	1.17 ± 0.10
JB	1.55 ± 0.28	0.97 ± 0.08

ratios of the two sets of data (Table 1) show that for neither π -mechanism do the ratios differ greatly from unity; thus there is no indication of an opponent response involving the blue-sensitive cone mechanism. Further, contributions from a red-green opponent system can be ruled out by the large value of Δ at 540 nm, which is a neutral wavelength for red-green opponent systems measured both psychophysically and electrophysiologically (Wiesel and Hubel, 1966; Gouras, 1974; de Monasterio, 1978; Michael, 1978a, b; Hendricks *et al.*, 1982).

In these experiments we have shown that signals generated in the blue-sensitive cones are transmitted to central mechanisms with broad-band spectral responses. They may also converge onto peripheral luminance channels selectively responsive to transient stimuli, but the spectral responses of the ST2 mechanisms cannot be studied under conditions which also permit the π_3 component to be identified. Signals from blue-sensitive cones contribute little to apparent brightness, but have a major effect on colour appearance, which stimulated the suggestion that blue-sensitive cones send signals to colour-opponent, but not to luminance neural channels. This hypothesis is supported by the results of several experimental investigations, as was discussed in the Introduction. The present experiments, however, utilise novel methods of investigating the blue-sensitive response mechanism and the results are in clear contradiction of the hypothesis. The contribution of blue-cone signals to the total signal in luminance channels may be relatively small, but our experiments provide no evidence on this point.

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VISUAL SPATIAL FILTERING AND PATTERN DISCRIMINATION ARE ABNORMAL IN STRABISMIC AMBLYOPIA

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Summary—1. We report the results of an experimental study on normal and amblyopic vision, in which we have measured spatial filter characteristics and pattern discrimination performance.

2. Threshold responses, measured for each eye of amblyopes, in response to a moving target of either positive (light) or negative (dark) contrast, are displaced to lower spatial frequencies than those for normal vision. These data, which are similar to those reported previously for light targets, imply a loss of spatial resolution.

3. Discrimination of target orientation, measured for multi-element stimuli of linear dimension 0.5 deg, is significantly impaired for the abnormal eyes of the amblyopic subjects compared with their performance under binocular conditions, whereas responses for the “normal” eyes are similar to the binocular data.

4. For larger targets (linear dimensions 1.5 deg), data for both “abnormal” and “normal” eyes are similar to those for binocular viewing, and the deficit observed with small targets can be simulated in normal subjects by degrading or demagnifying the retinal image.

5. We show that in amblyopia, discrimination losses for the “abnormal” eyes cannot be attributed solely to changes in the spatial filter responses. We argue that the discrimination losses observed in our experiments are consistent with blurring of images in amblyopia.

Key words—Amblyopia; strabismus; spatial filtering; orientation discrimination; Snellen acuity.

INTRODUCTION

The mechanism of amblyopia is not well understood, but the demonstration that neuronal responses and innervation of the striate cortex by fibres from the two eyes is modified by suturing of one eye (Wiesel and Hubel, 1963; Hubel *et al.*, 1977), stimulated considerable interest in the associated developmental factors. Subsequently, changes in receptive fields of X-, but not Y- type retinal ganglion and geniculate cells have been described in cats with surgically induced amblyopia (Ikeda, 1980). The receptive fields of both “on” and “off” centre X-type neurones were affected, but these findings have been disputed (Cleland *et al.*, 1982).

Several studies on human amblyopia have concentrated on losses of contrast sensitivity in threshold detection tasks (Hess and Howell, 1977; Hess *et al.*, 1980). At supra threshold contrasts, however, amblyopic responses in contrast matching are essentially normal (Hess and Bradley, 1980), and it has been suggested that visual deficiencies in amblyopia may result from distortion of space (Hess *et al.*, 1978; Levi and Klein, 1982; Bedell and Flom, 1983). Bradley

and Freeman (1985), however, concluded that deficits in amblyopic vernier acuity are “due primarily to poor visibility of the stimulus contours” and are “uncorrelated with perceptual distortions”. Reduced shape discrimination in amblyopia has been interpreted as evidence for spatial distortion (Pointer and Watt, 1986).

The study to be described utilizes two methods developed in the investigating laboratory, one designed for the determination of spatial and temporal response characteristics (Barbur and Ruddock, 1980; Holliday and Ruddock, 1983) and the other for the measurement of pattern discrimination in response to multi-element stimuli (Ike *et al.*, 1986). It has already been shown that spatial responses of one mechanism, called ST1, involved in the detection of bright targets is distorted in amblyopes, whereas that of a second mechanism, called ST2, is not (Grounds *et al.*, 1983). We now demonstrate that similar effects occur in the detection of dark targets, and that amblyopia leads to loss of discrimination performance with the multi-element patterns. We also examine the possible relationship between the changes in the ST1 spatial responses and the loss of discrimination.

EXPERIMENTAL METHODS

Apparatus

The equipment required for the experimental measurements was designed and, in part, constructed within our laboratory. The stimuli required for determination of the ST1 responses were generated by a Maxwellian view optical system, which has been described fully in previous publications (Barbur and Ruddock, 1980; Holliday and Ruddock, 1983). The only additional requirement of the present study was for a target of negative contrast, which was provided by a photograph transparency with appropriate density distribution. This was obtained by exposure of high contrast Kodalith film, and the appearance of the visual field is illustrated in Fig. 1. The multi-element targets required for the discrimination experiments were generated on a visual display unit (Microvitec Cub) controlled by a Sharp micro-computer (Type MZ-80B) via a Plutoboard (IO Research Ltd). The system generates random arrays of the pattern elements of the kind illustrated in Fig. 2(a), and has been described in detail elsewhere (Ike *et al.*, 1986).

Procedure for measurement of the ST1 spatial responses

The circular target, of diameter 3.5 deg, moved along the horizontal meridian at 15 deg s^{-1} , and traversed the central 8.5 deg of the field. The non-localized nature of the target eliminates the influence of eccentric fixation in the determination of detection thresholds, the 8.5 deg traverse of the moving target being significantly greater than the angles of eccentric

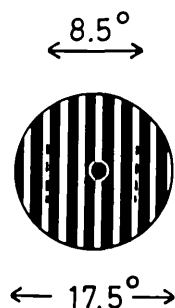


Fig. 1. The visual field used in determination of the ST1 spatial responses. The circular target (diameter 3.5 deg) moved along the horizontal meridian at 15 deg s^{-1} , traversing the central 8.5 deg of the circular background grating (diameter 17.5 deg). The dark and light bars of the background grating had the same width d , and the periodicity, f_s , of the target is defined as $(2d)^{-1}$.

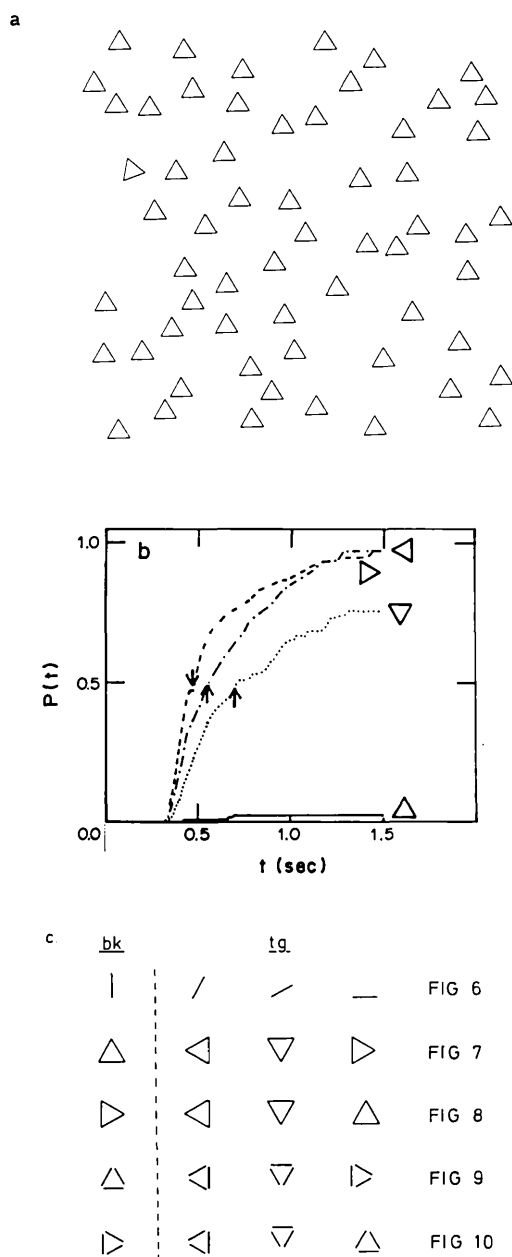


Fig. 2. (a) Appearance of the visual field used in the measurement of pattern discrimination. In these experiments there were 40 identical background elements and the triangles were all equilateral. The lines were of width 0.03 deg and the gap in elements such as $\triangle$ was 0.12 deg, measured from the line termination to the apex of the nominal triangle. (b) Typical experimental data obtained in the measurement of pattern discrimination. The probability of detection of the target, $P(t)$, is plotted against time, t , from the time of stimulus presentation. Measurements refer to background elements $\triangle$, and the different targets are marked on the figure. The time for 50% probability of detection, marked with an arrow at $P(t)$ equals 0.5, provides the characteristic response time, T . (c) Combinations of background and target elements used in the experiments; the figure numbers refer to the presentation of the different sets of data.

Table 1. Details of the five strabismic amblyopes

Subject	Sex	Age	Class	Fixation angle	V.A. "normal" eye	V.A. "abnormal" eye
M.G.	M	22	Con.	1.5°w	6/5	6/18
A.M.N.	F	20	Con.	0°	6/5	6/6
J.P.	M	19	Div.	8°t	6/4	6/12
P.D.	M	19	Con.	0.5°n	6/4	6/5
D.G.	M	24	Div.	1.5°t	6/6	6/12

The fourth column gives the classification as convergent (Con.) or divergent (Div.).

The fifth column gives the angle of eccentric fixation in the amblyopic eye, either nasal (n), temporal (t) or wandering (w), determined with the Linksz star graticule (Lyle and Wybar, 1967). Visual acuity (V.A.) was measured with the Snellen test chart, with refractive correction. All subjects had normal fundi and none was able to perceive images in random dot stereograms.

fixation in all but one of the amblyopic subjects (Table 1). Grounds *et al.* (1983) considered in detail and rejected the possible contribution of eccentric fixation to the threshold values. The direction of movement was reversed on successive presentations and the subject was instructed not to track the target, although no fixation point was provided. The target was superimposed on a background, which consisted of alternate light and dark bars of equal width d , giving a grating of periodicity $(2d)^{-1}$, orientated vertically. The appearance of the visual field is illustrated in Fig. 1. Threshold illumination, I_t , for detection of the target was determined as a function of $(2d)^{-1}$, and the mean illumination and contrast of the background grating were constant for each set of measurements. I_t was determined by the double interleaved staircase method (Cornsweet, 1962), target illumination being controlled by a neutral density wedge under computer control and each value was determined from ten turning points in the double staircase. The data so obtained are presented as $\log I_t$ plotted against $(2d)^{-1}$, the latter being expressed in cycles per degree. The alignment of the observer's eye was maintained by a dental bar, and the field was focussed by adjustment of the object plane. Where required, the subjects wore refractive correction.

Procedure for measurement of pattern discrimination

Discrimination measurements were made with patterns consisting of multiple, non-intersecting elements [Fig. 2(a)]. The elements were all of identical shape and size (e.g. Δ) and in these experiments, the single target, which the subject had to detect, was distinguished from the background only by its relative orientation (e.g. ∇). Four different target orientations were used for each background orientation, one of

them being a "null" target orientation, identical to that of the background elements. The "null" targets provided a check on the accuracy of the subjects, and the rate of false positives was $\leq 5\%$ of presentations for all subjects. The locations of the target and background elements were randomized for each presentation, and the subject pressed a button on detection of the target. A second button provided for a "no target" response, and as soon as either button was released, the next pattern was generated. The computer logged the time after presentation at which each positive response occurred, and computed the cumulative number of positive responses, expressed as probability of detection, as a function of time [Fig. 2(b)]. Stimuli for a given background element were presented in blocks of 100, consisting of 25 presentations of each target orientation, plus 25 "null" patterns. The probability values presented in Figs 6–10 are based on 50 presentations of each target, and for the purposes of this study, each response is characterized by the time, T , at which the subject achieved detection of the target on 50% of presentations [Fig. 2(b)], separate values of T being determined for each target orientation. The aim of these experiments was not to study the variation of discrimination for different orientations, which has been considered elsewhere (Ike *et al.*, 1987), thus in presenting the data, no distinction is made between the different target orientations for a given background, and each is given equal weight in analysing the data. The different combinations of target and background elements are illustrated in Fig. 2(c).

The subjects were seated 1.9 m from the VDU which at this distance subtended 8.5 deg horizontal by 6.3 deg vertically at the subjects eye. The screen colour was green (C.I.E. coordinates $x = 0.310$, $y = 0.485$) and the average

luminance was 10^{-1} cd/m². Subjects were instructed to scan the field in order to detect the target, and measurements were made under binocular viewing conditions, and then with each eye separately. In the latter case, the "unused" eye was covered with an eyepatch. The values of T obtained in binocular measurements, designated T_b , acted as a reference with which the values of T for each eye could be compared.

Subjects

Data are given for 12 subjects, five amblyopic and seven normal, aged 19–24 years. All but one of the normal subjects were, like the amblyopes, naive visual psychophysical observers. The details of the amblyopes are given in Table 1. In presenting the results, we differentiate between the "normal" and "abnormal" eyes of subject PD, although he reported that when young, he alternated fixation freely between the two eyes. Ophthalmic examination failed to confirm that this is currently the case, however. [Grounds *et al.* (1983) showed that visual responses were similar for each eye of a subject with alternating fixation.]

RESULTS

Mean values of the ST1 spatial responses, determined for four normal subjects with both positive and negative contrast targets, are plotted in Fig. 3. The responses for the two types of

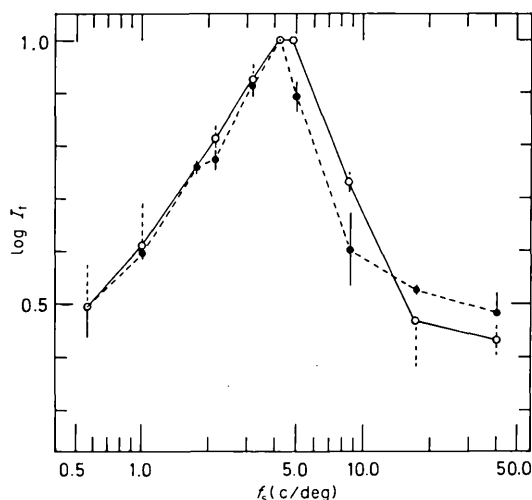


Fig. 3. Threshold illumination, I_t , for detection of a circular target moving across a background grating of periodicity f_s (see Fig. 1). Average values for four subjects with normal vision; dark circles refer to dark (negative contrast) targets and light circles to light (positive contrast) targets. The data are normalized to a peak value of $\log I_t$ equal to one. Error bars denote the standard errors, amongst the subjects.

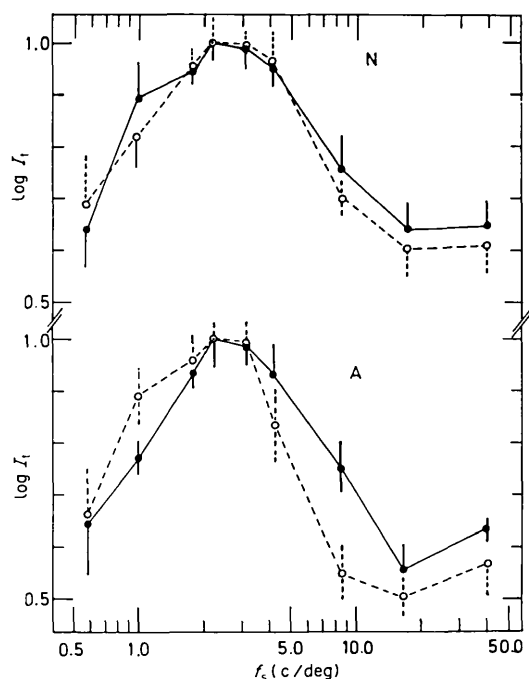


Fig. 4. As Fig. 3, but mean values for 5 subjects with strabismic amblyopia. Average data for the "normal" eyes, N, and the "abnormal" eyes, A.

target are closely similar, peaking at 4–5 c/deg, and those for the light target are consistent with previously published data (Barbur and Ruddock, 1980; Holliday and Ruddock, 1983). The ST1 responses for both normal and abnormal eyes of five amblyopes are shown in Fig. 4, and all four sets of data (both target contrasts measured for each eye) peak at 2–3 c/deg, significantly below the frequency for peak response in the normal subjects. The overall low frequency shift of the amblyopic responses relative to normal (Fig. 5) is similar to that found with light targets for either eye of a large group of amblyopes (Grounds *et al.*, 1983).

Pattern discrimination performance in response to the multiple element stimuli is expressed in terms of the observation time, T , required for 50% detection of the target (see Methods Section, Fig. 2). In Figs 6–10, T values obtained for observations made with one or other eye are plotted against the value, T_b , obtained with both eyes, each figure referring to a different background element. For a background consisting of vertically orientated, straight line elements, T values recorded for each eye separately are similar to those for both eyes. Results obtained with the triangular background elements orientated $\triangle$ (Fig. 7) and $\triangleright$ (Fig. 8) show that T values are, for most

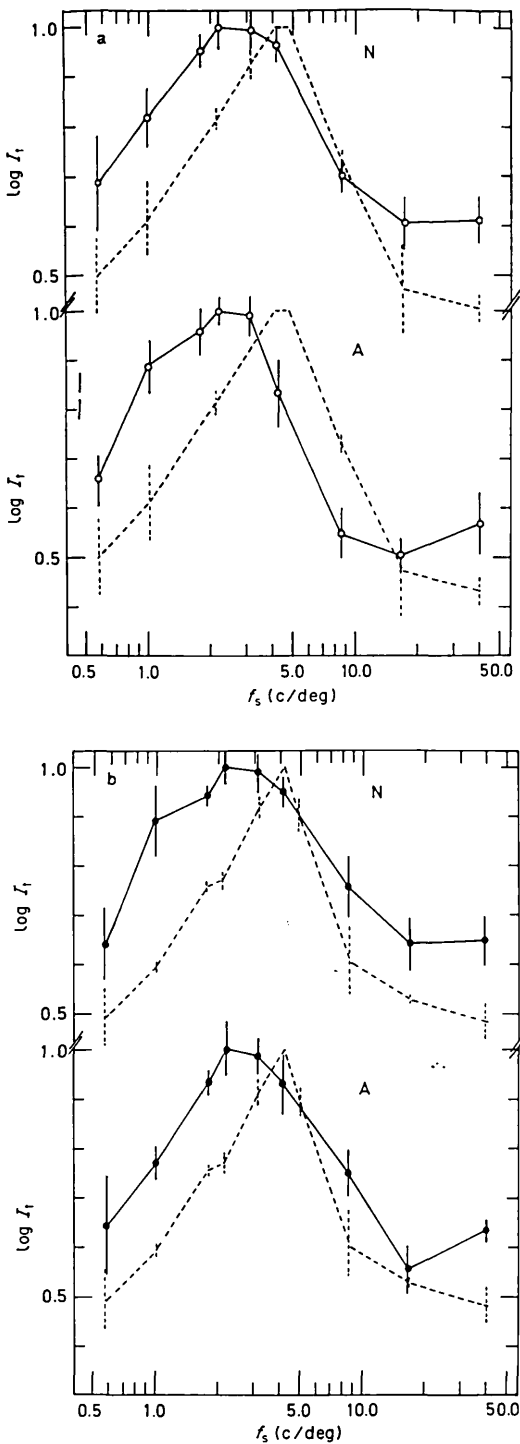


Fig. 5. Comparison between the experimental data of Figs 3 and 4 for normal subjects (broken lines) and amblyopic subjects (full lines with data points; N refers to the "normal" and A to the "abnormal" eyes). a—light targets; b—dark targets.

subjects, significantly greater than those obtained with the single lines. For the smaller elements [Figs 7(a), 8(a)], response times for "abnormal" eyes of the amblyopic subjects

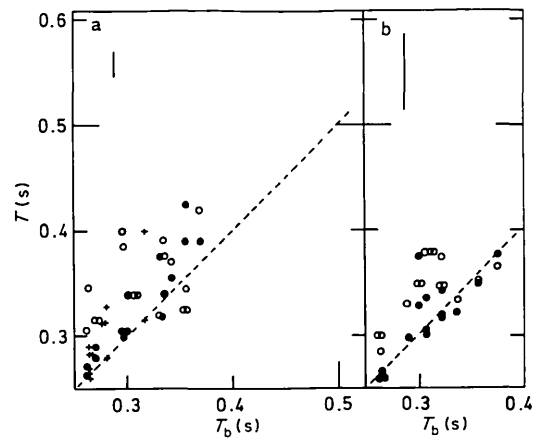


Fig. 6. The time T , for 50% probability of detection of the target using one eye, plotted against the equivalent time, T_b , obtained with binocular viewing. The background elements were vertically orientated straight lines. Open circles—data for the "abnormal" eyes of the amblyopic subjects. Closed circles—data for the "normal" eyes of the amblyopic subjects. Crosses—data for either the right or left eyes of the normal subjects. Data set (a) refer to lines of length 0.5 deg and (b) to lines of length 1.5 deg.

(open circles) are, in most cases, greater than those for the "normal" eyes (full circles), the vast majority of the latter being approximately equal to T_b . This difference between the results for the "normal" and "abnormal" eyes disappears in the responses to the larger elements [Fig. 7(b), 8(b)], where results for both eyes are clustered around the line $T = T_b$. Measurements were made with triangular elements lacking corners (background orientations $\triangle$, Fig. 9, and $\triangleright$, Fig. 10), but for only one size, corresponding to the smaller elements $\triangle$ and $\triangleright$. The discrimination task is still more difficult for the background elements $\triangle$ and $\triangleright$, thus the T values are increased, but again, those for the "abnormal" eyes of the amblyopes (open circles, Figs 9 and 10) are significantly greater than those for the "normal" eyes (solid circles). The comparison data given for the normal subjects (crosses) show no systematic deviation from the line $T = T_b$, regardless of the elements studied (Figs 6–10).

DISCUSSION

The experimental data establish two characteristics of visual function in amblyopia, one relating to the filtering of images by the visual system and the other to the discrimination of pattern orientation. The ST1 mechanism responsible for the detection of negative contrast targets is characterized by abnormally low spa-

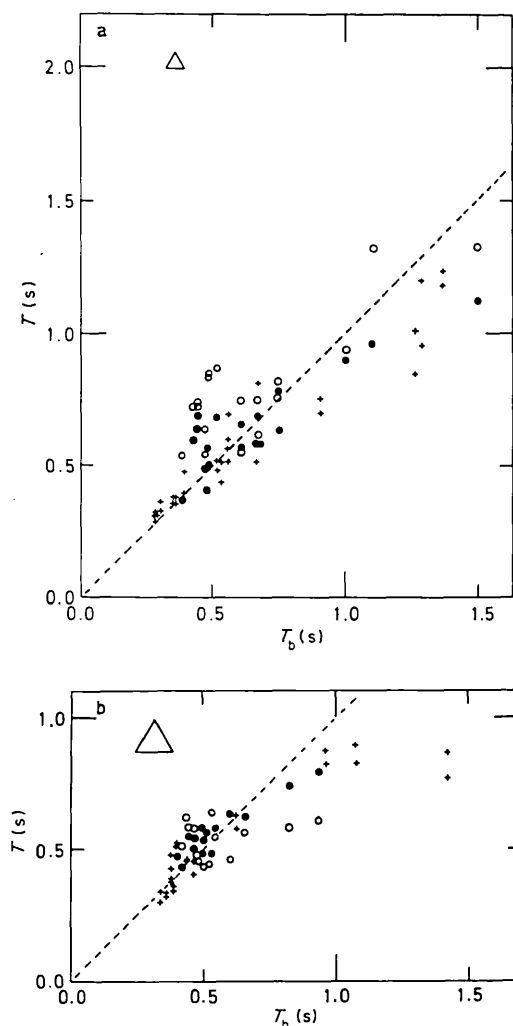


Fig. 7. As for Fig. 6, but for background elements Δ . Data set (a) refer to elements constructed from lines of length 0.5 deg and (b) to elements constructed from lines of length 1.5 deg.

tial frequency response (Fig. 5) and this occurs in both the "normal" and "abnormal" eyes of the amblyopic subjects. Grounds *et al.* (1983) found a similar effect in the ST1 responses measured for light targets and argued that the low frequency characteristics in the "normal" eyes were caused by patching treatment given during childhood. The amblyopic subjects of this study had, with one exception (J.P.), received such treatment (see Table 1), and the ST1 responses for J.P.'s "normal" eye were normal. The explanation offered by Grounds *et al.* therefore retains validity in relation to these new data. The ST1 filters have small spatial extension, with circular symmetry, and low pass (sustained) temporal response, thus they appear to correspond, functionally, to X-type

mechanisms located pre-cortically in the primate visual pathways (see Discussion section, Holliday and Ruddock, 1983). It is tempting to extend the analogy of equating ST1 mechanisms for dark and light targets to "off" and "on" centre electrophysiological mechanisms respectively. This, however, requires that the two ST1 mechanisms be mutually independent, which has yet to be established. Nonetheless, it should be noted that in their experiments on strabismic amblyopia, induced by surgical manipulation of the cat eye, Ikeda and her co-workers found increased sizes in the receptive field centres of both "on" and "off" centre X-type ganglion and geniculate cells (Ikeda and Tremain, 1978, 1979; Ikeda *et al.*, 1978; Ikeda, 1980).

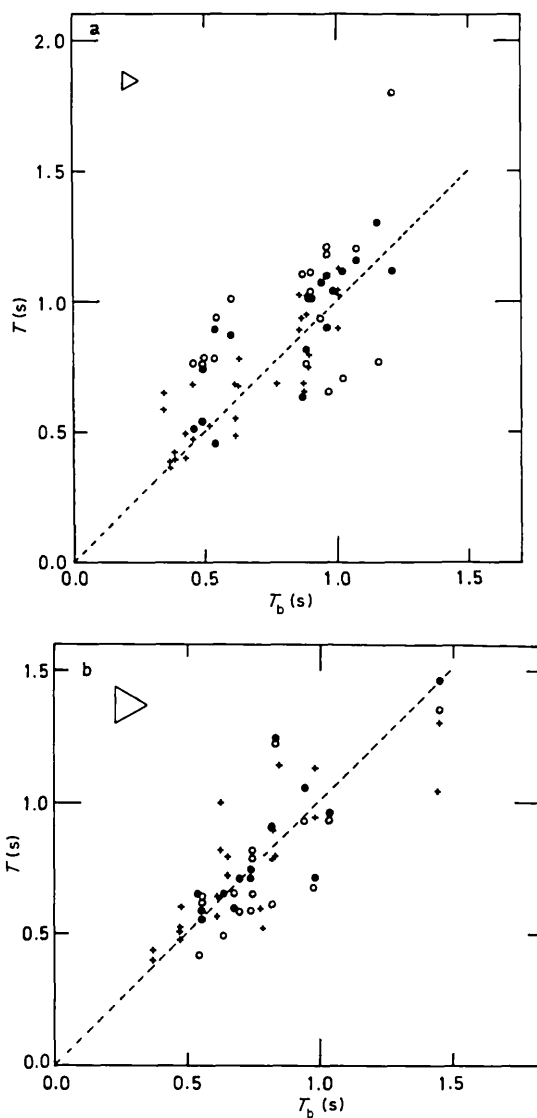


Fig. 8. As Fig. 7, but for background elements $\triangledown$. Data set (a) refer to line length 0.5 deg and (b) to line length 1.5 deg.

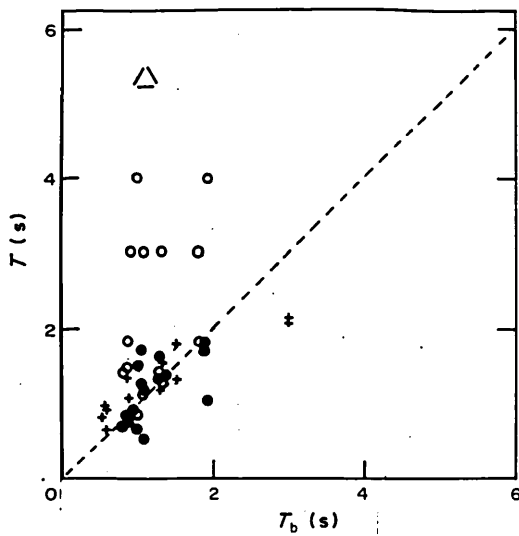


Fig. 9. As Fig. 8, but for background elements Δ . The line lengths were 0.5 deg.

Orientation discrimination for single lines appears to be unimpaired in amblyopia [Figs 6, 11(a)], a result similar to that found with long [15 deg] lines by Vogels *et al.* (1984). Discrimination performance with the "abnormal" eyes in response to small (side-length 0.5 deg) triangular elements is, however, significantly slower than that with the "normal" eyes or with both eyes together (Figs 7–10). There is considerable variation between T values for the

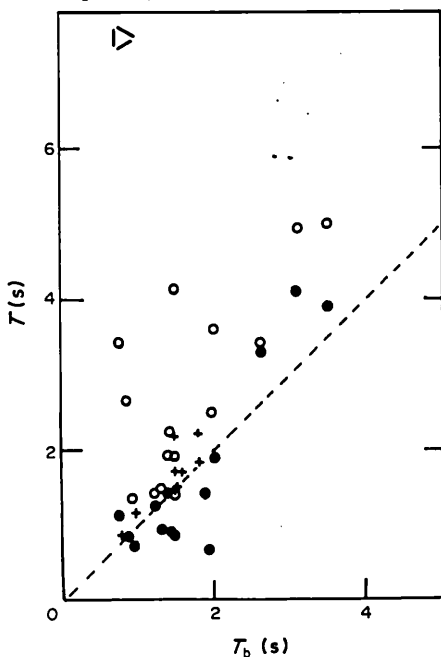


Fig. 10. As Fig. 9, but for background elements $\triangleright$. The line lengths were 0.5 deg.

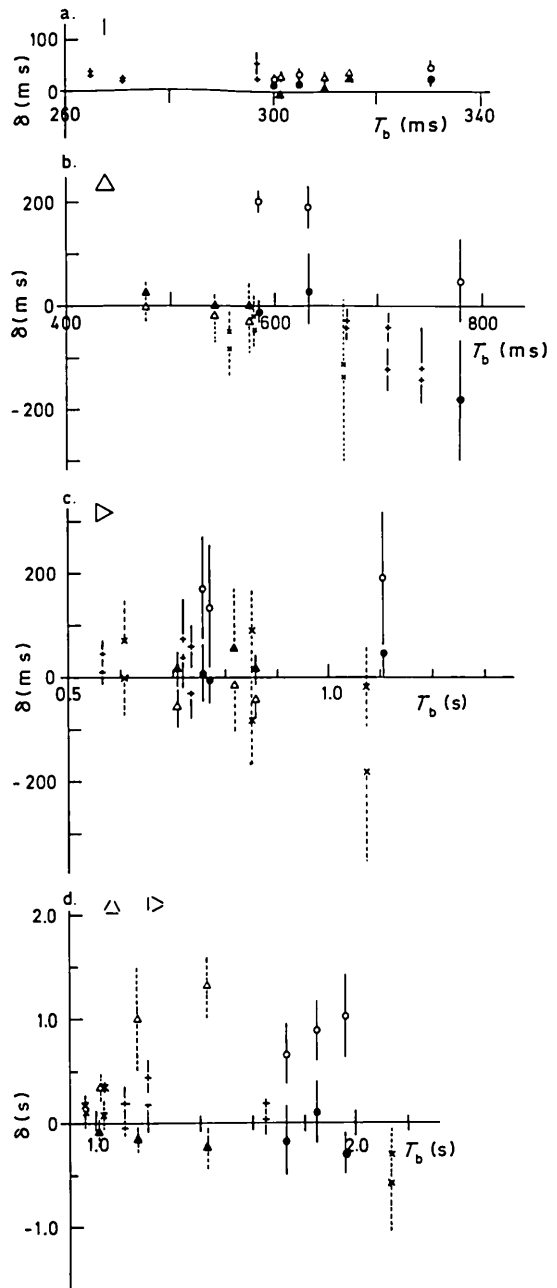


Fig. 11. Values of δ , equal to $(T - T_b)$, plotted against T_b . Data taken from Figs 6 to 10. (a) For background elements | (Fig. 6). Data for the "abnormal" eyes of the amblyopes are denoted by open circles (0.5 deg line length) and open triangles (1.5 deg line length); those for the "normal" eyes are denoted by full circles (0.5 deg line length) and full triangles (1.5 deg line length); for normal subjects are denoted by crosses (+, -0.5 deg line length and $\times$, -1.5 deg line length). (b) For background elements Δ (Fig. 7). Symbols as for Fig. 11(a). (c) For background elements $\triangleright$ (Fig. 8). Symbols as for Fig. 11(a). (d) For background elements Δ (Fig. 9) and $\triangleright$ (Fig. 10); data for "abnormal" eye of amblyopes denoted by open circles (elements Δ) and open triangles (elements $\triangleright$); data for "normal" eyes of the amblyopes denoted by full circles (Δ) and full triangles ($\triangleright$); data for normal subjects denoted by crosses (+, elements Δ and $\times$, elements $\triangleright$).

different amblyopes, but in almost every experiment, performance with the amblyopic eye was relatively slow. This result is demonstrated by plotting the average values of the difference δ , between T , obtained with a single eye, and T_b obtained with both eyes, (i.e. $T - T_b$), against T_b . Each set of data from Figs 6 to 10 has been replotted in this way (Fig. 11) and the large positive values of δ for the "abnormal" eyes [open circles and, in Fig. 11(d) only, open triangles] are immediately apparent. Figure 11 also shows that for normal subjects (crosses) and the "normal" eyes of amblyopic subjects (full symbols), $T \approx T_b$ in almost every case. Comparison between the δ values for smaller and larger elements establishes that performance for the "abnormal" eyes of the amblyopes improves in the latter case, becoming similar both to that for their "normal" eyes, and to that for normal vision [open triangles, Fig. 11(b) and (c)].

The improved discrimination performance for the "abnormal" eyes produced by increase in the size of the elements suggests that discrimination may be limited by resolving power. Thus, the question arises as to whether or not poor discrimination can be attributed to the loss in spatial resolution implied by the low frequency ST1 spatial response. Two observations suggest that this explanation cannot, in itself, account for the experimental data. Firstly, ST1 re-

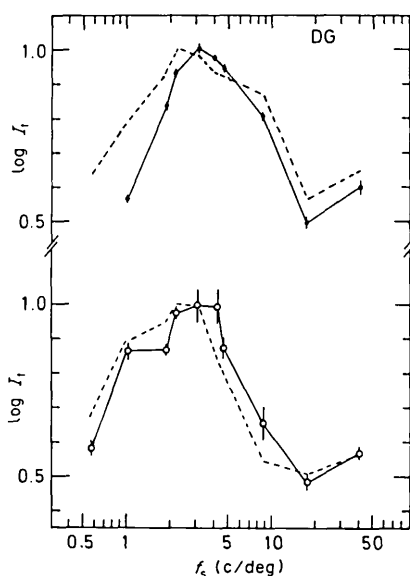


Fig. 12. ST1 data for the "abnormal" eyes of subject D.G. (full lines with symbols), plotted with the mean data for the "abnormal" eyes of the five amblyopes, taken from Fig. 4. Upper data sets refer to a dark target and low data sets to a light target. Error bars give standard errors of D.G.'s data.

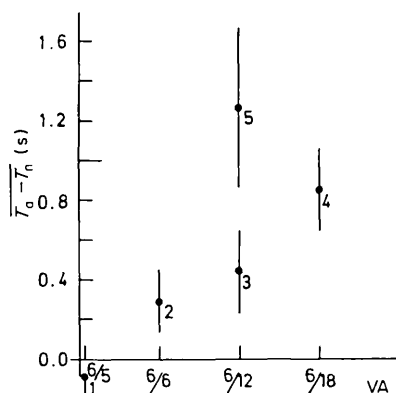


Fig. 13. The difference between the characteristic response times recorded for the "abnormal" and "normal" eye of each amblyope, ($T_a - T_n$), plotted against the Snellen visual acuity recorded for the "abnormal" eye. Data are averaged for elements of line length 0.5 deg, taken from Figs 7(a), 8(a), 9 and 10, and error bars denote the standard errors of the means; subjects P.D. (1), A.-M. N. (2), J.P. (3), M.G. (4) and D.G. (5).

sponses for the amblyopes "normal" eyes are similar to those for their "abnormal" eyes (Fig. 4), but there is no corresponding increase in T -values for the "normal" eyes, these being in most cases similar to T_b , and for the small elements are always less than T -values for the "abnormal" eyes (Fig. 11). Secondly, the difference between the T -values for the "normal" and "abnormal" eyes is greatest for subject D.G. (Fig. 13), yet D.G.'s ST1 responses are, if anything, displaced to the high frequency side of the mean amblyopic data (Fig. 12), indicating smaller spatial extension and, correspondingly, higher resolution. There is a similar lack of correlation between Snellen visual acuity and the ST1 response (Grounds *et al.*, 1983), thus we also plotted the difference between T -values for the "abnormal" and "normal" eyes, averaged over all small triangular elements, against Snellen visual acuity (Fig. 13). Although data for four of the subjects show that $(T_a - T_n)$ increases as resolution decreases, the value for the fifth subject, D.G. is greater than those for the other four, yet his resolution is intermediate between those of the others. D.G. has a severe refractive error in his "abnormal" eye (Table 1) which was, as with other subjects, corrected during the experiments. Generally, however, he wears no correction, thus his strabismic deficit is compounded by a refractive deficit, which may give rise to the very large T -values for his "abnormal" eye.

Our data demonstrate that orientation discrimination with single lines [Fig. 6; Fig. 11(a)]

is unimpaired in strabismic amblyopia, despite severe losses in Snellen acuity. Vogels *et al.* (1984) obtained the same result using a different method of measuring discrimination of line orientation. Levi and Klein (1982) showed that vernier acuity in strabismic amblyopes is related to Snellen acuity, but neither can be predicted from resolution for simple gratings. The triangular elements which show loss of orientation discrimination (Figs 7–10) are similar to the Snellen acuity targets, thus there should be some correlation between measurements made by the two methods, as is indeed seen in Fig. 13. The STI spatial response relies upon grating stimuli and probably represents an early stage of visual filtering (Holliday and Ruddock, 1983). The lack of correlation between this response and the orientation discrimination data for triangular elements is, therefore, consistent with Levi and Klein's (1982) conclusions.

The STI spatial response for normal, non-foveal vision is displaced to low frequencies relative to the foveal response (Barbur and Ruddock, 1980) and is similar to that found for central vision in amblyopia. Levi and Klein (1986) concluded that both normal peripheral vision and central vision in strabismic amblyopia are characterized by sparse sampling in the spatial domain, and the low frequency STI spatial characteristics imply precisely such a mechanism.

It is possible to simulate the amblyopic discrimination responses by degrading or demagnifying the images presented to normal subjects. Thus insertion of a scattering glass or a defocussing lens increases T -values; for example, with a +4 D lens, T -values for J.M.B. increase by a factor of five (background elements Δ). Reduction of the elements to half the previous minimum size (linear dimensions 0.25 deg) increases T by a factor of 1.5 (subject J.M.B.) and of 1.6 (subject A.J.) with the background elements Δ , and of 1.25 (subject J.M.B.) and of 1.7 (subject A.J.) with background elements $\triangleright$.

Although the discrimination deficits in amblyopia cannot be attributed solely to the changes in the STI spatial responses, they are, nonetheless, consistent with overall loss of spatial resolution. It is clear that other factors, arising centrally with respect to the STI filter, must contribute to both the loss of visual resolution and reduced discrimination suffered by the amblyopes. Our experiments do not identify these factors, but examination of both the

present data and those of Grounds *et al.* (1983) suggest that the time of onset of the amblyopic deficit may be a critical factor. Unfortunately, it was not possible to obtain sufficiently precise records for our subjects to assess this proposal quantitatively. Our results also demonstrate that if, indeed, there is distortion of visual space in amblyopia, its effects on discrimination are equivalent to those of spatial blurring.

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Visual discrimination of target displacement remains after damage to the striate cortex in humans

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Damage to the striate cortex usually causes blindness in those regions of the visual field which map to the area of neural damage^{1,2}. Nonetheless, there are reports that some patients with such damage can localize and perform certain visual discriminations between light stimuli presented within the 'blind' area of the visual field³⁻⁶. Experiments on animals with different brain areas ablated suggest that visual function is served by two principal projection pathways from the retina^{7,8}. That to the striate cortex is primarily responsible for fine discrimination between stimulus parameters such as colour and spatial pattern, whereas that to the superior colliculus in the midbrain is responsible for visual localization of stimuli. The residual visual functions in patients with cortical damage are usually attributed to the non-striate retinal projection to the superior colliculus. We now present measurements of spatial discrimination in two observers with large visual field defects (scotomata) caused by damage to the striate cortical region. Both exhibit a near normal ability to discriminate displacements of targets when two lights are flashed sequentially in their defective visual field, but they are unable to discriminate spatial pattern or size. We argue that these results are consistent with the 'two visual systems' interpretation of ablation studies on non-human species^{7,8}.

The representation of the visual field on the human striate cortex was first established from the study of patients who developed permanent blindness in localized areas following gunshot wounds to the striate cortex¹. However, visual discriminations in response to light stimulation within 'blind' areas of the visual field have been reported^{3-6,9} and two qualitatively different responses have been described. In one, visual discrimination can be shown only as forced-choice judgements between alternatives and the subject has no conscious visual sensation; these responses are thus termed 'blindsight'⁵. In the other, subjects report a sensation, usually described as a 'dark shadow', in response to bright, transient lights presented within visual field areas classed as 'blind' on the basis of conventional perimetry using steady or low-illumination transient stimuli⁹. The two subjects of the present study show the latter response, and the data presented relate to conscious detection of stimulus lights.

G.Y., a 28-year-old male, is hemianopic, suffering homonymous loss of vision in the right hemifield with sparing of about 3° around the fovea. R.C., a 27-year-old male, has a field loss covering the upper right quadrant, homonymous for the two eyes. The first subject received brain injuries in a motor accident, while the second sustained a cortical infarct following an attack of migraine. Degeneration of the left striate cortex, total for G.Y. and partial for R.C., has been established by computer tomography X-ray scans of the brain. Objects lying within these scotomata are detected only if displaced rapidly or presented transiently, and in the former case, the subjects experience a sensation of movement. Both G.Y. and R.C. perform accurate eye movements in order to fixate foveally on a flashed stimulus presented within the 'blind' hemifield, but neither can identify the colour, size or shape of the stimulus. For example, movement of the experimenter's hand cannot be differentiated from movement of a black, square card of much greater area. We have

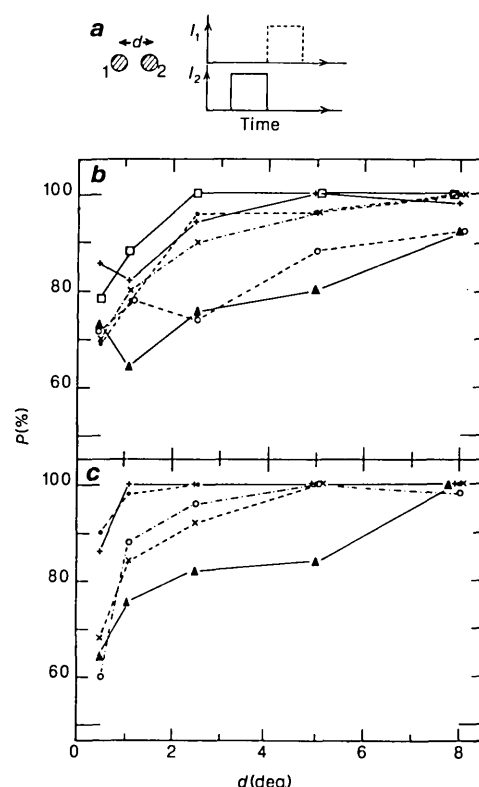


Fig. 1 *a*, The stimulus configuration used to elicit apparent displacement. The two circular targets were displaced centre to centre by distance d which was the variable parameter of the measurements, and were presented successively for 800 ms each. The value of d and the order sequence of the two spots were varied randomly between presentations. Each stimulus configuration was repeated 10 times. I_1 and I_2 denote the (equal) illumination levels of the two targets. *b*, Data of subject G.Y.; probability for correct discrimination of the target, $P(\%)$, is plotted against d , the separation of the two spots, expressed in degrees. The spots were of 1° diameter and the illumination level was 3.2 log Troland. Measurements were made in the 'blind' hemifield, at 5° (+), 10° (●), 15° (×), 20° (○) and 30° (▲) off-axis along the horizontal meridian, and at 5° off-axis in the normal hemifield (□). *c*, As for *b*, but for the normal subject I.B.; symbols are as for *b*.

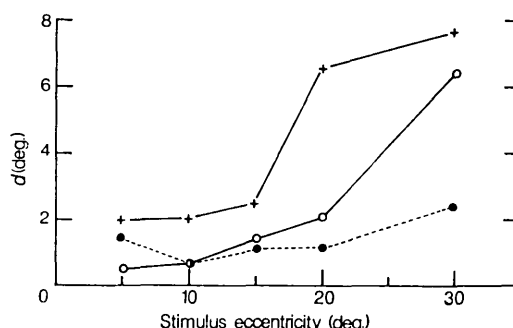


Fig. 2 *a*, Values of d required for 90% probability of correct discrimination of the direction of target displacement from right to left, or vice versa. Data for subject G.Y., blind hemifield (+) and I.B. (○), plotted against stimulus eccentricity, are taken from Fig. 1. Data for G.Y.'s normal hemifield (●) were obtained by similar methods.

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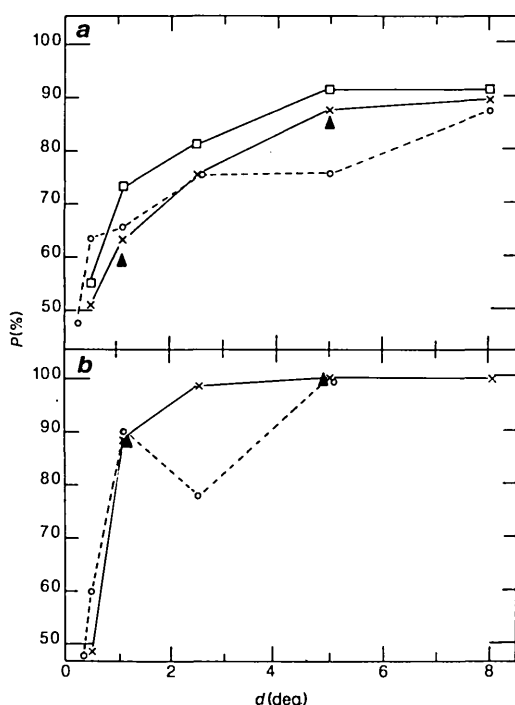


Fig. 3 *a*, As Fig. 1, but measurements were made at a single retinal location, 10° off-axis relative to both the vertical and horizontal meridians, placing the target in the upper right quadrant, that is, within R.C.'s 'blind' field area. The data for R.C. refer to circular targets (Fig. 1*a*) of 0.2° (▲), 0.5° (○) and 1.0° (×) diameter. Comparison data are also given for an equivalent location in the normal left upper quadrant for targets of diameter 1° (□). *b*, As *a*, but for the upper right quadrant of the normal subject I.B. Data refer to spots of diameter 0.2° (▲), 0.5° (○) and 1.0° (×).

studied systematically the responses of the two subjects elicited by transient, white-light stimuli, provided by a maxwellian view optical system. All measurements were made monoptically, with the right eye, and the observer's head was kept steady relative to the instrumental exit pupil by a dental clamp.

Spatial discrimination was measured for the displacement of two spots, with centre-to-centre separation d in a direction parallel to the horizontal meridian, presented sequentially for 800 ms each (Fig. 1*a*). Such stimuli normally elicit a strong sensation of movement, directed from the first to the second flash, and this was reported by the two subjects for stimulus presentation within either the normal or 'blind' areas of the visual field. The probability P of correctly identifying spot displacement to the right or to the left was measured as a function of spot separation d . Data for subject G.Y., measured at several retinal locations, show that P rises rapidly as d increases, and that the value of d for a given value of P increases as stimulus eccentricity increases (Fig. 1*b*). Values for G.Y.'s 'blind' hemifield are somewhat larger than those for his normal hemifield and larger than those measured for a normal subject I.B. (Fig. 1*c*), the differences being more significant at higher eccentricities (Fig. 2).

Data for R.C. are given for a single stimulus location, but for different spot sizes, and his responses are essentially independent of spot size (Fig. 3*a*). These data are again similar to those obtained for the normal field (Fig. 3*a*) and for the normal subject I.B. (Fig. 3*b*), although, as with G.Y., R.C.'s 'blind' field yields lower discrimination for displacement than does I.B.'s normal field.

For the 'blind' field, neither subject was able to resolve the targets used in the determination of displacement thresholds.

For example, G.Y. was presented with either a single circular target (diameter 1.1°) or with two such targets, separated spatially by 7° (as in Fig. 1*a*) but coincident in time, both targets being centred 13.5° off-axis along the horizontal meridian. The illumination of the single target was double that of each component, and so the two stimuli could not be distinguished on the basis of total flux. G.Y. was instructed as to the nature of the two stimuli, and in a random sequence of 100 presentations, he correctly identified the single target on 23 of 50 presentations and the pair on 26 of 50 presentations, that is, at chance level. He achieved 100% correct discrimination for presentation of the targets in the corresponding region of his normal hemifield.

The subjects were also unable to identify geometrical patterns formed by sequentially flashed spots, for example, by three spots (1.1° diameter), flashed for 800 ms and separated centre to centre by 5° (that is, a triangle with a spot at each corner), presented in the 'blind' field. The subjects reported the sensation of movement along a curved line, but the triangle was not identified; thus, discrimination of displacement cannot be exploited to provide pattern discrimination. Further, neither subject could discriminate at greater than chance level targets of different shapes or sizes presented within their visual field scotoma, as long as different targets were matched in total flux. For example, at no point in their 'blind' fields could they discriminate between circles of diameter 4° and equilateral squares and triangles constructed from lines of length 4°, the different targets being presented in random sequence for 300 ms at 2-s intervals. They were also unable to distinguish between a square-waveform grating of 1 cycle deg⁻¹ periodicity and a uniform field of illumination equal to the average illumination of the grating. It is difficult to compare such complete lack of spatial vision with normal function, but as an example, gratings of 10 cycles deg⁻¹ located 7° off-axis can be resolved in normal vision, whereas under the same conditions, neither subject was able to resolve a 1 cycle deg⁻¹ grating located in the 'blind' field.

Computer tomography X-ray scans show that in both subjects brain damage is restricted to the striate cortex, thus lack of pattern recognition or discrimination is attributed to disturbance of this area, which receives direct input from the retino-geniculate pathway. It has been argued that the characteristics of residual vision in one of these two subjects are similar to those of electrophysiological responses recorded from the superior colliculus⁹, which itself projects via the pulvinar to the prestriate cortex. Subsequently, however, a direct, albeit sparse, projection from the primate lateral geniculate nucleus to the prestriate cortex has been demonstrated^{10,11}. Although we cannot identify the non-cortical pathway which mediates the residual vision described here, our results demonstrate a complete functional dissociation between visual localization of transients and pattern discrimination, as would be predicted by the 'two systems theory' of visual organization^{7,8}.

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