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MONOCULAR AND BINOCULAR RESPONSES OF THE HUMAN VISUAL SYSTEM TO SPATIALLY STRUCTURED STIMULI

by

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Abstract

Two separate studies of visual responses to spatially structured stimuli are described. The first study is concerned with binocular aspects of the contrast threshold elevation effect. Thresholds for a test grating were determined after adaptation to a high contrast spatial frequency matched grating (in the test eye) and a conditioning grating of comparable illumination level but variable spatial frequency (in the alternate eye). It is shown that the threshold elevation effect observed in this configuration never exceeds that found in the absence of the conditioning grating. Indeed, for conditioning gratings in the range 1 - 4 c/°, the threshold elevation is much reduced, this reduction being independent of the conditioning spatial frequency except when test, adaptation and conditioning gratings are matched. The time course, intensity specificity and wavelength independence are comparable to those of the contrast threshold elevation effect itself, but the orientation specificity is not. Suppression is found only when all three gratings are within 20° of the vertical meridian. Suppression is also found to decrease for increasing horizontal displacements of a 5 c/° test field from a central fixation spot, but remains constant for increasing vertical displacements. It is not observed in stereoblind subjects nor in those who have been astigmatic in the vertical meridian since early childhood. Possible neural pathways for this suppression effect and its significance for overall visual performance are discussed.

In the second study, a spatial frequency filtering bench suitable for visual experiments is described. The experiments performed on this bench establish that an observer's ability to recognize and discriminate spatially structured stimuli (at both threshold and suprathreshold illumination levels) can be improved by the introduction of small non-transmitting disc filters into the diffraction plane.

CONTENTS

Chapter 1.

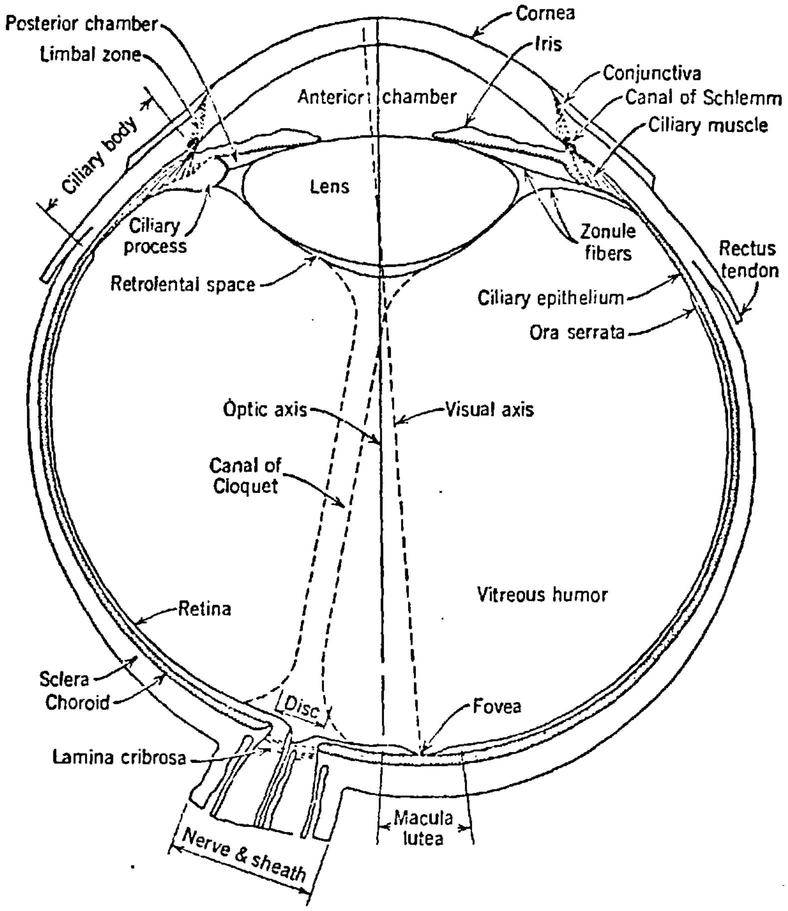
INTRODUCTION

A visual stimulus consists of a retinal distribution of energy, whose intensity can change with time or retinal location. In the receptors, photochemical absorption of light leads to neural signals transmitted via the retina, the optic nerve fibres and the geniculate body to the brain. The different characteristics of the stimulus activate neurones with the appropriate specificity, distributed throughout the visual nervous system.

There are two main methods for investigating the functional mechanisms of vision: direct electrophysiological experimentation on single cells in animals, and indirect, psychophysical techniques which can be used to measure responses of the whole human visual system. Before considering these functional aspects, a brief review of the anatomy of the eye is given.

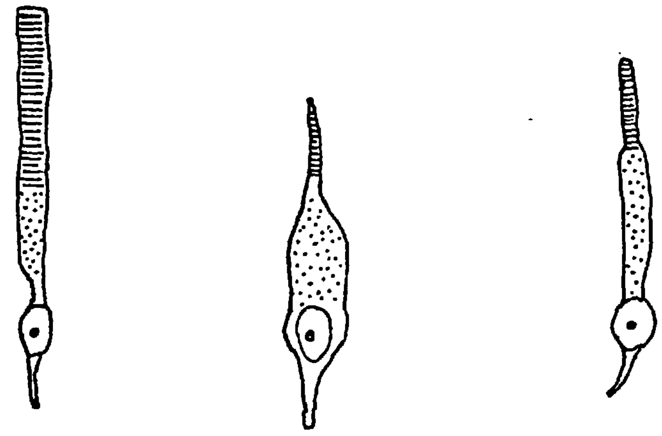
Anatomy

Light enters the eye via the transparent corneal membrane and passes through the anterior chamber containing the aqueous humour (fig. 1). It is refracted by the crystalline lens into the posterior chamber containing the vitreous humour and through the retinal membrane to the receptoral layer. In the human retina, this layer consists of two classes of receptors possessing different functional and morphological characteristics. The rods have an average width of 2 µm and an average length of 60 µm. They are made up of two distinguishable segments, both long and cylindrical in shape (fig. 2a). There is a small (1.5 mm) retinal indentation lying close to the optical axis of the eye, called the fovea, and this is virtually rod-free. It contains only the second class of receptor, the cones, some 10^5 in number which are responsible



Horizontal section of the right human eye.

fig. 1



(a) rod

(b) cone

(c) foveal cone

fig. 2

for about half the total optic nerve connections. The foveal cones are very rod-like in appearance, whilst those found extra-foveally have greater variations in their dimensions (figs. 2b and c). The outer segments of this latter type of cone are similar in shape to those of the rods, whilst the inner segments are bulbous and conical and up to four times the outer segment diameter. The population density of cones decreases away from the fovea whilst that of the rods increases to a maximum about 15° off axis, after which point, it ~~again~~ also falls off (Østerberg, 1935; fig. 3). The rod population is not smoothly distributed; rather the peripheral rods form small functional clumps.

The receptors contain photosensitive pigments, the most easily isolated of which was named rhodopsin (e.g. Kuhne, 1878). On exposure to light, it undergoes a series of well documented chemical changes, but regenerates when the light is withdrawn (Wald and Brown, 1956; Brindley, 1970). The rate at which the eye adapts to changes of illumination represents the time course of these chemical reactions. Rhodopsin is a rod pigment, but cone pigments have proved much more difficult to isolate with different experimenters ascribing different spectral characteristics to supposedly the same pigment. One of the most successful extracts was obtained by Wald (1937) when he isolated a cone pigment, iodopsin from the chicken retina. Its absorption spectrum showed a maximum at 562 nm and another secondary maximum at 370 nm. Recent experiments (Knowles, 1976) have suggested, however, that iodopsin is simply a by-product of bleaching rhodopsin.

Spectrophotometric measurements made in situ on the photopigments in monkey and human cones have shown three different absorption spectra, indicating three pigments operating a trivariant system of colour vision (e.g. Marks, Dobelle and MacNichol, 1964).

Each rod has a terminal spherule, invaginated by the dendrites of rod bipolar~~s~~ and horizontal cells. The terminal pedicle of each cone is

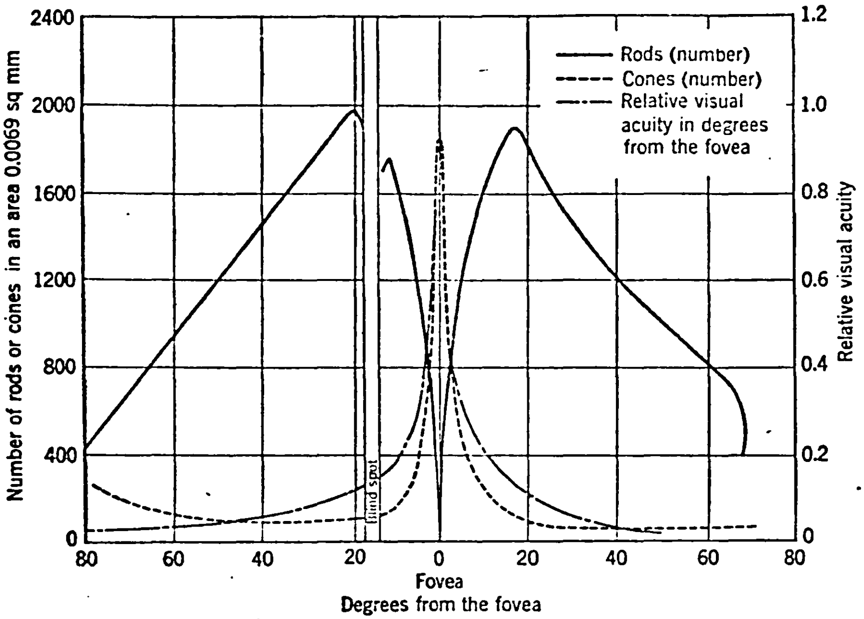


fig . 3

Distribution of rods and cones along a horizontal meridian. Parallel vertical lines represent the blind spot. Visual acuity for a high luminance as a function of retinal location is included for comparison.

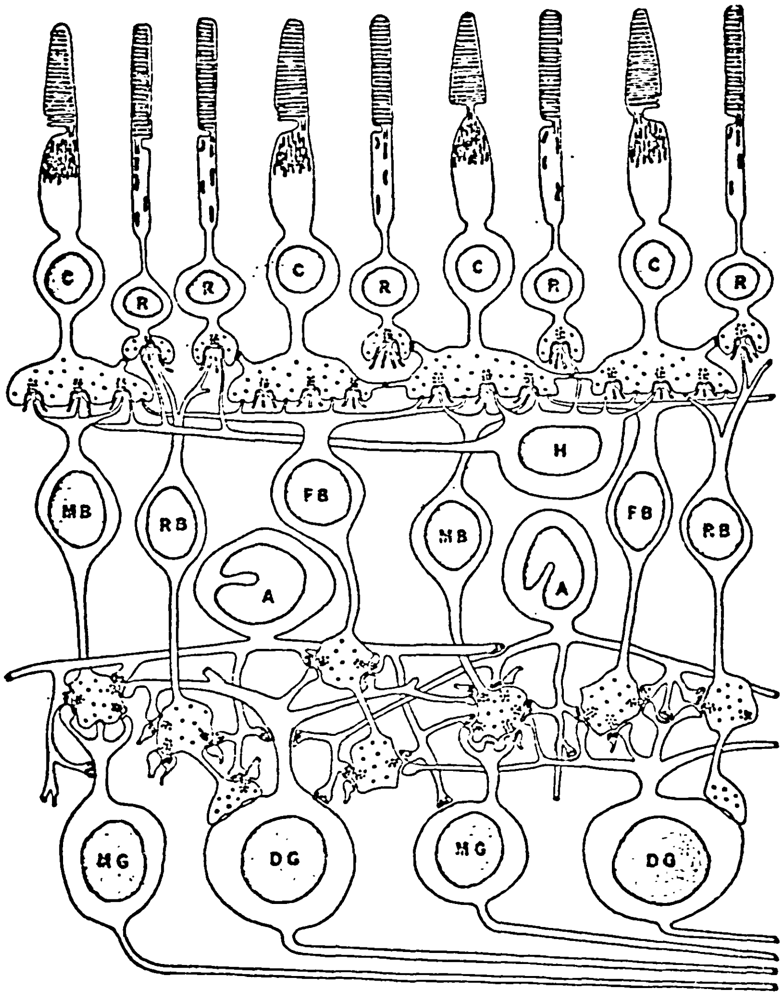


fig . 4

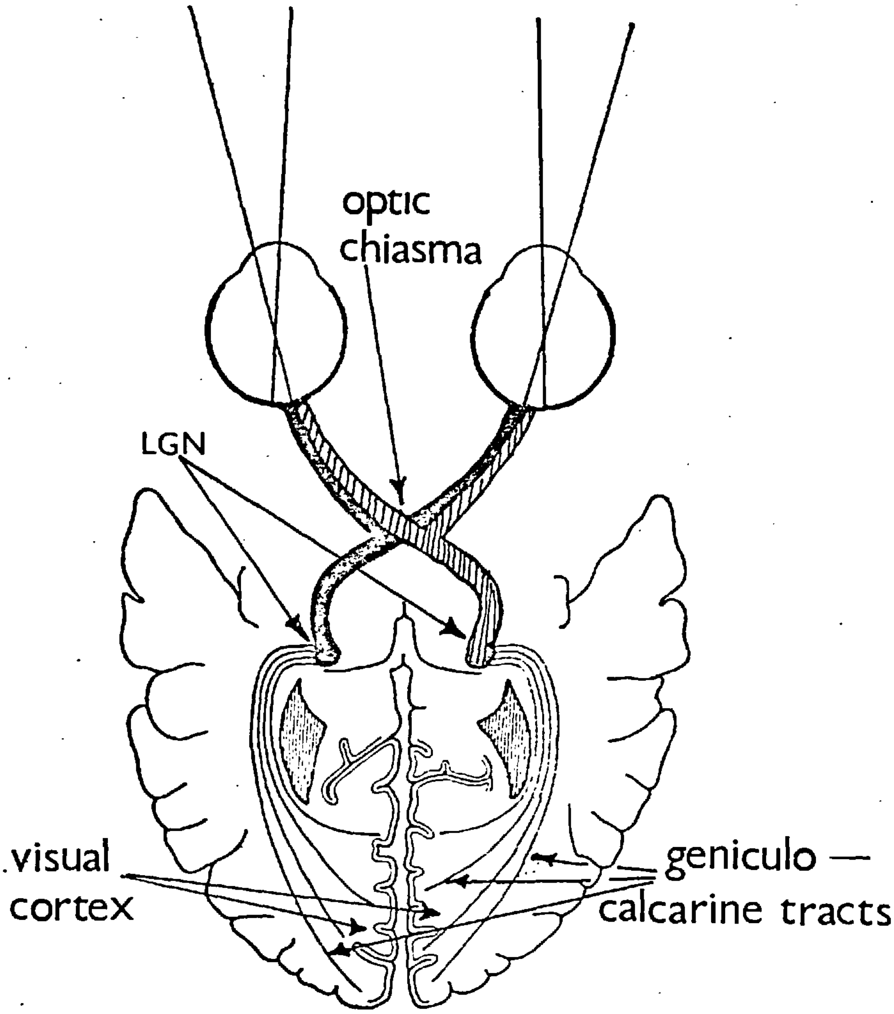
– Diagram of the synaptic connexions of the primate retina (rhesus monkey and man). R, rod; C, cone; MB, midget bipolar, probably receiving only from one cone; FB, flat bipolar, receiving from several cones, but probably from no rods; RB, rod bipolar, receiving from several rods, but probably from no cones; H, horizontal cell; A, amacrine cell; MG, midget ganglion cell; DG, diffuse ganglion cell (from Dowling & Boycott, 1966).

chapt. 1

invaginated by clusters of three dendrites, up to 25 clusters per cone. Dowling and Boycott (1966) suggest that the middle one originates in a midget bipolar cell and the other two in horizontal cells. As well as receptors, bipolar cells and horizontal cells, two other types of cell are found in the retina: amacrine and ganglion cells. All five groups are supported in the retina in two layers by Muller fibres and Glial tissue. Receptor, horizontal and bipolar processes make up the outer plexiform layer; bipolar amacrine and ganglion cell processes make up the inner plexiform layer. See fig. 4.

Axons of bipolars have long terminals which synapse with ganglion cell dendrites and amacrine cell processes; these latter connections appear to function in the amacrine-bipolar direction as well. Amacrine cells synapse with each other as well as with ganglion cells to make horizontal connections across the retina.

The six classes of primate ganglion cells described by Polyak (1941) are now classified as either midget or diffuse ganglion cells (Boycott and Dowling, 1969). The midget ganglion cell is unique to primates and is distinguished by its single dendrite, unbranched up to the synapse which it makes with a midget bipolar cell. The diffuse ganglion cell possesses many branching dendrites which make many synapses throughout the inner plexiform layer. The axons of the ganglion cells form the optic nerve fibres which pass from the retina to the optic chiasma where decussation occurs, fibres from the nasal half of one eye crossing over to join fibres from the temporal half of the other eye. The decussated nerve then passes into the lateral geniculate nucleus, the L.G.N. 80% of the optic nerve fibres terminate within the L.G.N., whilst the others go on to terminate in the superior colliculus (fig. 5). The function of these nongeniculate fibres is not well defined. It has been shown (Brindley, Gautier Smith and Lewin, 1969) that they produce pupilliary responses in cortically blind patients, but it seems



Schematic diagram of visual paths from the retinæ of the two eyes through the optic chiasma to the opposite sides of the brain. (From Traquair's "Clinical Perimetry.")

fig. 5

unlikely that this is their sole purpose.

There are six distinct layers in the L.G.N., the crossed fibres of the optic nerve, representing the nasal portion of the contralateral retina, going to the 1st, 4th and 6th layers, whilst the termporal portion of the ipsilateral retina terminates in the 2nd, 3rd and 5th layers. The geniculo-calcarine tract connects the L.G.N. to the striate cortex, a disproportionately large region of which receives signals from the foveal region of the retina. Talbot and Marshall (1941) estimated that 100 cortical cells received inputs from a single foveal cone. This correlates with the superior visual acuity of the fovea. The mapping between the retina and the L.G.N. is quite regular and, by studying war-wounded patients, a similar systematic representation of the L.G.N. on the striate cortex was found (Holmes, 1918; Teuber, Battersby and Bender, 1960).

Functional Experiments ... Electrophysiology

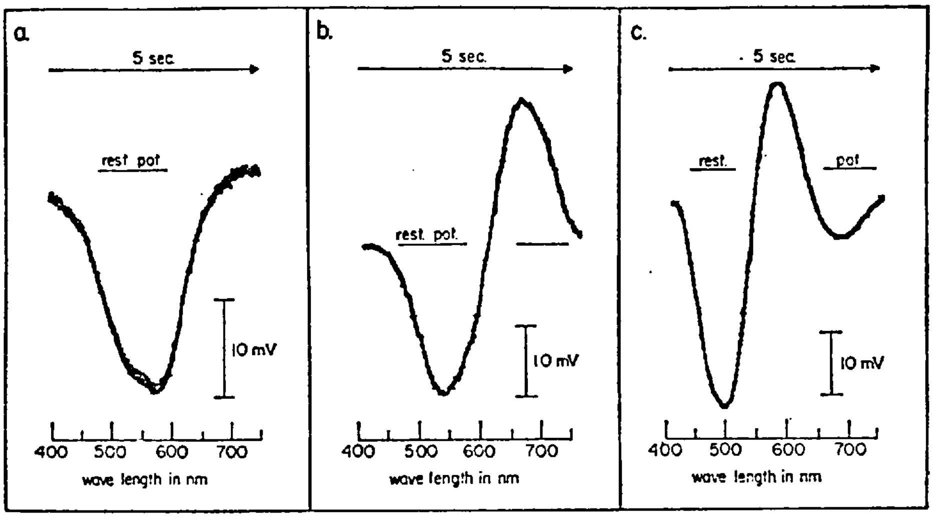
Receptor Activity

The first cone responses were recorded in the carp retina using fine-tipped (0.2 μm diameter) electrodes (Oikawa, Ogawa and Motokawa, 1959). The response amplitude was found to be independent of the stimulus size, indicating a lack of summation between the individual cones. Initial problems of locating and identifying the source of the response were overcome by the simultaneous recording and staining techniques of Werblin and Dowling (1969) who showed that the tip of the electrode must be within the inner segment of the cone in order to record successfully. Their experiments were carried out on mudpuppy retinae. The rod and cone responses were found to have different time courses of recovery and different absolute sensitivities. The response characteristics of single cones of the turtle retina have been studied by Baylor and Fuortes (1970) who found a relationship between the pattern of the retinal illumination and the cone response. If the receptive field of a cell is defined as the retinal area within which any illumination will alter the cell's response, then cones were found with 'centre-surround' receptive fields. Such receptive fields exhibit antagonistic on-off responses between the central and peripheral regions. All cone recordings have been restricted to fish and amphibian retinae because of limitations on the receptoral size of other groups.

Bipolar and Horizontal Cell Activity

Svaetichin (1953) was the first to record what are now known as S-potentials, but were at the time thought to be receptor responses. At the appropriate depth, some 80 - 120 µm below the surface of the retina, the microelectrode records a 20 - 50 mV negative resting potential. The amplitude of the electrical responses are graded with the illumination level and are more-or-less maintained during the period of stimulation. There are two classes of S-potentials: one, the luminance or L-type response which is always in a negative, hyperpolarizing direction, whereas the other, the colour or C-type response is depolarizing at some wavelengths and hyperpolarizing at others (fig. 6a and b).

The S-potentials are generated in the horizontal cells which are classified in terms of the type of receptor from which they receive signals (e.g. MacNichol and Svaetichin, 1958; Oikawa, Ogawa and Motokawa, 1959). Rod horizontal cells show hyperpolarizing responses to all wavelengths and have a spectral sensitivity equivalent to that of rhodopsin. Cone horizontal cells are subdivided into those with either L- or C- type responses. L-type responses are again hyperpolarizing for stimuli of all wavelengths. C-type responses are of two types: (i) those that show hyperpolarization for short wavelengths and depolarization for long wavelengths, (ii) those that hyperpolarize for long wavelengths and depolarize for short. A third type has been identified in

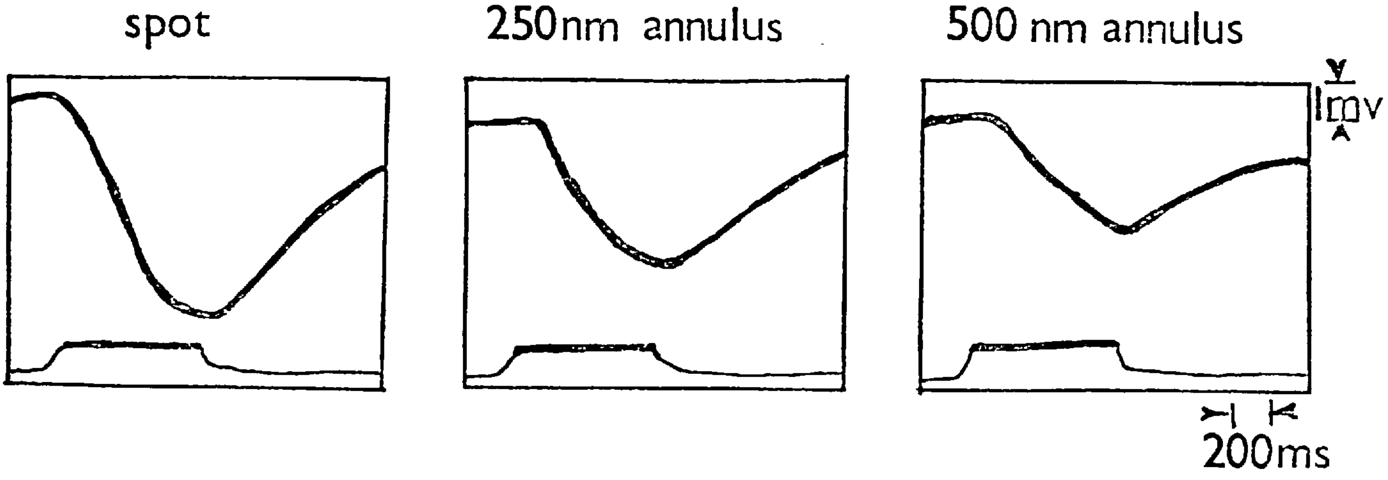


Three common types of S-potentials: monophasic (a), biphasic (b), and triphasic (c). In all records a negative potential deflection (hyperpolarizing) at the recording electrode is downward. Horizontal traces—marked *rest*(ing) *pot*(ential)—indicate the potential level in the absence of a light stimulus. Direction and duration of the spectral scan for each record are indicated by arrow at top. Intensity of the stimulus at 650 nm is 9 μw/cm^2.

C-TYPE S-POTENTIALS

Norton et al. (1968)

fig. 6(a)



L-TYPE S-POTENTIALS

(redrawn from Werblin & Dowling 1969)

fig. 6(b)

the carp and the goldfish which gives a triphasic response of depolarization-hyperpolarization-depolarization for successively longer wavelengths. There is no interaction between the rods and the cones at horizontal cell response level, although the horizontal cells do sum their respective inputs. Some have restricted receptive fields, others sum over the whole retina. There is, however, no antagonism between different regions within the receptive fields.

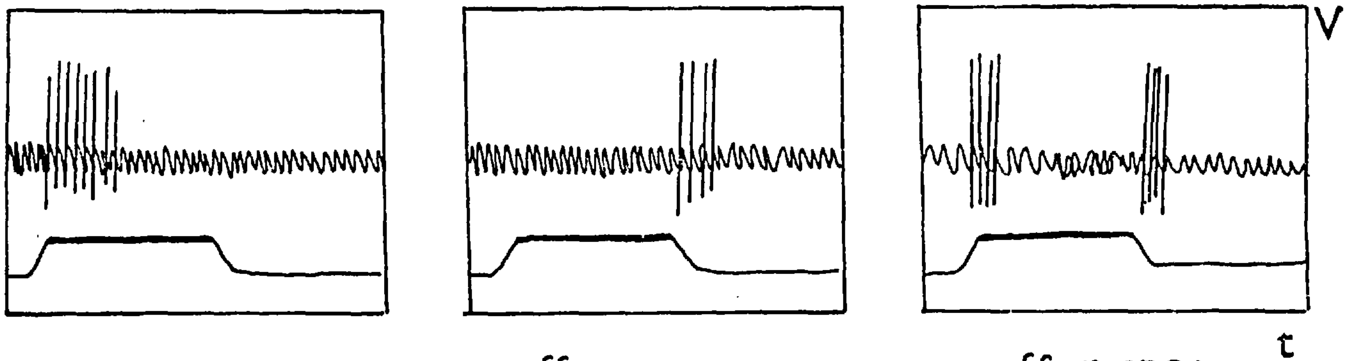
Bipolar cells receive signals from either the receptors or from horizontal cells. Their receptive fields are characterized by an antagonistic centre-surround organisation. The central region of the receptive field of a particular cell shows either a hyperpolarizing or depolarizing response whilst the surrounding region shows the opposite response. These bipolar cells can be further subdivided into two groups of colour-coded and non-colour-coded neurones.

Amacrine Cell Activity

Werblin and Dowling (1969) found all responses in the mudpuppy amacrine cells to be depolarising in nature, up to a critical level where spikes were produced (fig. 7). The spike response could occur at the onset or at the offset of the response, or at both onset and offset, depending on the position of the stimulus. The amacrine cells are the only cells in the inner nuclear level to produce spike responses.

Ganglion Cell Activity

The first electrophysiological measurements on ganglion cells were made in the cat retina by bringing the tip of a metal electrode very close to the cell body (Granit and Svaetichin, 1939). Trains of spikes were recorded which were later shown by Rushton (1949) to be from individual ganglion cells. Direct measurements on single optic nerve fibres of the frog were made by Hartline (1938) and showed the fibres to belong to one of three groups: on - off fibres of two kinds, those giving a burst of spike discharge at illumination onset and sustained discharge for the duration of the illumination and those responding whilst light was on, with spike discharge when it was extinguished, and a third group, off-fibres, which responded only when the light was terminated (fig. 8). Intracellular measurements were made by Kuffler (1953) in the cat retina and showed the ganglion cell receptive field diameters to be 0.8 - 2.0 mm. The response was concentric within the field with a spike discharge, either transient or maintained, occurring at the onset or offset of the flashing test light spot, depending on the position of the spot within the receptive field and its colour (Spekreijse et al., 1972, fig. 9, goldfish). Approximately equal numbers of cells were found with on-centre, on-surround characteristics. Enroth-Cugell and Robson (1966) further classified these cells into those which exhibit linear spatial summation of excitation over the receptive field



on response off response on–off response

fig. 8

ganglion cell responses drawn from Kuffler (1953)

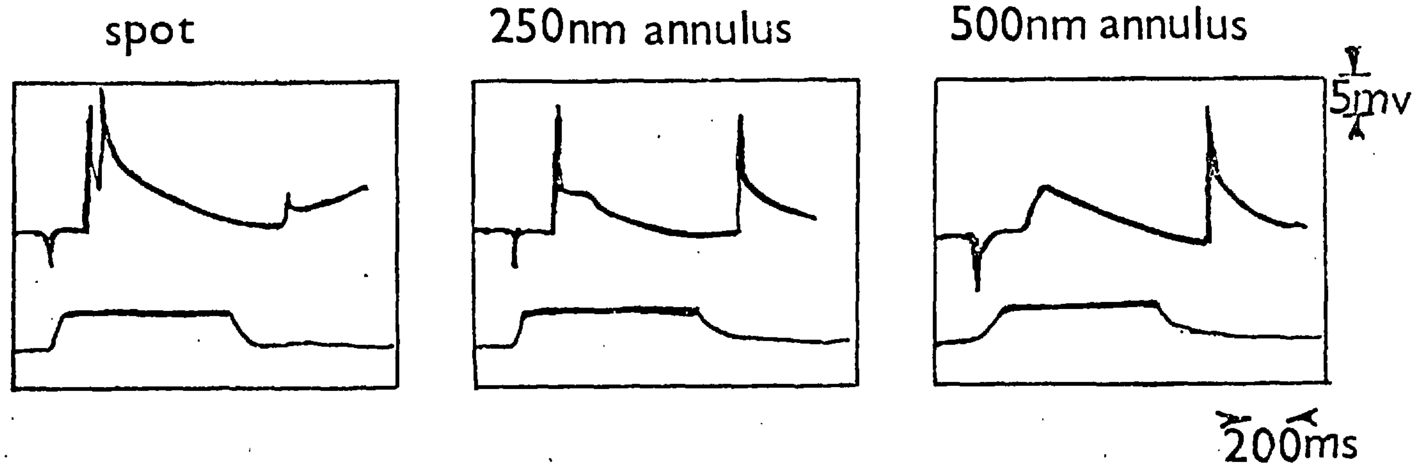
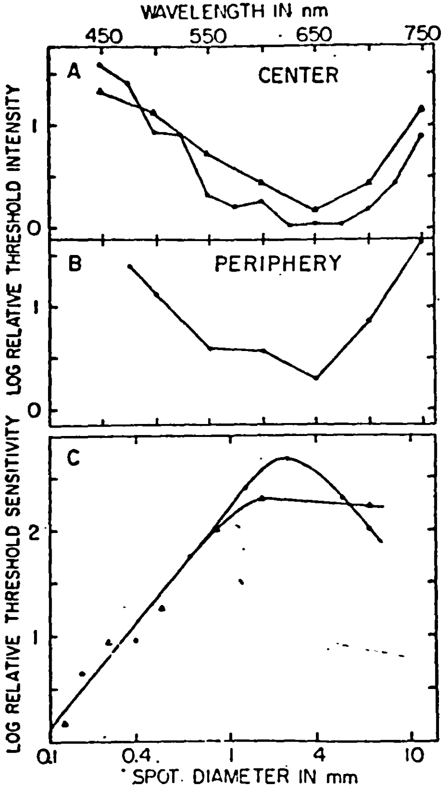


fig. 7

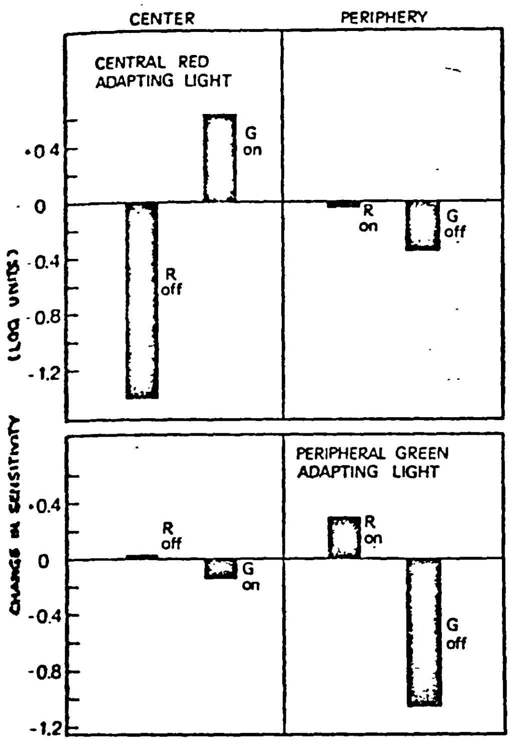
AMACRINE CELL RESPONSES

(redrawn from Werblin & Dowling 1969)



A and *B* show the wavelength dependence, as determined with a constant threshold criterion, for a red-on central, red-off peripheral type unit. In *A*, illumination of the retina with a 1-mm-diameter central spot resulted in the spectral characteristics shown by the filled circles (●). Stimulation of the periphery with an annulus resulted in a curve with identical spectral characteristics as shown in *B*. After the spontaneous, sudden loss of the peripheral information channel, stimulation of the center of the receptive field gave the curve with the filled triangle (▲) in *A*. *C* shows the full-summation plots as determined before (●) and after (▲) the loss of the peripheral process. Zero log intensity is 2×10^{12} quanta cm^{-2} sec^{-1} and zero log sensitivity corresponds to an intensity of 1×10^{13} quanta cm^{-2} sec^{-1}.

(a)



Bars in this figure represent the average shift in sensitivity of the spectral response curves of the information channels in the center and the periphery by selective color adaptation. Data are obtained from four red-off, green-on central type units with red-on, green-off antagonistic peripheral fields. Red adaptation (650 nm; 5×10^{12} quanta cm^{-2} sec^{-1}) of the central field does not influence the sensitivity of the peripheral fields. Neither does green adaptation (500 nm; 3×10^{13} quanta cm^{-2} sec^{-1}) of the periphery influence the sensitivity of the central information channels. Central spots had a diameter of 1 mm, the adapting annuli had an inner diameter of 1.4 mm.

(b)

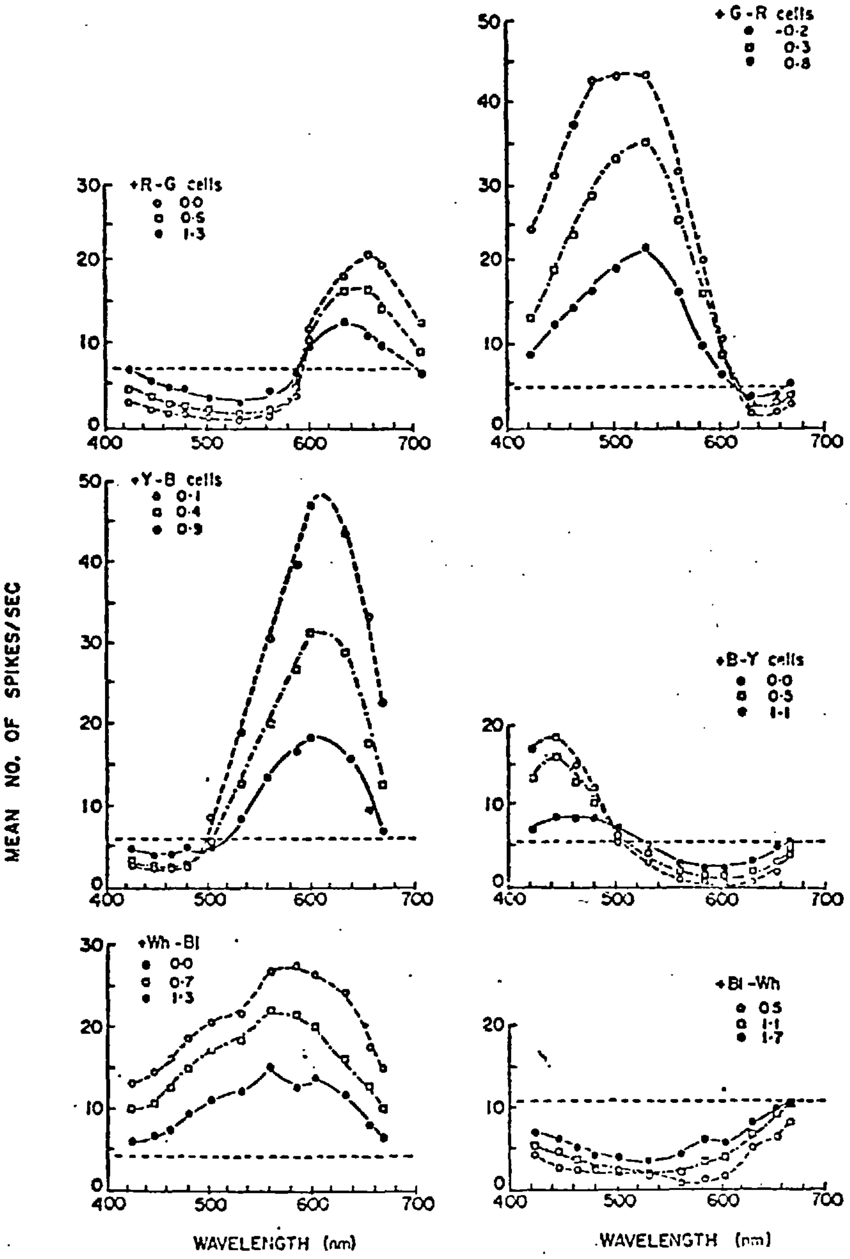
fig. 9

Spekreijse, Wagner & Wolbarst (1972)

and those which did not (X and Y cells respectively). These recordings were again taken from the cat. Further subdivisions of these cells into brisk and sluggish, transient and sustained response types, have been made (Cleland and Levick, 1974a and b). A third, totally distinct type of ganglion cell has recently been encountered which possesses a non-concentric receptive field; this group has been called the W cells (Stone and Fabian, 1966; Rodieck, 1973). By comparing the morphological data of Boycott and Wässle with the conduction time and receptive field size measurements of Cleland and Levick, attempts have been made to ascribe the different types of cat ganglion cell response to the three morphological groups which have been identified (e.g. Wässle, Levick and Cleland, 1975).

Lateral Geniculate Nucleus Activity

The responses of L.G.N. units consist of spike trains very similar to those of ganglion cells. The receptive fields are circular, usually concentric regions which are antagonistic in their responses to stimulus onset and offset. There is some slight indication of binocular interaction at this level in the cat, but none at all in the monkey. Wiesel and Hubel (1966) classified the opponent colour responses of the L.G.N. cells into five groups, each group responding either with an 'on' or an 'off' of the spike discharge when a particular colour is presented at the centre of the receptive field, and with an antagonistic response if the stimulus is presented to the surround region. There are, however, other cells with the same spectral response over both centre and surround regions of the receptive field. The purpose of the L.G.N. may be to compress, sort or perhaps to recode the information received from the retina before the signals enter the cortex (fig. 10).



Average firing rates of six LGN cell types to three different luminance levels of monochromatic light.

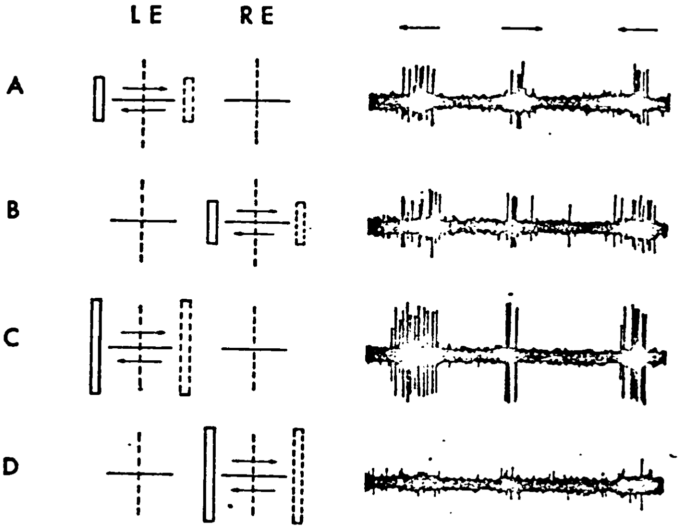
fig. 10

Cortical Cell Activity

Hubel and Wiesel (1959, 1962, 1965a, 1968) classified the cells of the striate cortex of the cat and the monkey into four groups: (i) circular concentric, (ii) simple, (iii) complex, (iv) hypercomplex. The three latter response groups differ in receptive field organisation from all earlier classes in two respects. Firstly, they are orientation selective. The receptive fields are not concentric in general and hence, in order to obtain the optimum response from a particular cell, the stimulus must be positioned at a particular orientation on the receptive field. Secondly, cortical cells are frequently binocularly driven. Retinal and L.G.N. cells respond only to stimulation of the eye with which they are associated, whereas some cortical cells, which ~~since they~~ lie beyond the optic chiasma, respond to stimulation of either eye. Cells may give a greater response to one eye, than to the other; this indicates a degree of ocular dominance in that cell. Some cells respond equally well to either eye, whilst others are monocularly driven (fig. 11a and b). A further type of cortical cell will respond only when there is a particular disparity between the retinal images of the two eyes.

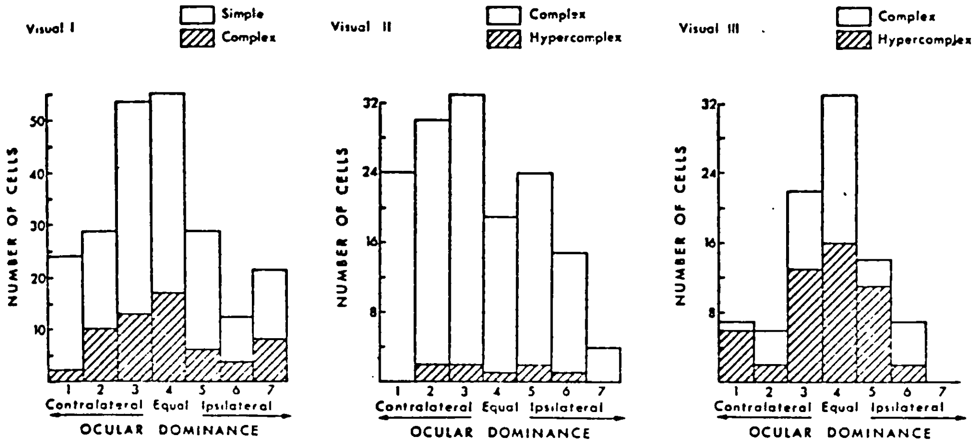
The circular concentric cells of group (i) were found to behave in a very similar manner to the L.G.N. cells and it was suggested that they were geniculo-calcarine fibres.

The simple cells were also similar to the L.G.N. cells in some respects. They displayed antagonistic centre-surround properties, but the shape of the receptive fields was elongated with straight line boundaries. A stimulus of the same shape and orientation as this new, longer field gave the most effective response, particularly when this stimulus was in motion in the direction indicated by crossing the border within the receptive field which marked the antagonistic regions. Although the optimum rate of movement varied from cell to cell, summation was seen to occur in such a way that a stimulus larger than that required for optimal response of an on-centre cell, for example, would reduce the response because of its overlap into the inhibitory



Two cells simultaneously recorded from area 19; these were cells 35 (complex, large spikes) and 36 (hypercomplex, small spikes), in Fig. 4, penetration V. *A* and *B*: responses of the hypercomplex cell (no. 36) to a vertical slit, ½° x 2°, moved rapidly back and forth across the receptive field of the left eye (*A*), and the right eye (*B*); no response from the complex cell. *C* and *D*: movement of a slit ½° x 12° produces no response from the hypercomplex cell, but a brisk response from the complex cell (no. 35), in the left eye only. Intensity of stimulus, 1.0 $\log_{10}$ cd/m^2; background, 0.0 $\log_{10}$ cd/m^2. Rate of movement about 20°/sec. Sweep duration, 1 sec.

(a)



Distribution according to ocular dominance of (*A*), 223 cells in visual I , (*B*), 149 cells in visual II, and (*C*), 89 cells in visual III. Cells of group 1 are driven only by the contralateral eye; for cells of group 2 there is marked dominance of the contralateral eye; for group 3, slight dominance. For cells in group 4 there is no obvious difference between the two eyes. In group 5 the ipsilateral eye dominates slightly, in group 6, markedly; and in group 7 the cells are driven only by the ipsilateral eye.

(b)

fig. 11

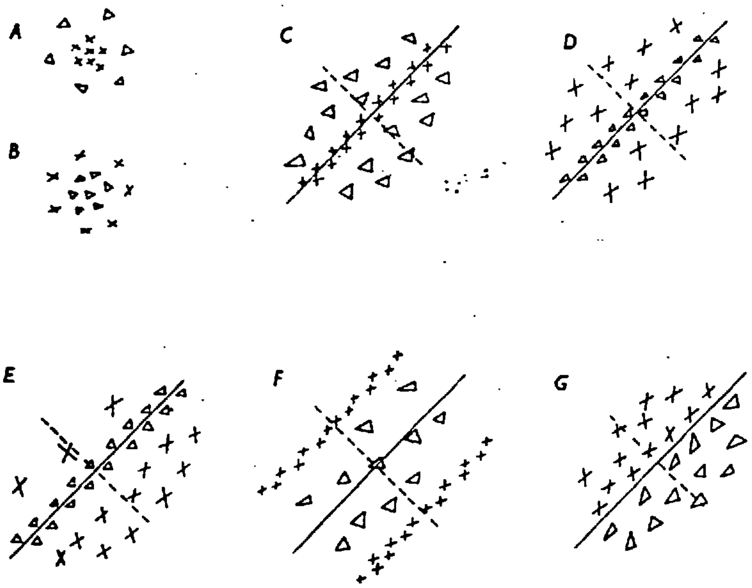
Hubel & Wiesel (1965)

region of the receptive field. There was no indication that a particular preferred orientation was commoner than any other. As well as receptive fields with central zones of different widths, some cells responded to just one edge of a particular orientation, i.e. only one antagonistic border constituting an edge. A variety of typical receptive fields are mapped out in fig. 12.

It was found that the response of complex cells could not be predicted from a map of the receptive fields as the arithmetic summation observed in simple cells did not hold. The technique of mapping out the receptive field of the cell with small dots of light which had been used for simple cells and all the earlier cells, could not be employed in the complex cells. A specific stimulus such as a narrow slit positioned with a certain orientation, was required. Such a slit might evoke an 'on' response anywhere within one region of the receptive field and an 'off' response everywhere else. If the stimulus dimensions or orientation were changed, then the optimum response of the cell was found to be much reduced. It was also a frequent requirement of such a cell that a good response was elicited only if the stimulus was in motion across the receptive field. Complex cells were found which responded to an edge stimulus of a particular orientation, but unlike the simple cells of this kind, it was only the orientation of the stimulus and not also its position within the receptive field that was important for maximum response. Movement of the edge across the field again produced a much stronger discharge than did a stationary stimulus (fig. 13a and b).

Hypercomplex cells were found in the cat and the rhesus monkey with properties very similar to those of the complex cells, the termination of one, or sometimes both ends of the bar or edge (depending on the specificity of the cell) within the receptive field was needed in order to elicit a response (fig. 14a, b and c). A summary table of cortical cell types is given in fig. 15.

Hubel and Wiesel (1963, 1968) found the cortical cells to lie in columns



Common arrangements of lateral geniculate and cortical receptive fields. *A*. 'On'-centre geniculate receptive field. *B*. 'Off'-centre geniculate receptive field. *C–G*. Various arrangements of simple cortical receptive fields. ×, areas giving excitatory responses ('on' responses); △, areas giving inhibitory responses ('off' responses). Receptive-field axes are shown by continuous lines through field centres; in the figure these are all oblique, but each arrangement occurs in all orientations.

fig. 12

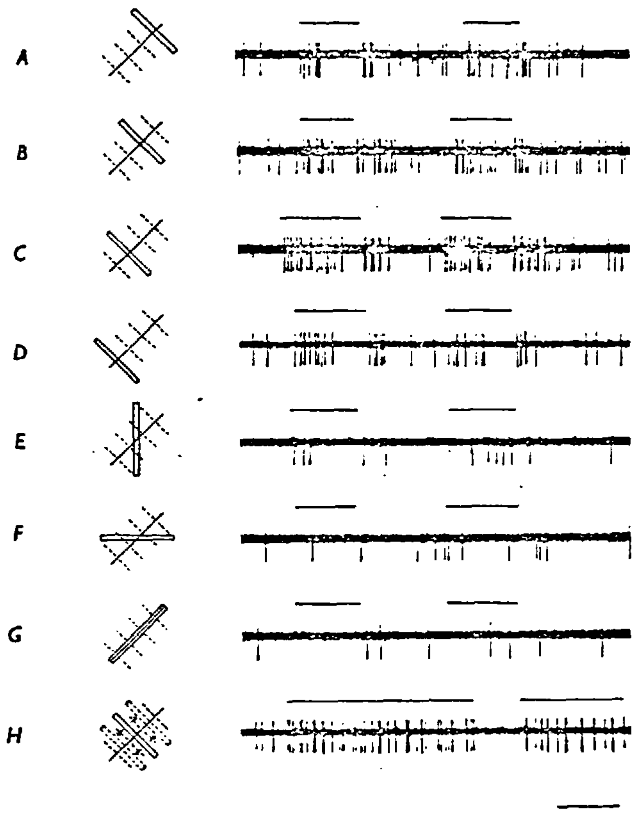


fig. 13(a)

Responses of a cell with a complex field to stimulation of the left (contralateral) eye with a slit $\frac{1}{8} \times 2\frac{1}{2}$°. Receptive field was in the area centralis and was about 2×3° in size. *A–D*, $\frac{1}{8}$° wide slit oriented parallel to receptive field axis. *E–G*, slit oriented at 45 and 90° to receptive-field axis. *H*, slit oriented as in *A–D*, is on throughout the record and is moved rapidly from side to side where indicated by upper beam. Responses from left eye slightly more marked than those from right (Group 3, see Part II). Time 1 sec.

Hubel & Wiesel (1962)

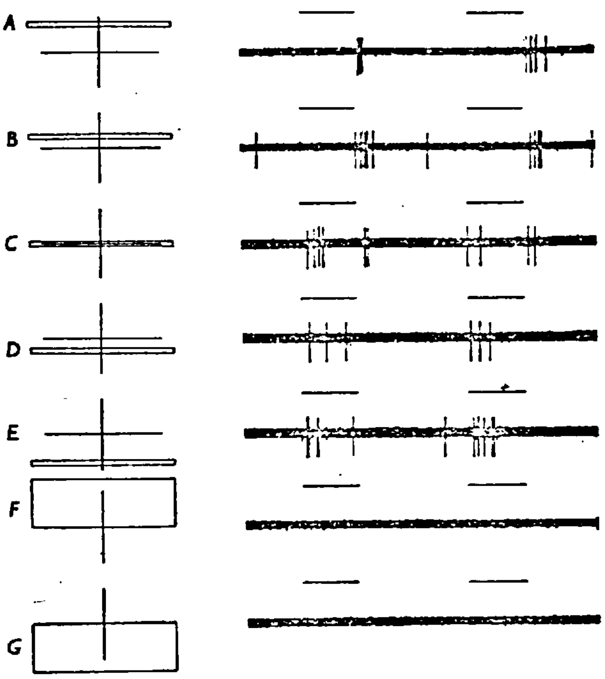
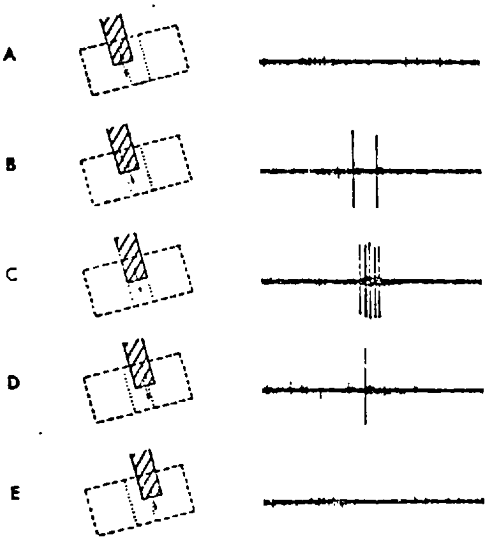


fig. 13(b)

Responses of a cell with a complex receptive field to stimulation of the left (contralateral) eye. Receptive field located in area centralis. The diagrams to the left of each record indicate the position of a horizontal rectangular light stimulus with respect to the receptive field, marked by a cross. In each record the upper line indicates when the stimulus is on. *A–E*, stimulus $\frac{1}{8} \times 3^\circ$, *F–G*, stimulus $1\frac{1}{2} \times 3^\circ$ (4° is equivalent to 1 mm on the cat retina). For background illumination and stimulus intensity see Methods. Cell was activated in the same way from right eye, but less vigorously (ocular-dominance group 2, An electrolytic lesion made while recording from this cell was found near the border of layers 5 and 6, in the apical segment of the post-lateral gyrus. Positive deflexions upward; duration of each stimulus 1 sec.

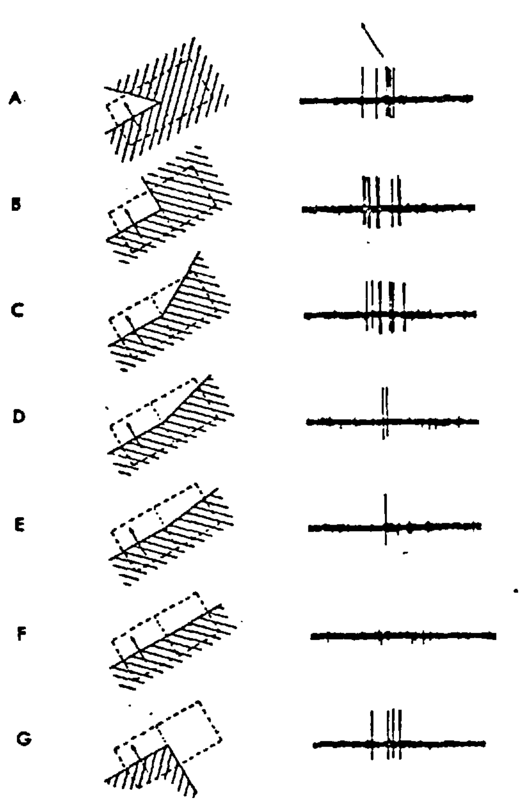
Hubel & Wiesel (1962)

fig. 14(a)



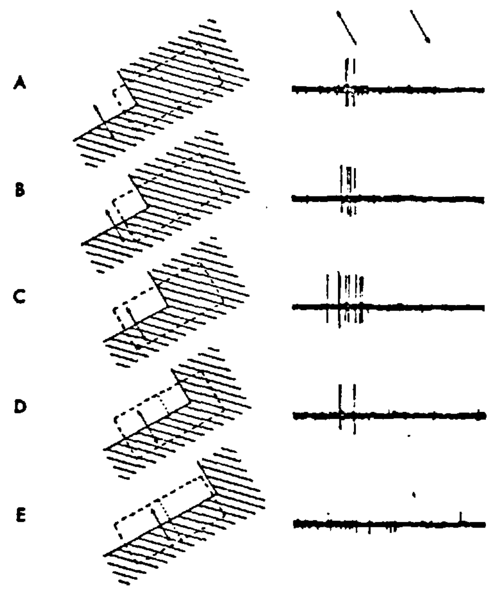
A dark tongue 2½°-wide crosses receptive field from above downward, in different positions. Maximum excitation occurs when the central (activating) strip of field is stimulated. Varying the position by 1/2° either way greatly reduces the response. Duration of each sweep, 1 sec.

Hubel & Wiesel (1965)



Stimulation with two intersecting edges moved up across the receptive field as shown. Inhibition is maximum when the right (antagonistic) half of the receptive field is stimulated with an edge having the same orientation as the optimum edge for the left (activating) half (*F*). Duration of each sweep, 2 sec.

(b)



Records from a hypercomplex cell in visual II . Stimulation of right (ipsilateral) eye, ocular-dominance group 6. Receptive field, 2° x 4°, indicated by interrupted rectangle. Stimulus consisted of an edge oriented at 2:00, with dark below, terminated on the right by a second edge intersecting the first at 90°. Brighter regions, 1.3 $\log_{10}$ cd/m^2; dark areas, 0.0 $\log_{10}$ cd/m^2. *A* through *C*: up-and-down movement across varying amounts of the activating portion of the field; *D–E*: movement across all of the activating portion and varying amounts of the antagonistic portion. Rate of movement 4°/sec. Each sweep 2 sec.

(c)

fig. 14

290 cells recorded in areas 18 and 19

Cell Type	Activated by	Visual II	Visual III
Complex	Edge	38	6
	Dark bar	12	12
	Slit	72	23
	Mixed	17	0
	Uncategorized	34	5
Total		173	46
Hypercomplex*	Edge		
	single-stopped (corner)	6	18
	double-stopped (tongue)	0	33
	Slit (double-stopped)	2	5
	Dark bar (double-stopped)	0	3
	Uncategorized	0	4
Total		8	63
Totals		181	109

* Eleven of the cells in visual III were classed as higher order hypercomplex.

fig. 15

Hubel & Wiesel (1965)

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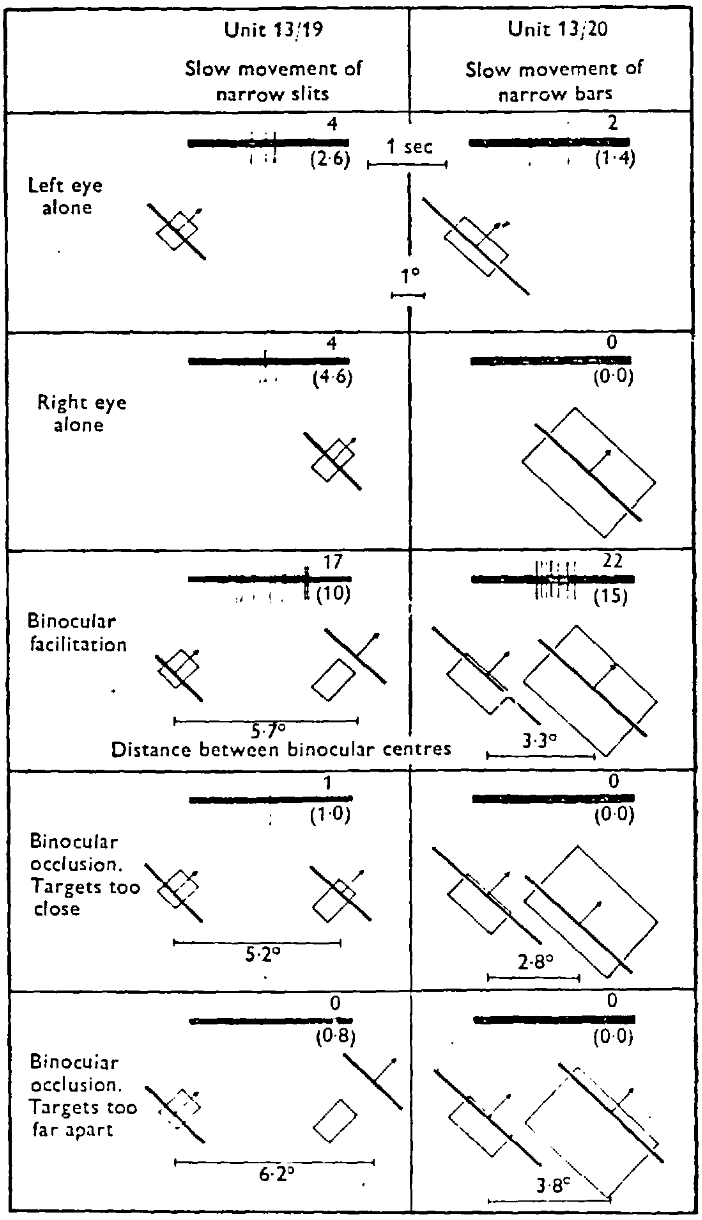
within which all cells had the same receptive field orientation. Similar columns were found in which all the cells possessed the same ocular dominance, movement response, optimum stimulus characteristics or, less well defined, colour selectivity. When recordings are made from cells lying adjacent to each other in a direction parallel to the surface of the cortex and scanning across the columns, the type of specificity was often found to change abruptly from one cell to another. It seems that about 28% of cortical cells are colour selective in their response (e.g. Boles, 1971; Gouras, 1972; Dow and Gouras, 1973).

Stereovision, the ability to perceive depth, is an important attribute of vision, resulting from the overlapping of the visual fields of the two eyes. The interocular separation means that these two fields will be slightly shifted one from the other ... that is, a retinal disparity is introduced between the images of any object in the visual scene. Binocularly driven units in the cortex of the cat were investigated by Barlow, Blakemore and Pettigrew (1967), who found that a stimulus presented with the correct disparity elicited a better response than a monocular stimulus presented alone. Two binocularly-presented non-corresponding images produced even less excitation than one correctly positioned monocular image (fig. 16). The range of horizontal disparities of corresponding retinal images giving the greatest response was 6.6°, but for vertical disparities, it was just 2.2° (fig. 17).

Hubel and Wiesel (1970a) recorded from cells sensitive to binocular depth in area 18 (behind the striate cortex) in the monkey. Just under half the cells in this region displayed characteristics indicative of binocular depth perception, whilst the remainder responded to stimulation of either eye. The former cells responded maximally to similarly orientated shapes presented to both eyes with a certain retinal disparity. These cells tended to lie in groups which responded to one value of retinal disparity, but with different receptive field orientations. There were very few cells with near horizontal receptive fields. A further study of the grouping



. Binocular interactions showing that facilitatory responses occur at different disparities in two cortical neurones from the same cat. The units were studied consecutively, their receptive fields lay close together in the visual field, and their axis orientations were the same. For each unit five stimulus conditions are illustrated—monocular stimulation for each eye alone, and three examples of binocular stimulation. Each box contains a sample record (retouched for reproduction, positive deflection downward) with the number of spikes in that sample and the average number for five repetitions in parentheses. The positions of the stimuli and the minimum response fields on the tangent screen are illustrated diagrammatically. Eye torsion and elevation have been corrected, but no correction has been made for the divergence of the visual axes or the separation of the two eyes. The projections of the areae centrales would be separated by about 6·4° in this diagram. Minimum response fields were plotted with a bright slit for both units, but binocular facilitation showed up better with a dark bar for unit 13/20, and these responses were chosen for this illustration. Slits and bars were 3 min of arc wide and several degrees long. Optimum facilitation occurs at 5·7° separation of targets for unit 13/19, 3·3° separation for unit 13/20. These were estimated to be equivalent to 0·7° and 3·1° of convergent disparity.

fig. 16

Barlow et al. (1967)

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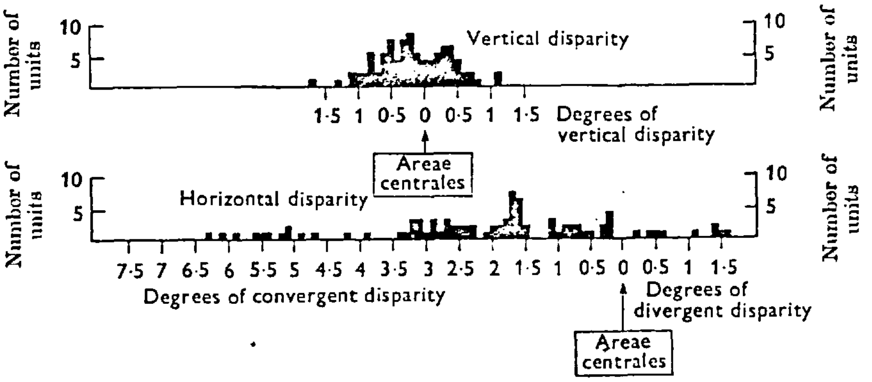
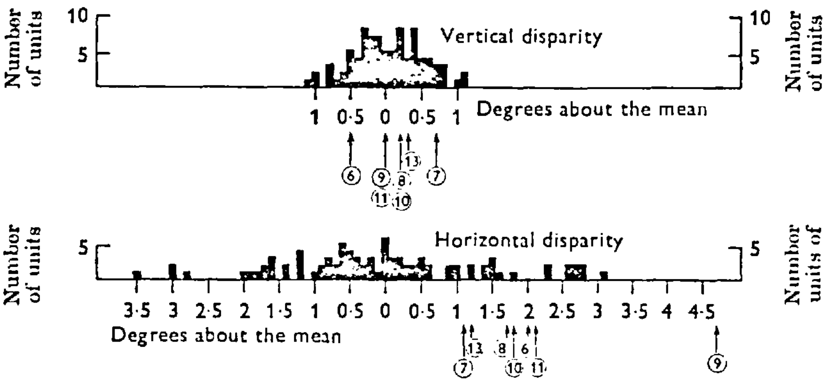


Histograms of horizontal and vertical disparities of the binocular centres for 87 units in seven cats. The positions of the two areae centrales were estimated in each cat, and their vertical and horizontal separations were assigned zero disparity in that cat. If the horizontal angular separation of the binocular centres was less than the areae centrales, the unit had convergent disparity; if greater, the unit had divergent disparity. These units would be optimally stimulated by objects lying closer than, or beyond, the fixation point in the normal cat.

(a)



Histograms of horizontal and vertical disparities with means superimposed. In Fig.   the results from different cats were combined by measuring disparities relative to the areae centrales, but since the estimate of area centralis position is subject to considerable error. Fig.   may indicate too wide a spread of disparities. In this figure the mean vertical and horizontal angular separations of the binocular centres for each cat have been assigned zero disparity and these reference points have been superimposed. This gives a more conservative estimate of the range of disparities than Fig.   Below the scale of each histogram are seven circles containing the identifying numbers of the cats. Arrows from these circles indicate the horizontal and vertical separations of the estimated areae centrales with respect to the mean disparities of the binocular centres. Much of the dispersion of these estimates is likely to be caused by errors in estimating the position of the area centralis.

(b)

Barlow et al. (1967) fig. 17

(Blakemore, 1970a) revealed two types of columns: (a) constant depth columns whose cells view a thin sheet of visual space, subtending a few degrees ~~wide,~~ of visual angle located at a particular depth; (b) constant direction columns with cells responsive to a ~~cylinder~~ cone of visual space directed towards the contralateral eye (fig. 18).

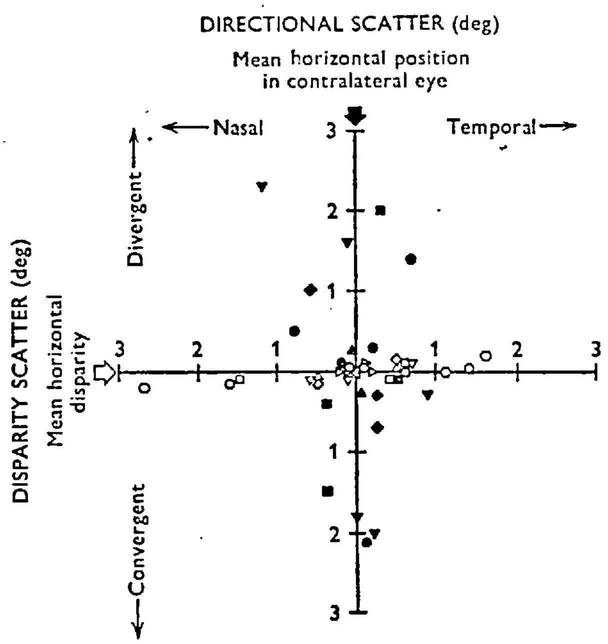
Further measurements made on disparity specific neurones in area 17 of the cat (Blakemore and Pettigrew, 1970) found that the responses were often dominated by the contralateral eye. The receptive fields were plotted for each eye and it was found that the horizontal receptive field spread over a number of cells was greater for the ipsilateral eye than for the contralateral eye. There was no significant vertical difference. The authors suggest that depth perception may result from retinal-cortical mapping of the ipsilateral eye being less accurate than that of the contralateral eye.

Psychophysical Approach

Psychophysical methods are applied to the study of human visual responses. Experiments of this kind require an observer to make judgements regarding the visual stimuli. Generally he will be required to indicate whether or not he can differentiate two stimuli. Such operations as setting the threshold of a test to the level of its background or matching the colour, brightness or spatial characteristics of two separate stimuli are examples of this type of experiment.

Some of the earliest reported psychophysical experiments were designed to measure visual performance. Ricco (1877) found that the threshold for detection of a circular test stimulus was inversely proportional to its diameter, up to a diameter of 42' 40". This relationship, in later studies, was found to hold for the extra-foveal region of the retina.

Another example of a psychophysical experiment designed to test the effect of spatial characteristics of a stimulus on its detectability, is the measurement of visual acuity. The spatial configuration of the test stimulus



The variation of depth and oculocentric direction within each column sample is analysed in this diagram. For each set of units, judged to belong to one column, the horizontal disparities and the horizontal positions or visual directions of the binocular centres in the contralateral eye were determined. The variation in disparity (on the ordinate) is plotted against the variation in oculocentric direction (on the abscissa). Zero on the ordinate, marked with a large open arrow, is the mean horizontal disparity of the binocular units in the columnar sample. Disparities in a convergent direction from the mean fall below zero, those more divergent fall above zero. On the abscissa, zero, marked with a large filled arrow, is the mean horizontal position or azimuth of the binocular centres for the sample, in the contralateral eye. Nasal-ward points fall to the left and temporal-ward to the right. Each point represents one unit and plots its horizontal disparity (relative to the mean for the whole columnar sample), and the horizontal position of its binocular centre in the contralateral eye (relative to the mean). The symbols are filled for direction columns and open for depth. Depth columns are supposed to have much larger variation in eccentricity from unit to unit than variation in depth. They should, therefore, cluster around the abscissa. Direction columns, on the other hand, should have much less scatter of response field position in the contralateral eye than variation of horizontal disparity. They should, therefore, be grouped around the ordinate.

fig. 18

Blakemore (1970)

is modified until a particular threshold is attained, e.g. two adjoining lines are displaced laterally until a misalignment is detected (vernier acuity). Acuity varies with parameters such as pupil size, illumination level and retinal position. It improves rapidly with initial increases in pupil size, and then less rapidly until a maximum is reached (Leibovitz, 1952; fig. 19). The variation of acuity with intensity is attributable to two components: that due to the cones, functioning at high intensities, and that characteristic of the rods, at low light intensities (fig. 20). In the foveal region, only the cone component is detectable (Shlaer, 1937). The fovea, the portion of the retina with the highest acuity, has limits of resolution beyond those to be expected from a consideration of the size of the retinal receptor mosaic. The fovea is capable of resolving a light spot subtending one minute of arc at the retina. Outside the fovea, the resolution is less than that which might be expected from the same considerations, indicating that some of the information related to the spatial content of the image is, perhaps, being discarded by the visual system, although any measure of the acuity of the eye is also affected by optical refractive errors within it.

An alternative experimental approach is to keep the spatial configuration of the test constant, but to reduce its contrast to a level corresponding to 'just see' or 'just not see'. As well as being much more versatile, this technique avoids the problem of particular points within the pattern changing contrast as the threshold is approached (as was the case in the measurement of vernier acuity, for example). Patterns made up of alternating dark and bright bars are commonly used for this type of study. The optics of the eye, as with other imaging systems, can be described in terms of Fourier analysis. A sine wave grating, i.e. one in which the intensity distribution measured across the bars varies sinusoidally with distance, is imaged on the retina as a sine wave grating. The modulation depth, that is, the ~~separation~~ relative illumination difference of the

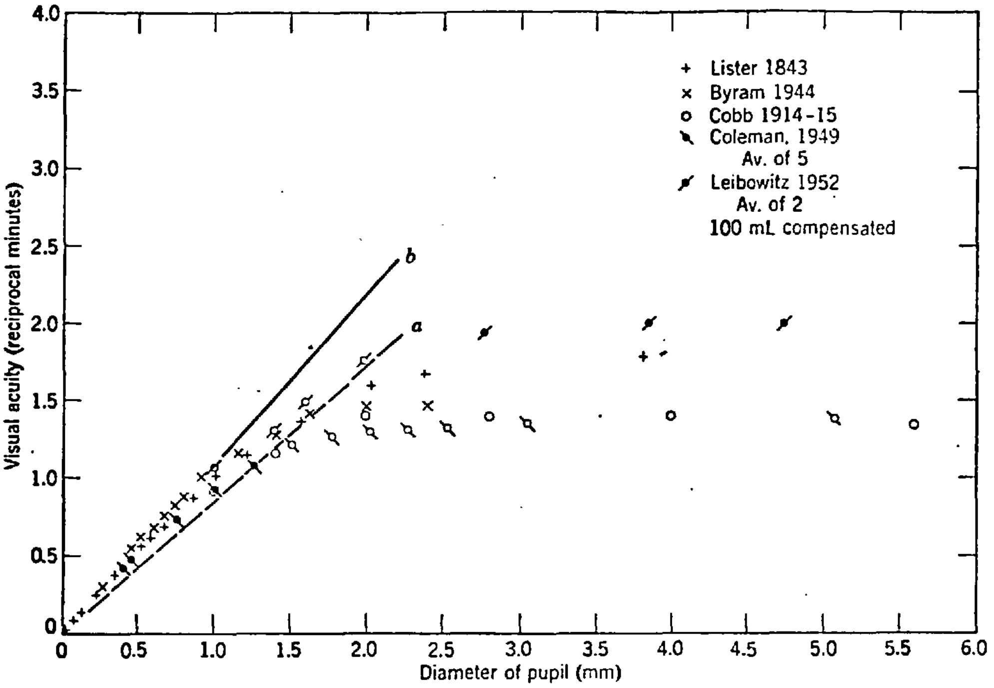


fig. 19

Effect of pupillary diameter on visual acuity. Points are experimental data of several investigations. Straight lines define (*a*) the "Rayleigh Limit" and (*b*) the "Dawes Limit" attributable to diffraction.

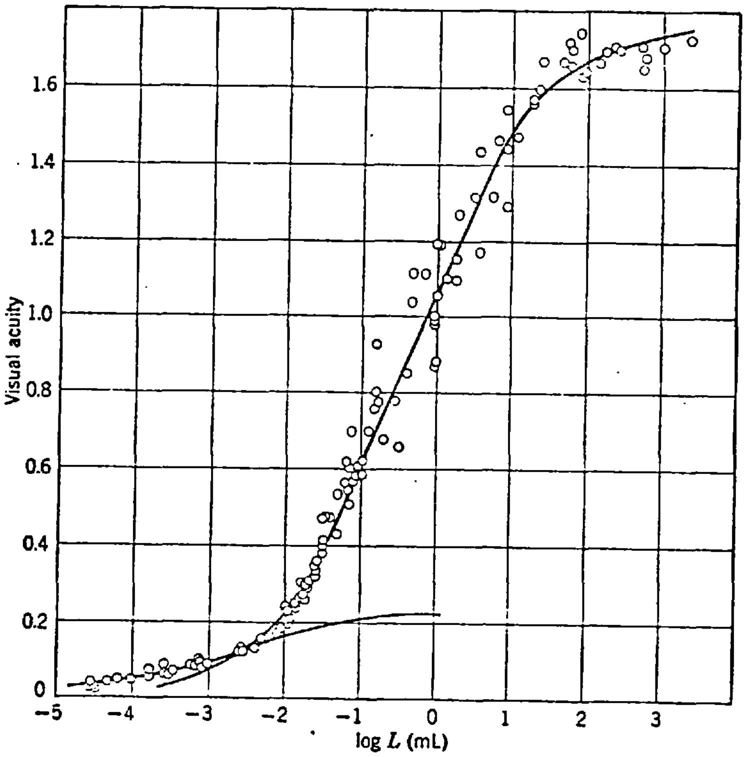


fig. 20

König's data for the relation between visual acuity and illumination, as replotted by Hecht (1934). The shallow curve for the lower limb of the data is an equation for rods, whereas the upper curve is for cones. The task is one of recognizing the orientation of a hook form of test object.

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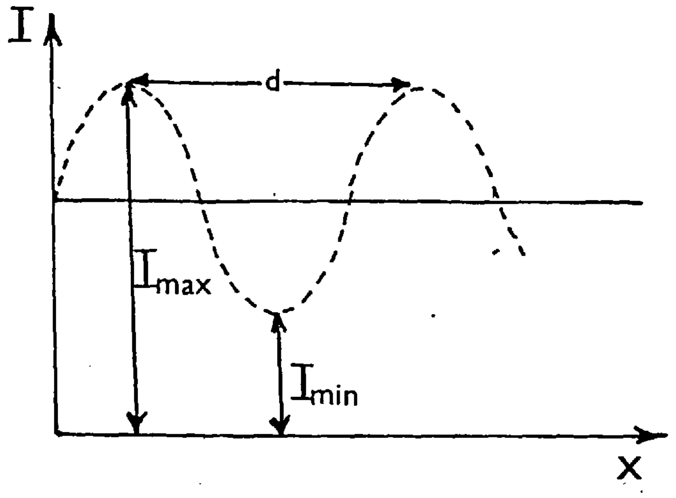
maximum and minimum intensities within the pattern, fig. 21a, is reduced from object to image grating in accordance with the quality of the optics and the spatial frequency of the grating. If a plot is made of the spatial frequency of the object grating and the demodulation incurred at that frequency, the resulting curve represents the spatial modulation transfer function, the MTF, of the eye. If the object modulation is kept constant over the range of spatial frequencies studied, it is found that the image modulation decreases with increasing frequency, reaching zero at a particular cut-off frequency. Objects other than sine wave gratings can be described in terms of their sine wave Fourier components, which, when allocated their respective MTF's, will yield the MTF of the original object.

Visual MTF's

If it were assumed that the whole visual system working at threshold were linear, linearity being ~~the~~ a necessary criterion for the application of Fourier analysis, then it would be possible to predict the visual response of the system to complicated patterns by measuring the individual sensitivities of the Fourier sine wave components of the pattern. If the threshold contrast C_t is defined as in fig. 21b, and the contrast sensitivity $S_t(f)$ at the spatial frequency f is defined as the reciprocal of this value, then a plot of $S_t(f)$ against f yields the contrast sensitivity function, which became known as the MTF of the visual system. This function (see fig. 21c) shows a sensitivity maximum at 3 - 5 c/°, i.e. cycles per degree of visual angle. The high frequency fall-off could be explained in terms of receptoral grain, but the reduction in sensitivity at low frequencies must be a result of the visual processing performed on the retinal image, perhaps associated with some inhibitory interaction (Lowry and de Palma, 1962). The lower the overall illumination level, the lower the frequency where the maximum is to be observed. Fiorentini and Maffei (1973) showed that a maximum could be located for very



sinusoidal distribution of illumination I.
spatial frequency $f = 1/d$
modulation depth = C

(a) $C = \dfrac{I_{max} - I_{min}}{I_{max} + I_{min}}$

(b) C_t : defined as C with I_{max} and I_{min} taking threshold values.

(c) $S_t(f) = 1/C_t$ = contrast sensitivity

(d) $s(x) = \int_{-\infty}^{+\infty} S_t(f) \exp(2\pi i f x)\, df$

(e) $r(x) = \int_{-\infty}^{+\infty} g(x') s(x - x')\, dx'$ x' being a dummy integration variable

fig. 21

low light levels, providing that measurements were made at sufficiently low frequencies.

Assuming that Fourier theory can be applied, a line spread function s(x), can be calculated (see fig. 21d). The visual response r(x) to some other intensity distribution g(x) is found by convolving the new intensity distribution with the line spread function of the sine wave grating (see fig. 21e).

Campbell and Robson (1968) showed that the contrast thresholds of sine wave gratings and also those of square wave, rectangular and saw-toothed gratings, were determined only by the amplitude of their first fourier harmonic over a wide range of grating frequencies. Only when the contrast of the gratings was raised sufficiently for the higher harmonics within the patterns to reach their indivisual thresholds, could the complex gratings be distinguished from sine wave gratings. From these results they postulated the existence of linear independent mechanisms, each responding to a limited range of spatial frequencies.

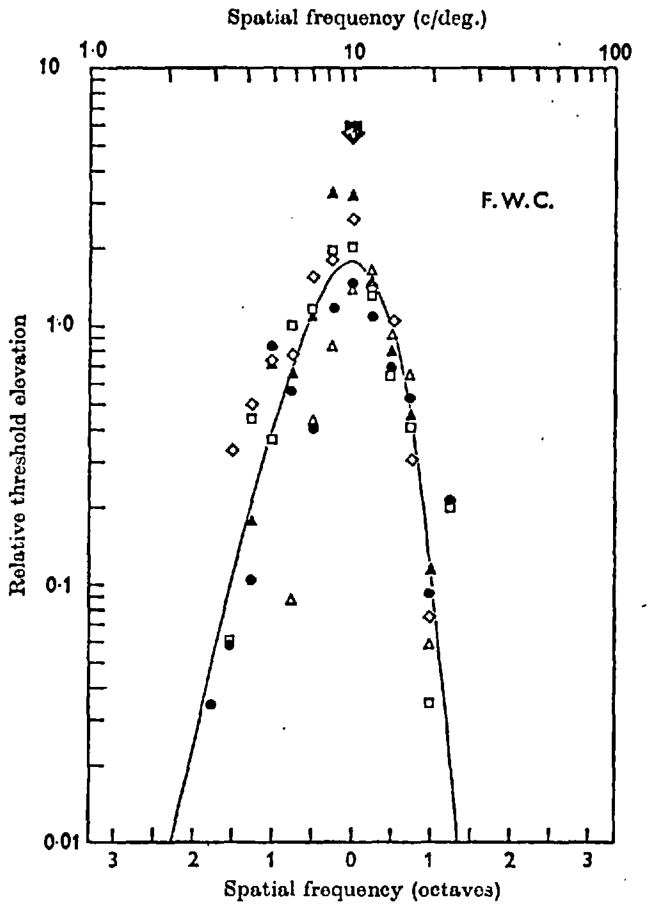
These experiments were performed with the gratings being displayed on an oscilloscope screen. An alternative experimental method is the formation of the gratings, as high contrast, sinusoidal interference fringes, directly on the retina. The advantage of this latter technique is that the MTF of the retina plus the visual pathways can be measured without any distorting contribution from the ocular media and optics of the eye. There are several methods for producing the fringes, the first being developed by Le Grand (1935). More recently, a laser interference technique has been described which produces the necessary high contrast fringes and for small pupil diameters, these undergo virtually no degradation (Campbell and Green, 1965).

Prolonged viewing of different linear stimuli has been found to induce a series of response phenomena known as visual after effects. Interpretation of the characteristics of these after effects has given much information as to the various ways in which the visual system can operate.

The Contrast Elevation Effect

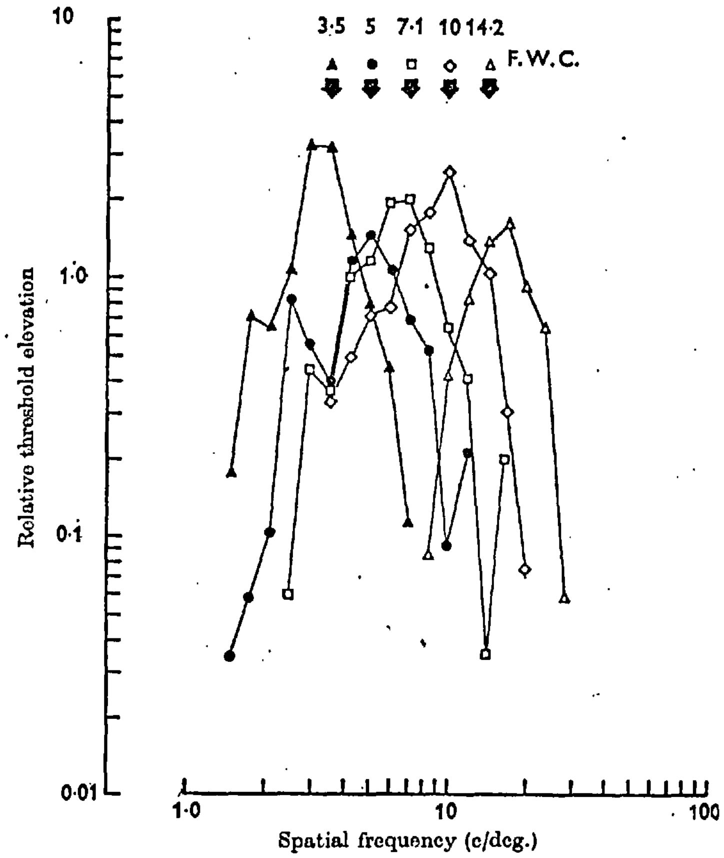
The channels, frequency specific or otherwise, responsible for the detection of linear gratings have been shown to be desensitized by prolonged exposure to an adaptation grating of the spatial frequency to which they are specific. Two or three minutes adaptation to a high contrast, periodic grating raises the contrast threshold of a test grating of the same spatial frequency (Gilinsky, 1968; Blakemore and Campbell, 1969a and b; Pantle and Sekuler, 1968 and 1969.) The test can only be presented for a maximum of three seconds as the adaptation effect falls off rapidly with time, so further adaptation periods of 20 secs, alternated with the 3 sec test presentation are required in order to obtain a satisfactory contrast threshold setting, T_g, for the illumination level of the test grating. The experiment is repeated with a uniform field adaptation stimulus of the same mean luminance as the adaptation grating used previously. Again the threshold contrast, T_u, of the test grating is recorded. The amount of contrast threshold elevation Δ is measured as $\Delta = \log T_g - \log T_u$. The effect is frequency selective (fig. 22), e.g. Blakemore and Campbell (1969a and b) and orientation selective, e.g. Gilinsky and Doherty (1969) and Maudarbocus (1973) (fig. 23), requiring adaptation and test gratings to be of the same spatial frequency . and similarly orientated in order to observe the maximum elevation. It is also a function of adaptation time (fig. 24) and adaptation contrast (fig. 25).

The results of adaptation experiments have been interpreted as providing evidence for the hypothesis proposed by Campbell and Robson (1968) for the existence of linear independent detection mechanisms responding to narrow ranges of spatial frequencies. Blakemore and Campbell (1969b) found that adaptation to a square wave grating raised the contrast threshold for the detection of a sine wave grating whose spatial frequency was three times that of the adaptation grating, that is, the frequency of the third harmonic of the adaptation grating. Tolhurst (1972) found the degree of elevation for this experimental arrangement to be less than that predicted by the application



Adaptation characteristics normalized for spatial frequency. The data points have been shifted along the abscissa so that all the adapting frequencies superimpose at 10 c/deg., shown by the arrow. The abscissa is also expressed, on the lower scale, as octaves of spatial frequency on either side of the adapting frequency. There is no normalization on the ordinate

(a)

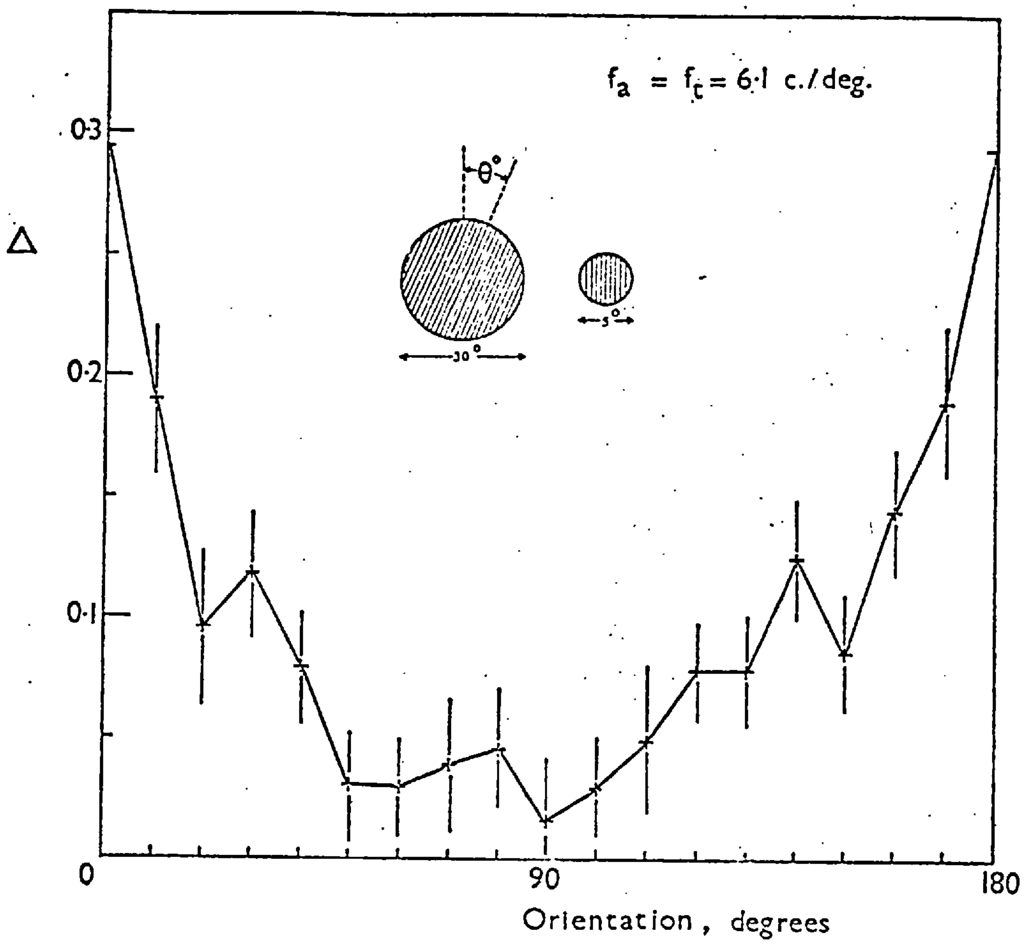


Adaptation characteristics for five adapting spatial frequencies. Each arrow marks the frequency of adaptation and above it is the symbol used for the relative threshold elevation caused by the adaptation. Points are joined in order of spatial frequency. The adapting frequencies were 3·5, 5·0, 7·1, 10·0 and 14·2.

(b)

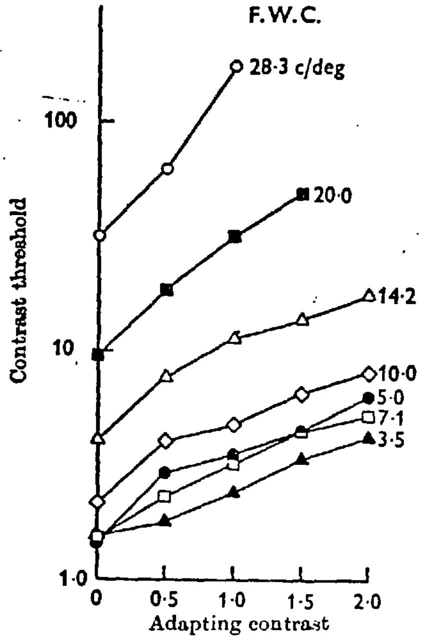
fig. 22

Blakemore & Campbell, 1969b



orientation selectivity of contrast elevation effect :Δ measured in log units (Maudarbocus 1973).

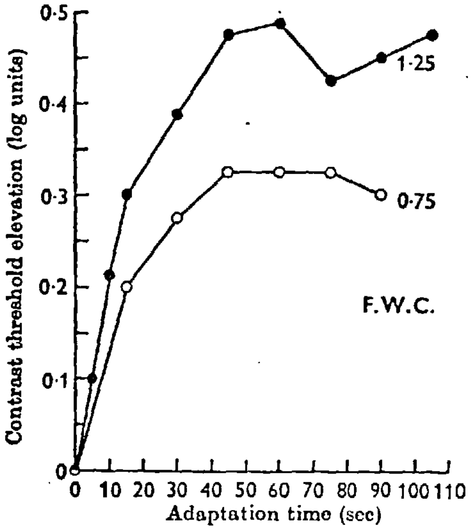
fig. 23



The effect of adapting contrast. The initial contrast threshold for F.W.C., after a period of adaptation, is plotted, on an arbitrary logarithmic scale, against the contrast of the adapting pattern in log units. Results are shown for a number of spatial frequencies: in each case adapting and test gratings were of the same frequency. The data points for zero adapting contrast are, of course, the normal contrast threshold values.

fig . 24

Blakemore & Campbell (1969b)



The effect of adapting time. The initial elevation of threshold for F.W.C. is plotted against the adaptation time. For the filled circles the adapting grating of 15 c/deg. was 1·25 log units above threshold. For the open circles it was 0·75 log units above threshold.

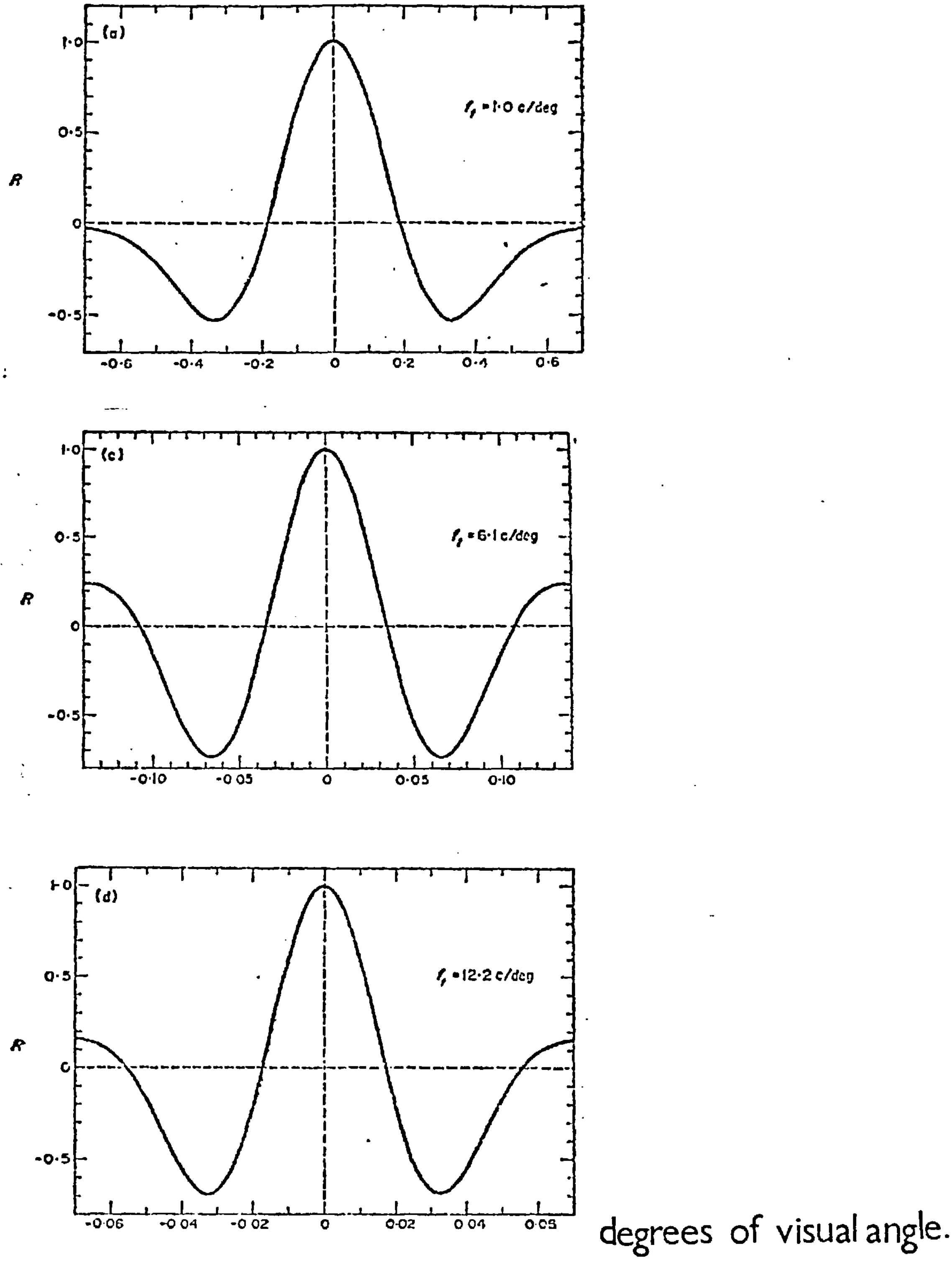
fig . 25

of Fourier theory. Further evidence against the original hypothesis was found in the experiments of Nachmias et al. (1973), who could obtain no elevation at all in the threshold setting of the test equivalent to the third harmonic of the adaptation grating.

If the adaptation grating is presented to one eye and the test grating of the same spatial frequency is presented to the other, contrast elevation of the test threshold of the same order as the monocular experiment is obtained. This would indicate the origin of the effect to be central, sited in the visual cortex.

Sullivan, Georgeson and Oatley (1972), described experiments in which observers adapted to sine wave gratings before making threshold settings of single test bars. They found no elevation specifically dependent on the width of the single bars and concluded that many cycles were necessary for the stimulation of the channels. Carter and Henning (1971) found, however, that a single cycle test was detectcd with less contrast than a many cycle test. It would appear, therefore, that different criteria are used in the two detection tasks, for the single bar and for the grating, and it is thus difficult to draw a meaningful comparison between them.

Maudarbocus and Ruddock (1973b) measured the contrast elevation of threshold of a sinusoidal test grating for each of a range of adaptation gratings of different spatial frequencies presented to the non-test eye. ~~For~~ From the tuning curve thus obtained, the line spread function was computed. The experiment was repeated for a number of different test frequencies. The line spread functions were all similar in having one principal maximum lying between two minima (fig. 26). The separation of these minima was found to be equivalent to the width of one cycle of the test grating represented by the function. The amplitudes of the second and higher harmonics of a filtered sinusoidal test grating were shown to be almost as large as that of the fundamental for large input modulation depths, but the experimenters recorded no elevation of the test contrast



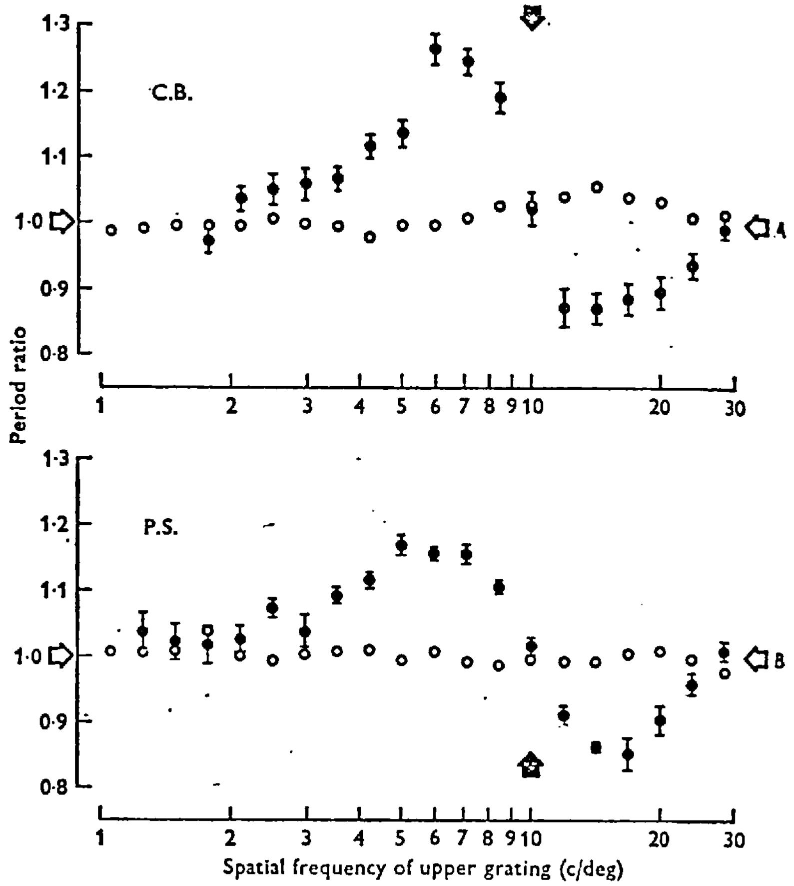
Fourier transform functions: fig. 26
Maudarbocus & Ruddock (1973)

threshold as a result of adapting to these higher frequency harmonics. This result is, again, in disagreement with the theory that the visual system acts as a Fourier analyser.

Kulikowski and King Smith (1973) performed subthreshold summation experiments in which a test pattern and a subthreshold background pattern were set to their combined threshold. The authors concluded from their results that there was evidence for the existence of line, edge and grating detectors in the human visual system, although the grating detector could well have represented a lateral facilitation between line detectors. They assumed linearity of the filter response for illumination levels near threshold and that only one detector was active at this level for the range of background contrasts that they employed. King Smith and Kulikowski (1975) made a detailed study of the detection of gratings, analysing their visibility in terms of the visibility of single lines. They concluded that whereas independent activation of a pair of line detectors could account for the level at which a two line stimulus was detected, the probability of seeing a multiple line test was slightly higher than that predicted. They reason that sub-units slightly more narrowly tuned than a line detector were being employed, rather than sharply tuned grating detectors. Such units had the necessary properties to correlate with the results of adaptation experiments.

Perceived Spatial Frequency Shift

This after effect was first reported by Blakemore, Nachmias and Sutton (1970). They found that adaptation to a high contrast grating produced an apparent shift in the spatial frequency of subsequently viewed test gratings. This shift was in such a direction as to make the disparity in the frequencies of the two patterns appear larger than it actually was. No such shift occurred if the two gratings were of the same spatial frequency, nor did it occur if the two spatial frequencies were separated by more than two octaves (fig. 27a).



The effect of spatial adaptation upon spatial frequency discrimination. The results for the two subjects C.B. and P.S. are plotted separately in Fig. 2*A* and 2*B*. The subject, fixating in between the two oscilloscopes, altered the spatial frequency of the grating on the lower screen until it seemed to match that of the grating on the upper screen. The test spatial frequencies. at which judgements were made, were spaced at 1/4 octave intervals. The ordinate is the ratio of the periods of the gratings on lower and upper oscilloscopes, when they appeared matched. The open circles are means ($n = 12$) of settings made with no pre-adaptation. (Period ratio $= p_1/p_0$.) The filled circles are the means with their S.E. ($n = 6$) of settings made after adapting to a grating of 10 c/deg on the upper screen alone, at a contrast of 1·5 log units above the subject's contrast threshold. (Period ratio $= p_2/p_0$.) For test frequencies below 10 c/deg a greater period (lower spatial frequency) is needed on the lower screen to match the apparent period of the upper grating. Above 10 c/deg the apparent period of the upper pattern is reduced. The effect is limited to spatial frequencies near that of the adapting grating, marked with a filled arrow, but at the adapting frequency itself there is no significant disturbance of spatial frequency.

Oscilloscope phosphor: P-7. Mean luminance: 1·7 cd/m². Contrast of test gratings: 0·6.

fig. 27(a)

Blakemore, Nachmias & Sutton (1970)

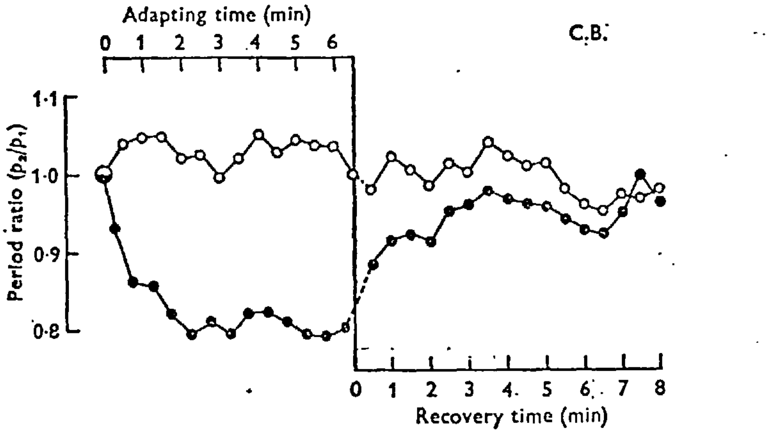
The effect increased to a saturation value with both increase in adaptation exposure time and increase in adaptation grating contrast (fig. 27b and c). If the adaptation grating were presented to one eye and the test grating to the other eye, 80% of the monocular frequency shift was obtained. Blakemore and Nachmias (1971) studied the orientation specificity of this effect, compared with that of the contrast elevation effect, and found the two to be identical. They presented evidence that the neural origins of the two effects were the same and provided further support for the theory of spatial frequency detection units in the visual cortex.

Tilt Aftereffect

The first reports of this effect were published by Gibson (1933). Later analyses have been made by Campbell and Maffei (1971) and Lovegrove and Over (1973). Adaptation to a tilted grating produces an apparent tilt in the opposite direction to that of the adaptation grating on subsequently viewing a vertical test grating. The effect is almost completely transferred between the two eyes. The magnitude of the induced tilt rises sharply as the adaptation grating is tilted away from the vertical (the test grating being itself vertical), reaching a maximum of four degrees for a tilt of the adaptation grating of eight degrees. After this point, the effect falls rapidly away to zero as the adaptation is tilted towards 45° (fig. 28). It has been suggested that this aftereffect provides evidence for the existence of specific channels in the visual system for the detection of limited bands of angles (Coltheart, 1971).

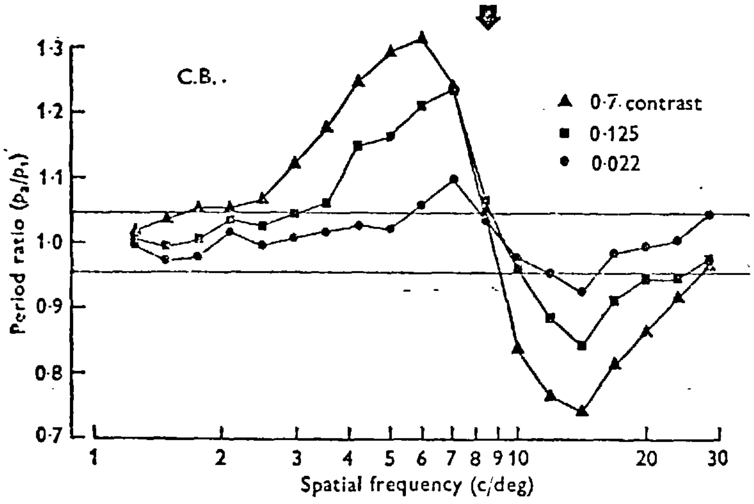
McCullough Effect

This effect was originally described by McCullough (1965). The procedure for observing it is to adapt for alternate three second intervals to a vertical orange grating and a horizontal blue grating. If after three to five minutes the observer views a test grating made up of blocks of white light, horizontal



(b)

Frequency matches were made as described in the text at 11·9 and 8·4 c/deg (contrast = 0·32) during and after adaptation to a grating of 8·4 c/deg (contrast = 0·72). Only one setting was made at a time but the whole procedure was performed three times. The ordinate is the ratio of the period of the lower grating during and after adaptation, to the mean period (n = 12) of four settings made without adaptation, before each session. The means of these unadapted settings are plotted with large symbols at zero adapting time and they have, of course, a value of 1·0 on the ordinate. The other open circles are the mean (n = 3) settings at 8·4 c/deg itself and the filled circles the mean (n = 3) readings for 11·9 c/deg. The abscissa is time and the vertical line through the graph marks the end of adaptation. (Phosphor: P-31; luminance: 2·2 cd/m^2.)



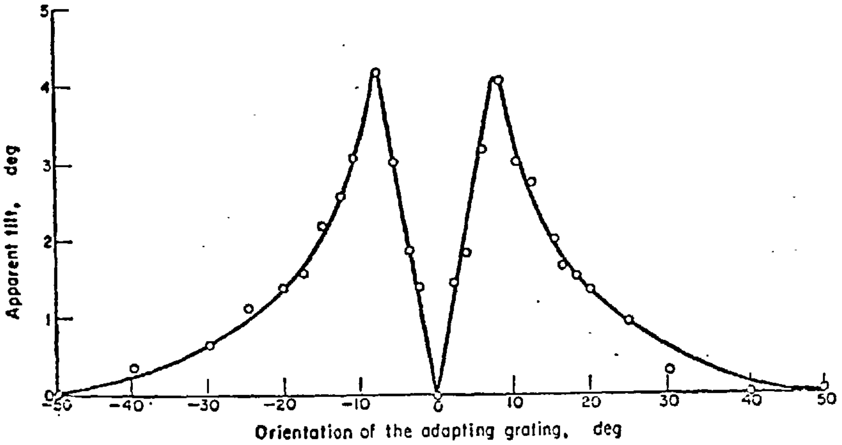
(c)

Subject C.B. adapted to gratings of 8·4 c/deg at contrast levels of 0·022 (●), 0·125 (■) and 0·70 (▲). There were four separate experimental sessions, taking, at each test frequency, four unadapted settings and then four settings during adaptation. The effect plotted is the mean (n = 16) effect of adaptation and is expressed as a ratio of the mean unadapted match (n = 16). The stippled band delimits the 95 % confidence level ($2\sqrt{2}$ times the mean S.E. of the unadapted settings) for significant deviation from the unadapted settings.

Phosphor: P-31. Mean luminance: 2·2 cd/m^2. Contrast of test gratings: 0·32.

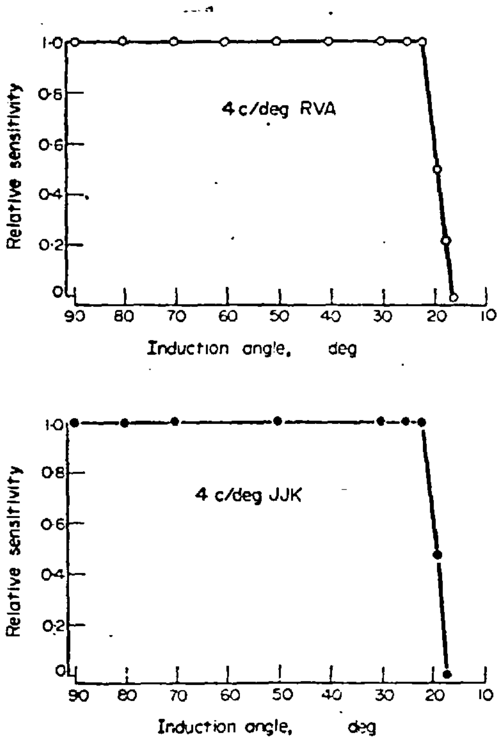
fig. 27

Blakemore, Nachmias & Sutton (1970)



The test grating was kept vertical (0°) and its apparent tilt was measured for different orientations of the adapting grating. Anticlockwise (—) and clockwise (+). Each point is the mean of 10 observations. The continuous line is the best symmetrical curve that could be fitted by eye.

Campbell & Maffei (1971) fig. 28



This demonstrates the change of relative sensitivity for each change of induction angle. Note that for both RVA and JJK (b) the amount of contrast required to suppress the suprathreshold induction input becomes less from around 21° downwards. Heights of symbols represent ±2 S.E. Relative sensitivity scale normalised.

Threshold sensitivity of one grating as a function of the angle of the induction (rivalry) grating of the same spatial frequency.
Abadi (1976).

fig. 29

and vertical gratings, the horizontal gratings appear tinged with orange and the vertical gratings tinged with blue. Channels were proposed, sensitive to both colour and orientation of gratings. When these are in the adapted state, viewing a white light grating produces an illusion of the complementary colour. The manner in which the effect decays with time appears to be rather different from the other after effects in that it is much more long term. This has been studied in detail by MacKay and MacKay (1974). Mikaelian (1975) has recorded some interocular transfer of the effect, although the other experimenters have found none. Lovegrove and Over (1972) and May (1972) induced colour and spatial frequency specific after effects by an analogous technique.

Psychophysical Experiments into the Basis of Stereovision

The retinal images are essentially two dimensional. These images may contain cues to their depth in space, for example, cues from the relative sizes of familiar objects within the scene or from the manner in which these objects occlude one another, but precise judgement of near depth is achieved through stereovision. Because of the interocular separation, the two eyes receive slightly different views of any object in the visual field. The difference in the relative retinal positions of any one point in the scene is termed the 'retinal disparity' of that point. With the eyes focused at infinity the nearer the point, the larger is its retinal disparity. The disparities represented by distances greater than twenty metres from the observer are so small that depth perception becomes reliant on the monocular cues mentioned above. Tyler (1973) found that the presentation of a sinusoidal line to one eye and a straight line to the other produced the illusion of a line varying sinusoidally in depth. He measured the minimum amplitude of the sinusoid for which depth could still be perceived, as a function of its frequency. His results show that no sensation of depth can be achieved for frequencies above 3 c/°. He concludes that stereovision does not cater for the positioning of fine structure, but tolerates large disparities when representing large objects. He suggests that this latter flexibility is a result of large objects often being near and hence, an exact measure of their depth is important.

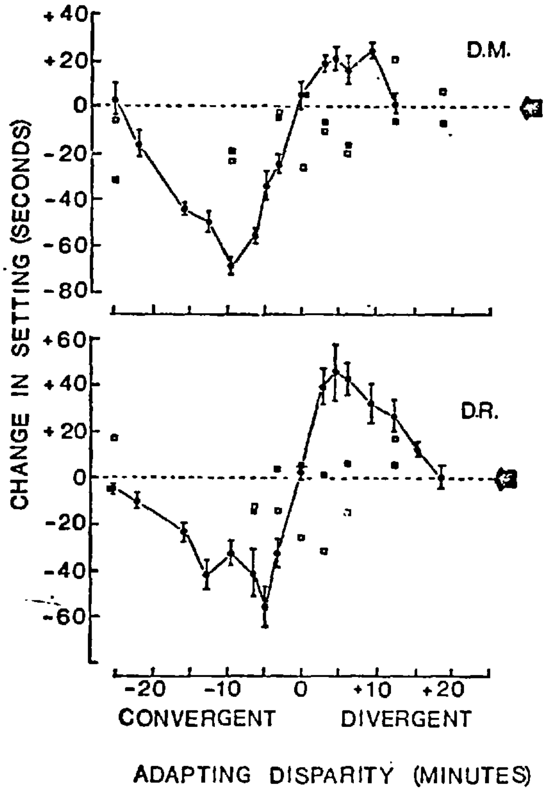
If two visual inputs, differing widely in spatial content or in colour are fed separately, one into each eye, then rivalry occurs, the observer seeing first one input and then the other. Fusion of the two is generally impossible. One of the most recent studies on this type of suppression has been made by Abadi (1976) in relation to grating stimuli. The author concluded from his experiments that high spatial frequencies are more easily suppressed than lower ones when the two gratings are presented vertically. He also studied the angular dependence of the suppression when the gratings were of the same spatial frequency, but one was rotated with respect to the other (fig. 29).

Experiments were carried out by Blake and Fox (1974) into the extent of this phenomenological suppression, by linking binocular rivalry with the contrast elevation effect. They measured the monocular elevation in the threshold contrast when the adaptation grating was continuously visible in the eye to which the test grating was subsequently presented; secondly, they measured the elevation in test threshold contrast when the adaptation grating was rivaling with a second pattern presented in the other eye, and hence being perceived for only half of the total adaptation period. It was found that there was no significant difference in the two threshold values, indicating that the adaptation grating still functioned as such even when it was perceptually suppressed. The site of the contrast elevation effect must, therefore, be located prior to the rivalry site.

Blakemore (1970b) found that presenting two vertical square wave gratings of slightly differing spatial frequencies simultaneously, one to each eye, produces a complete impression of a three dimensional grating, tilted about its vertical axis. If the difference in spatial frequencies exceeds 30%, irrespective of the actual spatial frequency values, it is no longer possible to fuse the two gratings in this way. The phenomenon does not occur for spatial frequencies less than 0.6 c/° or greater than 15 c/°. He suggests that this kind of stereopsis may be dependent upon a comparison of spatial frequencies, rather on an analysis of the disparity at each individual retinal location. It is thus possible to conceive the existence of binocularly driven neurones with different optimal spatial frequency disparities.

Blakemore and Hague (1972) performed experiments where observers adapted to gratings presented stereoscopically with a particular disparity. They found maximum contrast elevation effect for test gratings of the same disparity as the adaptation gratings. They found also that adaptation to a grating of this type produced an apparent, transient shift in the perceived depth of the test grating when the disparity of the latter was close to, but not actually the same as, that of the adaptation grating. The disparity differences and the effect itself are analogous to the perceived frequency shift effect. Further aspects of this apparent depth shift were studied by Mitchell and Baker (1973) who found the direction of the shift to be cyclical with respect to the original position of the test as the disparity difference between the two gratings is increased (fig. 30).

These experiments indicate the existence of disparity-specific neurones in man similar to those previously described in the visual cortex of the monkey and the cat where they were located by electrophysiological methods. If these cells represent, however, the only means of depth perception, then a problem arises in the consideration of central vision. An object lying behind or in front of an observer's fixation point produces retinal images which lie across the nasal-temporal division of the retinae. These images will project information to both hemispheres of the brain. It would seem necessary that at some stage, this information must be collated in order to produce a complete measure of the disparity of the images and hence of the true depth of the object. It would appear that an interhemispheric,or perhaps



The stereoscopic aftereffects (circles) for two subjects measured with lines subtending 6·75′ in width and 2° in height as stimuli. The ordinate shows the difference (expressed in seconds of arc of retinal disparity) between the mean of six equidistance settings of the test target made immediately prior to, and immediately following, adaptation to the disparate target. The bars through the circles indicate ±1 standard error. The open and closed squares show the changes in the test target settings produced by adapting to a target visible to only the right eye or the left eye respectively. There is zero difference between the settings (marked by the horizontal dashed line and the arrow on right) if the adaptation produces no aftereffect.

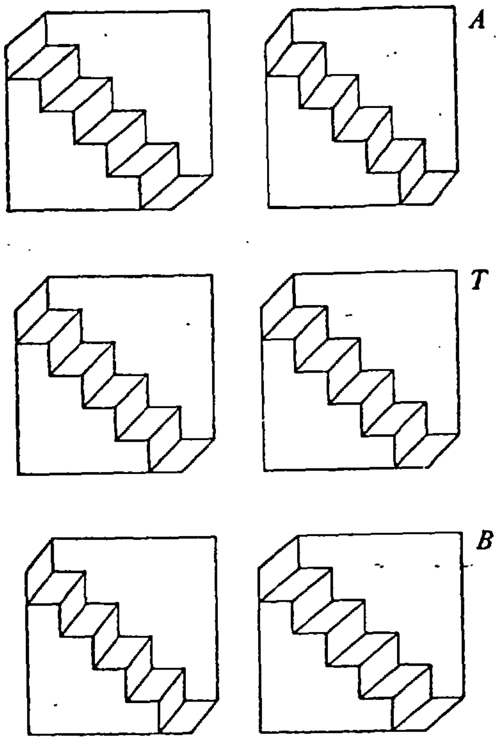
fig. 30

Mitchell & Baker (1973)

earlier, connection must be available in order to accommodate central stereovision. A study of a subject with a split optic chiasma (Blakemore, 1970c) revealed that he possessed nonetheless, normal central stereovision. This would ~~infer~~ imply that the connection must be made higher up in the visual system. Mitchell and Blakemore (1970) found that a patient with a split brain had normal peripheral stereovision, but no central stereovision. It would thus appear that such an interhemispheric connection does exist to deal with this aspect of depth perception.

If channels sensitive to binocular depth are present in the visual system, then it might be expected that they could be fatigued in the same way as size-tuned channels. Virsu (1975) used as a test pattern an ambiguous staircase stereogram (fig. 31a) which underwent alternating perceptual reversals. The adaptation stimulus was arranged to be a similar staircase stereogram which was made, by small disparity shifts within the pattern, to remain perceptually unambiguous in one of the two possible perspective views. After 60 seconds adaptation, the test was studied and found by 83% of the observers to present the alternative to the adaptation perspective. After 20 seconds, the reversal rate returned to the preadaptation value. This would indicate the possibility of channels more sophisticated than those related simply to disparity specific neurones (fig. 31b).

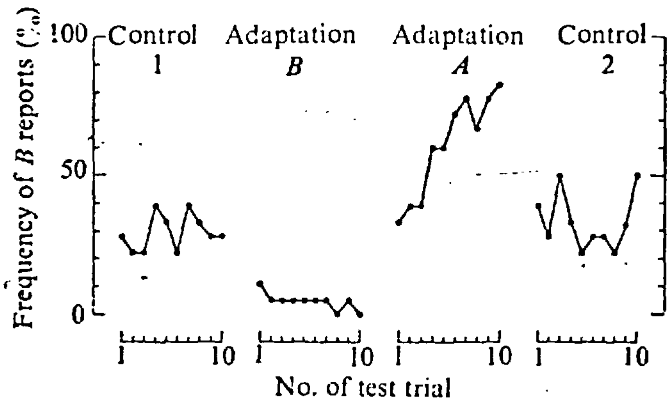
Blakemore, Garner and Sweet (1972) used the contrast elevation effect in their experiments to find the site of size constancy. Two gratings at different depths look the same when their actual frequencies, rather than their angular frequencies as measured at the observer's eye, are the same. In their experiment, an adaptation grating was placed three times further away from an observer than was the test grating. Despite the perceptual observation above, maximum contrast elevation was obtained when the angular frequencies of the test and adaptation gratings were the same. From these experiments, the authors concluded that size constancy scaling occurs after



Determination of perspective reversals through disparity specific adaptation. *A* and *B*, Adaptation stereograms with opposite disparities. *T*, Test stereogram without disparity. If reader stereoscopically fuses the test pair, an alternating perspective of the staircase is seen. Pairs *A* and *B* if properly fused produce a stereoimage which does not alternate in perspective. Adapt to *A* for a minute and observe then *T*: the apparent perspective of the test image now is opposite to that observed in *A*. Repeat the same by adaptation to *B* and notice that after adaptation to *A* or *B* the perspective of *T* is always opposite to the one observed in the adaptation figure.

(a)

Development of the disparity specific aftereffect during repeated testing after various forms of adaptation. Ordinate shows the percentage of subjects ($N = 18$) who saw perspective alternative *B* in the test figure which could be seen either as alternative *A* or alternative *B* during its 1-s presentation. Each test trial was preceded by a 5-s adaptation period. In control series the adaptation stimulus was the same as the test stimulus. In adaptation *B* the disparity of the adaptation stimulus evoked a perspective view of type *B*. Adaptation stimulus *A* evoked perspective *A*, respectively.



(b)

Virsu(1975) fig. 31

the site of adaptation, perhaps in the infero-temporal cortex.

Studies have been made on the tilt after effect and the contrast elevation effect as experienced by stereoblind subjects (e.g. Movshon, Chambers and Blakemore, 1972) and it has been found that whilst exhibiting normal monocular results, the degree of interocular transfer is much less in stereoblind than in normal observers (efficiency of 49% against an efficiency of 70%). Observers who are both stereoblind and strabismic show even less transfer, only 12%. Among normal observers, (Mitchell and Ware, 1974), it was found that the interocular transfer of the tilt aftereffect was greatest for observers with the highest stereoacuity. Movshon, Chambers and Blakemore (1972) found that for both normal and stereoblind observers, the dominant eye (that eye which the individual would choose to use for monocular detection tasks), transfers more of the after effect than does the nondominant eye.

Chapter 2.

APPARATUS AND EXPERIMENTAL METHODS

(a) Apparatus

In the introductory chapter, the advantage of using interference fringes as test gratings was discussed. This advantage is principally that the MTF of the retina and visual pathways can be studied without distortion from the ocular media and the optics of the eye. For the same reason, correcting lenses for observers with less than perfect vision were unnecessary. Interference fringes were first used for visual studies by Le Grand (1935) and later by Byram (1944), Arnulf and Dupuy (1960) and Westheimer (1960). A basic difficulty encountered by these experimenters was to find a light source of sufficient brightness and coherence to form the necessary high contrast fringes. This problem was resolved by Campbell and Green (1965) by using a He-Ne laser source. The technique was to focus two beams of monochromatic light from the coherent laser source in the plane of the eye pupil, close to the nodal points of the eye. The interference fringes, analogous to Young's double slit interference fringes, are produced over those retinal regions where the two beams overlap. Constructive interference, where the two beams are in phase, produces a maximum within the pattern; destructive interference where the beams are out of phase, gives rise to a minimum. The intensity distribution is given by

$$I(x) = I_1 + I_2 + 2\sqrt{(I_1 I_2)}\cos\frac{2\pi dx}{\lambda} \qquad (1)$$

with:

I_1, I_2 : intensities of the two beams,

λ : wavelength of the light,

x : angular distance across the retina,
d : separation of the two focussed beams.

In all the adaptation experiments described in subsequent chapters, the intensity of the two beams was the same ($I_1 = I_2$) and thus the fringe contrast is ideally unity. The basic experimental arrangement used by Campbell and Green (1965) is shown schematically in fig. 1. A reflecting plate RP splits the incoming divergent laser beam into two components, one of which is deflected by a mirror M, and the two components are refocussed by the microscope objective MO. The observer views the fringes by placing his eye so that the two images of the source are located close to the nodal point of the eye, although the spatial frequency of the pattern is, in fact, almost independent of the position of the observer's cornea.

The split level apparatus used in the present experiment was designed and built by G.J. Burton (1973) and incorporates a duplicated Mach-Zehnder interferometer (Born and Wolf, 1970). A schematic diagram of the apparatus is shown in fig. 2. For most of the experiments, lasers 1 and 2 were both Helium-Neon (Spectra-Physics type number 120), although laser 1 could be replaced by an argon laser (Coherent Radiation, model 54) for the purpose of changing the stimulus wavelength. In following the light path through the equipment, it should be noted that laser 2 is located at a lower level than laser 1. After deflection from the front-silvered mirror M1, the beam from laser 1 is focussed by a x10 microscope objective mo1 onto a 25-micron pinhole pn, to ensure the selection of a single laser mode. This beam is then collimated by lens Cℓ and enters the upper half of the interferometer through the beamsplitter bs4.

Light from laser 2 is divided by beam splitter bs6, one half passing through a double neutral density wedge w_1 and w_2 to be recombined with the other half by bs5. The beam is focussed by a x10 microscope objective, mo2,

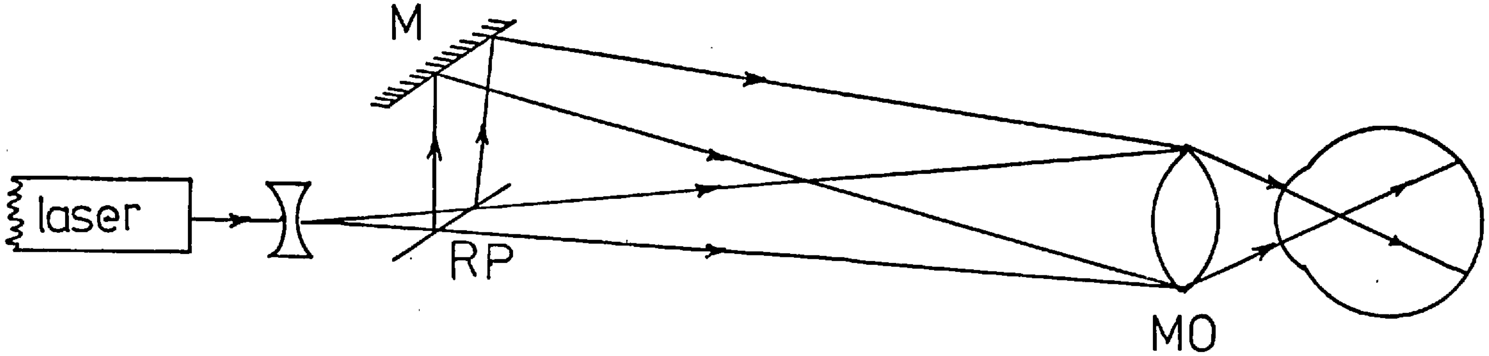


fig.1

schematic diagram of the interferometer

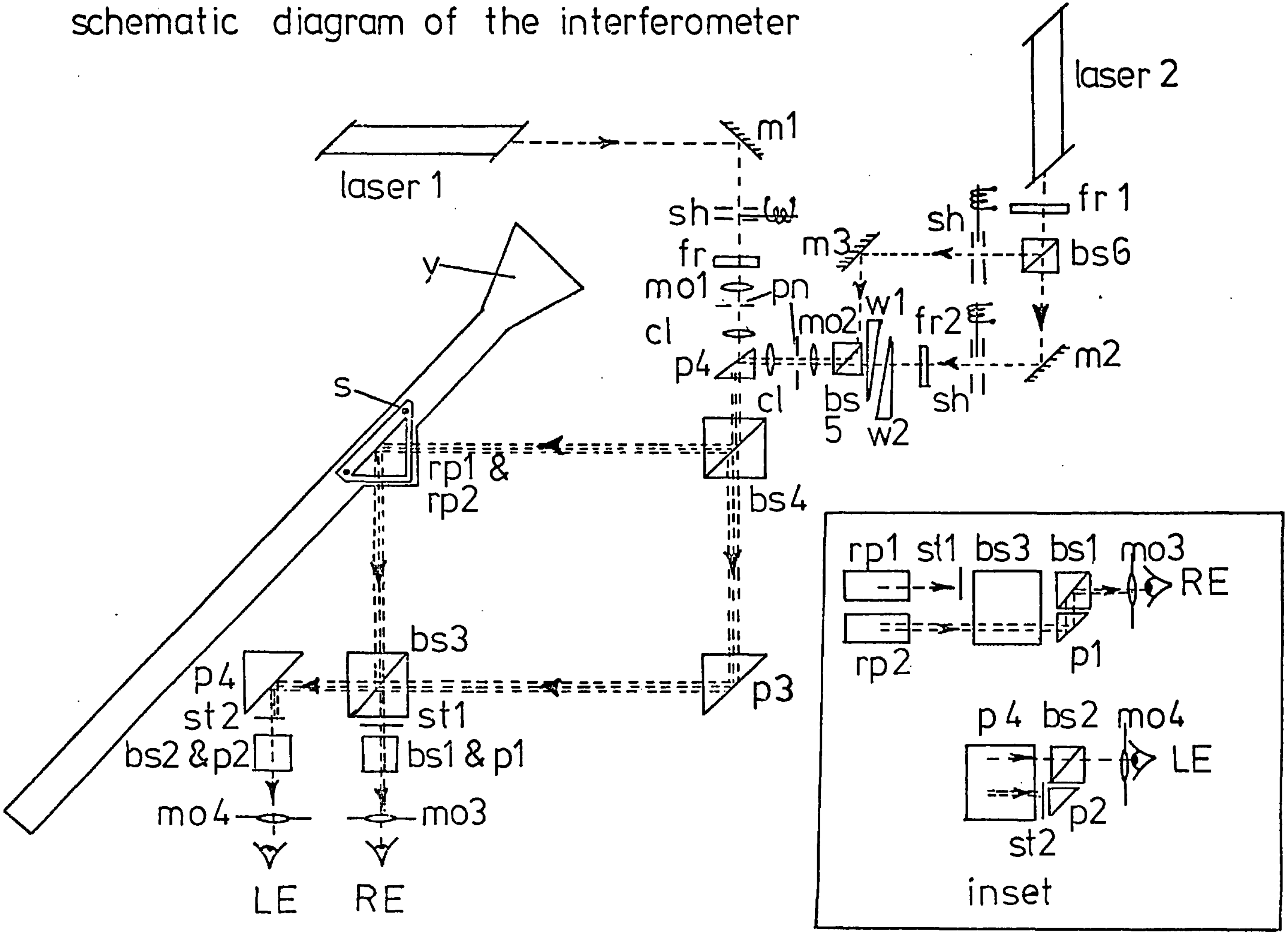


fig. 2

onto a 25-micron pinhole, pn, and collimated by a lens Cl, in the same manner as the beam from laser 1. After deflection by a prism, p4, the light from laser 2 passes into the lower half of the beam splitter bs4.

Three electromagnetic shutters (sh) are positioned in such a way that when the test beam (the component from laser 2 which passed through the wedges w1, w2) is revealed, the light beam from laser 1 and the second component beam of laser 2 are occluded. Conversely, opening the shutters to allow light from laser 1 and this second component from laser 2 to enter the system, occludes the test beam. A time switch controls the shutter in such a way that the test presentation period is limited to 3 seconds. Neutral density filters (fr) are positioned in all three beams, enabling the illumination levels of each to be controlled.

After division of the beams by bs4, light from both lasers is reflected by prism, p3, or by the reflecting prisms, rp1 and rp2, before passing through the beam splitter, bs3. The prisms rp1 and rp2 are positioned separately one above the other, with light from laser 1 passing through rp1 (the upper of the two) and light from laser 2, through rp2. Both rp1 and rp2 can be rotated and translated independently by means of two separate micrometer drive mechanisms attached to the metal arm, y. Stops can be placed in any of the beams emerging from bs3 according to the experimental configuration required. In the majority of the experiments described in this thesis, light from laser 1 provided the conditioning grating, CG, which was presented to the left eye as inset. As this beam is the upper of the two, a stop st2 was positioned after the prism p4 in order to prevent the lower beam from entering the eye via the small prism p2 and the beam splitter bs2.

The microscope objective, mo4, focussed the two collimated components from laser 1 to two points close to the nodal point of the observer's eye. As the two beams are mutually coherent, these points give rise to two interfering divergent beams which produce sinusoidally modulated interference fringes on the observer's retina.

In the studies to be described, a stop st1 (again, as in fig. 2) prevented the upper beam from entering the right eye, allowing only light from laser 2 to reach the eye. These laser 2 beams are deflected upwards by p1 (inset, fig. 2) and into the objective, mo3. Fringes are produced in the observer's right eye as described in the previous paragraph. Only one pair of collimated beams from laser 1 passes into mo3 at any instant. Depending on the position of the shutters, sh, the observer sees either the test grating TG which arises from the beam passing through the neutral density wedge, or he sees the adaptation grating AG, which is deflected around the wedge.

By adjusting the stops st1 and st2, the adaptation, conditioning and test gratings can be presented to either the left or the right eye, or, if necessary, to both eyes.

A more detailed examination of the production of the fringes on the retina is given in fig. 3. It was stated earlier in this chapter that Campbell and Green (1965) found that the spatial frequency of the gratings did not depend critically on the position of the observer's eye. The state of accommodation of the eye was also found to be unimportant with respect to spatial frequency. This would appear initially to be surprising, but a more detailed analysis was set out by Campbell, Kulikowski and Levinson (1966) (see fig. 3). Initially, the observer's eye is considered as being located with its nodal plane some distance D from the two focus points P1 and P2 of two coherent beams focussed by the microscope objective. Rays from these components which give rise to adjacent interference maxima (A' and B') on the retina are considered. The points conjugate to these are depicted in the diagram as A and B, for the particular state of accommodation of the eye. For A' and B' to be adjacent maxima of brightness, the optical

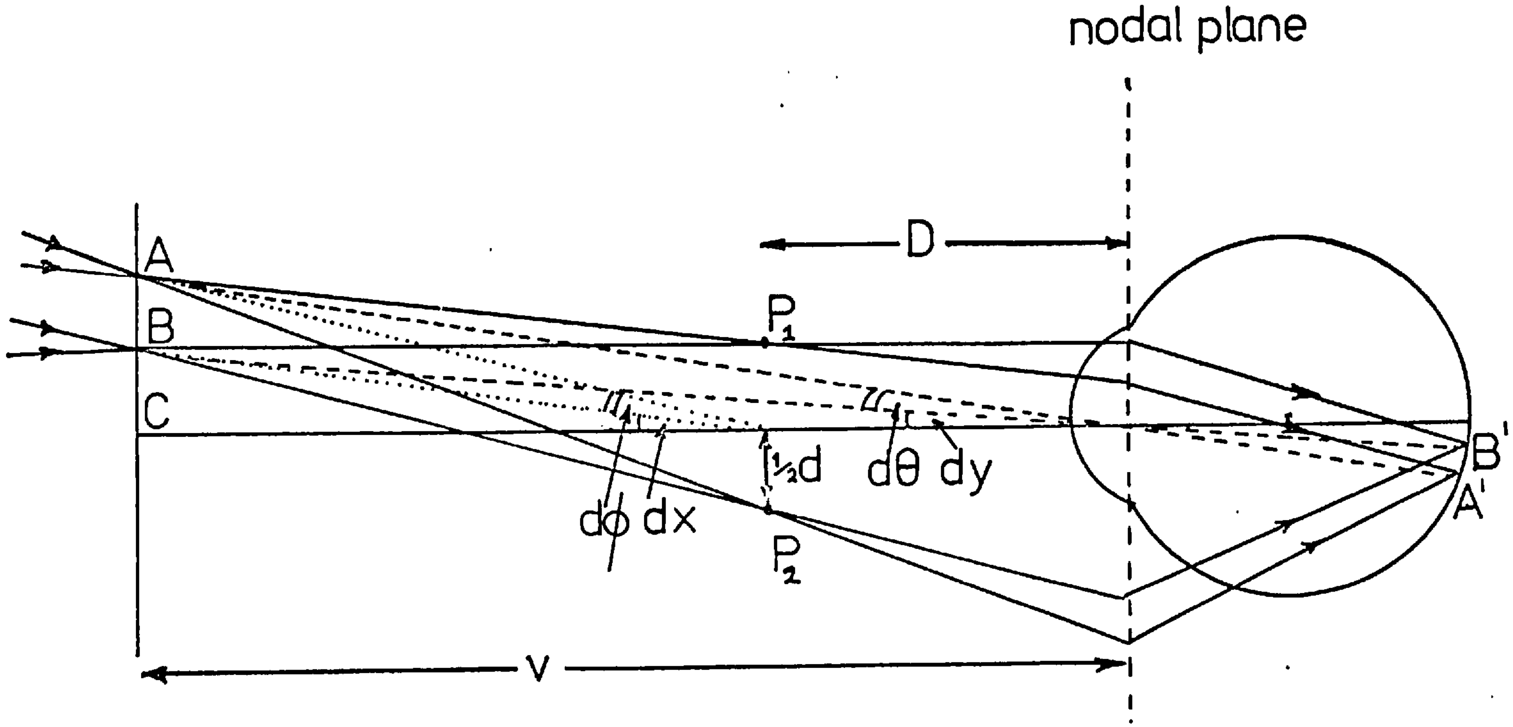


fig.3

path difference must equal one wavelength; i.e.

$$(P_1A' - P_2A') - (P_1B' - P_2B') = \lambda$$

λ : wavelength of laser light.

Also: $$(AP_2 - AP_1) - (BP_2 - BP_1) = \lambda$$

The angle subtended at P_1P_2 by AB, $\delta\phi$ is then $\delta\phi = \lambda/d$.

Then: $$\tan(\delta\phi + \delta x) = \frac{AB + BC}{v - D}$$

and $$\tan(\delta\theta \div \delta y) = \frac{AB + BC}{v}$$

$$\tan \delta x = \frac{BC}{v - D}$$

and $$\tan \delta y = \frac{BC}{v}$$

therefore: $$\tan(\delta\phi + \delta x) = \frac{AB}{v - D} + \tan \delta x$$

and $$\tan(\delta\theta + dy) = \frac{AB}{v} + \tan \delta y$$

Assuming small angles where $\tan\theta \longrightarrow \sin\theta \longrightarrow \theta$ (radians):

$$\delta\phi \longrightarrow \frac{AB}{v - D}$$

and $$\delta\theta \longrightarrow \frac{AB}{v}$$

$\delta\phi = \lambda/d$ from before

Therefore: $$\delta\theta = \frac{(\nu - D)}{\nu}\left(\frac{\lambda}{d}\right)$$

Thus the spacing between successive interference maxima ($\delta\theta$) is independent of the accommodation of the eye (ν) when $D = 0$, i.e. $\delta\theta = \lambda/d$. If $D \neq 0$, but is still very much less than ν, the fringe spacing can be still seen to depend very little on accommodation. In the Mach-Zehnder interferometer used in the experiments, variation of the spatial frequency of the fringes was achieved by changing the angle between the incident beams, as measured at the microscope objective. Referring to fig. 4 which gives a simplified description of the interferometer, this angle, β, is given by:

$$\beta = \arc\tan\,(q/B) \qquad (2)$$

where q is the separation of BS and P, and B the distance from BS to the microscope objective MO. To ensure precise intersection of the beams, the prism P must be rotated as well as translated and an experimental approximation to this theoretical requirement was designed by Burton (1973) and is incorporated in the interferometer. For visual experiments with grating stimulus patterns, the range of spatial frequencies required from the interferometer extends from zero to about 25 cycles per degree of visual angle. With a x10 microscope objective eye-piece, β is sufficiently small over this frequency range to approximate equation (2) to:

$$\beta = 2\,\arc\tan\left(\frac{q/B}{2 - q/B}\right)$$

A micrometer attachment y, drives the pivoted metal arm on which the prism, P, is mounted, in such a way that the pivot of the arm, O, forms an isosceles triangle with the microscope objective MO and the beam splitter BS. The simplified arrangement shown in fig.3 does not(by the finite size of

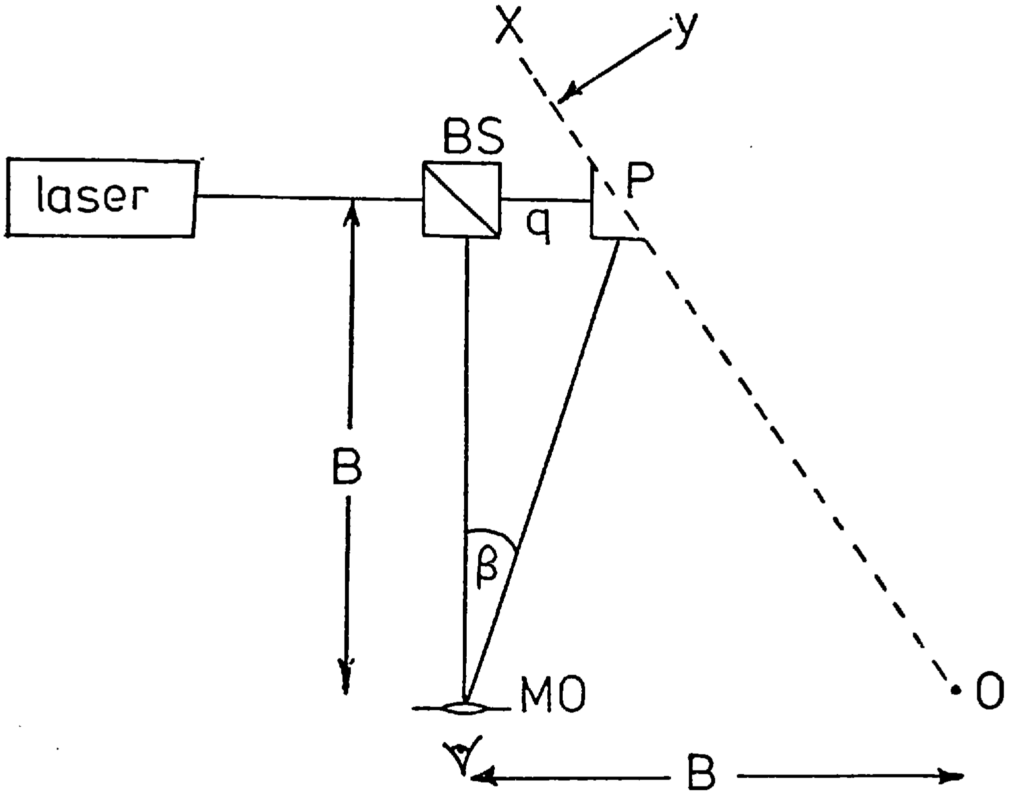


fig. 4

BS and P) allow the production of very low frequency fringes because β is limited. For this reason, the more complex apparatus described earlier was designed.

In most of the experiments described in the following chapters, the observer viewed the full 30° fields supplied by both left and right eye microscope objectives. In one group of experiments, however, the off-axis measurements described in section (e) of Chapter 3, the adaptation and test gratings as presented in the right eye-piece were restricted to 5° of visual angle by placing a stop of the appropriate diameter in the back focal plane of this objective. During the course of these experiments, it was required that the 5° test and adaptation gratings should be located at a series of distances from a central fixation spot. To meet this requirement, a series of stops were constructed with a small central aperture corresponding to ½° of visual angle with another larger (5°) aperture located at a chosen off-set from the centre. Stops were made with a series of off-set values in both the horizontal and vertical directions.

Calibration of Fringes

The spatial frequencies of both the upper and lower systems of interference fringes were calibrated in terms of the readings on the two micrometer screws which drive the arms on which the reflecting prisms are mounted, thereby changing the angle (β in fig. 4). Separate calibrations were required for both left and right eye pieces. A travelling microscope was used to measure the separation of the two coherent spots produced by each system (distance d in fig. 3) for various values of the micrometer setting y.

For any set of interference, the intensity distribution on the retina is given by:

$$I(x) = I_1 + I_2 + 2\sqrt{I_1 I_2}\,\cos\frac{2\pi dx}{\lambda}$$

as defined in equation (1).

If dθ is the angle in radians between successive maxima, then:

$$d\theta = \frac{\lambda}{d}$$

Thus the spatial frequency, f, in cycles per degree of visual angle is given by:

$$f = \frac{d}{\lambda} \cdot \frac{\pi}{180} \qquad (3)$$

(For the He-Ne laser, $\lambda = 632.8$ nm).

Therefore, a value of f could be derived for every value of the spot separation, d, and this quantity plotted as a function of its respective micrometer reading, y. The resultant graphs are plotted in fig. 5 (a and b) for two x10 microscope objective eye-pieces. Calibrations were obtained for the Argon laser by setting the value of λ in equation (3) to 476 nm.

After the initial adjustment and alignment of the instrument, all the components were rigidly mounted, except for the rotating prisms rp1 and rp2 (fig. 2). Two screw adjustments were available, one for each prism; rotation of the screw tilted the prism which in turn tilted the respective set of fringes to the required orientation. Unless otherwise specified, the fringes were set vertically with respect to the observer, whose head was stabilized by means of a bite bar.

The sinusoidal profile of the fringes was checked by G.J. Burton (1974) using a photomultiplier (EMI, type 9698) driven by a stepping motor, scanning with a 0.48' x 4° slit. A scan over one cycle is reproduced in fig. 6 (filled circles). A "least squares fit" of the experimental data is marked by the open circles.

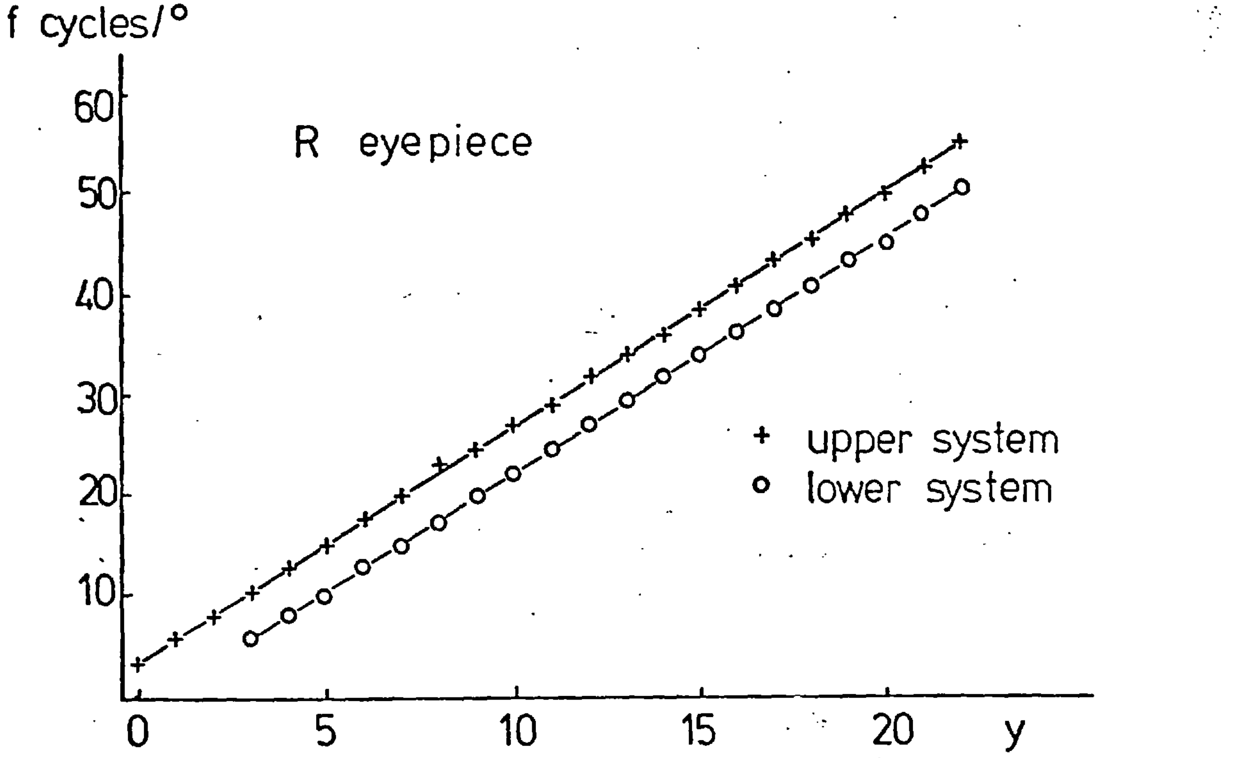


fig.5(a)

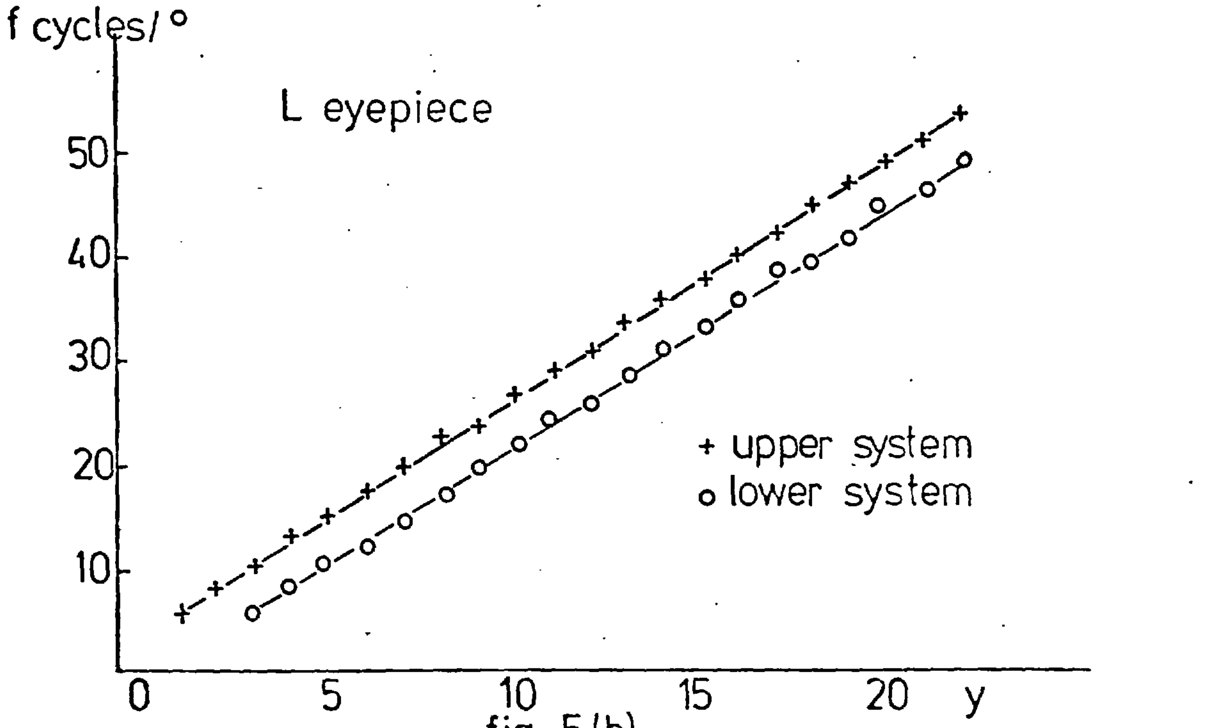
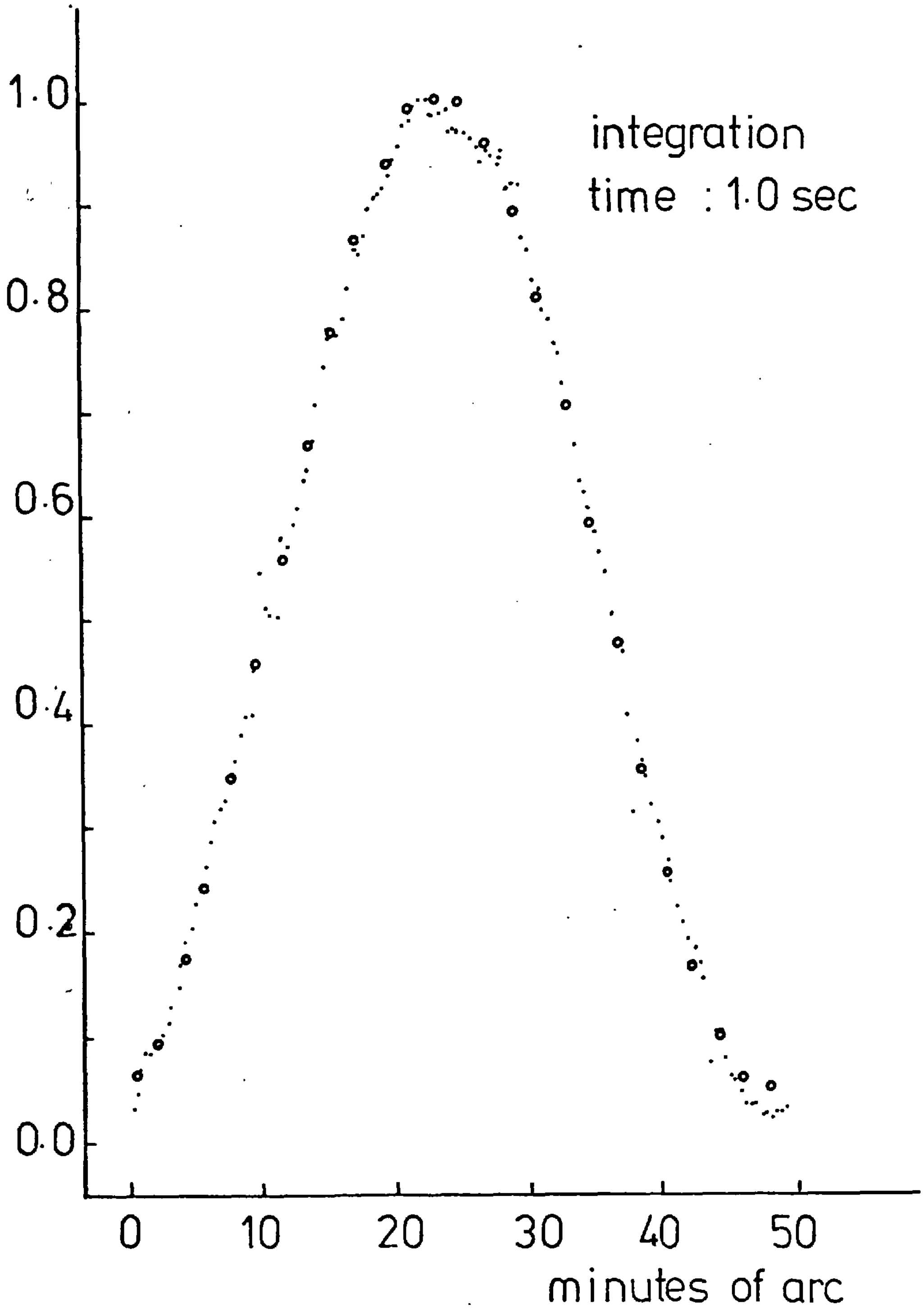


fig.5(b)

Spatial frequency calibrations.



Scan of one interference fringe
fig. 6

Neutral Density Filters and Wedge Calibrations

The neutral density wedge used in these experiments was made from blue glass and its density gradient resulted from the change of thickness along its length. The wedge and filters were calibrated "in situ" by means of an EMI photomultiplier (type 9558) placed immediately beyond the eyepiece MO1. A reading, R_1, was obtained without the wedge, and a second reading, R_2, obtained for the wedge at some position in the beam. The transmission at this point is given by:

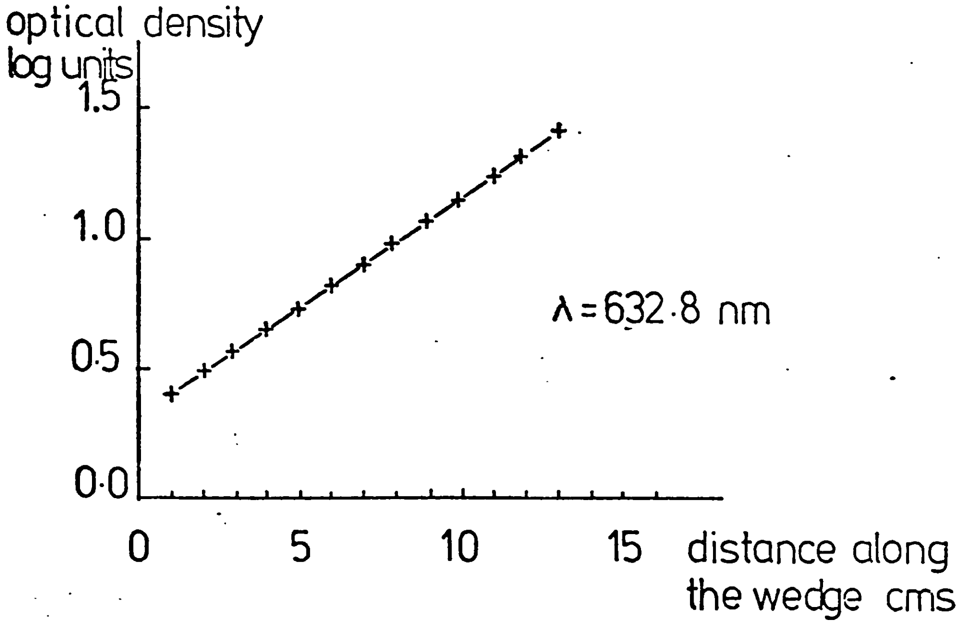
$$T = R_2/R_1.$$

The value of the optical density D in log units is given by:

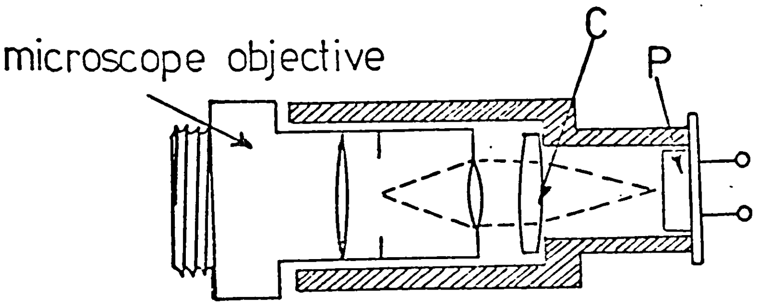
$$D = \log_{10} 1/T$$

The optical densities at a series of positions along the wedge are given in fig. 7. The relationship between the two quantities is seen to be linear. The neutral density filters were calibrated by determining the position along the wedge which gave an equivalent photomultiplier reading to that obtained when the wedge was replaced with a particular neutral density filter.

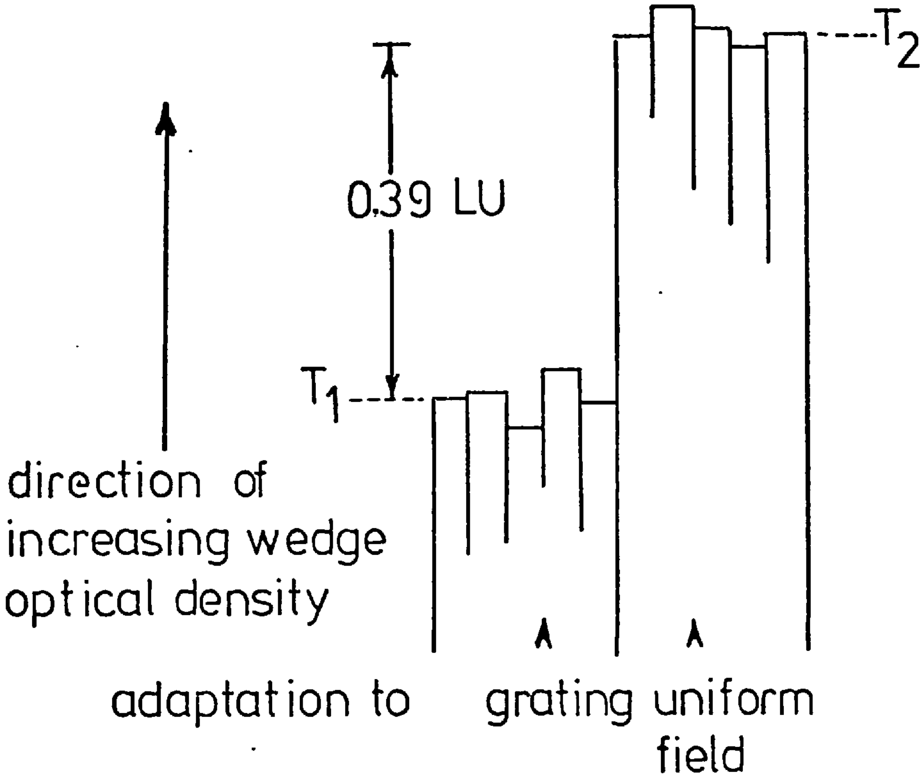
In order to monitor the output power of either laser, or to compare the illumination levels of the different field configurations studied, a photoconductor device was constructed by G.J. Burton (1974) for use with the interferometer. Mounted in a brass tube designed to slip tightly over the eye-pieces (fig. 8) it consisted of a condensing lens C and a photoconductor P which was connected in series to a 100 volt battery and a galvanometer (Pye, 7904/S). The lens produced an image of the field on the photocell, as shown by the broken lines in fig. 8. Since the device



Wedge calibration
fig. 7



Light monitoring device (Burton, 1974)
fig. 8



Typical data record

fig. 9

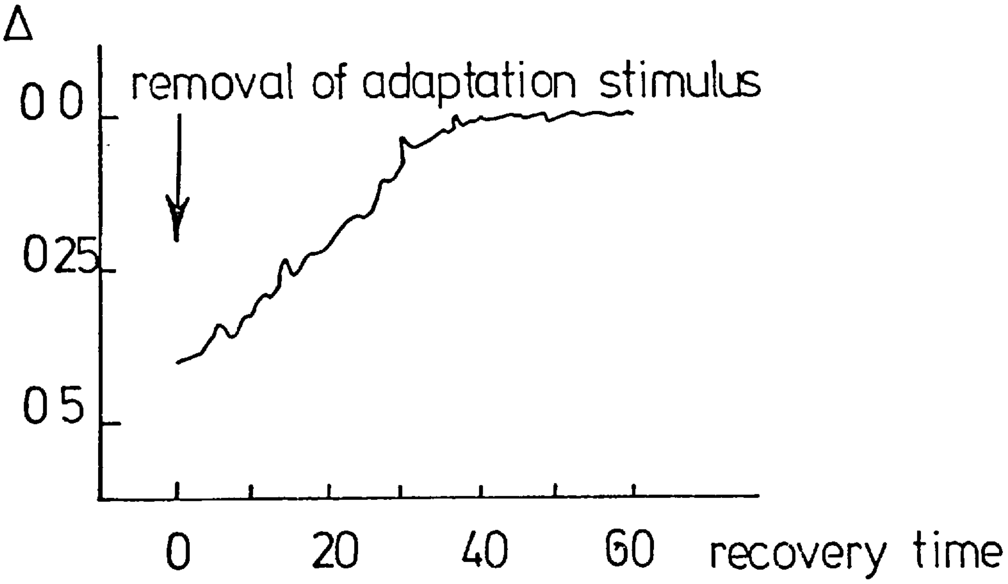


fig. 10

was used only for checking that fields were presented at the same illumination level and not for measuring differences in illumination level, no calibration was necessary.

The observer adjusted the neutral density wedge by turning a knob on the right hand side of the apparatus. This was attached to a rod and a system of pulleys which raised or lowered the wedge through the test beam. The same knob moved a pen-recorder across a metal drum; when a satisfactory reading had been obtained, the observer operated a switch which drove a small motor and thus rotated the drum. The system was arranged so that the distance marked out by the pen recorder corresponded exactly with the distance travelled by the wedge through the laser beam.

Experimental Procedure

The initial aims of these experiments were outlined in the introductory chapter and are concerned principally with aspects of the threshold elevation effect (also discussed in the introductory chapter). The observer typically views a high contrast adaptation grating for a period of approximately 2 minutes and is then required to set a test grating, which is presented for just 3 seconds, to its threshold illumination level, i.e. the illumination level where all the grating structure in the test field disappears. This threshold value is compared with that obtained after adaptation to a uniform field of the same mean illumination level as the adaptation grating presented for the same period. The magnitude of the elevation effect Δ was defined in Chapter 1, page 32 , in terms of these two threshold values. A more detailed account of the experimental procedure follows.

Before commencing the experiments, the observer was asked to adjust the position of the left-hand eye-piece (mo4 in fig. 2) so that the separation of the two eye-pieces (mo3 and mo4) matched his own interocular separation. This was to ensure that the two fields could be fused. A similar lateral adjustment was made to the prism p4 (fig. 2), thus giving uniform illumination over the entire left-eye field. The illumination levels of the various adaptation gratings are quoted in the subsequent chapters in terms of log units above their respective thresholds. In order to obtain these threshold values, the observer dark-adapted for thirty minutes after which time, a low illumination level grating of the required spatial frequency was presented to the right eye. Neutral density filters were inserted into the laser beam (see fig. 2: fr 1 for the adaptation grating) until the grating structure in the field just vanished. This threshold criterion of "just-not-see" was maintained throughout the experiments. The values of the filters required to reduce the illumination level of the particular grating to its threshold were noted. Sufficient filters were subsequently removed to raise the illumination level of the adaptation or conditioning field to that needed in experiments. This level was generally 4.5 l.u. above threshold for the adaptation grating, although other values were used in intensity variation experiments. Unless otherwise stated, the illumination level of the conditioning grating was matched to that of the adaptation grating using the photoconductor attachment (fig. 8) by adjustment of the filters fr in fig. 2.

The observer viewed the adaptation and conditioning gratings presented in the requisite experimental configuration for two minutes. During this period, the observer was asked to keep his gaze moving around the fields so as to avoid retinal afterimages. He then operated the shutters, SH, which occluded these gratings and presented the test gratings to either the left, the right, or in one experiment, to both eyes. The test presentation period was just three seconds and in this time the observer decided whether or not he could perceive the grating structure. If he could not, the experimenter changed the filters, fr2, to allow more light to pass through the wedge. If he could see the grating structure, the observer was instructed to adjust the wedge to reduce the illumination level of the test still further. After three seconds, the test beam was cut off automatically by the time switch on the shutters and the adaptation gratings and conditioning gratings presented once more. After 20 seconds readaptation, the test was again presented for a further 3 seconds; this cycle of 20 seconds adaptation, 3 seconds test was maintained until the observer had obtained a satifactory threshold setting. After marking this value on the recording drum, the experimenter re-set the wedge arbitrarily so as to make the test grating visible again, and the observer repeated the experiment.

When five threshold illumination levels for the test grating had been determined, the adaptation and conditioning gratings were replaced by two uniform fields of the same mean illumination level. This was done by blocking between bs6 and m3 (fig. 2) one of the pairs of beams provided by laser 2 (previously supplying the adaptation grating) and removing the stop st_1 (fig. 2, inset). A second stop was introduced, in the upper level only, between bs3 and p3. Thus during the adaptation period, only one of the two interfering components of laser 2 was visible, but this was presented to both left and right eyes. The illumination level of this uniform field was increased to an illumination level equal to the space average illumination level of the grating adaptation field by removing a 0.3 log unit filter from the filters, fr, thus compensating for the component of laser 1 which was being blocked.

After an initial two minutes of adaptation to the uniform fields, the same 3 seconds test, 20 seconds adaptation cycle described previously was continued until the observer found the new threshold illumination level. The test grating itself remained unaltered by the changes made to the adaptation fields. Again, five settings of the test threshold were made. A typical record of experimental values for a 7 c/° monocular adaptation experiment is shown in fig. 9. T_1 represents the mean of the five grating adaptation thresholds and T_2, the mean of the five uniform field adaptation thresholds.

A comparison of T_1 with T_2 shows that the test threshold following adaptation to a grating is slightly ~~lower~~ higher than that obtained following adaptation to a uniform field of the same mean illumination level. This effect is known as the contrast threshold elevation effect (see introduction). The error in the measurements, calculated in terms of the standard deviation, is approximately 0.05 log units. This compares with the magnitude of the threshold elevation of about 0.4 log units, for say a monocular experiment with no conditioning grating and test and adaptation presented to one eye only. Thus it can be seen that the magnitude of the threshold elevation, although small, is significant.

The test presentation period is necessarily limited to 3 seconds because the contrast threshold elevation effect itself is short-lived, with Δ quickly falling to zero following removal of the adaptation stimuli. The monocular recovery curve in fig. 10 illustrates this point and is in agreement with the data of Blakemore and Campbell (1969b). All data points presented in the figures of the subsequent chapters represent, unless otherwise specified, the mean of ten readings. The error bars drawn on these points represent the standard deviation about the mean.

It has been indicated that the conditioning, CG, adaptation, AG, and test, TG, gratings can be presented to the observer's left or right eye in almost any combination. Their spatial frequencies, f_{cg}, f_{ag} and f_{tg}, respectively, and the illumination levels of the conditioning grating, I_{cg}, and the adaptation grating I_{ag}, are specified for each experiment.

Chapter 3.

PRELIMINARY MEASUREMENTS

It was indicated in the introduction that prolonged viewing of a sinusoidal or square wave grating raises the detection threshold of a similar test grating (Pantle and Sekuler, 1968; Gilinsky, 1968; Blakemore and Campbell, 1969). The elevation of contrast threshold is maximal for test and adaptation gratings of the same orientation and spatial frequency. The elevation effect has also been extensively studied interocularly, that is, with the adaptation grating in one eye and the test grating presented subsequently to the other eye (Blakemore and Campbell, 1969; Maudarbocus, 1973). In the human visual system, pathways from the two eyes converge anatomically by partial crossing over of the optic nerve fibres at the optic chiasma. Neurophysiological studies of the visual cortex of primates show that these converging pathways carry signals from both eyes to the same cortical neurones. The interocular transfer of the contrast elevation effect would suggest the site of this kind of adaptation to be centrally located in the cortex, since any other interpretation would require retinal control by centrifugal fibres emanating from the cortex for which there is a lack of evidence (Brindley, 1970, p. 105).

The original purpose of this investigation was to study possible summation effects in grating adaptation experiments. The magnitude of the monocular and interocular contrast elevation effects were to be compared with that arising from a combination of the two, i.e. the same frequency and orientation adaptation gratings presented to both left and right eyes, but a test grating presented to only one. Summation of adaptation would be indicated by a greater elevation of threshold in this latter experiment than that from either the monocular or interocular set-ups measured in isolation. A series of experiments were undertaken:

(a) The variation of Δ, the elevation of threshold, with increasing illumination level of adaptation field as measured monocularly for both left and right eyes.

(b) The variation of Δ with adaptation illumination as measured interocularly, transferring from the left to right eye and vice-versa.

(c) The variation of Δ with the intensity of identical adaptation gratings presented to both eyes for a test presented to either the left or the right eye.

(a) Monocular measurements (All data refer to E.W., an emmetrope, unless otherwise indicated)

Figs. 1 and 2 show the ~~logarithmic~~ increase in the threshold of the test grating Δ (as defined in chapter 2, page 57) as a function of the log intensity of the adaptation grating I_{ag}, when the two gratings are presented to the ~~right~~ left eye. Figs. 3 and 4 refer to the same experimental situation applied to the ~~left~~ right eye. In both cases test and adaptation gratings are of the same orientation (vertical) and spatial frequency (either 7 or 2 cycles per degree of visual angle). The linear relationship between Δ and log I for low adaptation illumination levels is in agreement with that observed by other experimenters (Blakemore and Campbell, 1969). As a further check with the results of these earlier experimenters, the monocular (right eye) frequency and orientation selectivities were measured. Figs. 5 and 6 represent situations where the test grating spatial frequency was maintained at either 2 c/° or 7 c/° (f_{tg}) and Δ measured as a function of the frequency of the adaptation grating (f_{ag}). The observation that the threshold elevation is bandwidth-limited to ~~just over an~~ one to two octaves at half amplitude is consistent with the experiments of Blakemore and Campbell (1969),

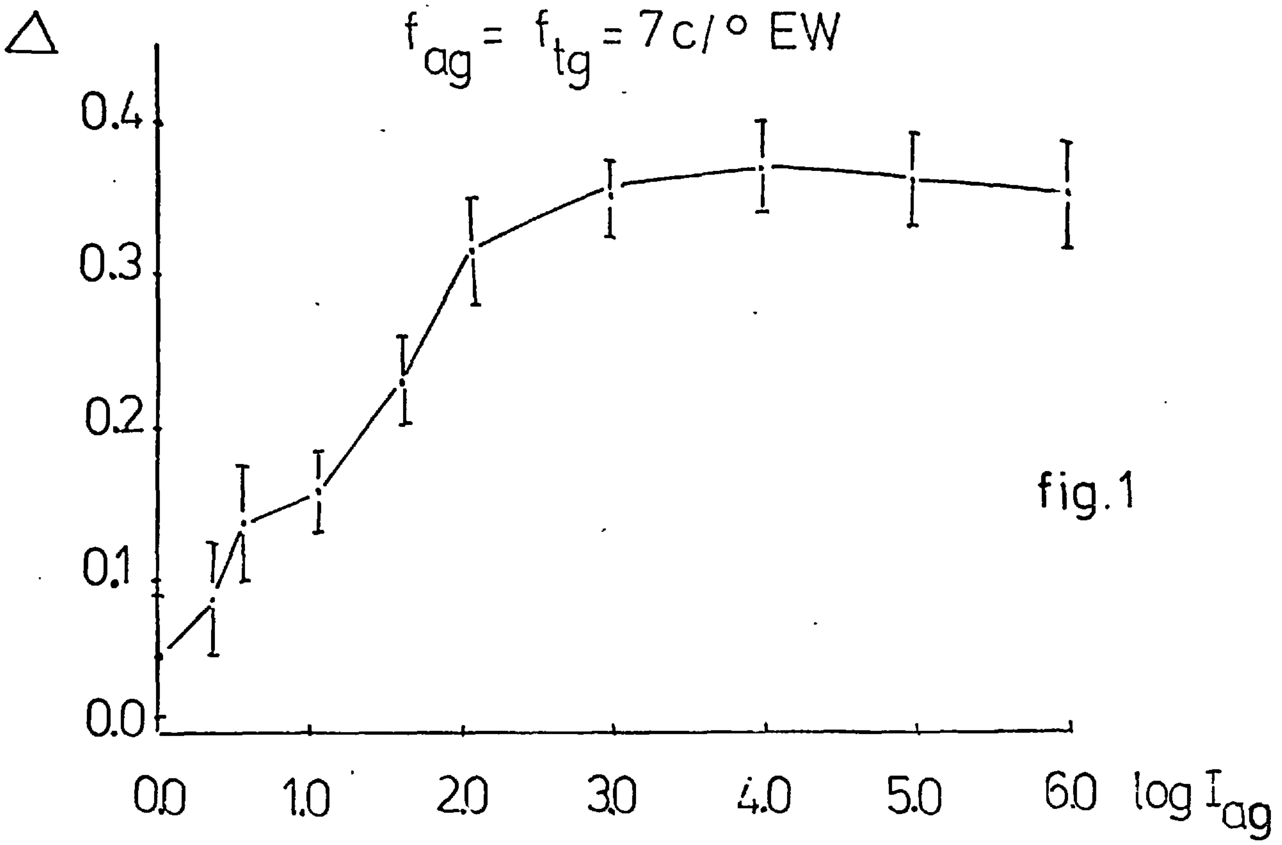


fig.1

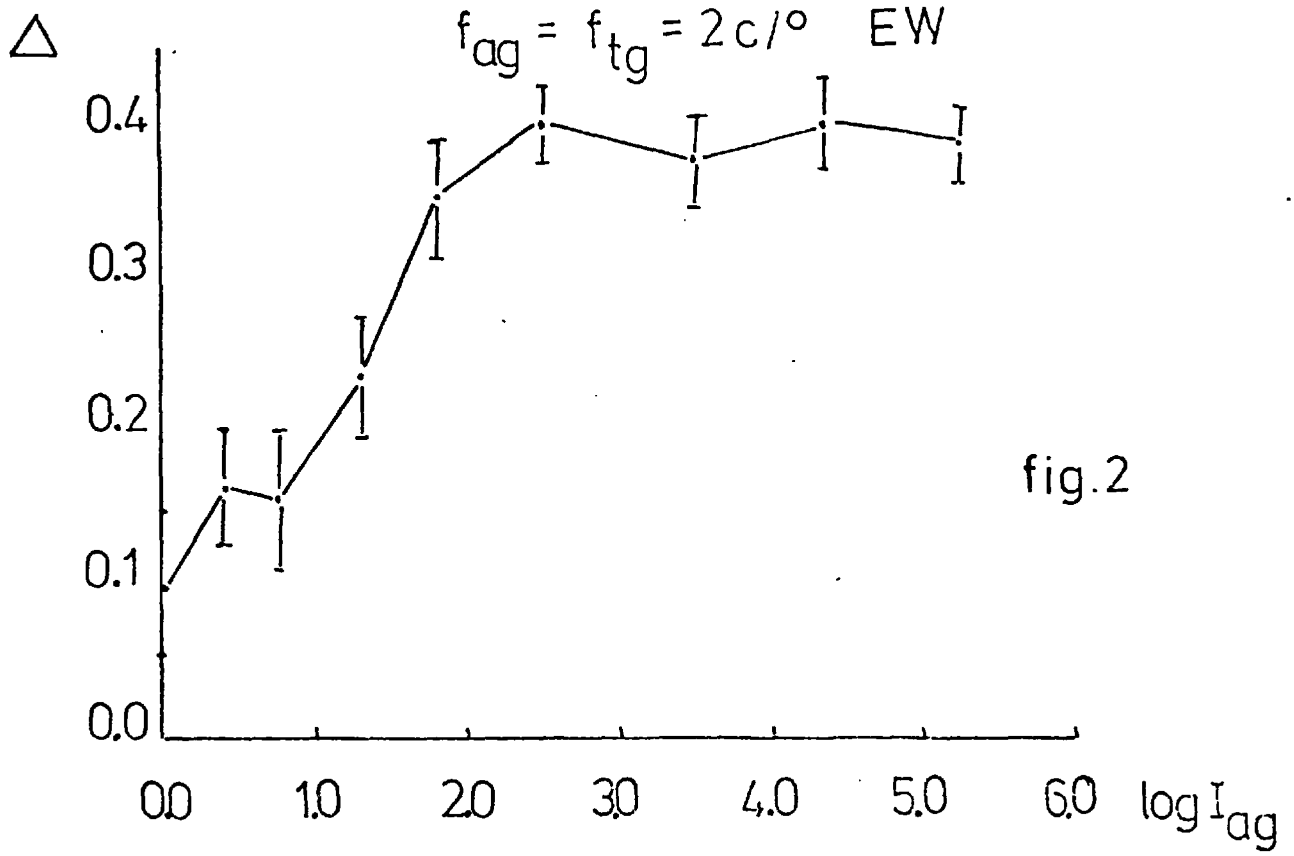


fig.2

test and adaptation in L eye

chapt. 3

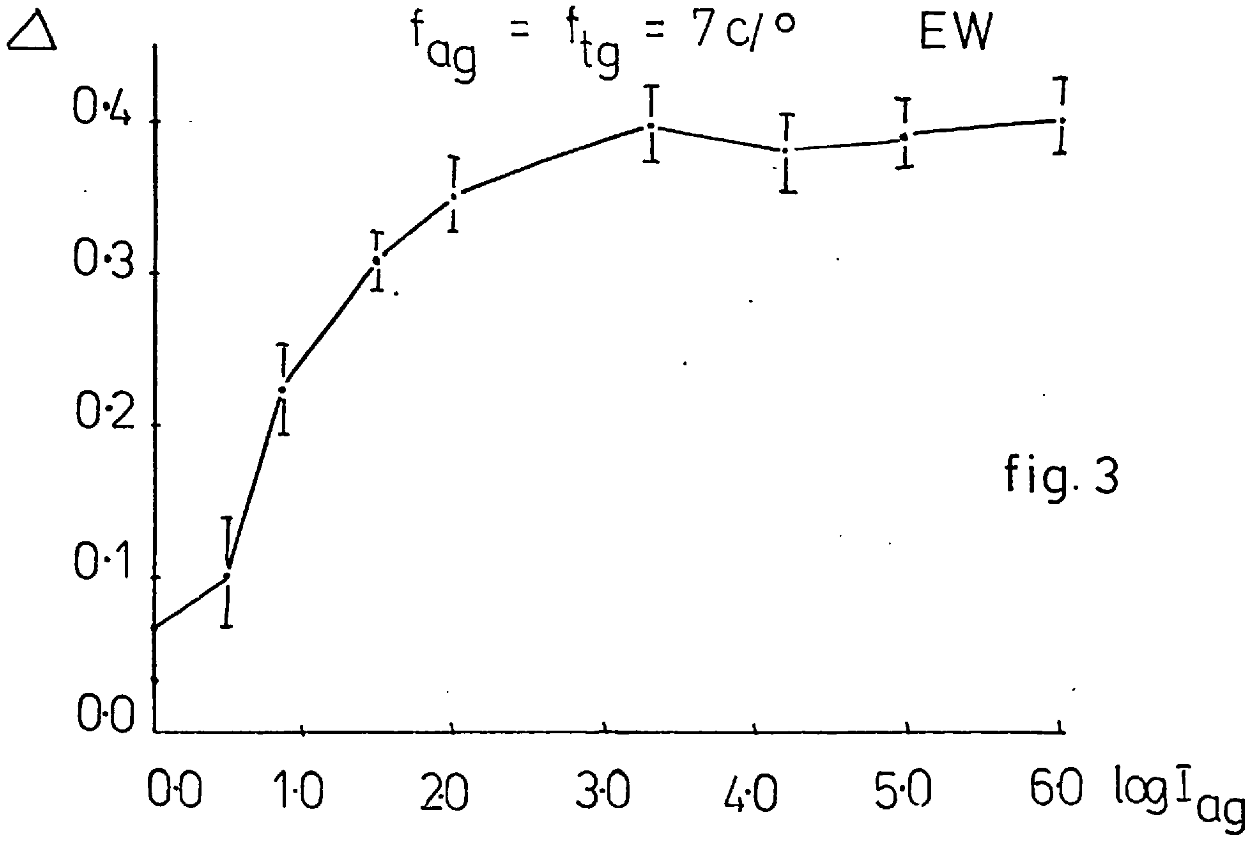


fig. 3

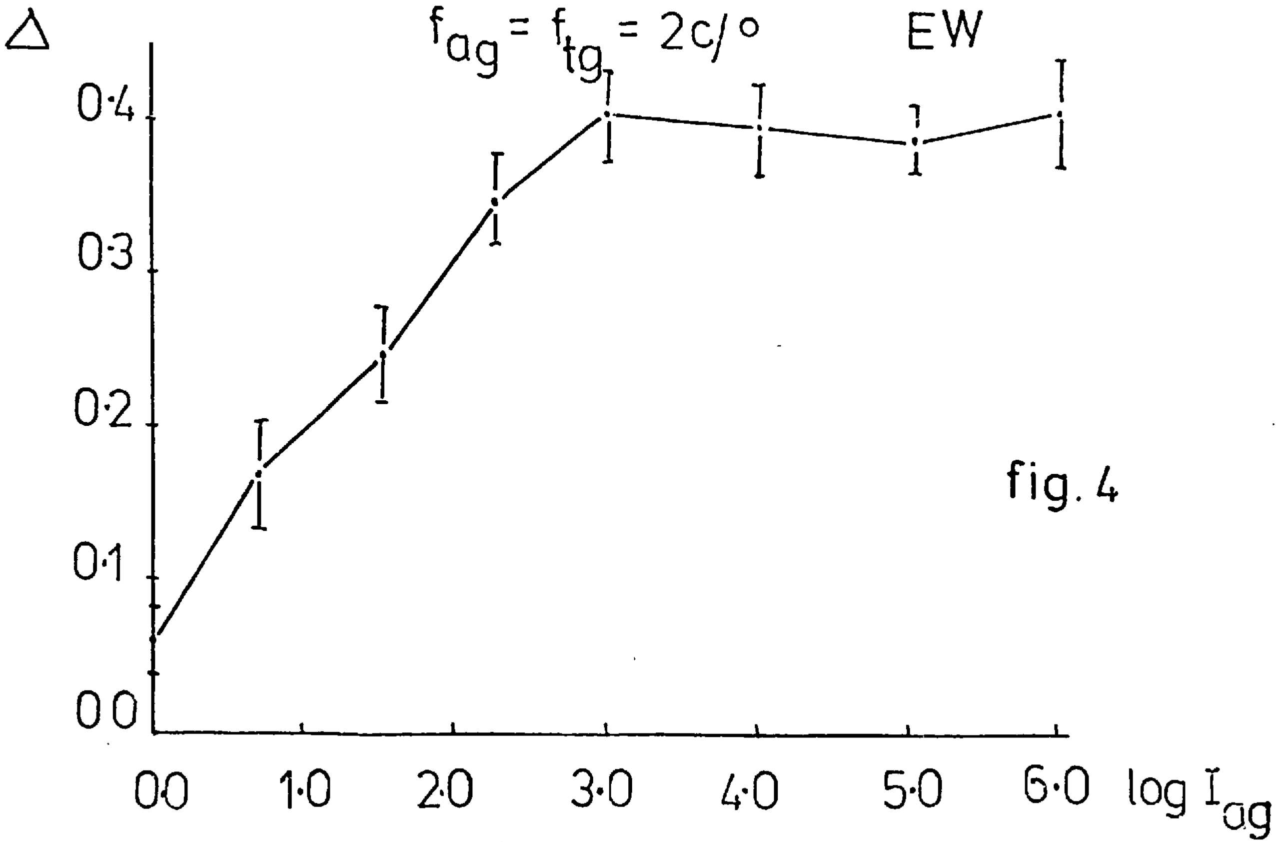


fig. 4

test and adaptation in R eye

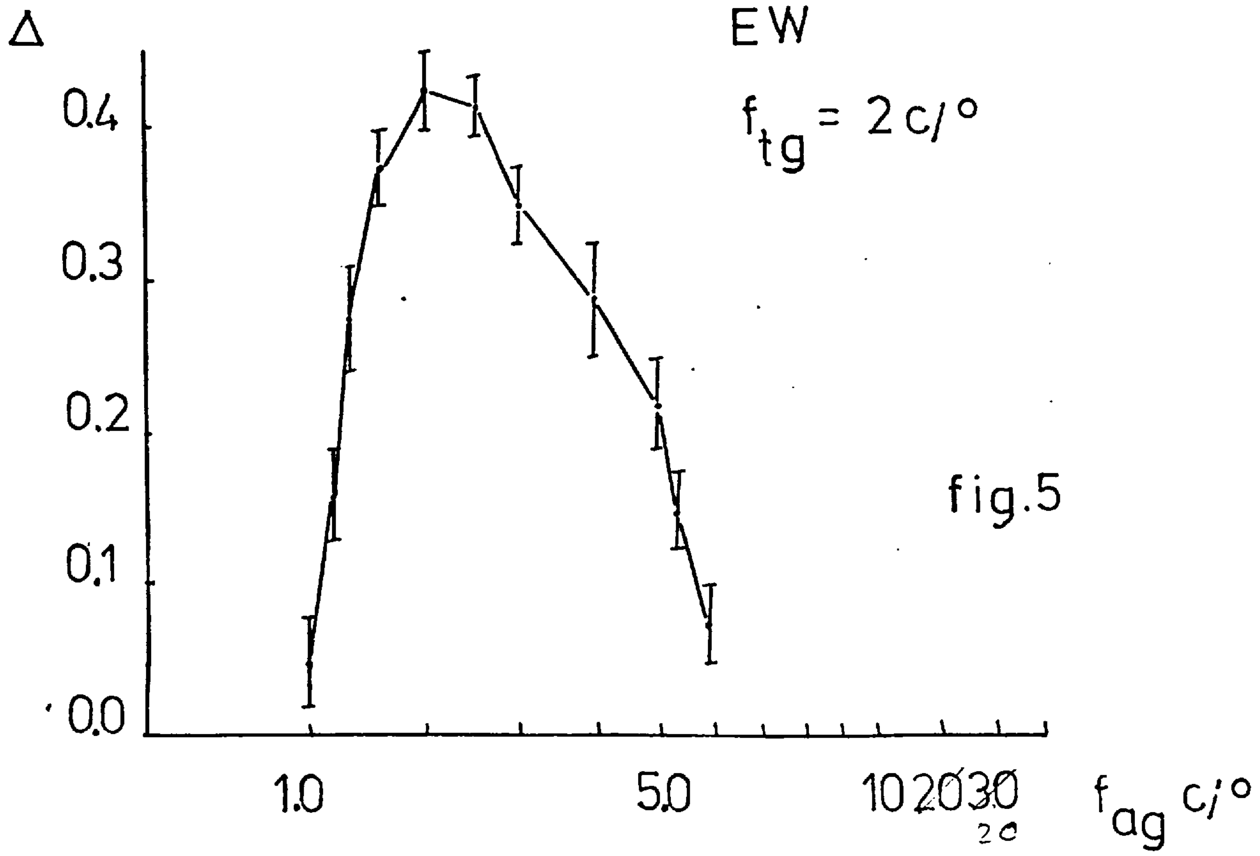


fig.5

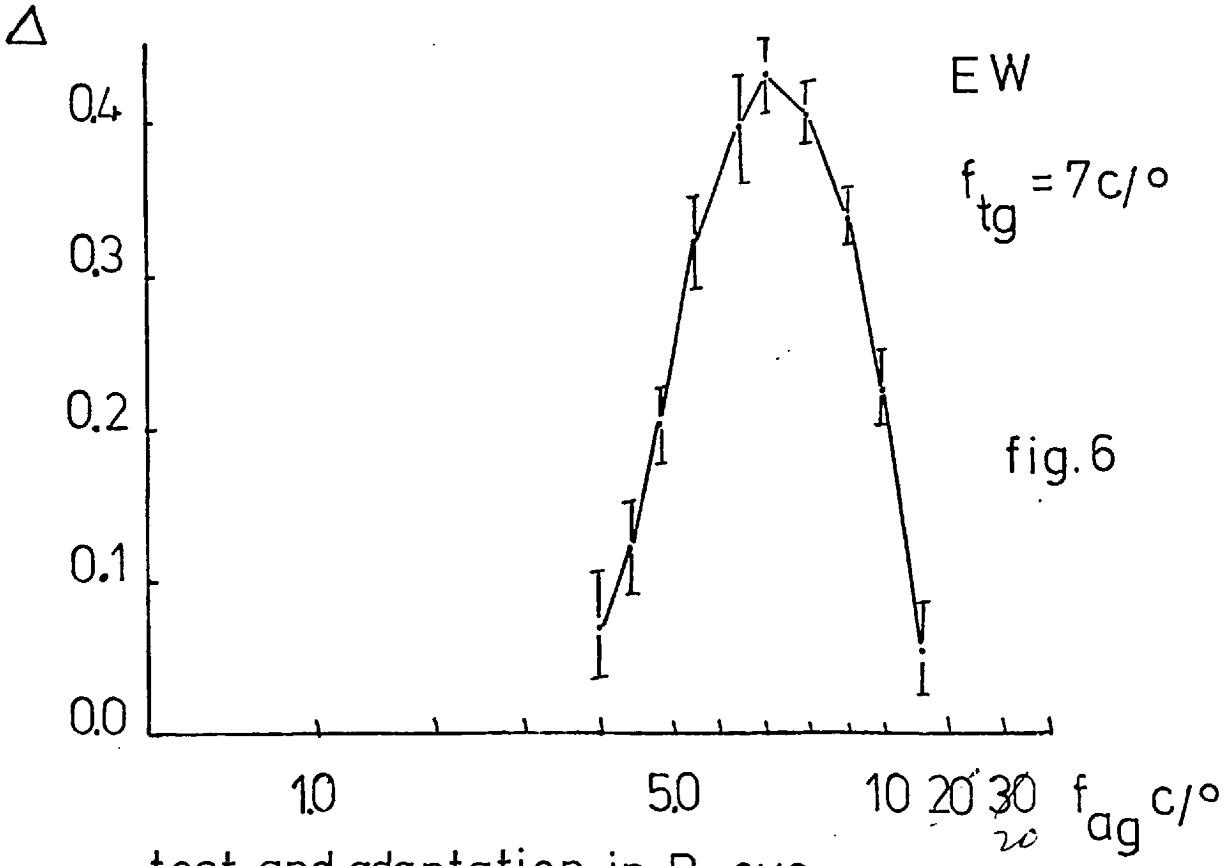


fig.6

test and adaptation in R eye

but whereas Blakemore and Campbell (1969) found the maximum response for test frequencies less than 3 c/° to occur at adaptation grating frequencies equal to 3 c/°, fig. 5 shows a maximum for $f_{ag} = 2$ c/°. This could perhaps be a result of the 30° test and adaptation fields used in the present series of experiments as compared with the 1.5° field used by Blakemore and Campbell (1969). Large fields would minimise any possible edge effects. Results comparable to those obtained here, again using larger adaptation fields than those of Blakemore and Campbell (1969) were reported by Maudarbocus and Ruddock (1973b). Figs. 7 and 8 show the variation of Δ (as measured for a vertical test grating) as a function of the orientation θ of the adaptation grating. The test and adaptation spatial frequencies were held at either 7 c/° or 2 c/°. The results are again consistent with those of other experimenters (Gilinsky, 1968).

(b) Interocular measurements

In this set of experiments, Δ was determined for a test grating presented to the dark adapted eye after adaptation of the other eye. Figs. 9 and 10 show the variation of Δ with intensity of the adaptation grating presented to the left eye for two spatial frequencies ($f_{ag} = f_{tg}$). Figs. 11 and 12 show the results of presenting the adaptation grating to the right eye. Again, two values of grating spatial frequencies were used. It can be seen that the maximum value of Δ transferred interocularly is less than the 70% of the monocular value recorded by other experimenters (Blakemore and Campbell, 1969; Gilinsky and Doherty, 1969). Experiments on the interocular transfer of the tilt after effect (described in the introduction) associate lack of transfer with reduced stereopsis (Movshon, Chambers and Blakemore, 1972; Ware and Mitchell, 1973). In these experiments, stereopsis was estimated from the clinical histories of the observers, their performance on random

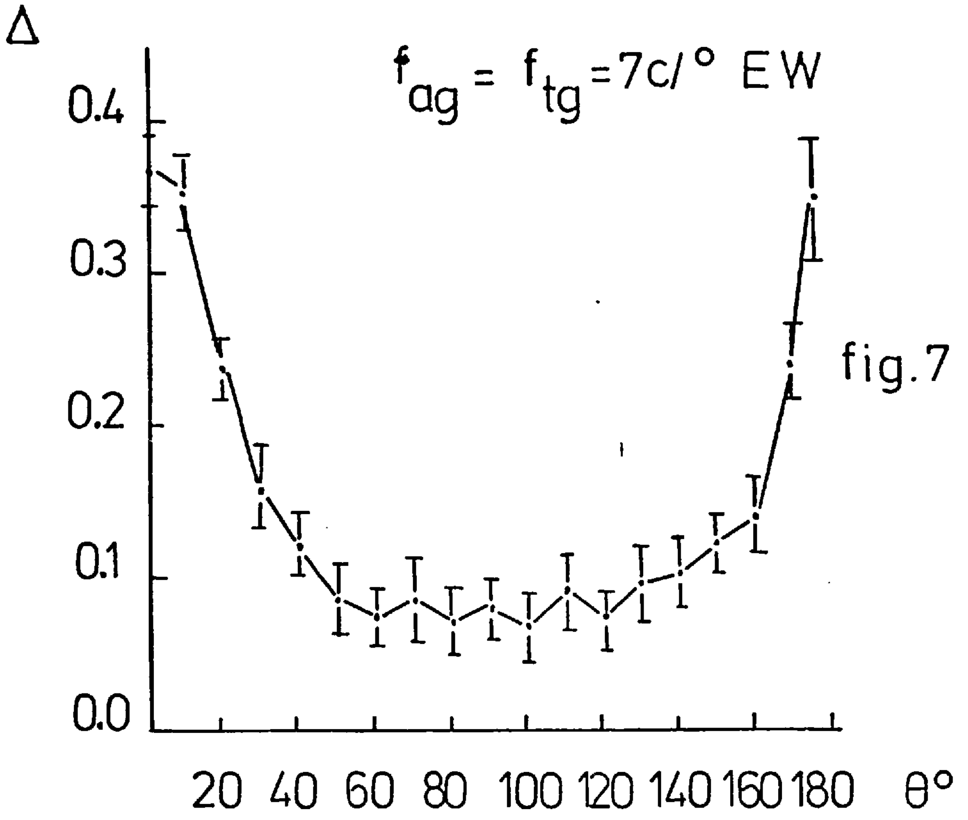


fig.7

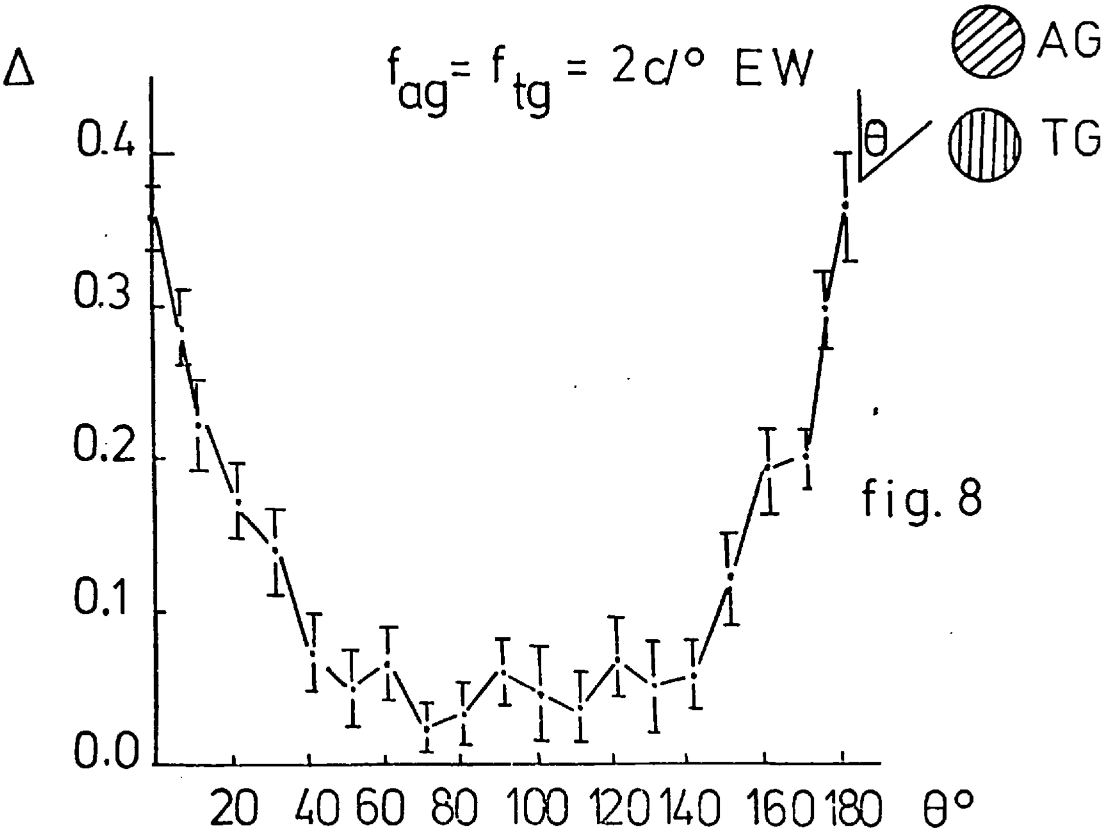


fig. 8

test and adaptation in R eye

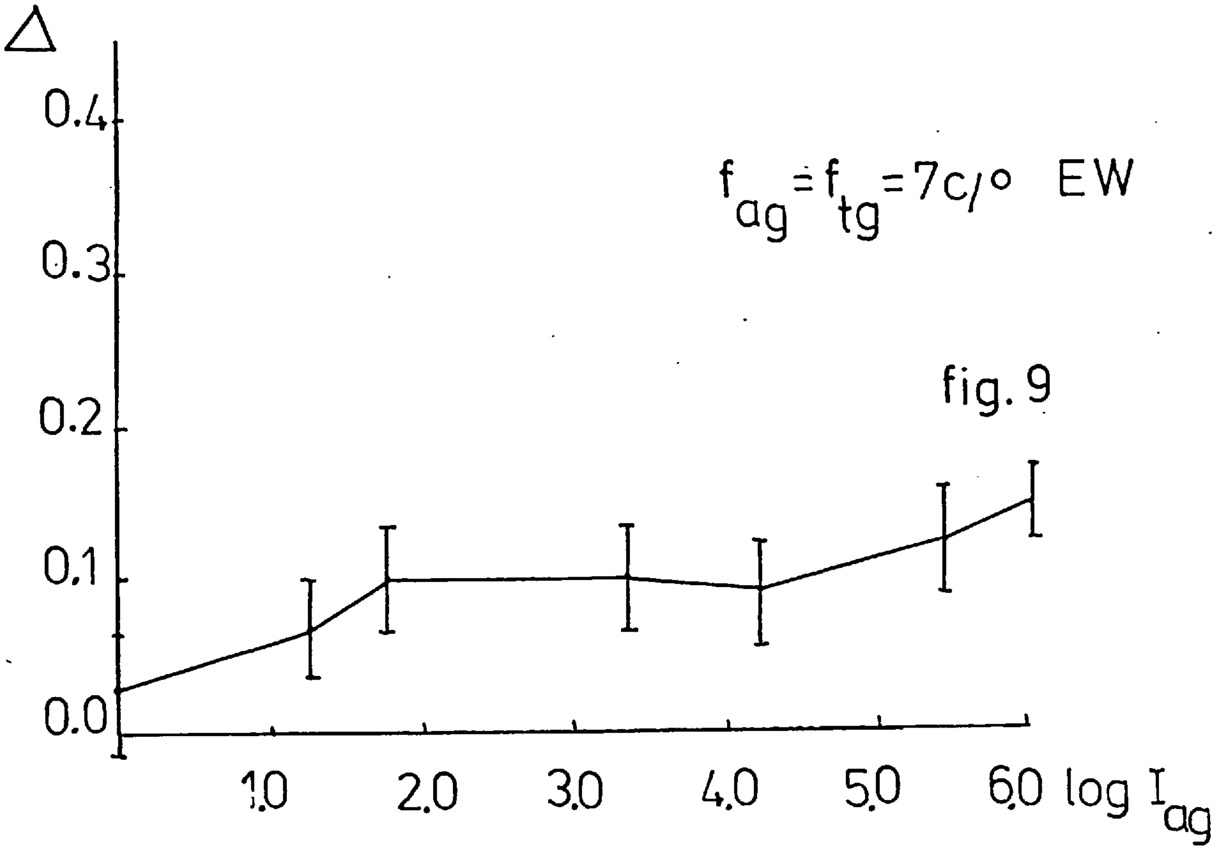


fig. 9

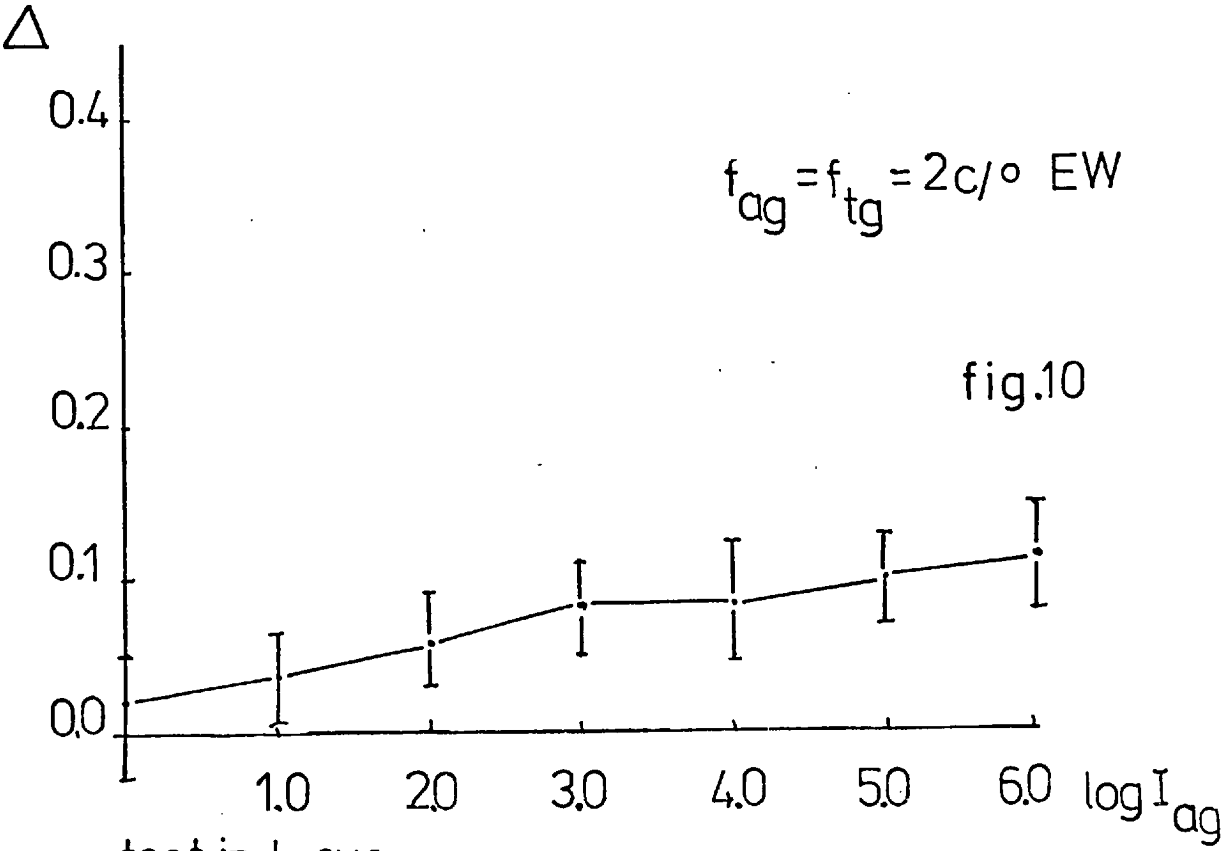


fig.10

test in L eye
adaptation in R eye

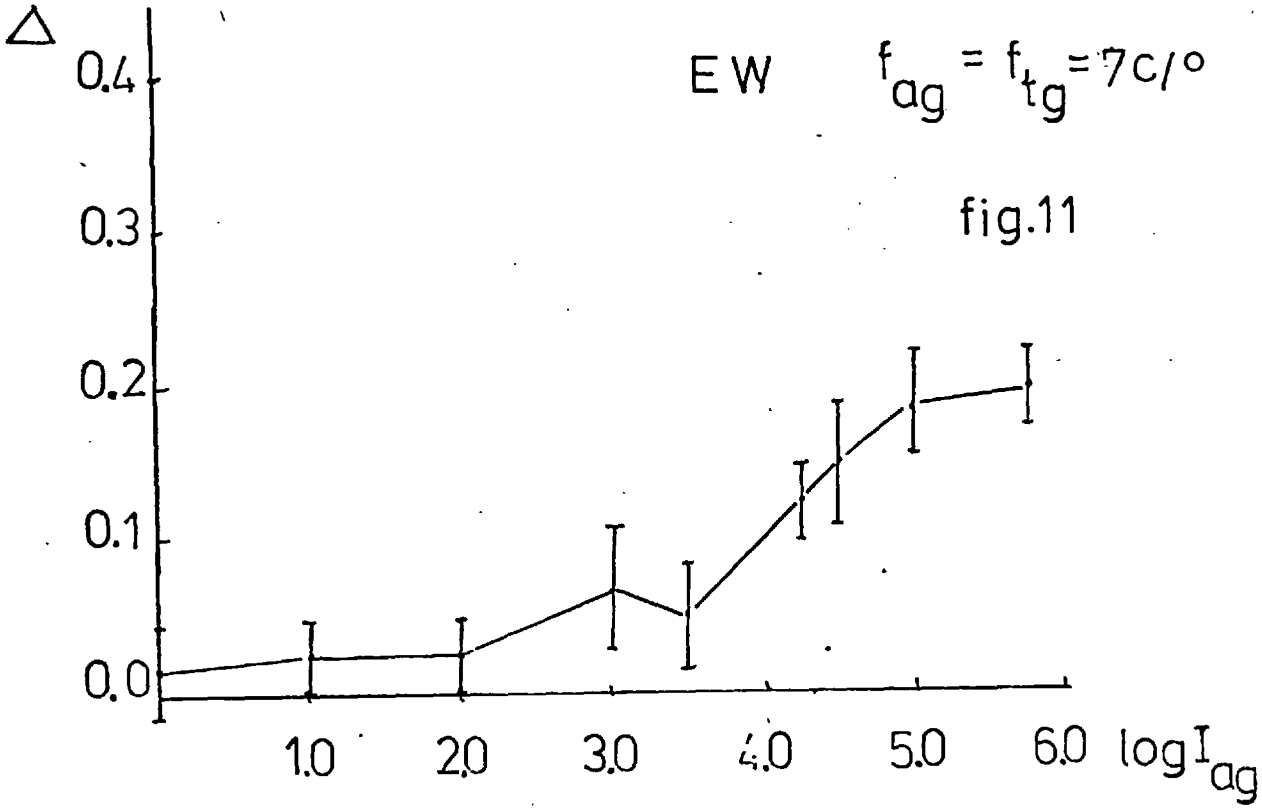


fig.11

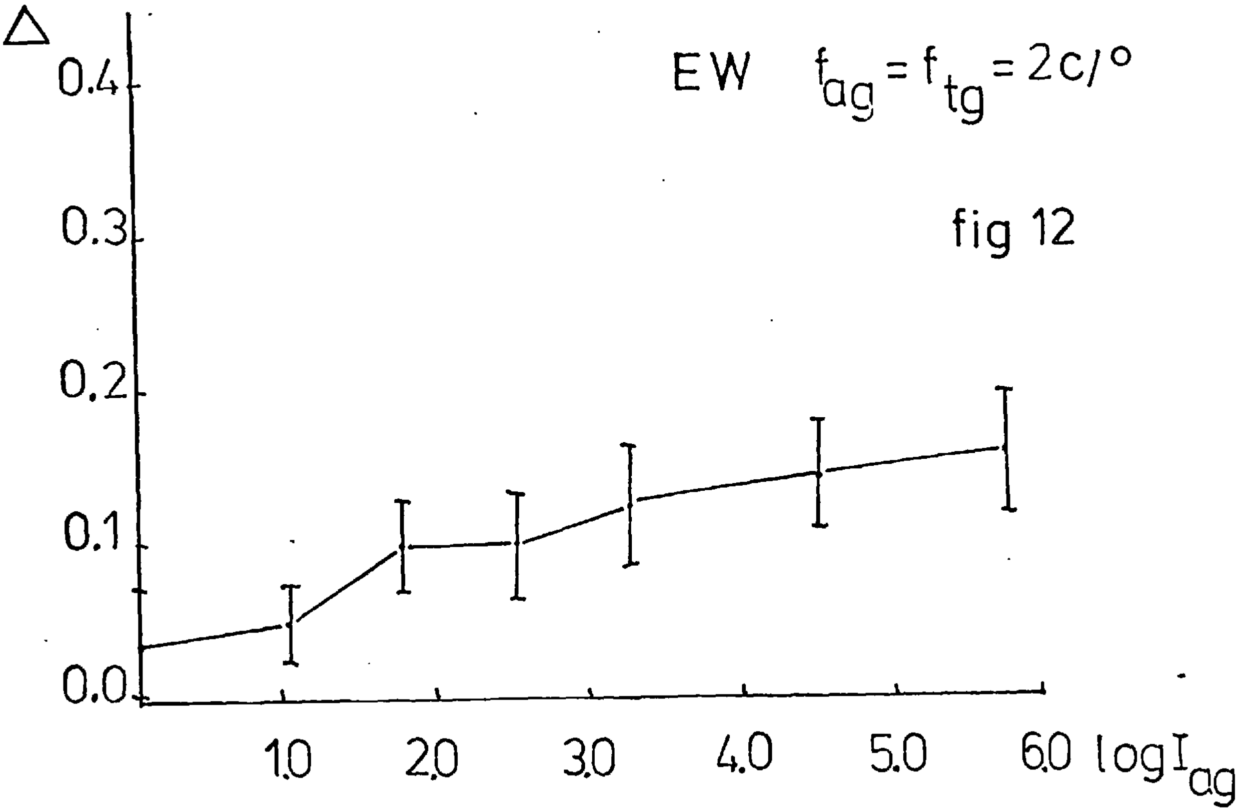


fig 12

test in R eye
adaptation in L eye

dot stereograms of varying degrees of decorrelation between the two fields and also from their performance on the Gulick-Lawson conventional stereogram (Julesz, 1971). Normal observers were defined by their ability to perceive depth in both the Gulick-Lawson stereogram and in Julesz stereograms above 70% correlation. In both these tests, E.W. showed normal stereopsis and her clinical history shows no record of strabismus (squint), astigmatism or other visual disorders. The disparity, therefore, between the amount of interocular transfer exhibited here compared with other observers seems to be due to statistical variations.Comparison of figs. 9 with 11 and 10 with 12 shows that the transfer from the left eye to the right eye (adaptation grating in left eye, test grating in right eye) exceeds the transfer recorded in the opposite direction. This is consistent with the observations made by Movshon, Chambers and Blakemore (1972) concerning interocular transfer of the tilt after effect. They found that all subjects with normal stereovision showed greater transfer from the dominant eye to the nondominant than vice-versa. The dominant eye, determined as that eye the observer would choose to use for any monocular sighting task, was found to be the left eye for E.W.

Because the interocularly transferred contrast elevation was less than anticipated, the orientation specificity and frequency selectivity were determined for two grating spatial frequencies. Figs. 13 and 14 represent the orientation selectivity for a vertical test grating and a series of oblique adaptation gratings. Figs. 15 and 16 show the spatial frequency tuning of the elevation effect around the test frequency. Although the maximum elevation of threshold is still less in all cases than that recorded by earlier observers, the characteristics of the selectivity curves are the same.

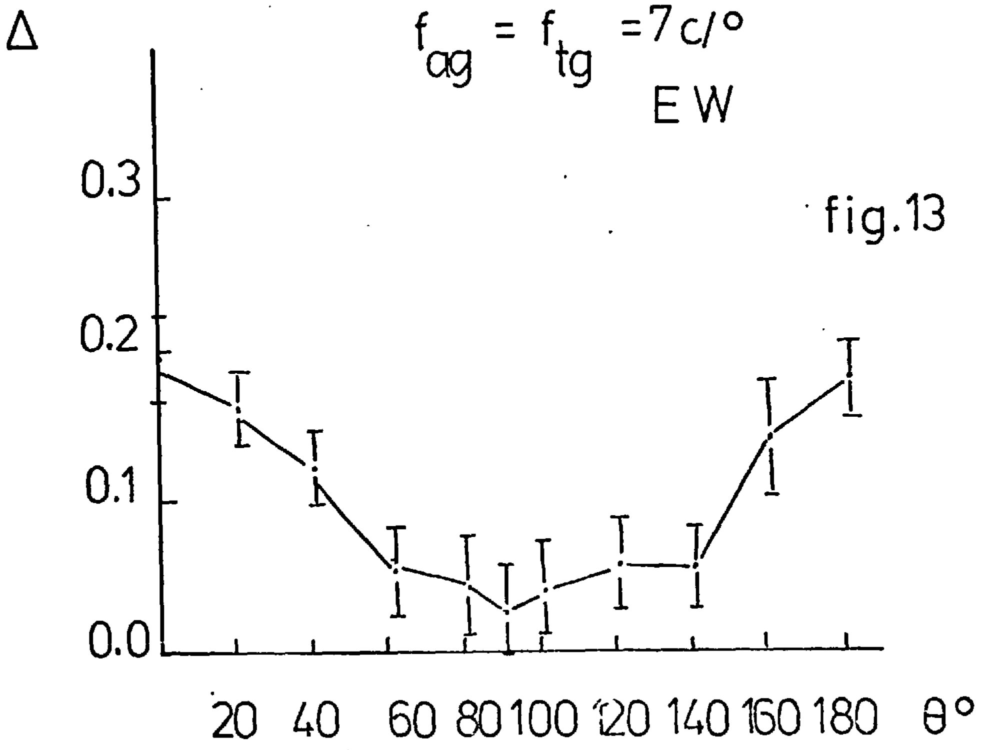


fig.13

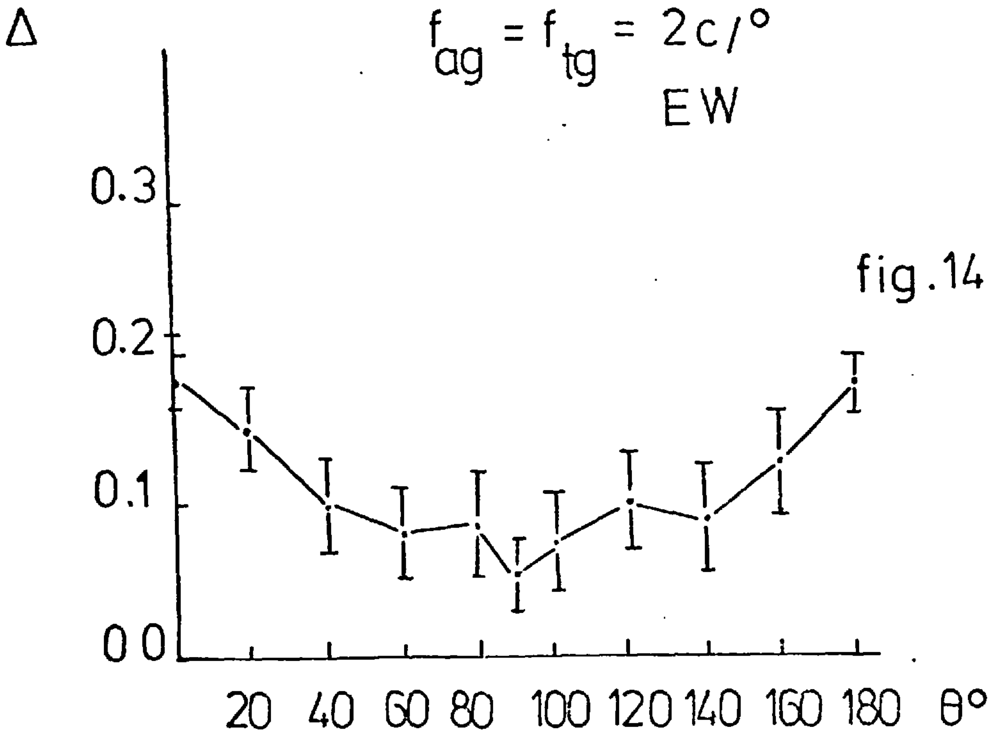


fig.14

test in R eye, adaptation in L eye

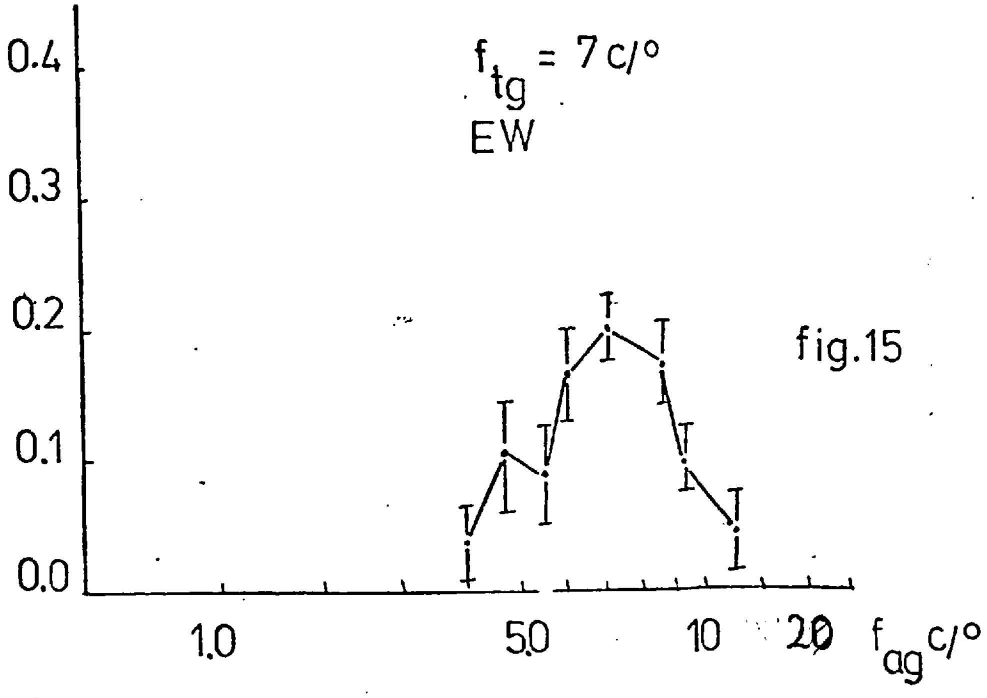


fig.15

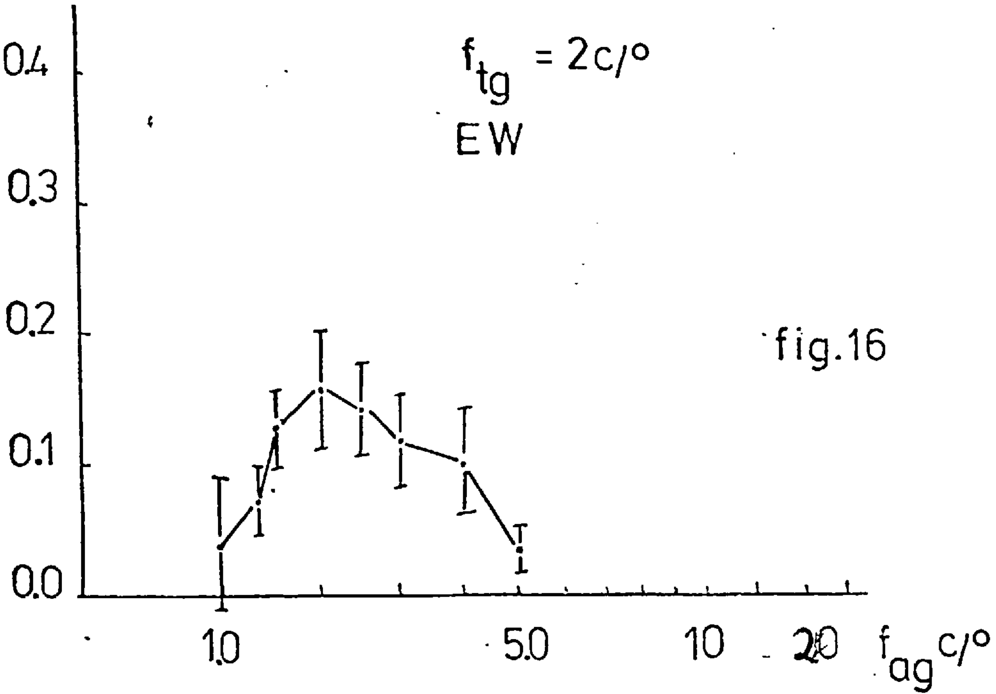


fig.16

test in L eye
adaptation in R eye

(c) Binocular experiments

Having measured the contrast elevation effect monocularly and interocularly, the following experiments were devised to combine these adaptation situations in order to determine whether summation of the two elevations of threshold could be achieved. The two experimental techniques consisted of the presentation of identical adaptation gratings to both left and right eyes for three minutes and a subsequent three second presentation of a test grating of the same spatial frequency as the adaptation gratings to either the left eye or the right eye. This was followed by alternate 20 second adaptation, 3 second test periods until the threshold of the test grating was determined. This threshold was compared with that of the same test grating as measured after adaptation to two uniform fields of the same mean luminance as the adaptation gratings, presented one to each eye. The difference in the two thresholds, Δ, was plotted as a function of the intensity of the adaptation fields. Figs. 17 and 18 show the results for two different values of the adaptation and test spatial frequencies, with the test grating presented in the right eye. Figs. 19 and 20 show the results for the same frequencies presenting the test grating in the left eye. In each case, the binocular set-up (open circles) is compared with the monocular set-up (filled circles) where the adaptation field was presented only to the test eye, the other eye remaining dark adapted. Without exception, the effect of adapting the non test eye is to reduce the amount of contrast elevation effect compared with that observed monocularly, rather than produce summation of the interocular and monocular effects. Repeating the binocular experiment for adaptation gratings of higher spatial frequencies (figs. 21 and 22) again produced less adaptation than the comparable monocular experiments. The results were confirmed by two observers, S.N. and P.D., both of whom possessed normal vision (figs. 23 and 24). The characteristics

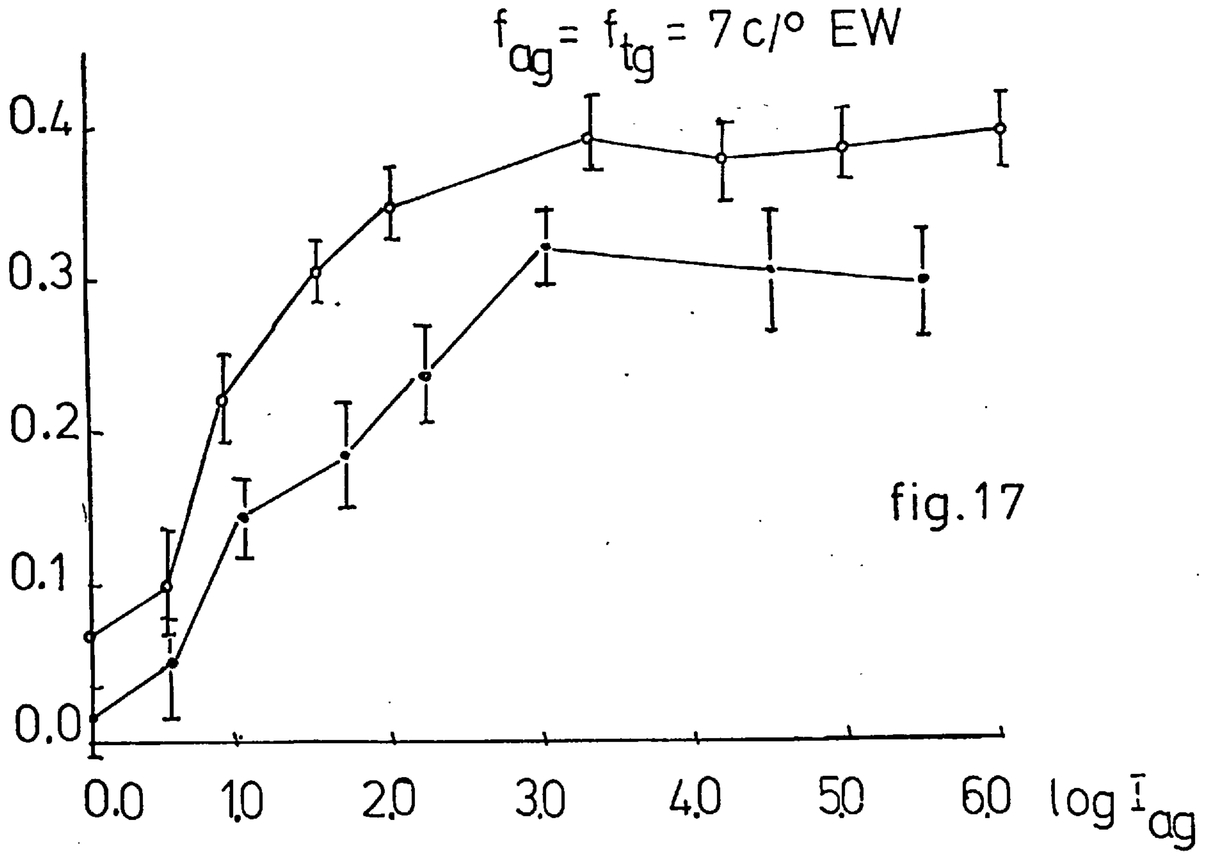


fig.17

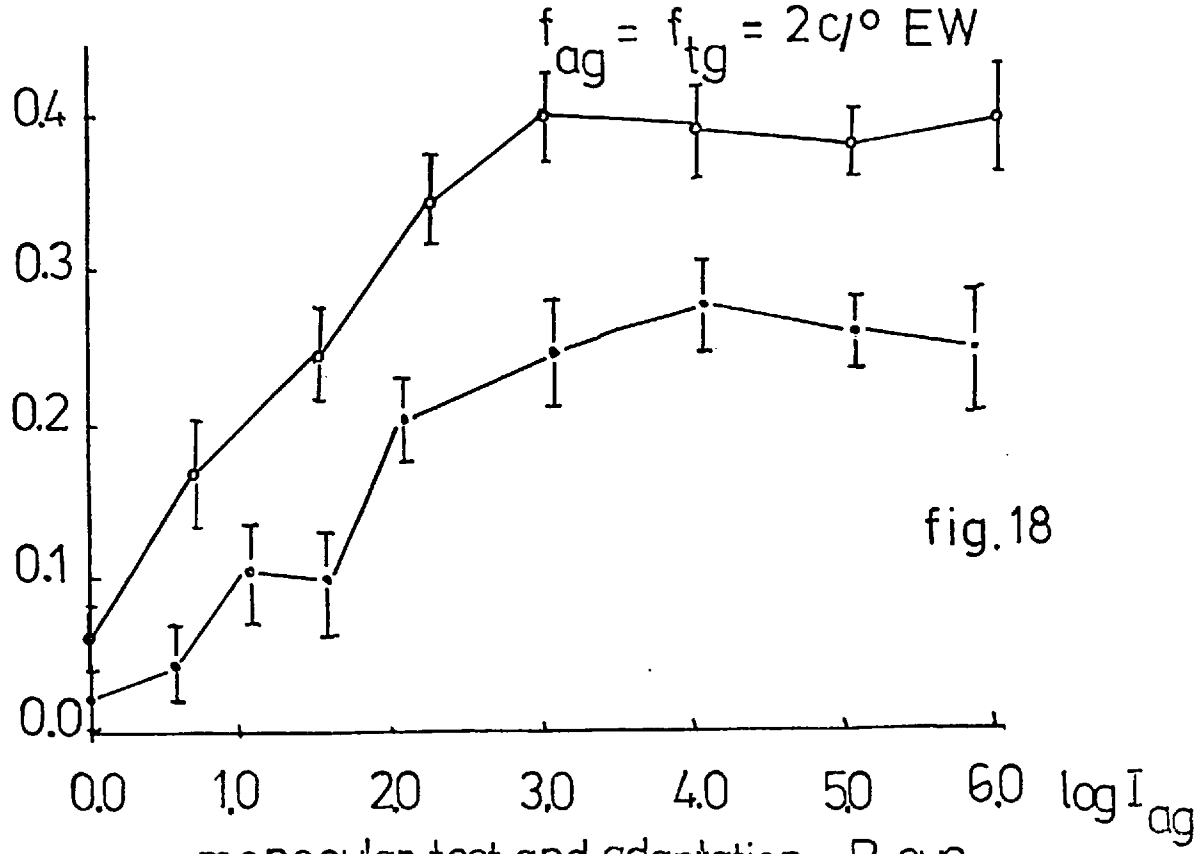


fig.18

∘ monocular test and adaptation: R eye

• R eye test; binocular adaptation

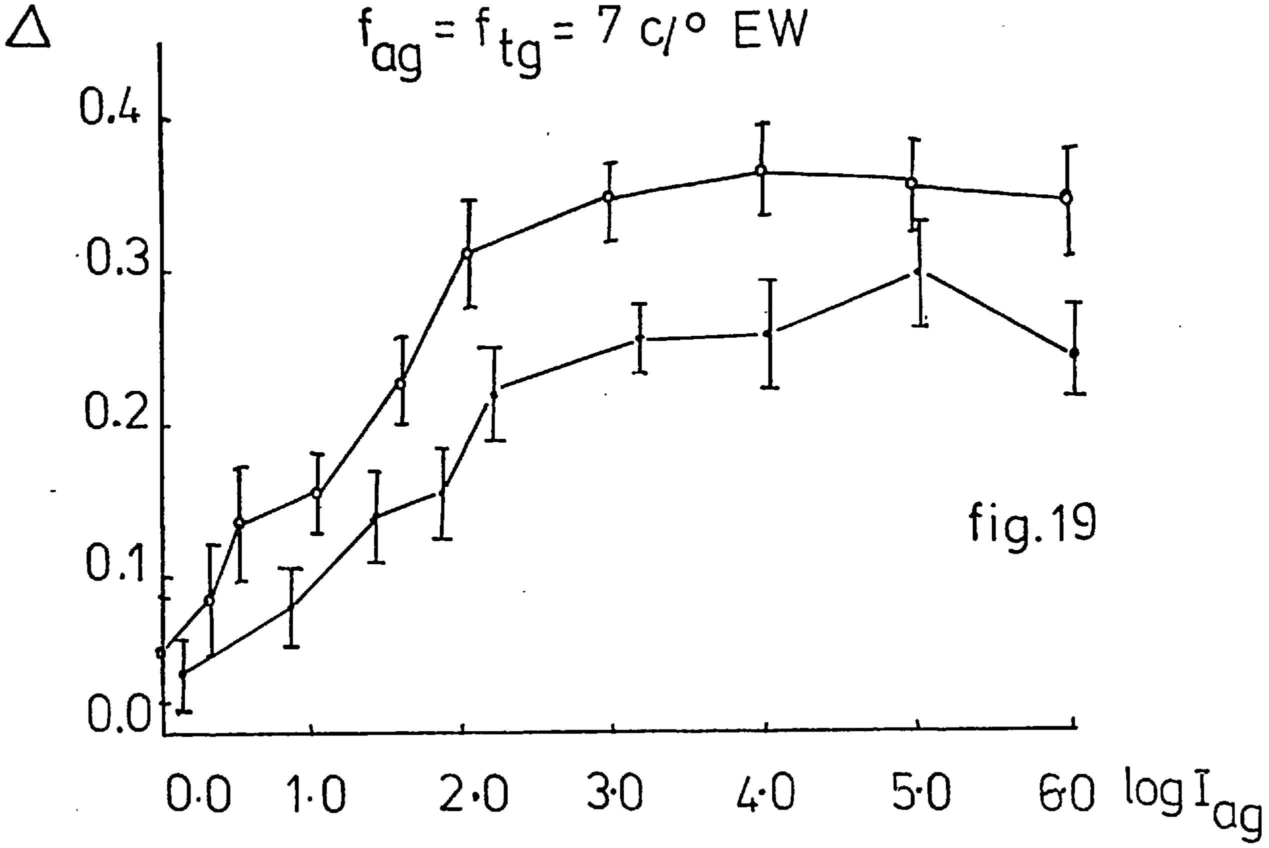


fig.19

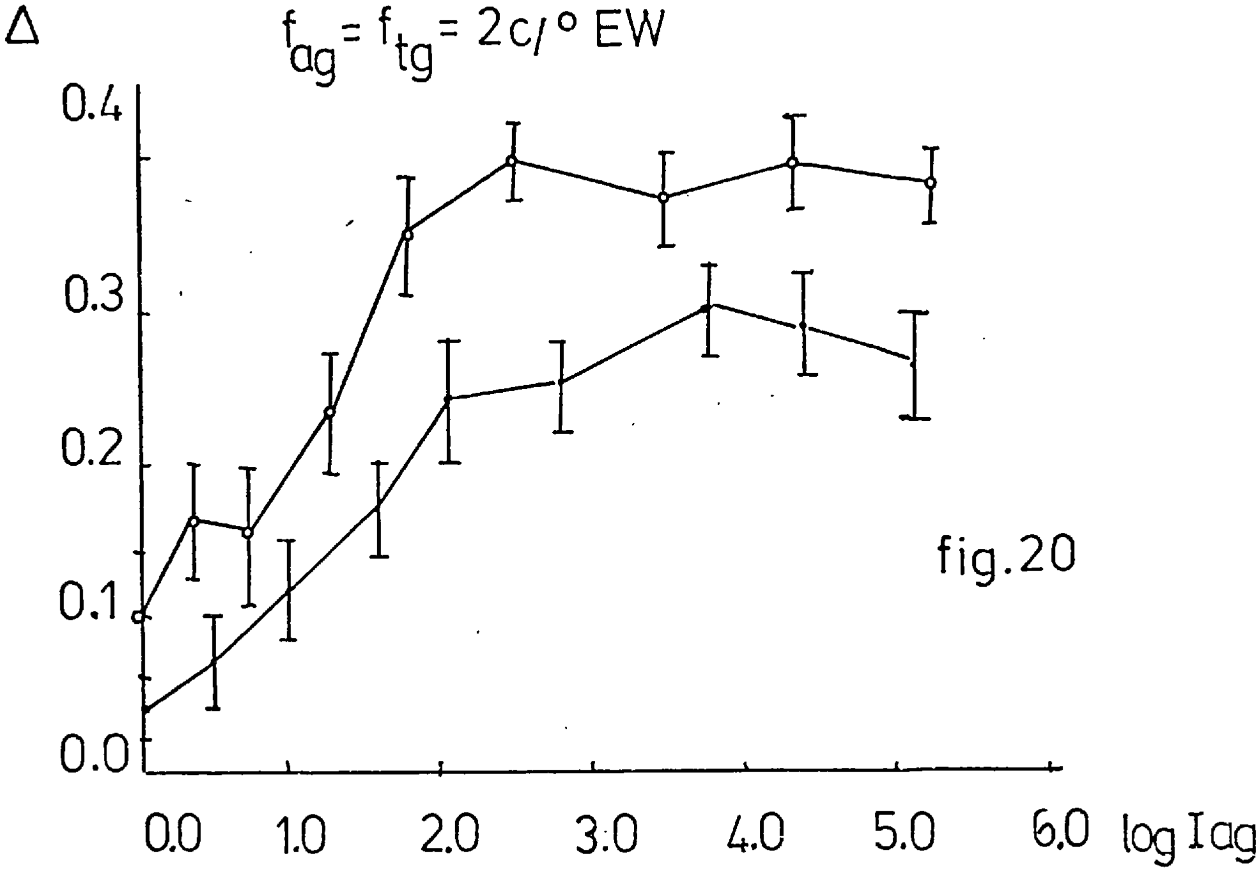


fig.20

∘ monocular test and adaptation: L eye

• L eye test ; binocular adaptation

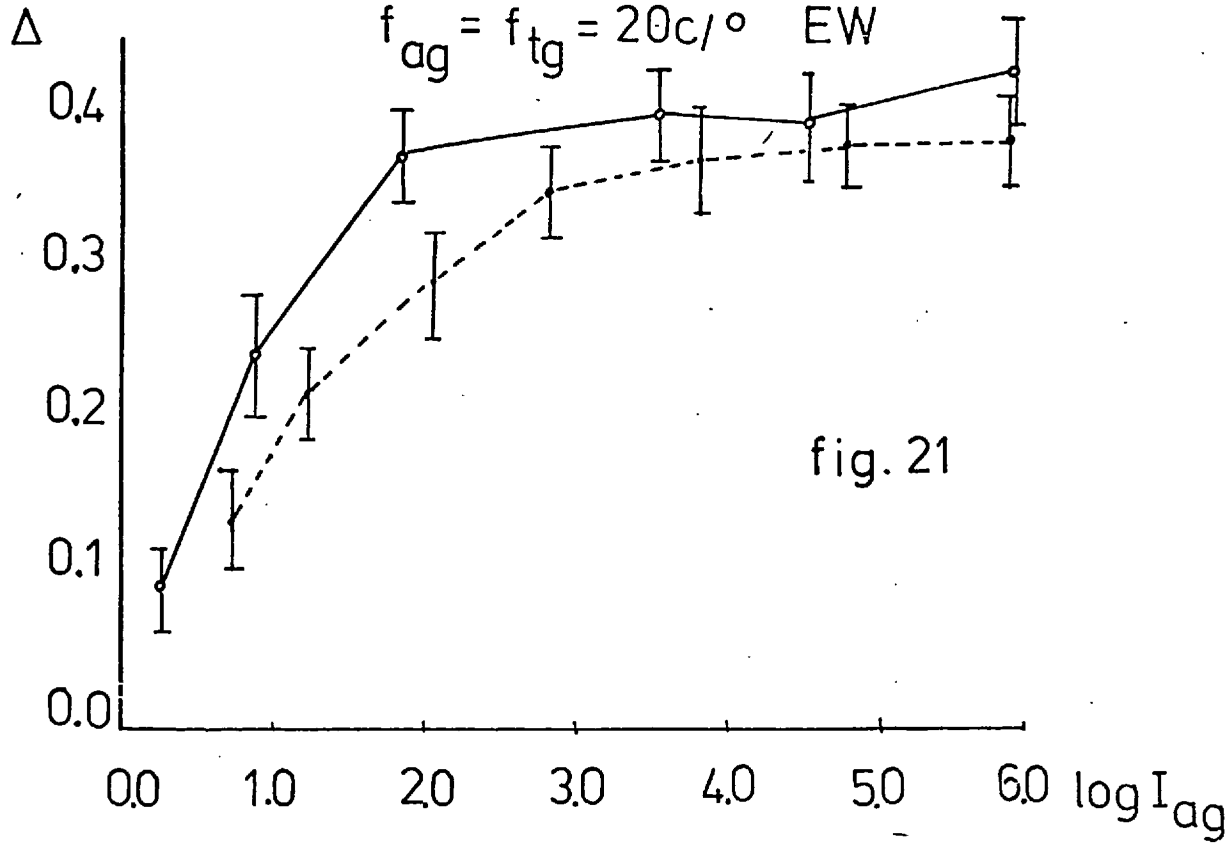


fig. 21

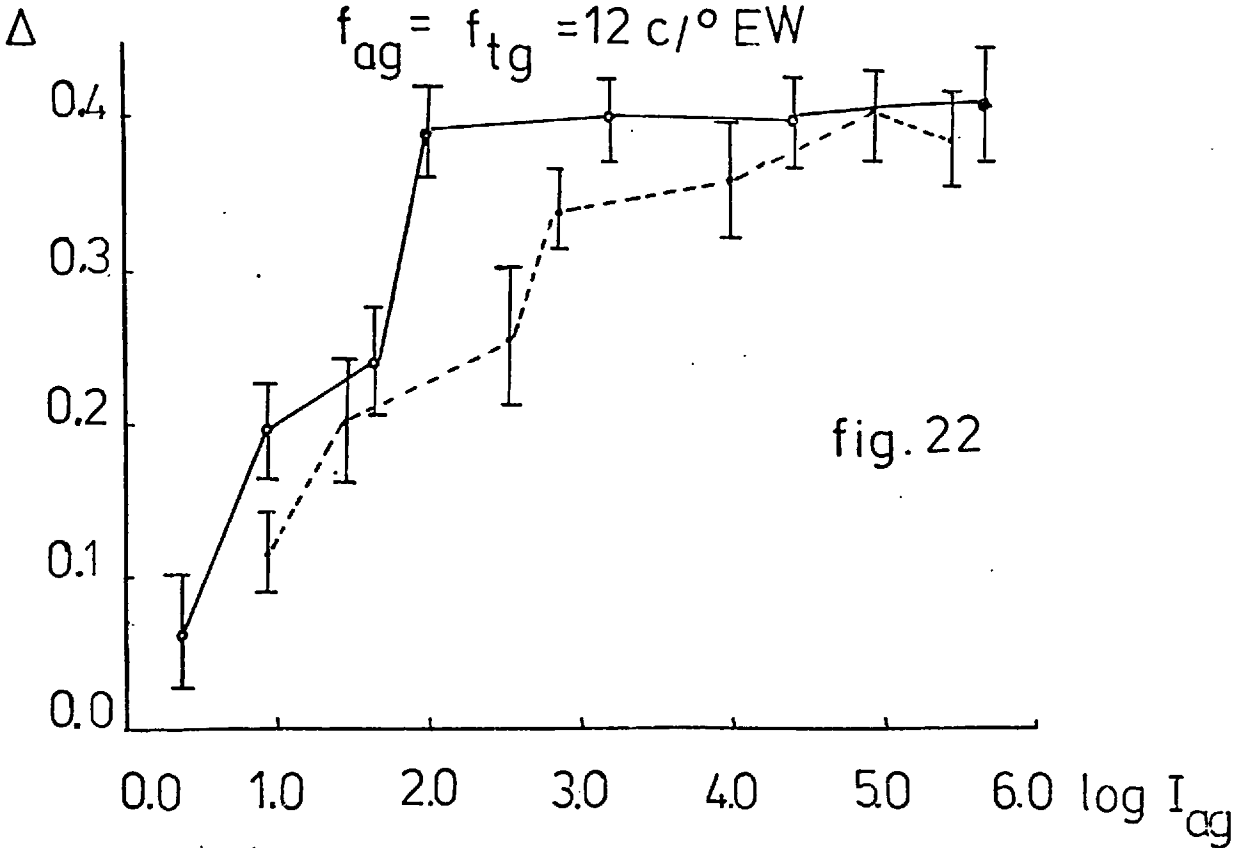


fig. 22

—monocular test and adaptation: R eye

----R eye test : binocular adaptation

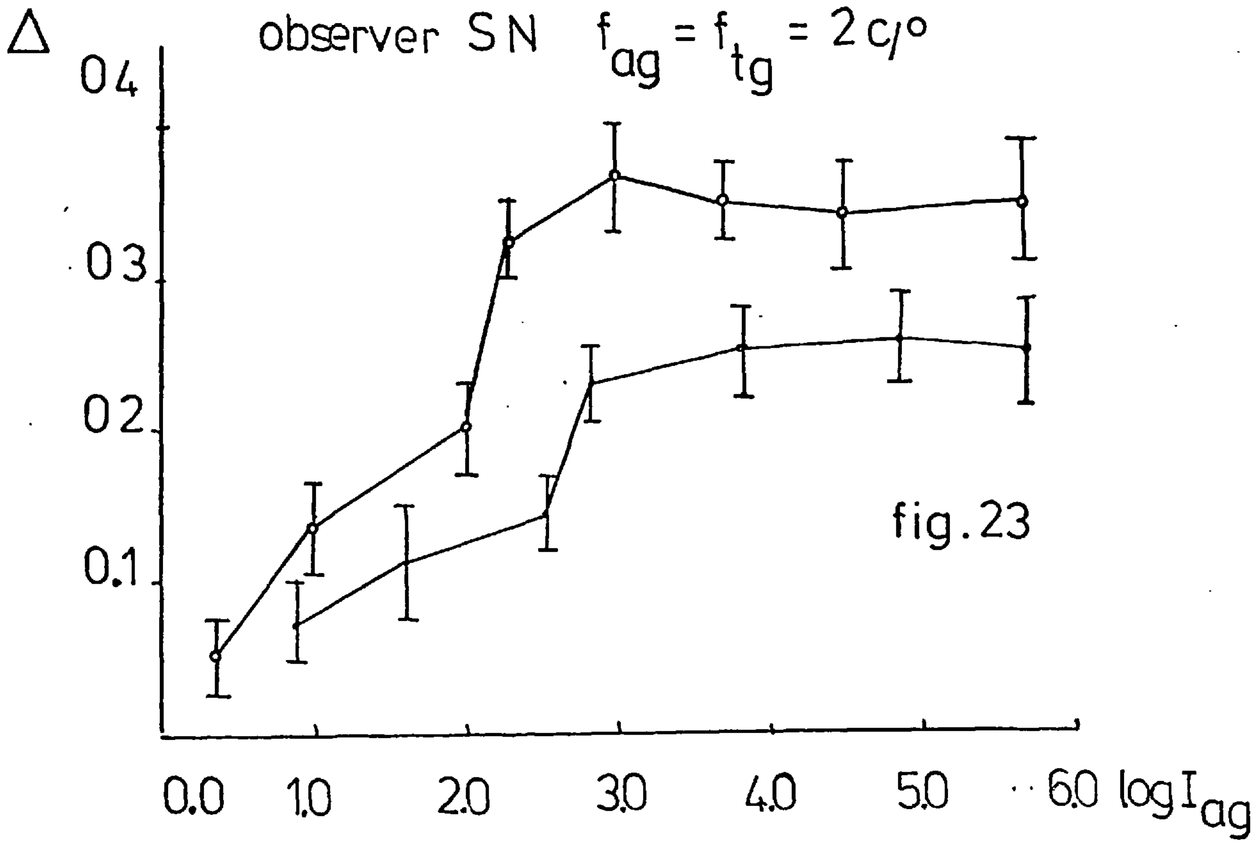


fig.23

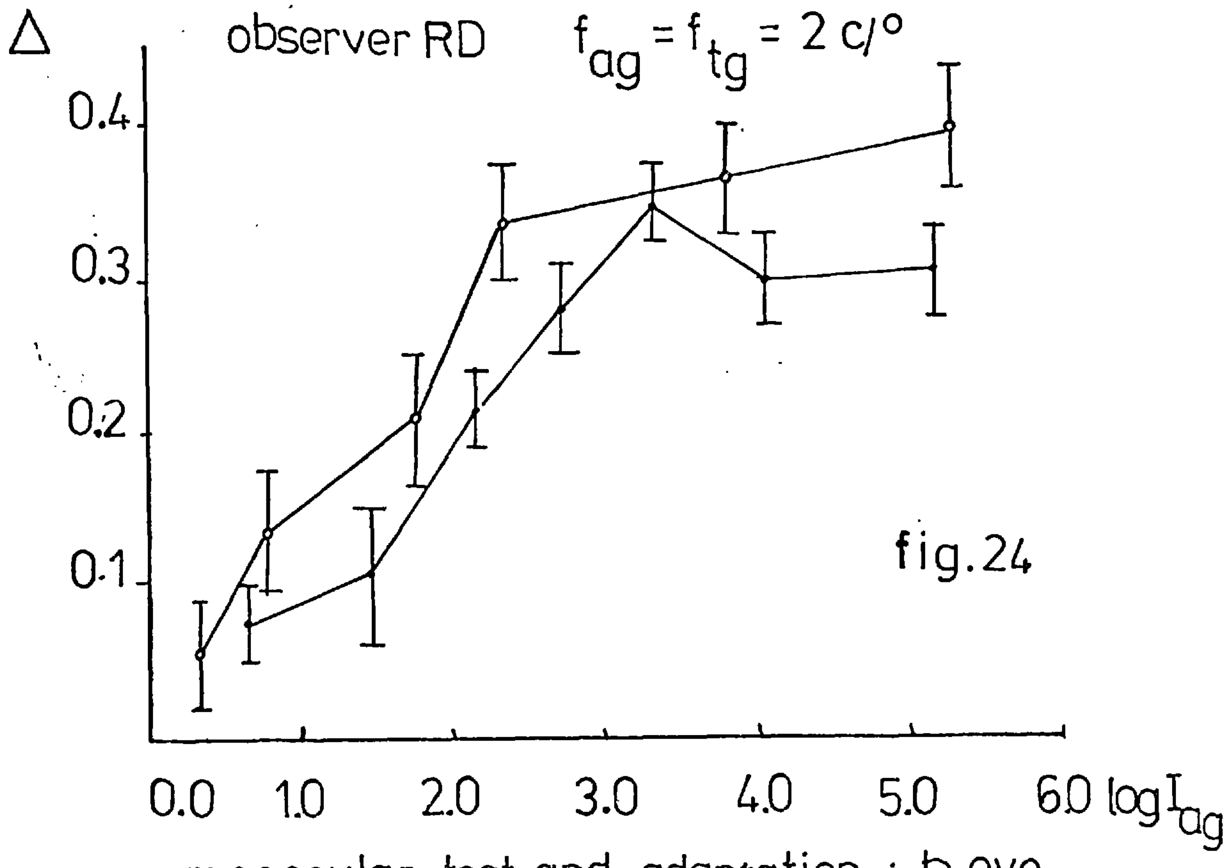


fig.24

∘ monocular test and adaptation : R eye

• R eye test ; binocular adaptation

of the inhibitory effect of adapting the non test eye are investigated in more detail later in this chapter.

It has been shown that the amount of interocular transfer of the contrast elevation effect shown by E.W. is relatively small. For this reason it is possible that the configuration chosen in the last section was not optimal for displaying summation if, indeed, summation is taking place. A configuration which combines two monocular experiments, rather than a monocular and an interocular experiment, utilizes two set-ups which both yield pronounced adaptation effects when carried out separately. Two identical adaptation gratings, therefore, were presented one to each eye and two identical test gratings, of the same spatial frequency as the adaptation gratings, were presented subsequently, again, one to each eye. Figs. 25 and 26 show the variation of Δ as measured for a binocularly presented test grating following binocular adaptation for two adaptation frequencies (dotted line). Both figures show the comparable monocular results (solid line). It can be seen that the results of the binocular set-up are not significantly different from those of the monocular experiment performed in isolation. Neither inhibition nor summation of adaptation is displayed.

Investigation into the effect of adapting the test and non test eyes simultaneously

In the following series of experiments the test eye was adapted with a vertical grating, at an illumination level of 4.5 l.u. above threshold, of the same frequency as the test grating. The illumination level, orientation, wavelength and spatial frequency of the adaptation grating presented to the non test eye were varied and the changes, if any, in Δ as measured in the test eye, were recorded. The non-test-eye grating is termed the conditioning

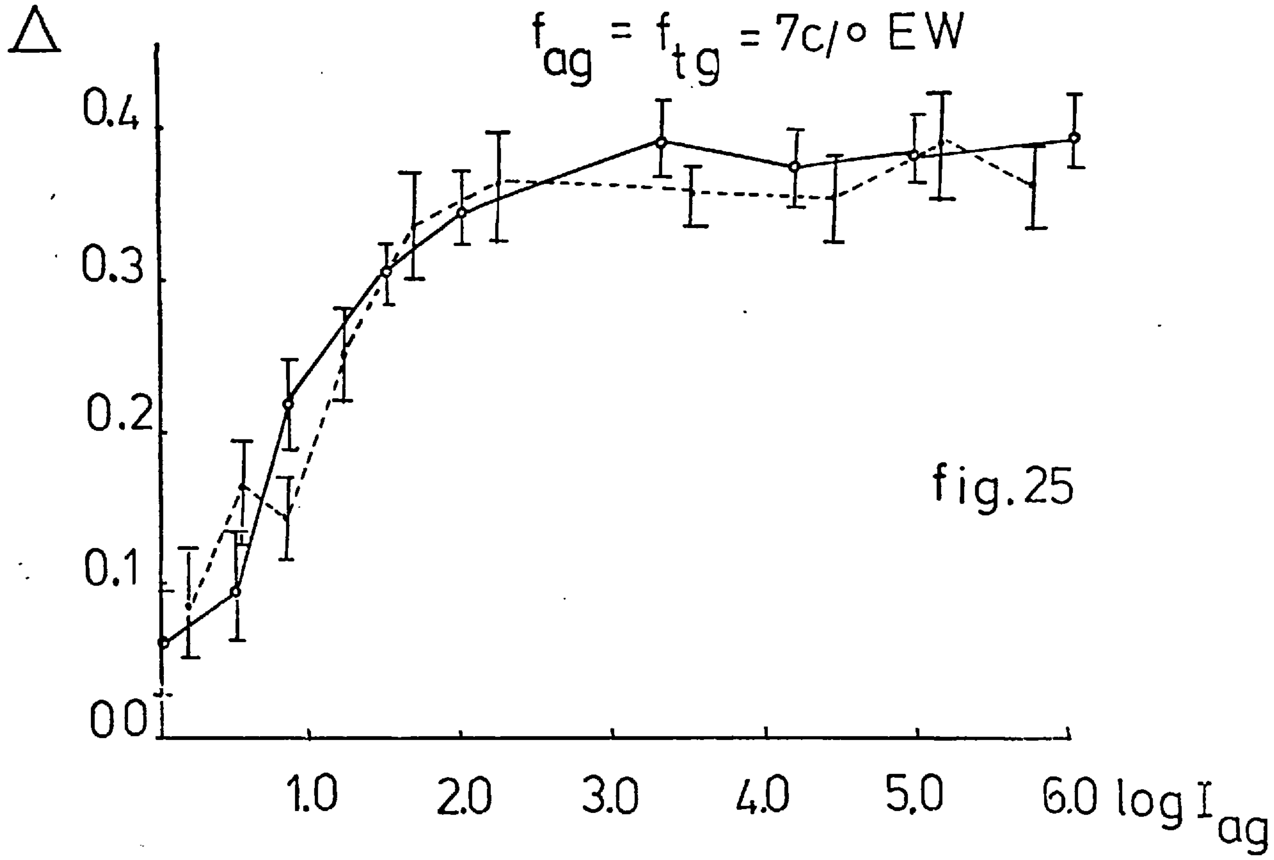

Δ
$f_{ag} = f_{tg} = 7c/°$ EW
0.4
0.3
0.2
0.1
0.0
1.0
2.0
3.0
4.0
5.0
6.0 $\log I_{ag}$

fig.25

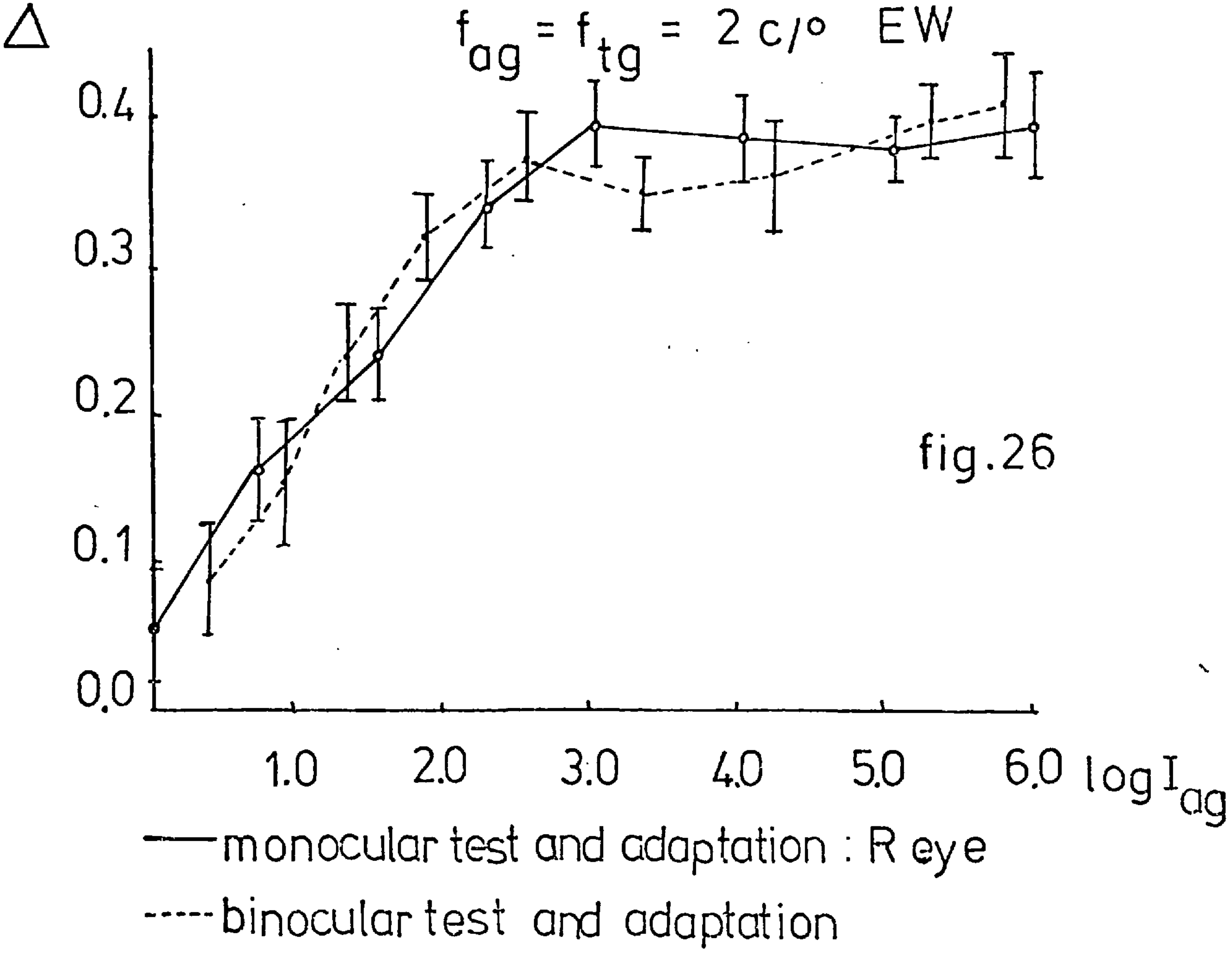

Δ
$f_{ag} = f_{tg} = 2 c/°$ EW
0.4
0.3
0.2
0.1
0.0
1.0
2.0
3.0
4.0
5.0
6.0 $\log I_{ag}$
—— monocular test and adaptation : R eye
----- binocular test and adaptation

fig.26

grating and its parameters subscripted CG. The test eye grating is called simply the adaptation grating and its parameters subscripted AG. Figs. 27 to 30 inclusive show the variation of Δ with increasing illumination level of the conditioning grating. The gratings, test, adaptation and conditioning, were all vertical and of the same spatial frequency, either 2 or 7 c/°. AG is 4.5 l.u. above its threshold. After setting the test threshold following adaptation to AG and CG, the test threshold was determined following adaptation to two uniform fields whose mean illumination levels were equal to that of AG in the test eye and CG in the non test eye. Δ was measured as the mean difference between the two thresholds. In all four figures, increase in the intensity of CG is accompanied by decrease in Δ over the intensity range of 0 to approximately 2.0 log units above threshold. Increasing the intensity of CG beyond 2.00 l.u. level does not further affect Δ which is maintained at a value of between 0.1 and 0.15 l.u. below its maximum. The initial decrease in Δ with increasing logarithmic intensity of CG is comparable in its approximate linearity and the limits of intensity for which the linearity holds with the monocular and interocular measurements described at the beginning of the chapter (figs. 1 to 4 and 9 to 12). In these latter experiments however, Δ is increasing rather than decreasing and the gradient of slope is steeper. The orientation characteristics of the inhibition are not, however, comparable with those of the monocular and interocular adaptation effects. In the orientation experiments, the test and adaptation gratings were held vertical whilst the conditioning grating, of the same frequency and illumination level as the adaptation grating, was rotated through 180°. It can be seen from figs. 31 and 32 that the reduction in Δ for the binocular as opposed to the monocular configurations, is not significantly orientation specific ... occurring as it does even when adaptation and conditioning gratings are at right angles to each other.

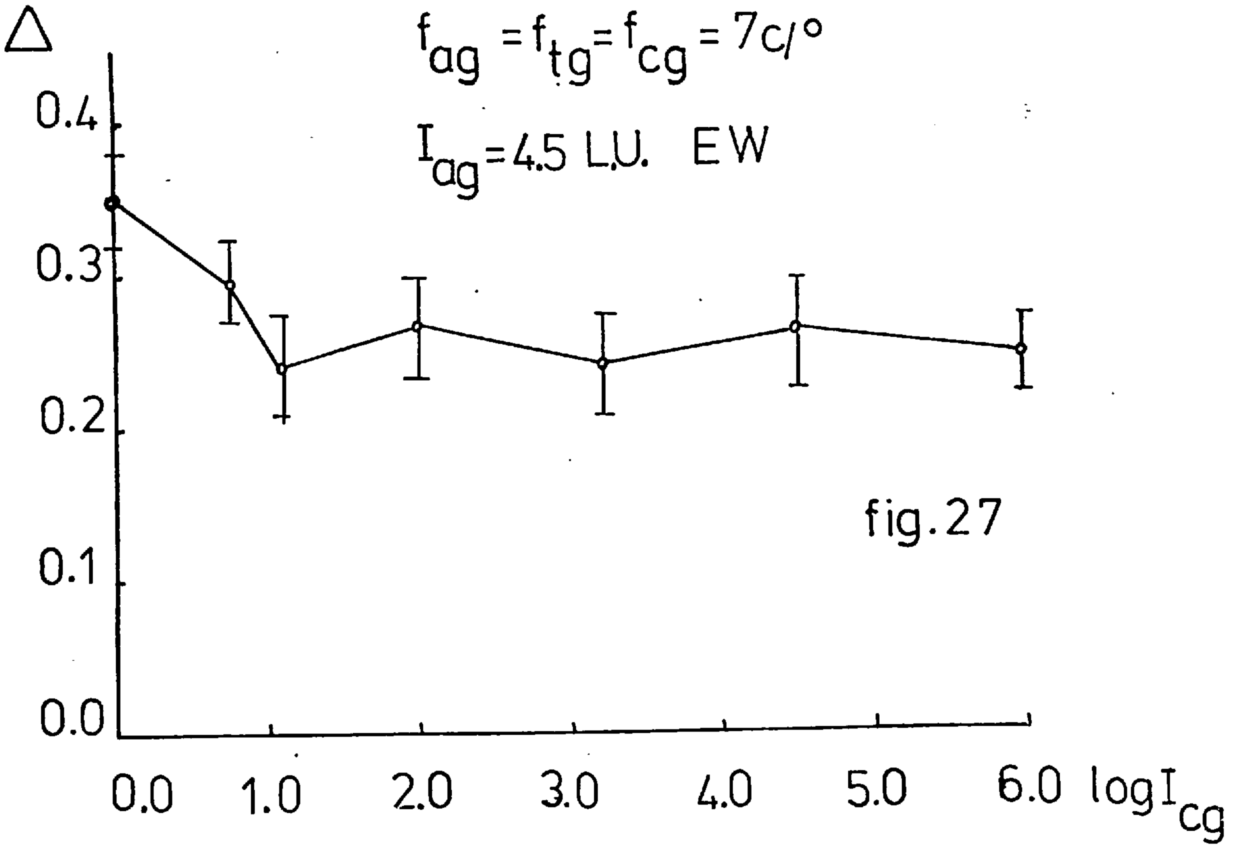

Δ
$f_{ag} = f_{tg} = f_{cg} = 7c/°$
$I_{ag} = 4.5$ L.U. EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$

fig.27

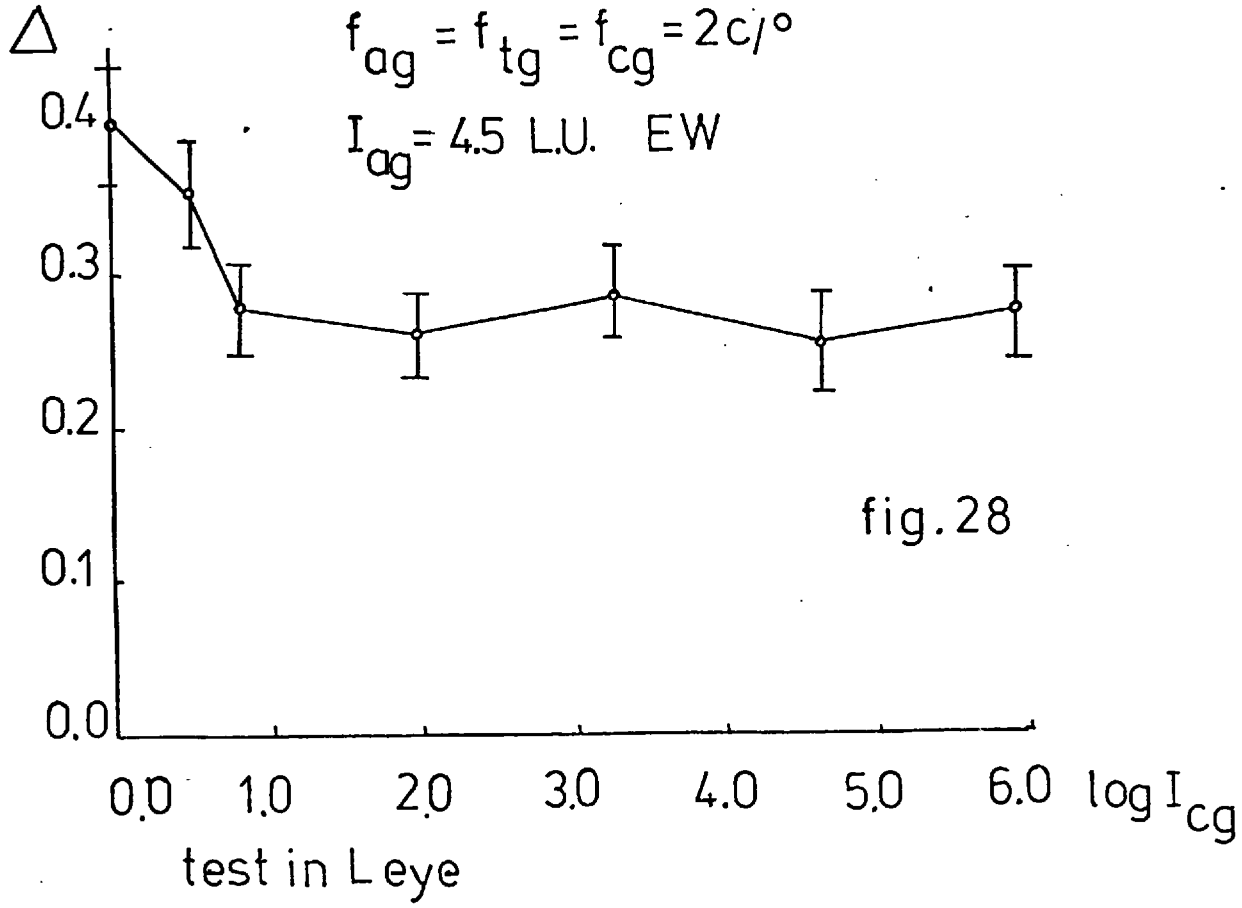

Δ
$f_{ag} = f_{tg} = f_{cg} = 2c/°$
$I_{ag} = 4.5$ L.U. EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$
test in L eye

fig.28

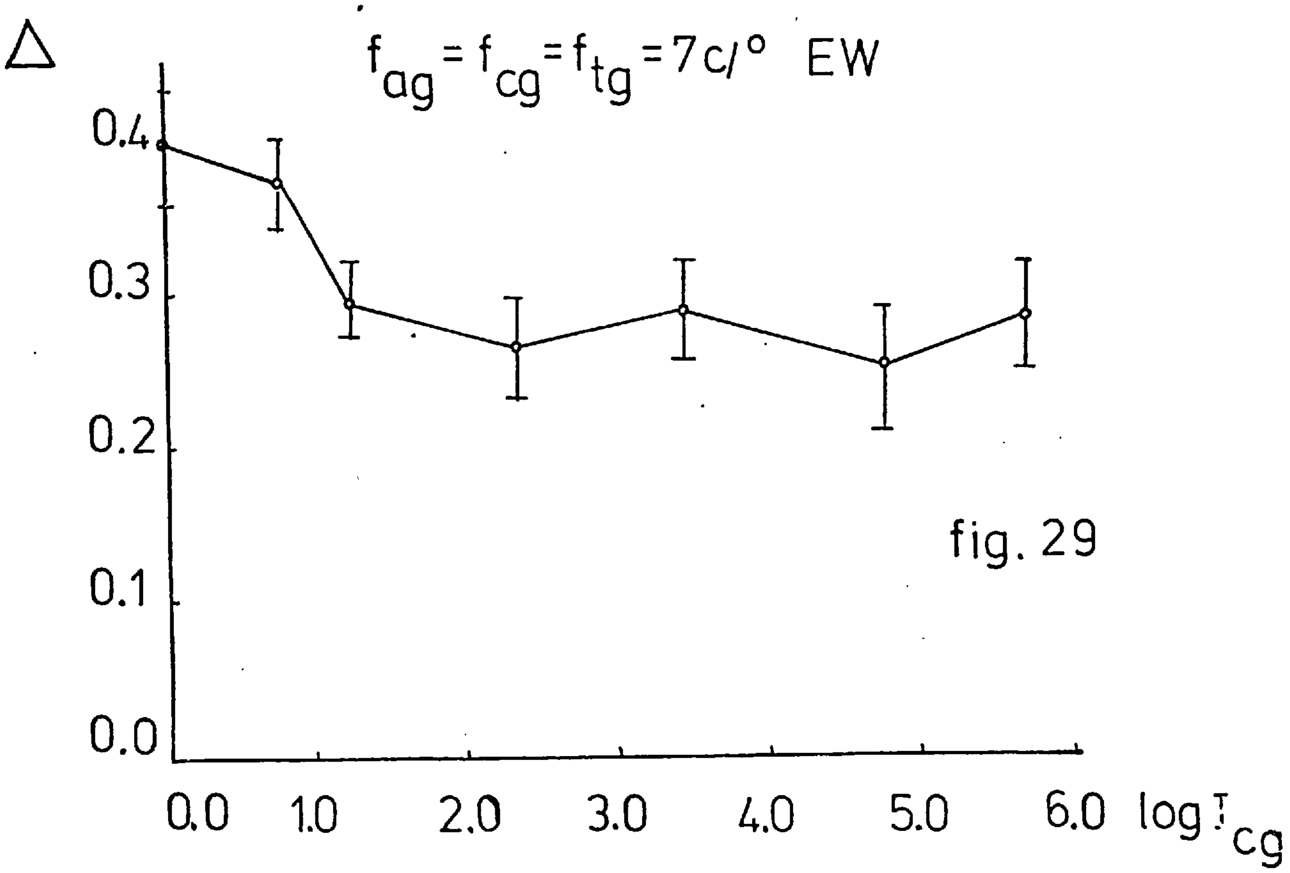

Δ
$f_{ag} = f_{cg} = f_{tg} = 7c/°$ EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$

fig. 29

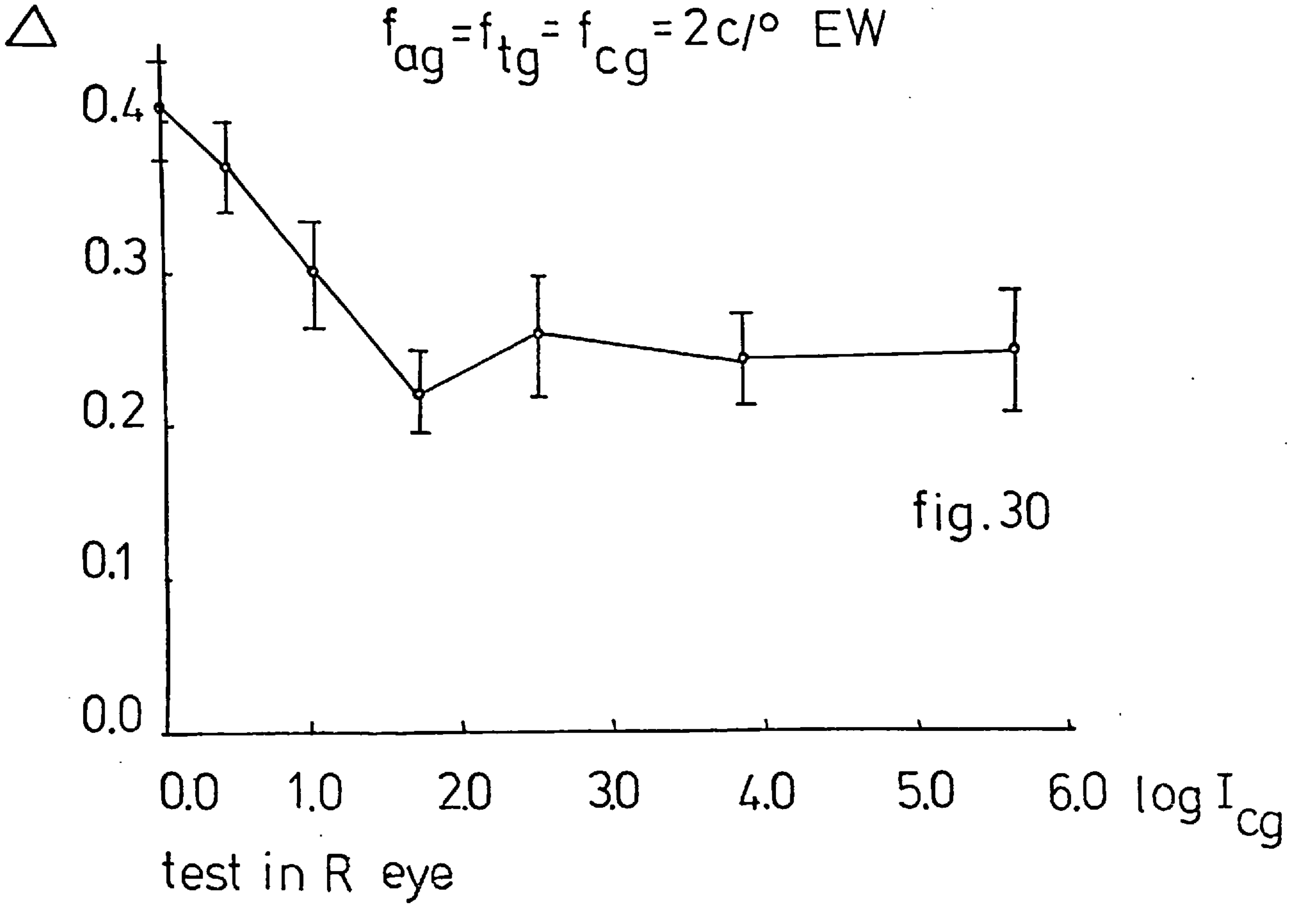

Δ
$f_{ag} = f_{tg} = f_{cg} = 2c/°$ EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$
test in R eye

fig. 30

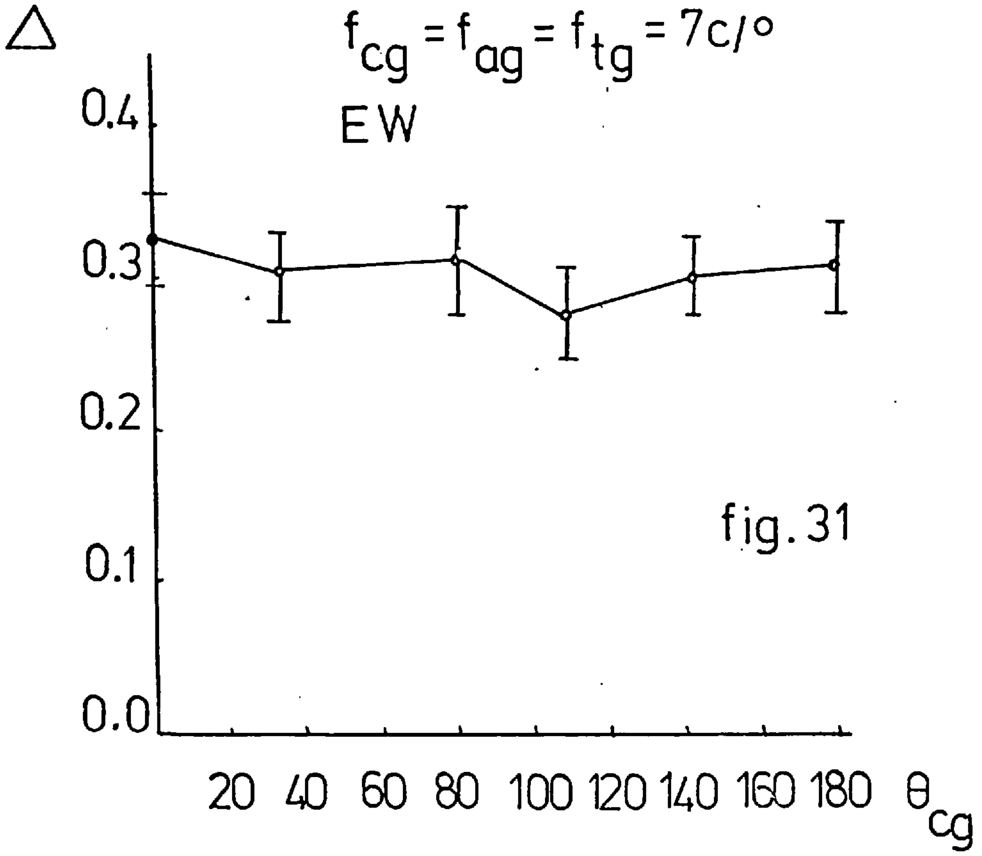


fig. 31

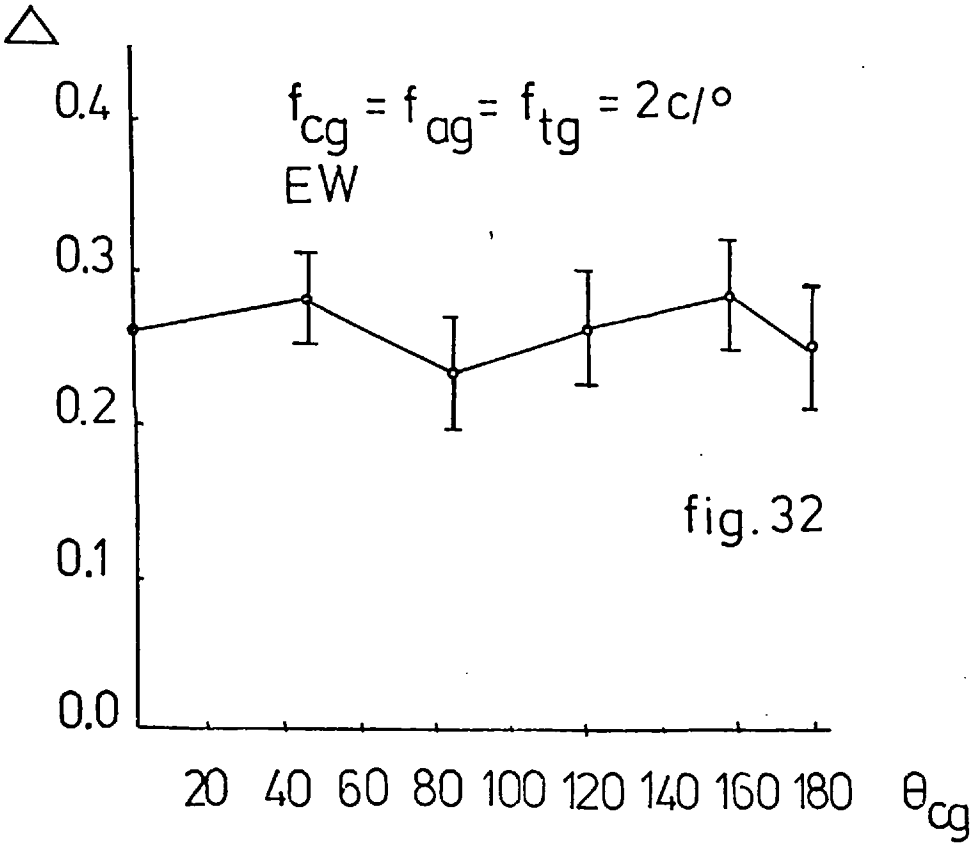


fig. 32

test in R eye

Having found the inhibition to depend on the intensity, but not on the orientation of the conditioning grating, the next experiment was to determine whether the inhibition was dependent on the wavelength of the conditioning grating. The red conditioning grating was replaced by a vertical blue grating (476.5 nm) of the same spatial frequency as the test and adaptation gratings. The variation in Δ with increasing conditioning grating intensity is shown in figs. 33 and 34 for two different spatial frequencies. The intensity of the conditioning grating was measured in log units above its threshold in blue light. The uniform field test threshold was taken after adaptation to two uniform fields: the red test eye field being of the same mean illumination level as the red adaptation grating, the blue non-test-eye field being of the same mean illumination level as the blue conditioning grating. The results are not significantly different from those obtained with a red conditioning grating (figs. 29 and 30), indicating that the conditioning effect of illuminating the non test eye is not wavelength specific. Experiments (e.g. Maudarbocus, 1973) have shown that the threshold elevation effect itself is also independent of wavelength.

The final section of this chapter is concerned with the changes in Δ to be observed on varying the spatial frequency of the conditioning grating. All three gratings were vertical and the same colour (632.8 nm), the test and adaptation gratings were maintained at 7 c/° and Δ measured for a series of conditioning grating spatial frequencies between 0 c/° and 12 c/°. Fig. 35 shows the results obtained when the test and adaptation gratings were presented to the right eye. When the conditioning grating is finer than the 7 c/° of the adaptation grating or coarser than 1 c/°, Δ remains unchanged at the 7 c/° conditioning grating value. However, for values of CG between 1 c/° and 7 c/°, a dip in the value of Δ occurs, reaching a minimum when the spatial frequency of CG equals 3 c/°. At this point Δ is exactly half of its maximum value. Since this result was unexpected, the experiment was

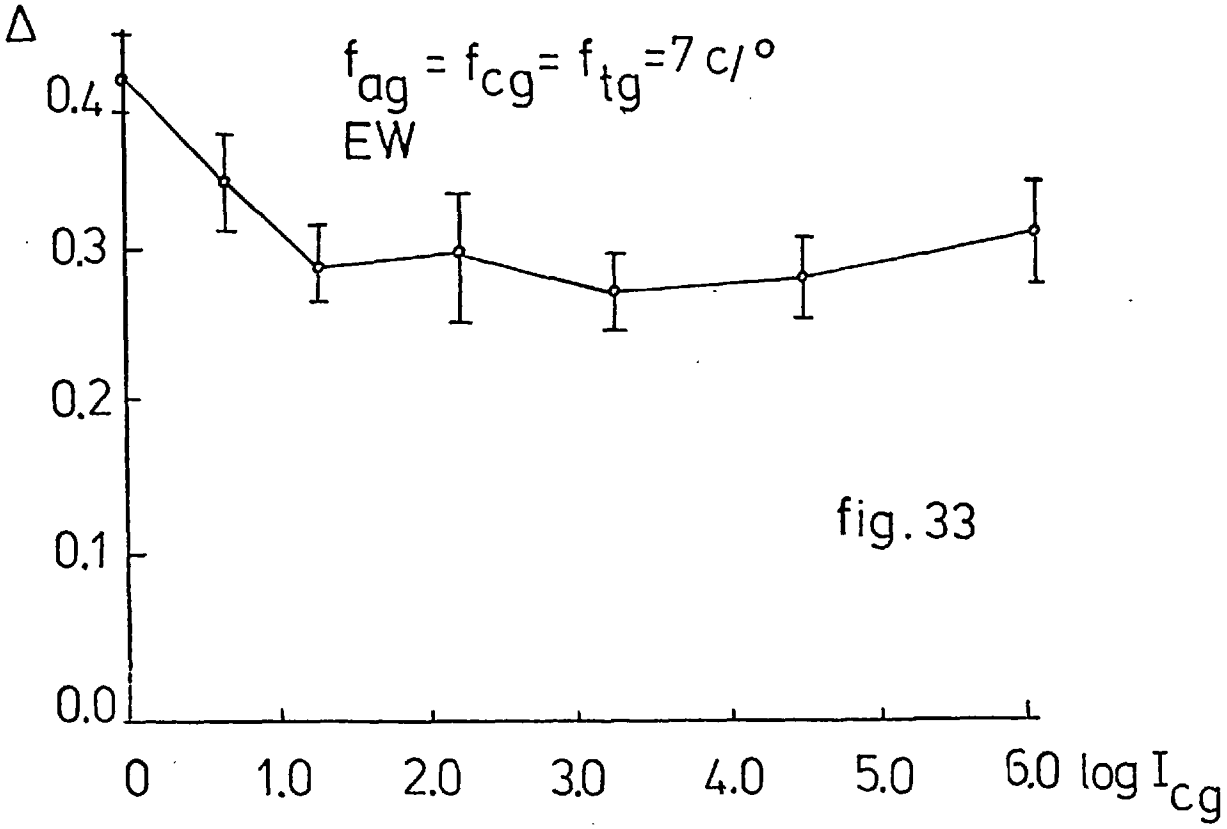


fig. 33

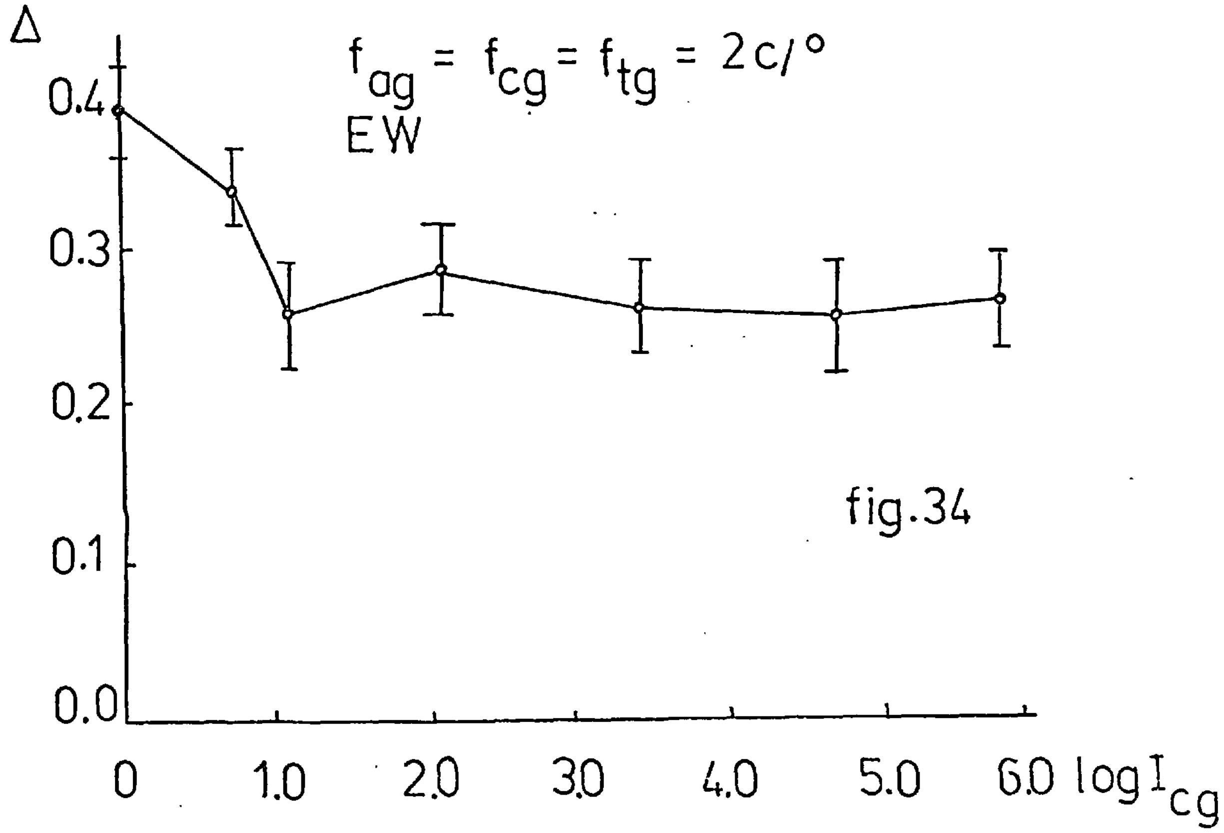


fig.34

red adaptation and test in R eye
blue conditioning grating in L eye

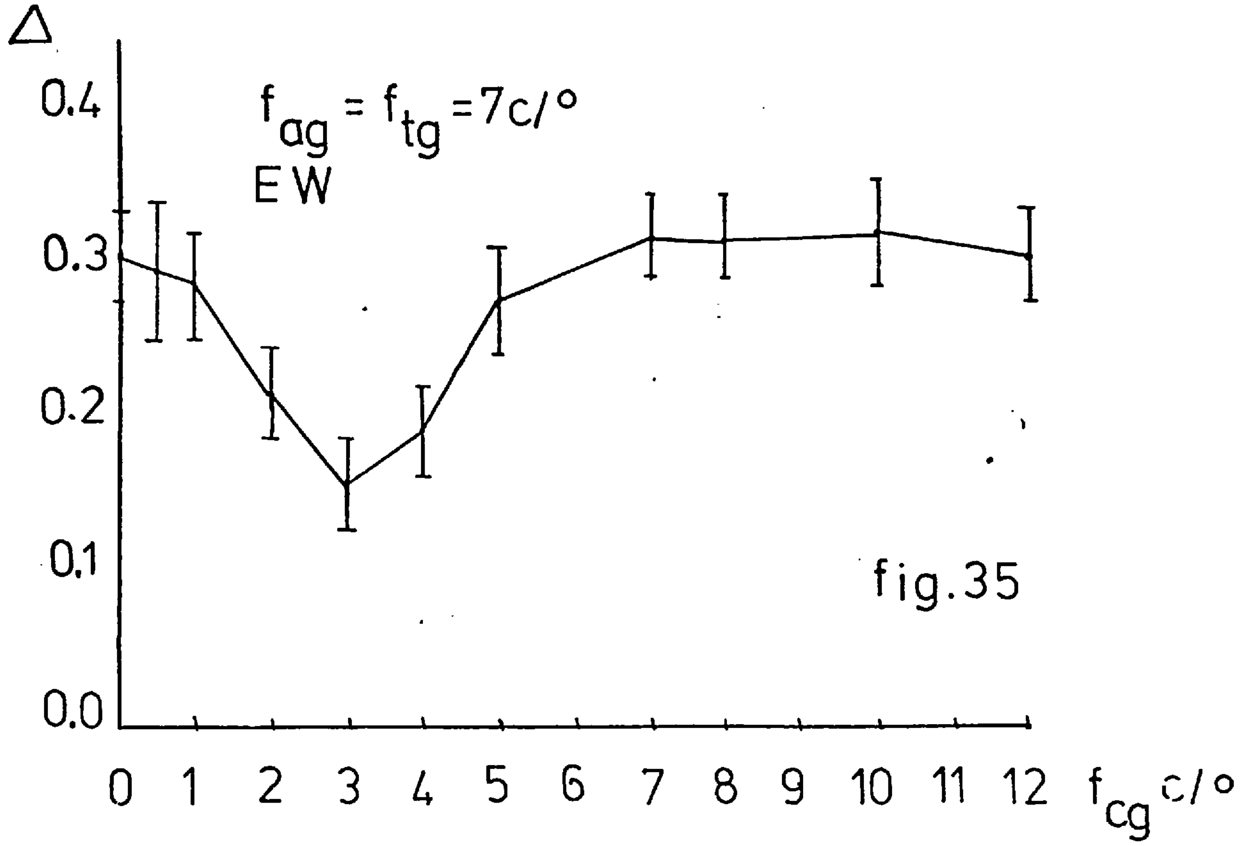


fig.35

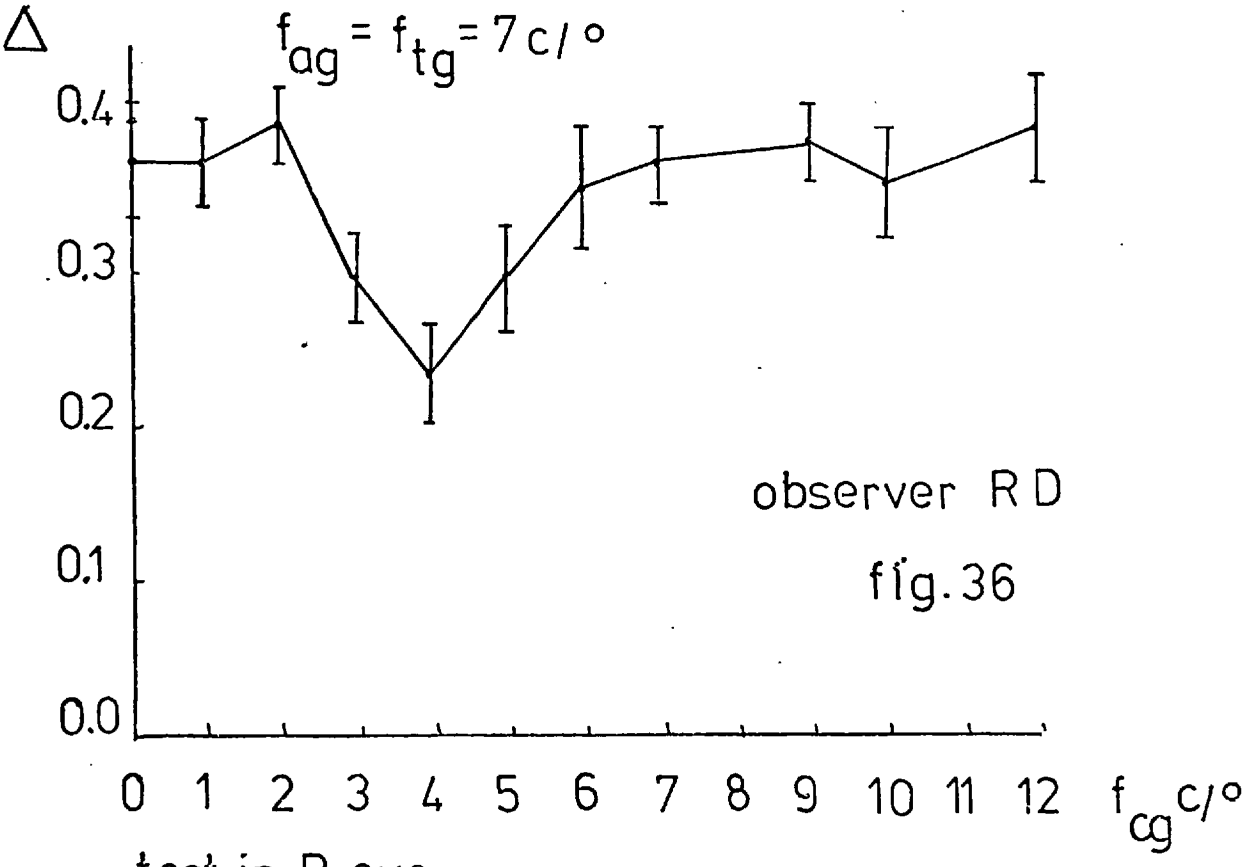


fig.36

test in R eye

repeated for two other observers, R.D. (fig. 36) who had normal vision and was unaware of the purpose of experiment, and K.H.R. (fig. 37) who also had normal vision. Both observers gave results essentially similar to those of E.W. There was also little difference to be observed in presenting the test and adaptation to the left eye and the conditioning grating to the right eye (fig. 38).

There seemed no obvious reason for such a significant frequency inhibition of the contrast elevation effect and it is the investigation of the various characteristics of this binocular interaction which is covered in the next two chapters. Although of greater magnitude and specificity, the inhibition observed in the last four figures does little to account for the more general inhibition produced by the conditioning grating which is described earlier in the chapter. A conditioning grating in one eye can reduce the amount of adaptation of a test grating produced in the other eye even though the test eye is already adapted. Reduction of response in the binocular compared with the monocular case has been observed in certain types of simple cortical cells. Hubel and Wiesel (1968) studied simple cells in level IV of the cortex of the monkey and found little binocularity: the response was almost totally dominated by either the ipsi or the contralateral eye. Using a different technique, however, Henry, Bishop and Coombs (1969) found these same cells to almost all be responsive to binocular inputs in a manner which, because of the lack of spontaneous activity in simple cells, had not been observed before. Although the simple cell fails to respond to stimulation of the non dominant eye alone, this same stimulation can have a very powerful inhibitory effect if it takes place at the same time as stimulation of the dominant eye. If the two eyes are activated independently, with the optimal stimulus being applied to the dominant eye so as to produce a maintained discharge, an inhibitory receptive field can be mapped for the non dominant eye within which, the stimulus will produce a reduction of the

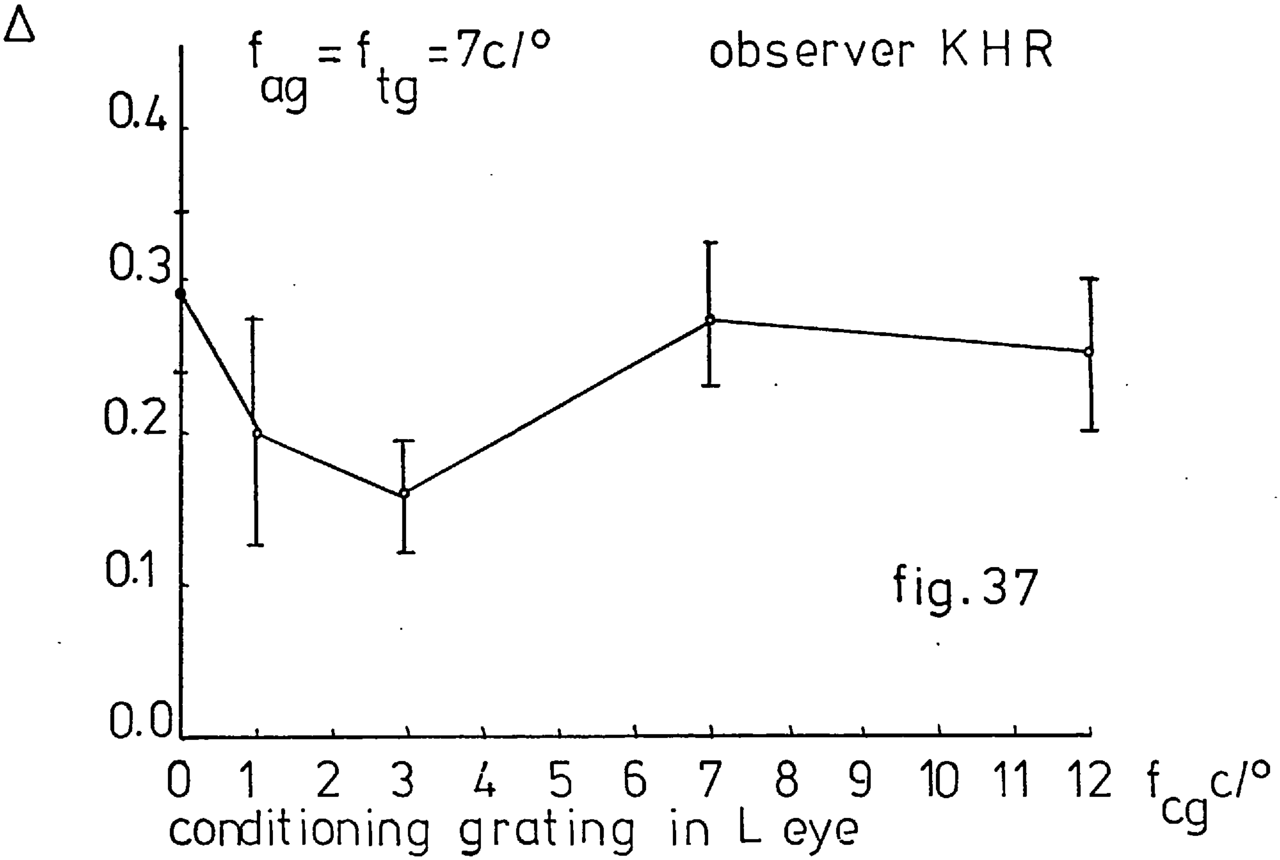


fig. 37

conditioning grating in L eye
test and adaptation in R eye

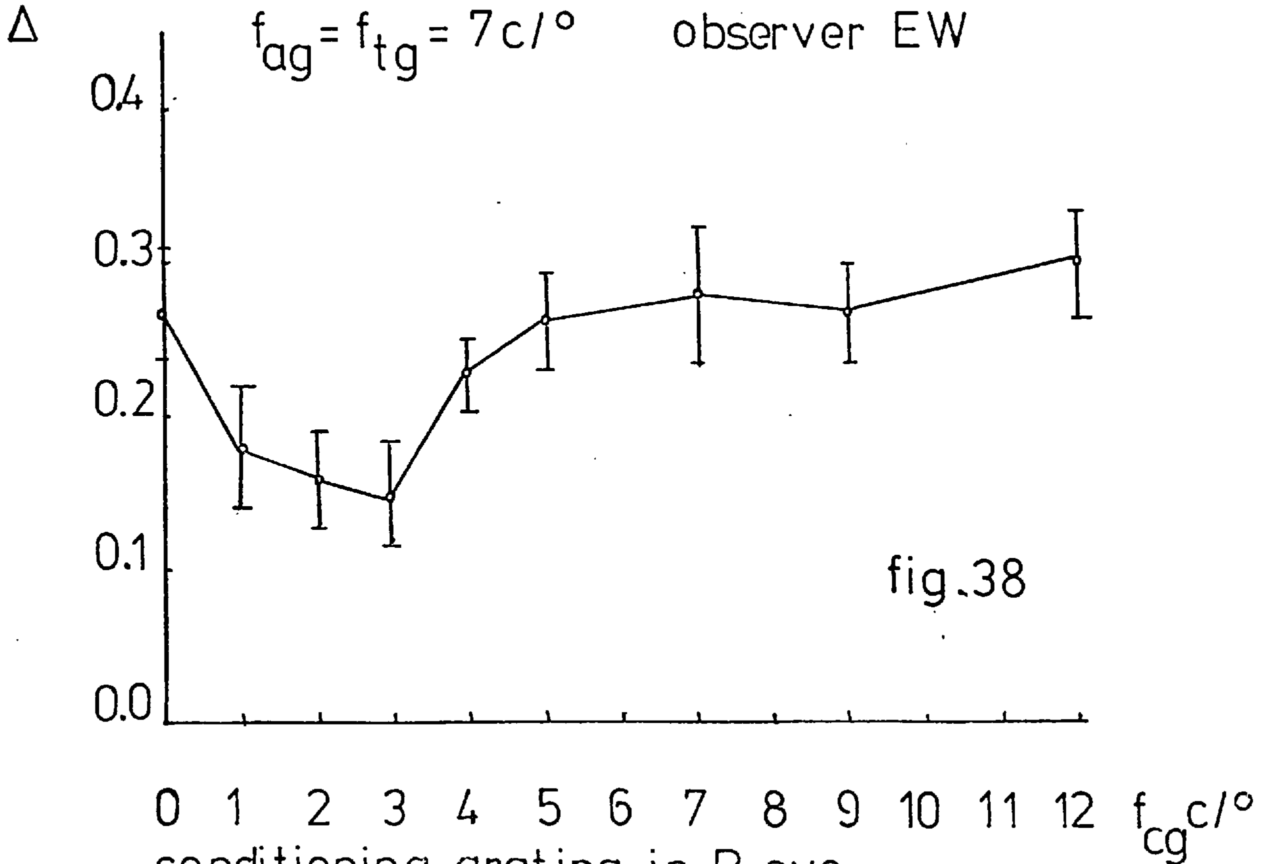


fig.38

conditioning grating in R eye
test and adaptation in L eye

dominant eye discharge. Such a receptive field would typically be 2° across. It was also found that a very small part of this field produced additional excitation of the discharge, although the conditions were very exact and the region itself only 0.3° across. Thus it would appear that under the experimental conditions employed in these observations, i.e. independent and separate stimulation of the two eyes, the response of the simple cells in the cortex would be reduced by the introduction of a field in the opposite eye, even though this eye is not directly involved in making the threshold measurements. The same eye movements which produce optimal conditions for the dominant eye of certain simple cells may bring the stimulus within the inhibitory receptive field of the non dominant eye and the overall response would therefore be reduced.

Joshua and Bishop (1970) showed most simple cells to be dominated by the ipsilateral eye, in which case, the inhibitory receptive field will lie in the contralateral eye. If the contralateral eye is dark adapted, there will be no inhibition of response, but increasing the intensity of the stimulus in this eye will result in a reduction of the response previously recorded from the ipsilateral eye. Such a reduction was observed in figs. 27 to 30. Since, however, the inhibitory region of the simple cell is such that a stimulus falling anywhere within it will reduce the response, one would not expect the reduction to be orientation selective with respect to the contralateral eye. No such selectivity was found (figs. 31 and 32).

Hubel and Wiesel (1968) found the majority of simple cells to be indifferent to colour so changing the conditioning field from red to blue might be expected to make little difference to the inhibitory effect of the field. This, from figs. 33 and 34, would appear to be the case.

The effect of the spatial frequency of the conditioning grating and its implications for more complicated binocular phenomena such as stereovision will be discussed in the next chapter.

Chapter 4.

AN INHIBITORY BINOCULAR INTERACTION

The experiments of the previous chapter have shown that the adaptation effects which arise from gratings presented individually to each eye do not exhibit positive summation when both gratings are presented, simultaneously. This is true regardless of which eye the test grating is presented to, or whether the test grating is presented to both adapted eyes. It was found that the magnitude of the contrast elevation effect obtained in an experimental situation where both eyes are adapted to identical gratings and a test grating of the same spatial frequency is subsequently presented to one eye, is slightly, but significantly less than the value found when the adaptation grating is presented only to the test eye. Further investigation of this reduction in the adaptation effect has shown that lowering the spatial frequency of the adaptation grating presented to the non-test eye (termed the "conditioning grating") to 3 c/° reduces the adaptation induced by a 7 c/° grating (termed simply the "adaptation grating") in a 7 c/° test grating to an even greater extent. Both 7 c/° gratings are presented to the same test eye ($\Delta = 0.15$ l.u. for a 3 c/° conditioning grating, c.f. $\Delta = 0.32$ for a 7 c/° conditioning grating). Further reduction of the spatial frequency of the conditioning grating is marked by an increase in the threshold elevation effect to its previous value. It is with this spatial frequency-specific binocular conditioning effect that this chapter is concerned. The different aspects which will be considered are as follows:

(a) The nature of the conditioning effect for adaptation gratings of spatial frequencies other than 7 c/°.

(b) The variation of the conditioning effect with changes in the intensity of the conditioning grating.

(c) The orientation specificity, if any, of the conditioning effect.

(d) The wavelength specificity.

(e) The influence of binocular rivalry and time course measurements.

(f) Off-axis measurements.

(a) Conditioning as a function of the spatial frequency of the test and adaptation gratings.

In these experiments the adaptation grating was presented to the right eye at a level of 4.5 l.u. above the threshold illumination level for detection of the grating. The conditioning grating of spatial frequency f_{cg} was presented to the left eye and its illumination level matched to the adaptation grating by means of the photocell (described in chapter 2). The test grating, of spatial frequency f_{tg} equal to f_{ag}, that of the adaptation grating, was presented subsequently to the right eye. The contrast elevation effect was determined by comparing the test threshold obtained under this adaptation configuration with that following adaptation to two uniform fields whose illumination level was the same as the space-average illumination level of the adaptation and conditioning gratings. Fig. 1 illustrates the results of setting the adaptation and test gratings to 2.5 c/° and determining Δ as a function of the spatial frequency of the conditioning grating. In the case where the conditioning and adaptation gratings are identical, Δ is the same as that determined for a fine high frequency conditioning grating, but Δ falls away sharply for values of f_{cg} slightly above or below the value f_{ag}. The same sharp tuning is observed for test and adaptation gratings of 4 c/° (fig. 2), this tuning occurring within the inhibitory region defined by values of f_{cg} below 6 c/°. If the adaptation and test gratings are set at a spatial frequency greater

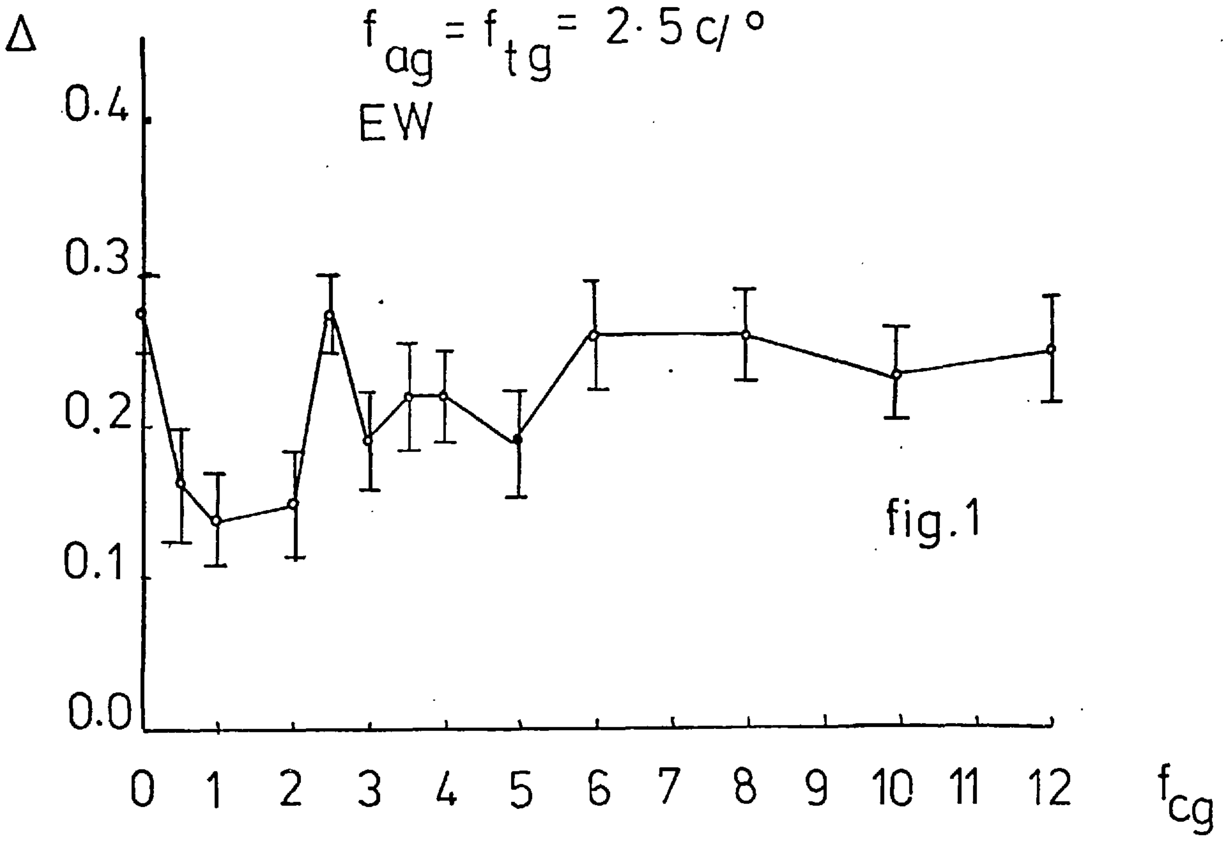


fig.1

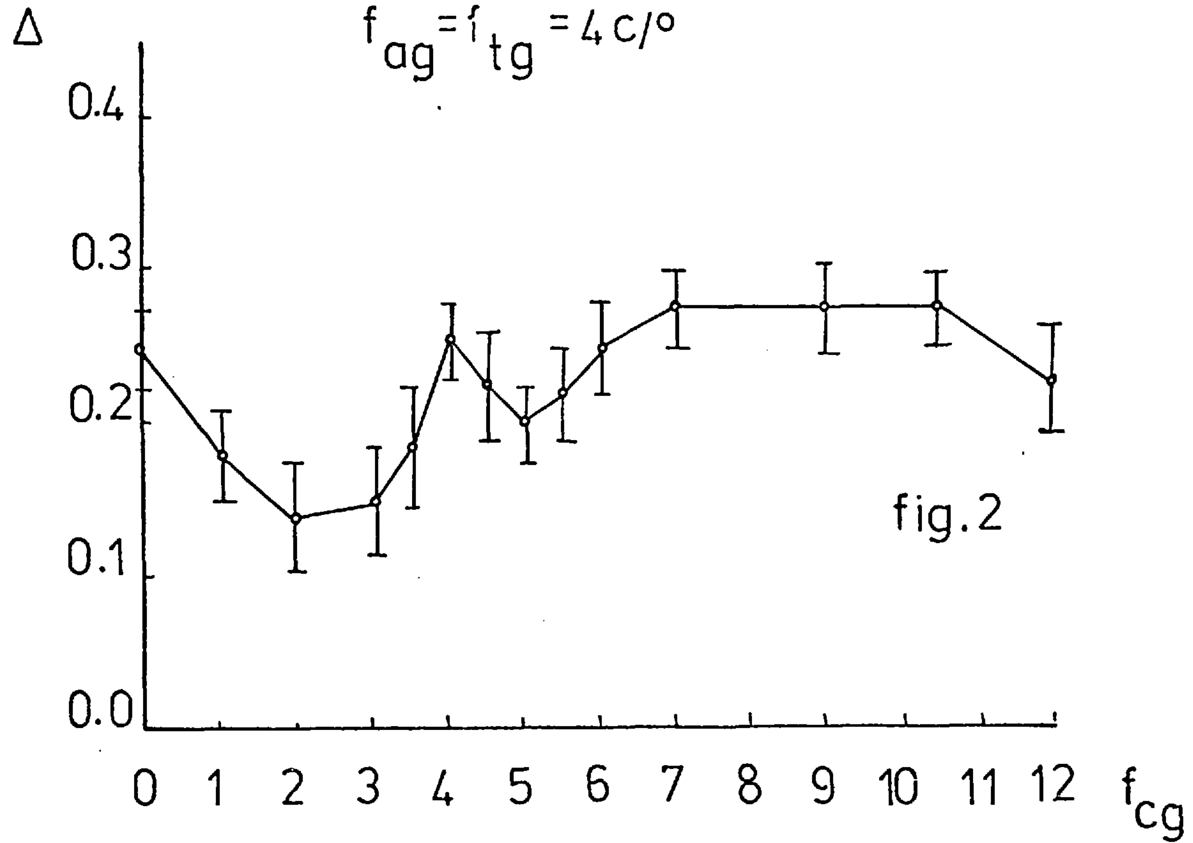


fig.2

test and adaptation in R eye
conditioning grating in L eye

than 6 c/° (fig. 3, f_{ag} = 7 c/°), no peak value of Δ is observed for f_{cg} equal to f_{ag} although the basic suppression effect of the conditioning grating, maximal in the region of f_{cg} equal to 3 c/° is still in evidence. Higher values of the spatial frequency of the adaptation and test gratings (fig. 4, f_{ag} = 12 c/°; fig. 5, f_{ag} = 20 c/°) produce less significant conditioning effects, although in each case these effects occur for the same range of f_{cg}, the spatial frequency of the conditioning grating.

The spatial frequency tuning observed for coarse adaptation gratings when f_{cg} equals f_{ag} can be compared with the spatial frequency tuning associated with the threshold contrast adaptation effect itself, although the experimental configurations are rather different. The tuning associated with the adaptation effect proper was determined under monocular presentation of the adaptation and test gratings, with no conditioning grating. The adaptation grating spatial frequency was varied whilst the test and spatial frequency was held constant. In the binocular set-up, both adaptation and test gratings remained constant whilst the spatial frequency of the conditioning grating was varied. The tuning curve for this experiment (for a 2.0 c/° test grating) is compared in fig. 6 with the tuning curves associated with the conditioning grating (for test gratings of 2.5 c/° and 4.0 c/°Δ. Both axes of fig. 6 are normalized, the maximum value of Δ being 1.0 and the spatial frequency variable, f, expressed as a ratio of f_{tg}, the spatial frequency of the test grating. For the monocular determination of the adaptation effect, f represents the spatial frequency of the adaptation grating; in the binocular experiment, with the conditioning grating, it represents the spatial frequency of this conditioning grating with $f_{ag} = f_{tg}$. Δ_{max} is that elevation of threshold obtained in one case when the test and adaptation gratings are of the same spatial frequency and in the other case, when the spatial frequency of the conditioning grating equals that of the adaptation and test gratings. It can be seen from fig. 6 that the normalized curves of the two conditioning grating

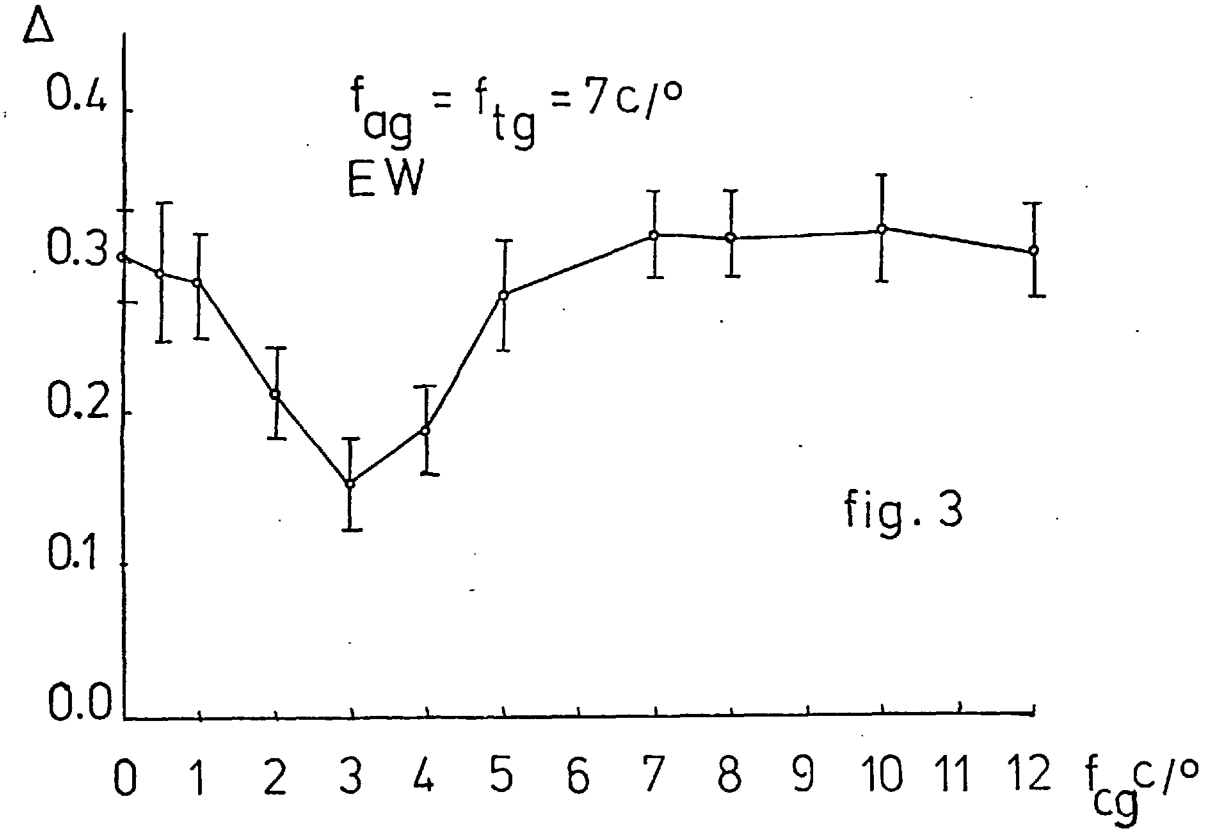

Δ
0.4
0.3
0.2
0.1
0.0
$f_{ag} = f_{tg} = 7c/°$
EW
0
1
2
3
4
5
6
7
8
9
10
11
12
f_{cg} c/°

fig. 3

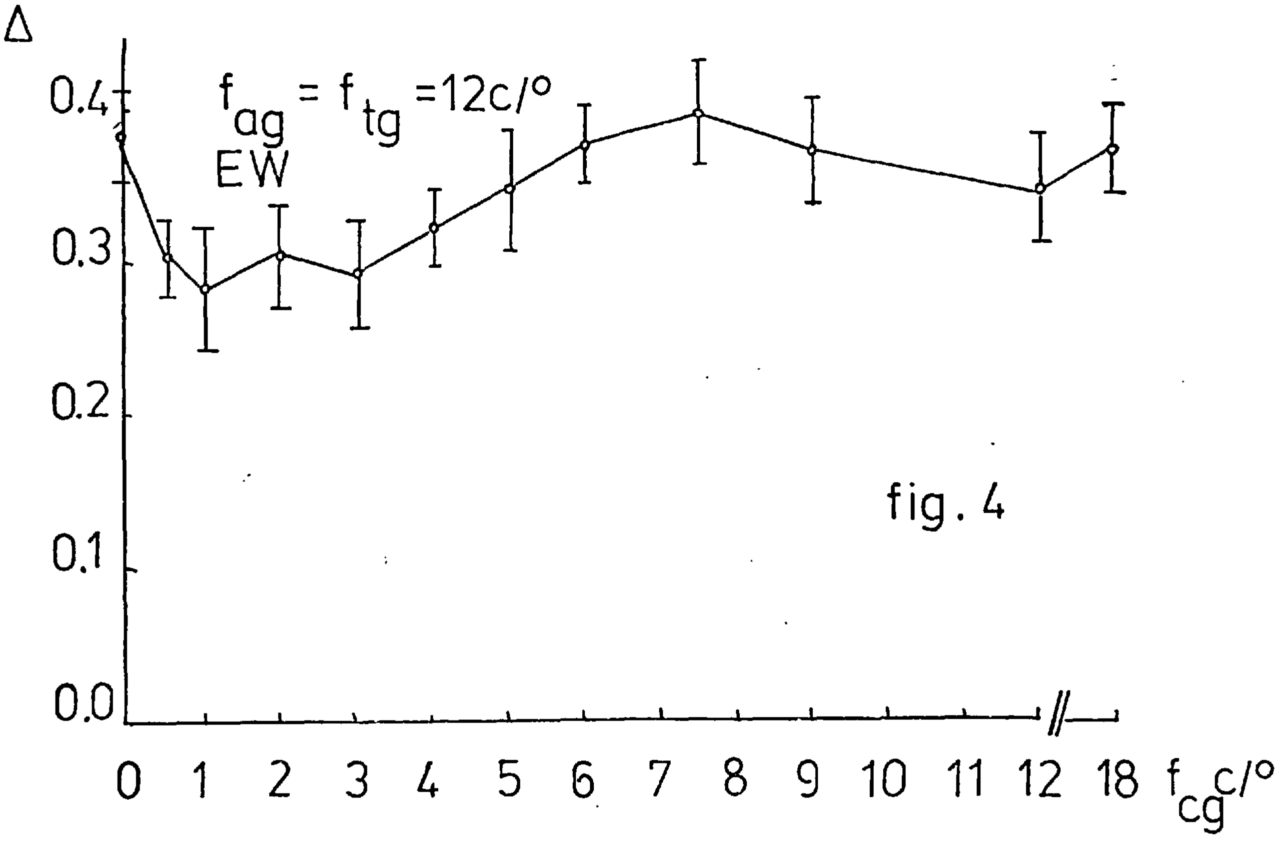

Δ
0.4
0.3
0.2
0.1
0.0
$f_{ag} = f_{tg} = 12c/°$
EW
0
1
2
3
4
5
6
7
8
9
10
11
12
18
f_{cg} c/°

fig. 4

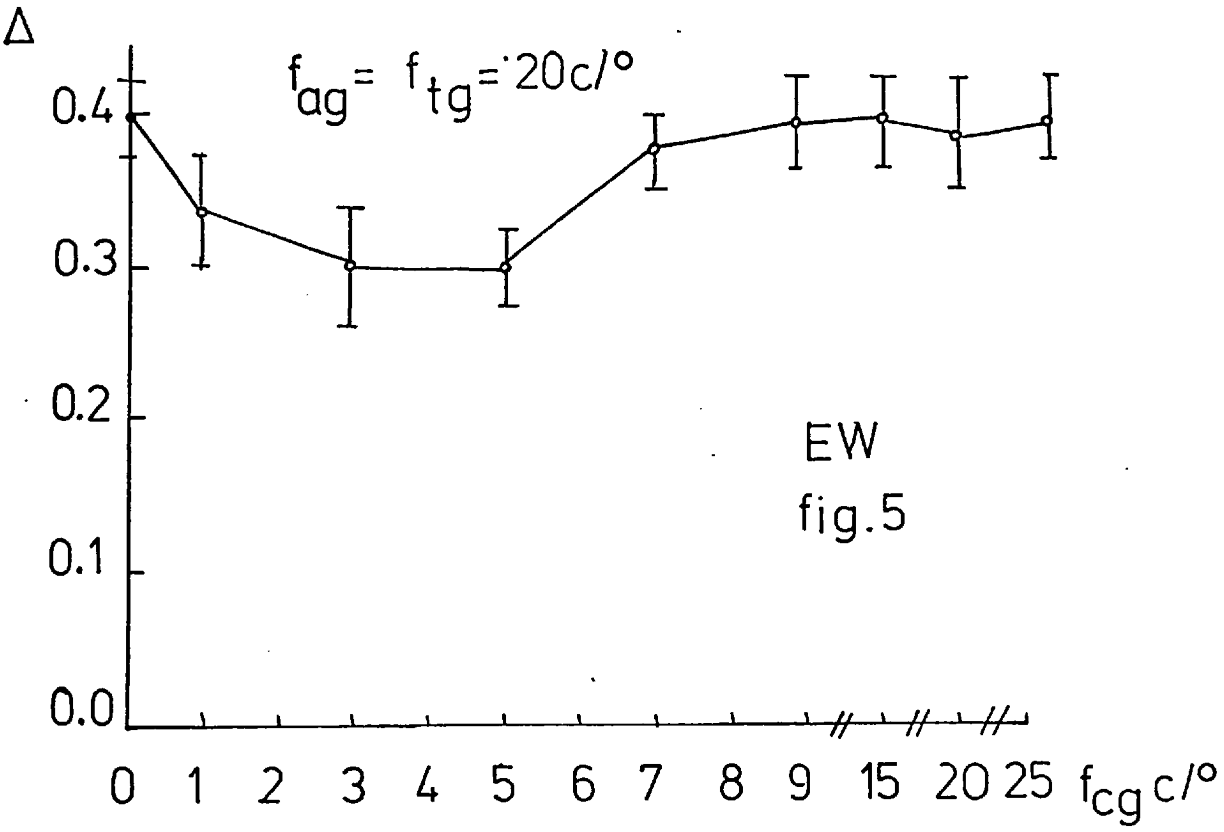


fig.5

test and adaptation in R eye
conditioning grating in L eye

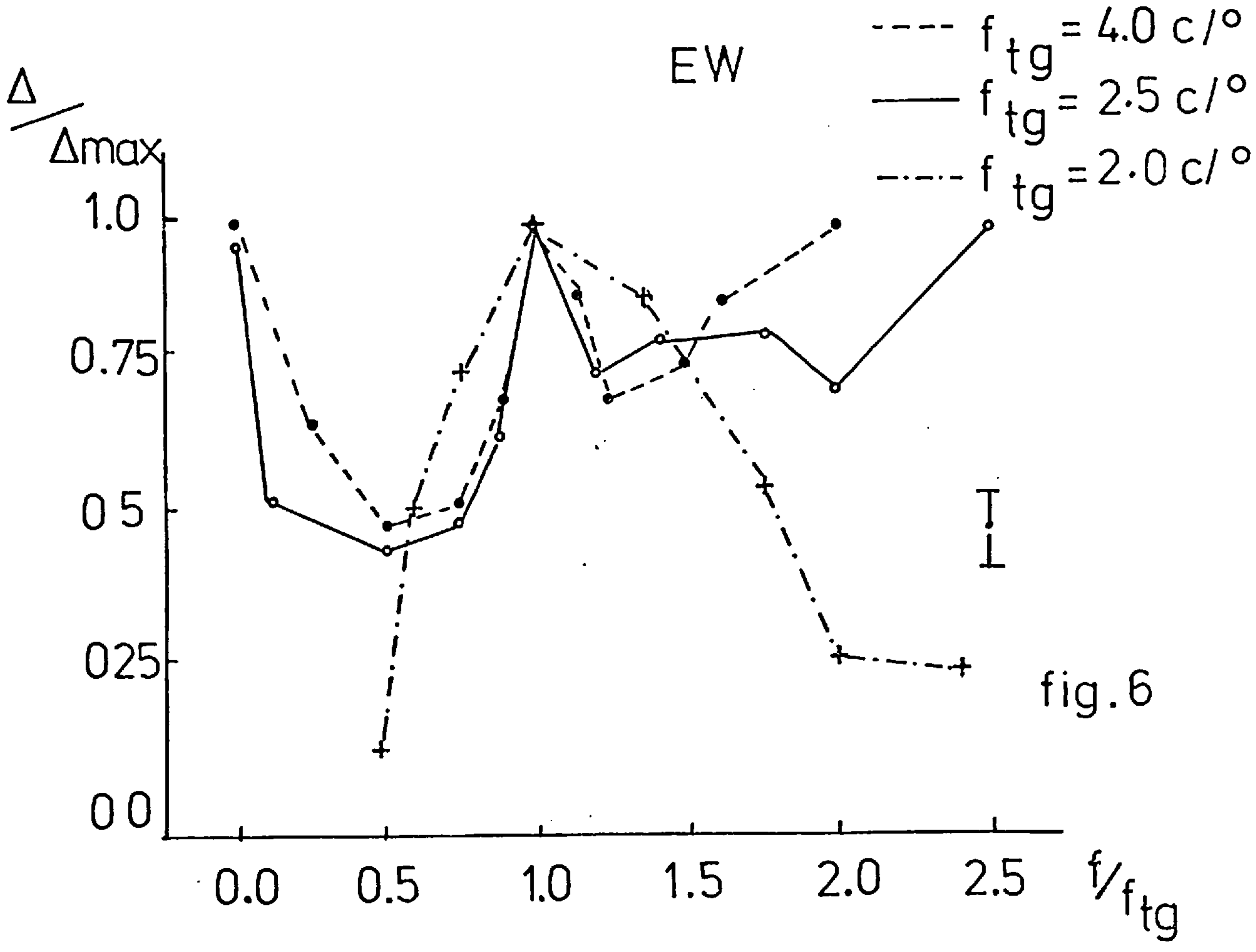
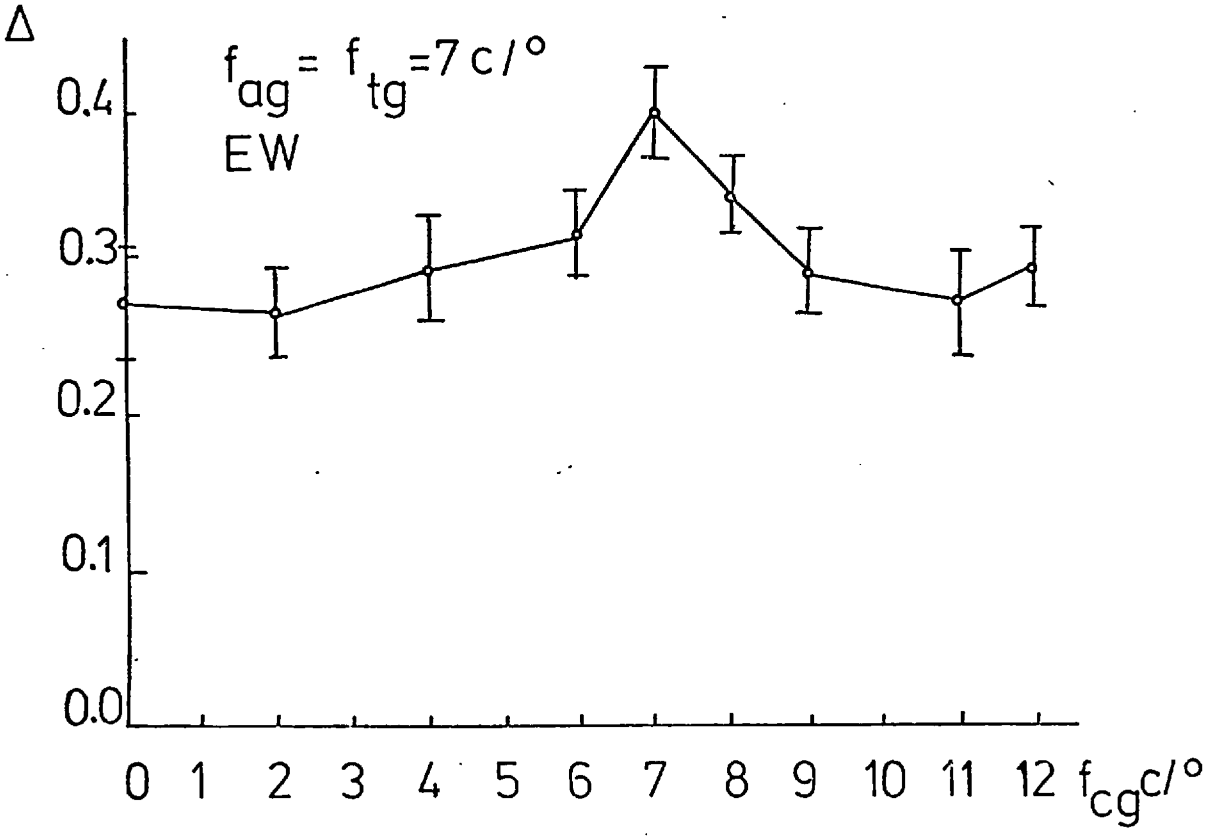


fig.6

experiments are very similar in the range $f/f_{tg} = 0.5$ to $f/f_{tg} = 1.5$. Both, however, are significantly sharper than the monocular tuning curve over the same region.

Experiments described so far deal with the effect of a 3 c/° conditioning grating presented dichoptically with respect to the adaptation grating. It was necessary to determine whether similar effects could be obtained by superimposing the conditioning grating on the adaptation grating in the right eye, whilst the left eye remained dark-adapted. The threshold illumination level found under these conditions for detection of the test grating also presented to the right eye, was compared with that found following adaptation to a single uniform field whose illumination level was the same as the mean of the superimposed adaptation and conditioning gratings. The adaptation spatial frequency was held at the test value of 7 c/°, Δ being measured as a function of the spatial frequency of the conditioning grating. The results of this experiment are shown in fig. 7. A maximum value of Δ was found when $f_{cg} = f_{ag}$. In this configuration, the adaptation and conditioning gratings were presented in phase. For values of f_{cg} other than 7 c/°, the adaptation field appeared confused and the resultant loss of visibility could account for the reduction in Δ observed for these values. Alternatively, inhibitory interactions between spatial frequency channels, such as those proposed by Tolhurst (1972) could reduce the adaptation effect. The reduction in values of Δ found for this experiment, however, remains constant over most of the range of values of f_{cg} and is not limited to low frequency conditioning gratings. The frequency specific suppression effect shown in figs. 3 - 5 is not observed, which implies that the conditioning effect is necessarily a binocular interaction.



adaptation and conditioning gratings superimposed
in test eye : R eye

fig. 7

(b) Conditioning as a function of grating illumination level.

In these experiments, the observer firstly adapted the right eye only to a grating presented at an illumination level of 4.5 log units above the threshold illumination level, and the value of Δ was determined in the usual way. Subsequent measurements were made to determine Δ as a function of increasing intensity, I_{cg}, of a conditioning grating presented to the left eye. The spatial frequency, f_{cg}, of the conditioning grating was set at 3 c/°, the value shown to yield the maximum inhibitory effect (figs. 3 to 5). The experiment was carried out for two spatial frequency values of the test and adaptation gratings, f_{ag} = 7 c/° and f_{ag} = 4 c/°. The two sets of data are shown in figs. 8 and 9. In both cases, increasing I_{cg}, the intensity of the conditioning grating, is accompanied by decrease in Δ, (to a value of about 0.12 l.u.) over the approximate range 0.0 to 2.5 l.u. above threshold. Further increasing I_{cg} does not reduce Δ below 0.12 l.u. These data (fig. 8) can be compared with the dependence of Δ on the illumination level of the adaptation grating when no conditioning grating is used. Such data were determined with the test and adaptation gratings both of spatial frequency 7 c/° presented to the right eye and are plotted together with the data of fig. 8 in fig. 10. Although changes in the value of Δ are obviously in opposite directions, the minimum intensity of the adaptation grating for which maximum Δ is obtained in the non-conditioned case is approximately the same as the intensity of the conditioning grating for which minimum Δ is obtained in the binocular experiment. The same linear relationship between log I and Δ for values of log I less than 2.0 noted for monocular and interocular experiments in the previous chapter, is evident in figs. 8 and 9.

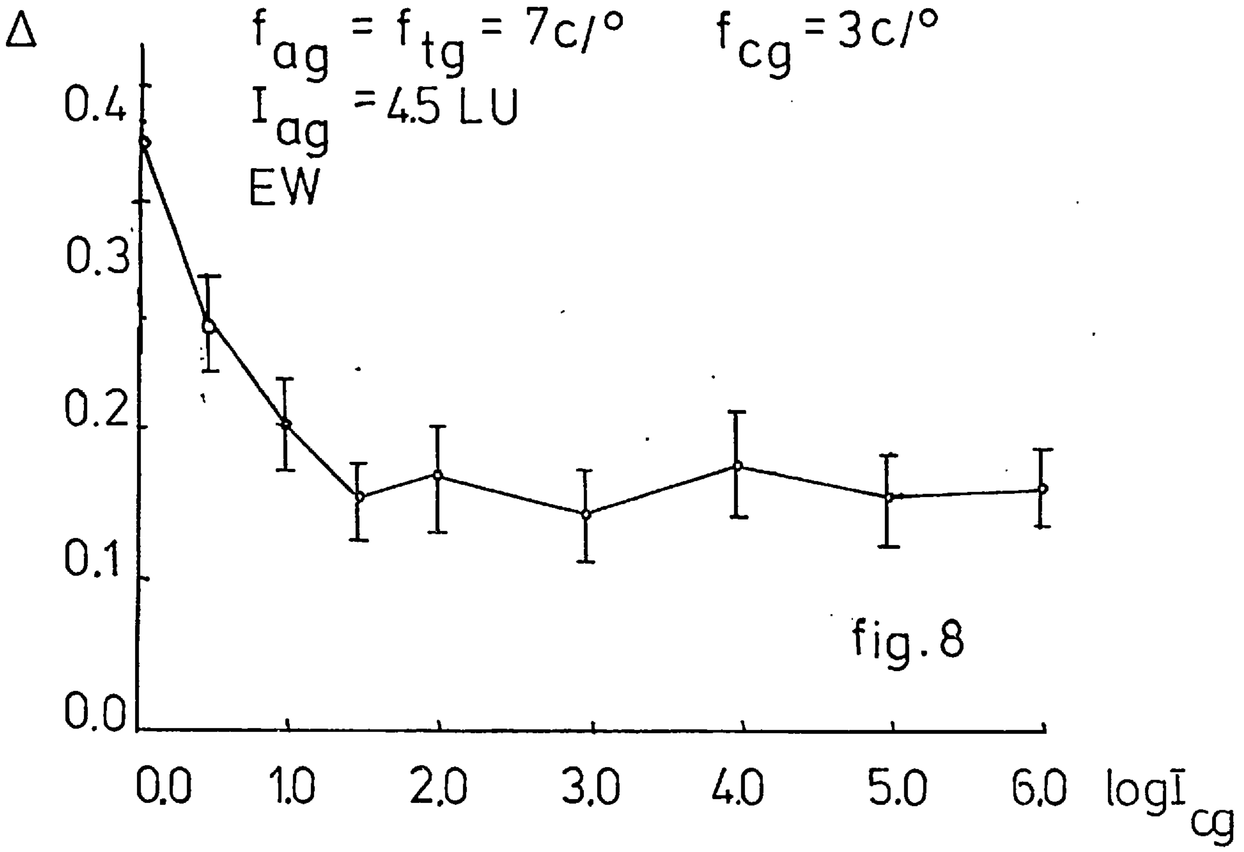

Δ
$f_{ag} = f_{tg} = 7c/°$
$f_{cg} = 3c/°$
$I_{ag} = 4.5$ LU
EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$

fig. 8

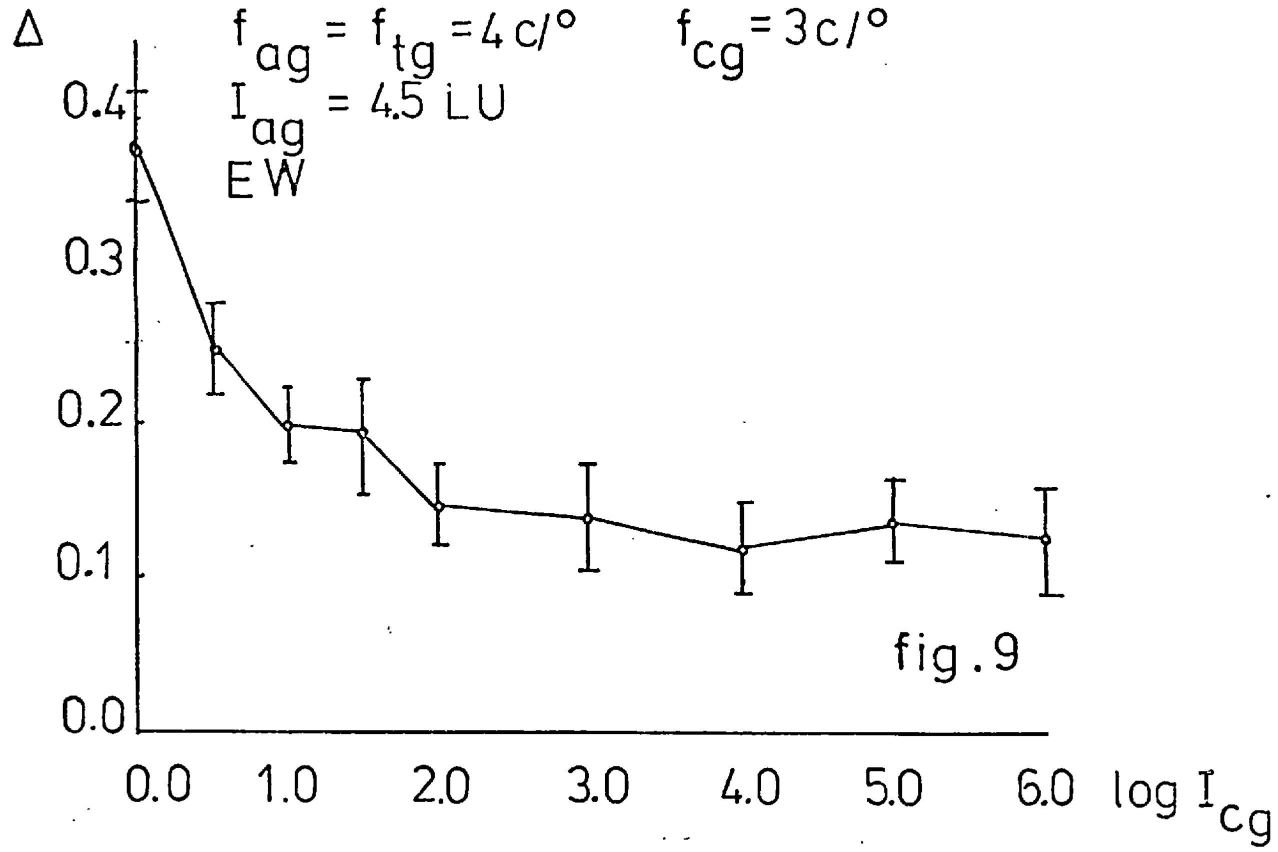

Δ
$f_{ag} = f_{tg} = 4c/°$
$f_{cg} = 3c/°$
$I_{ag} = 4.5$ LU
EW
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{cg}$

fig. 9

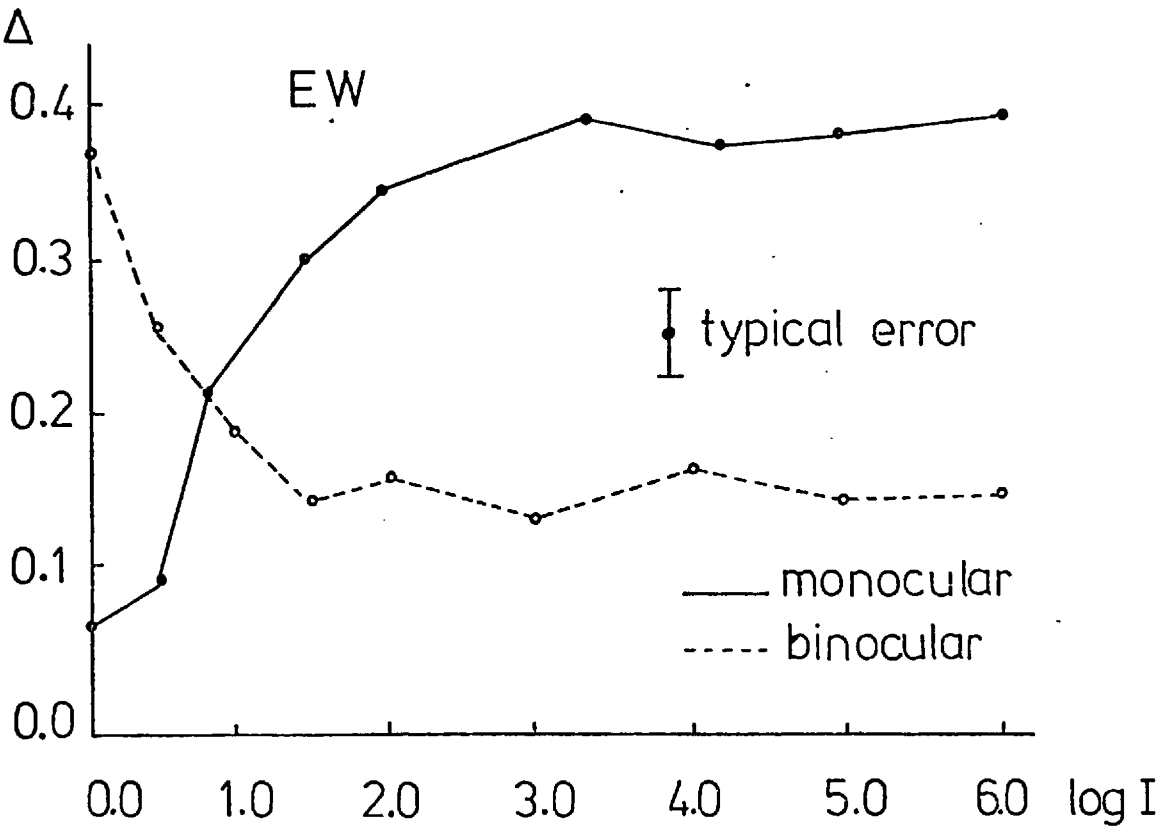


fig. 10

chapt.4

(c) Orientation Specificity

All the experiments described so far have been concerned with gratings oriented vertically. The orientation specificity of the conditioning and test gratings have been investigated in two ways: firstly, measurements were made with the adaptation, conditioning and test gratings rotated together through different angles up to 180 degrees and Δ was determined as a function of the angular displacement. Secondly, the adaptation and test gratings were held vertically and Δ measured for a series of conditioning grating orientations. The results of the first experiment are shown in figs. 11 and 12. In both graphs, f_{cg} was set at 3 c/° in order to maximise the conditioning effect, whilst f_{ag} was set at 7 c/° (fig. 11) and 4 c/° (fig. 12). It can be seen that the reduction in value of Δ, so significant for vertical gratings, is completely removed by rotating the gratings through 90°, the value of Δ returning to that found when $f_{ag} = f_{cg}$. The conditioning experiments shown in figs. 1, 2 and 3 were repeated using horizontal instead of vertical gratings so that the effect of orientation angle for the full range of f_{cg} (the spatial frequency of the conditioning grating) could be determined. The results of the experiments are plotted in figs. 13, 14 and 15. Although the values of Δ for $f_{ag} = f_{cg}$ are the same for both the horizontal and the vertical configurations, the inhibition produced by low spatial frequency conditioning gratings is not observed.

With the gratings oriented at 30° to the vertical and f_{tg} and f_{ag} equal to 7 c/°, a dip in the values of Δ is apparent (fig. 16), but its magnitude is less than half that observed when all the gratings are vertical (fig. 3).

The second series of orientation experiments was carried out with the adaptation and test gratings oriented vertically and only the conditioning grating was rotated to different orientation angles. Again, f_{cg} was set at 3 c/° to give maximum reduction of Δ and the spatial frequency of the adaptation

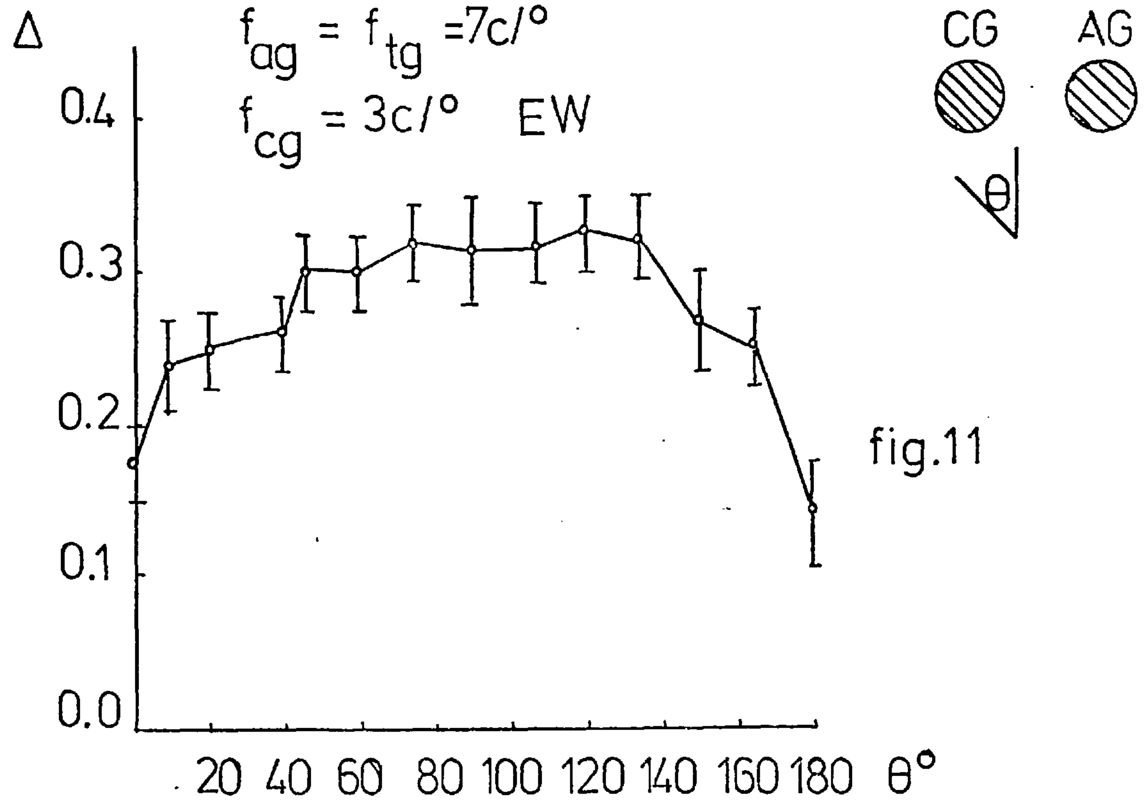

Δ
$f_{ag} = f_{tg} = 7c/°$
$f_{cg} = 3c/°$ EW
CG
AG
θ
0.4
0.3
0.2
0.1
0.0
20 40 60 80 100 120 140 160 180 θ°

fig.11

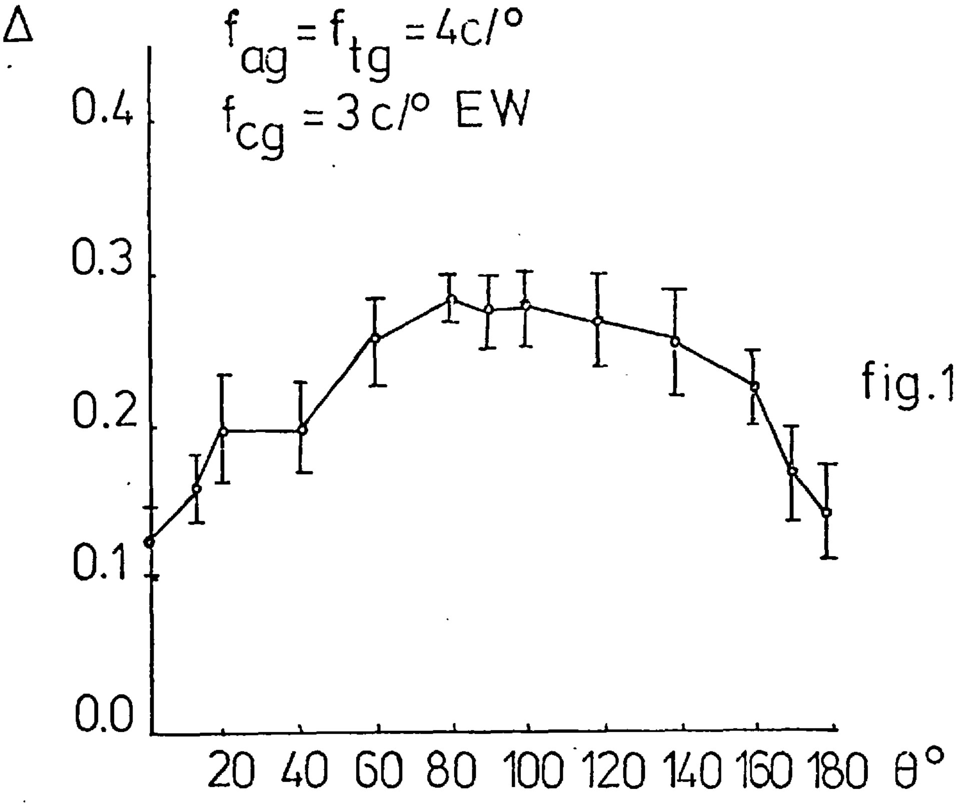

Δ
$f_{ag} = f_{tg} = 4c/°$
$f_{cg} = 3c/°$ EW
0.4
0.3
0.2
0.1
0.0
20 40 60 80 100 120 140 160 180 θ°

fig.12

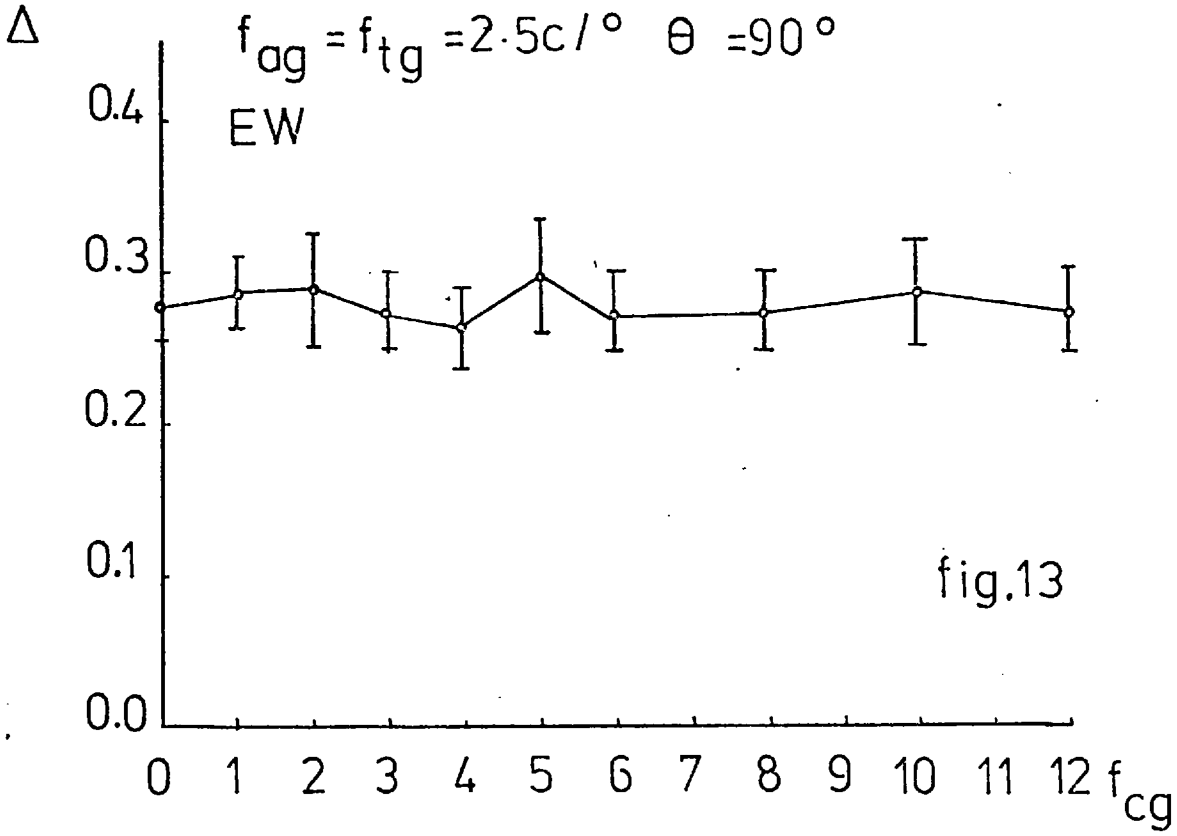

Δ
f_ag = f_tg = 2·5c/° θ = 90°
EW
0.4
0.3
0.2
0.1
0.0
0 1 2 3 4 5 6 7 8 9 10 11 12
f_cg

fig.13

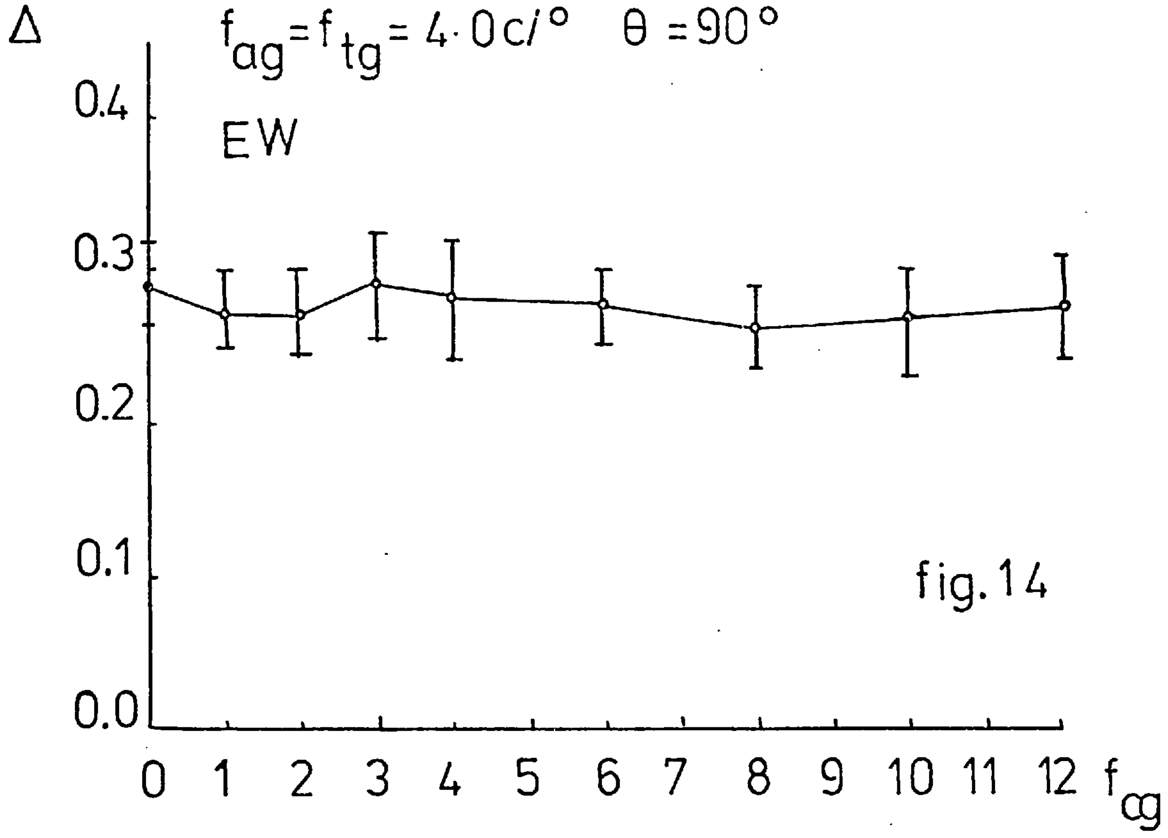

Δ
f_ag = f_tg = 4·0c/° θ = 90°
EW
0.4
0.3
0.2
0.1
0.0
0 1 2 3 4 5 6 7 8 9 10 11 12
f_cg

fig.14

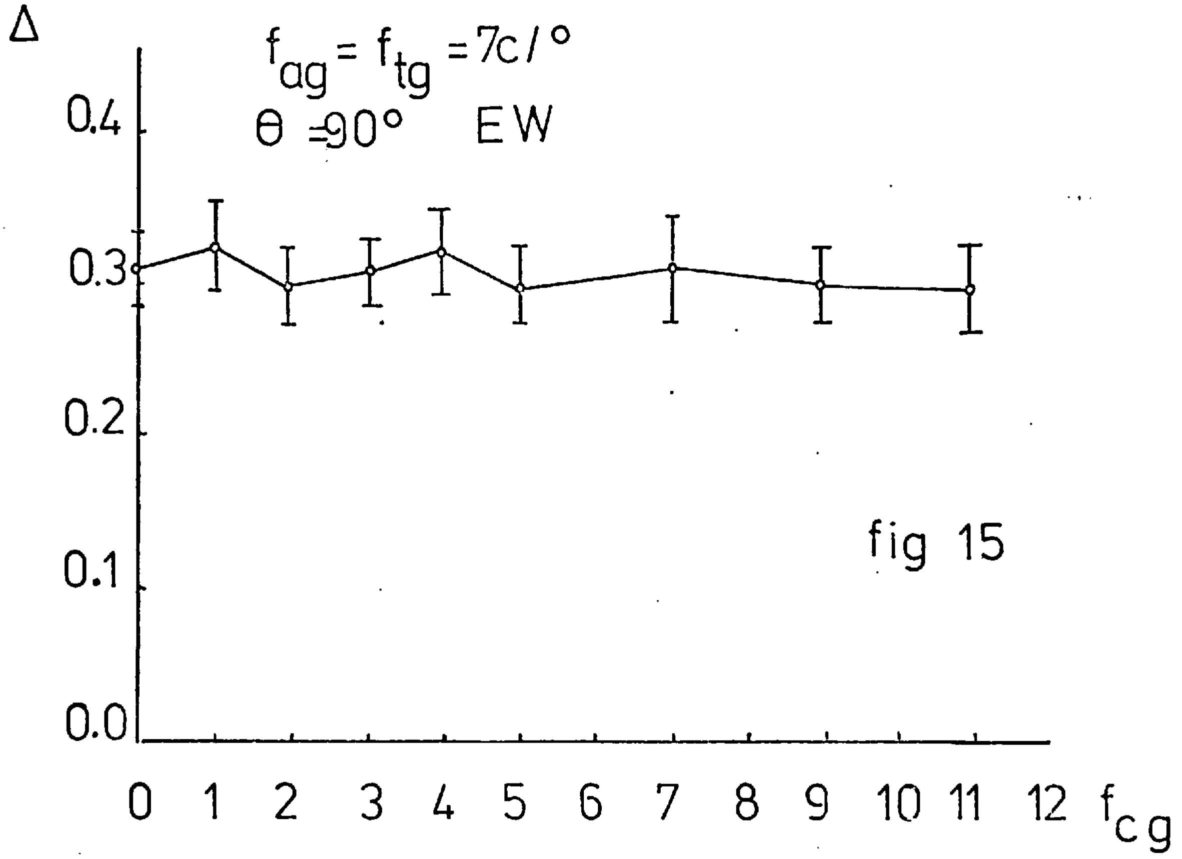

Δ
$f_{ag} = f_{tg} = 7c/°$
θ =90° EW
0.4
0.3
0.2
0.1
0.0
0 1 2 3 4 5 6 7 8 9 10 11 12
f_{cg}

fig 15

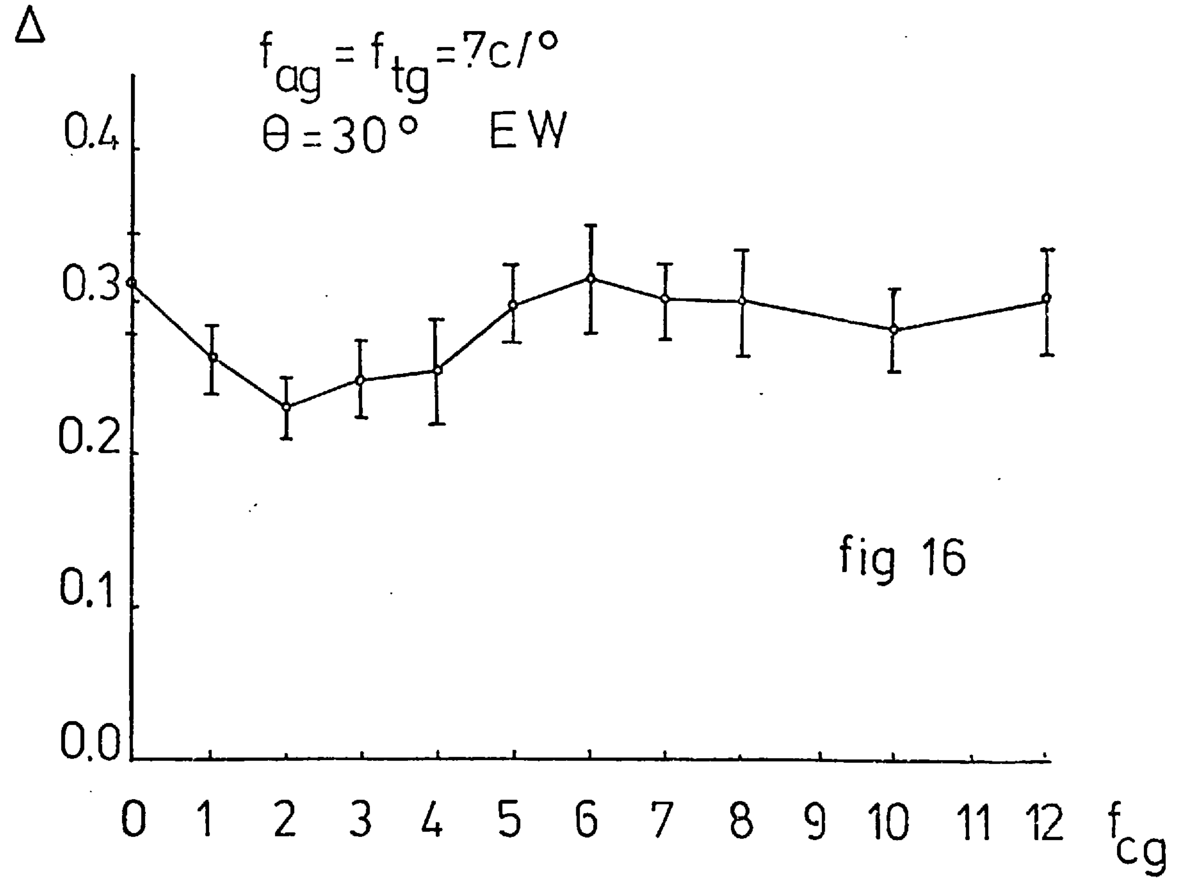

Δ
$f_{ag} = f_{tg} = 7c/°$
θ = 30° EW
0.4
0.3
0.2
0.1
0.0
0 1 2 3 4 5 6 7 8 9 10 11 12
f_{cg}

fig 16

and test gratings was set at either 7 c/° (fig. 17) or 4 c/° (fig. 18). The variation of Δ with angular rotation of CG alone is not significantly different from that seen when all three gratings are rotated together. A comparison of these two sets of data with the orientation selectivity of the grating threshold effect itself as discussed in the previous chapter, is provided in fig. 19. The similarity in general shape between the conditioning field measurements and the monocular adaptation measurements suggests that the mechanisms responsible for orientation specificity of these two effects are comparable.

(d) Wavelength Specificity

It has been found that the interocular transfer of the contrast elevation effect is not colour specific (Maudarbocus and Ruddock, 1973a); that is, adaptation to, say, a blue grating in one eye will elevate the threshold of a red test grating presented to the other eye. In all the experiments concerned with the conditioning field effect described so far, the gratings were of one wavelength - 632.8 nm. By keeping the test and adaptation gratings at this wavelength, but changing that of the conditioning grating to 476 nm, it was possible to determine whether the binocular suppression effect of the conditioning grating was colour-selective. In these experiments, the blue conditioning grating was of spatial frequency 3 c/° for maximum inhibitory effect and the red adaptation and test gratings were of spatial frequencies 7 c/° (fig. 20) or 4 c/° (fig. 21). Values of Δ were determined for different illumination levels, I_{cg}, of the conditioning grating field and a fixed illumination level of the adaptation grating - 4.5 l.u. above its threshold level. Comparisons of these two sets of data with those of figs. 8 and 9 (in which experiments the conditioning gratings were red instead of blue) reveals no significant difference, indicating that the conditioning effect is not colour selective.

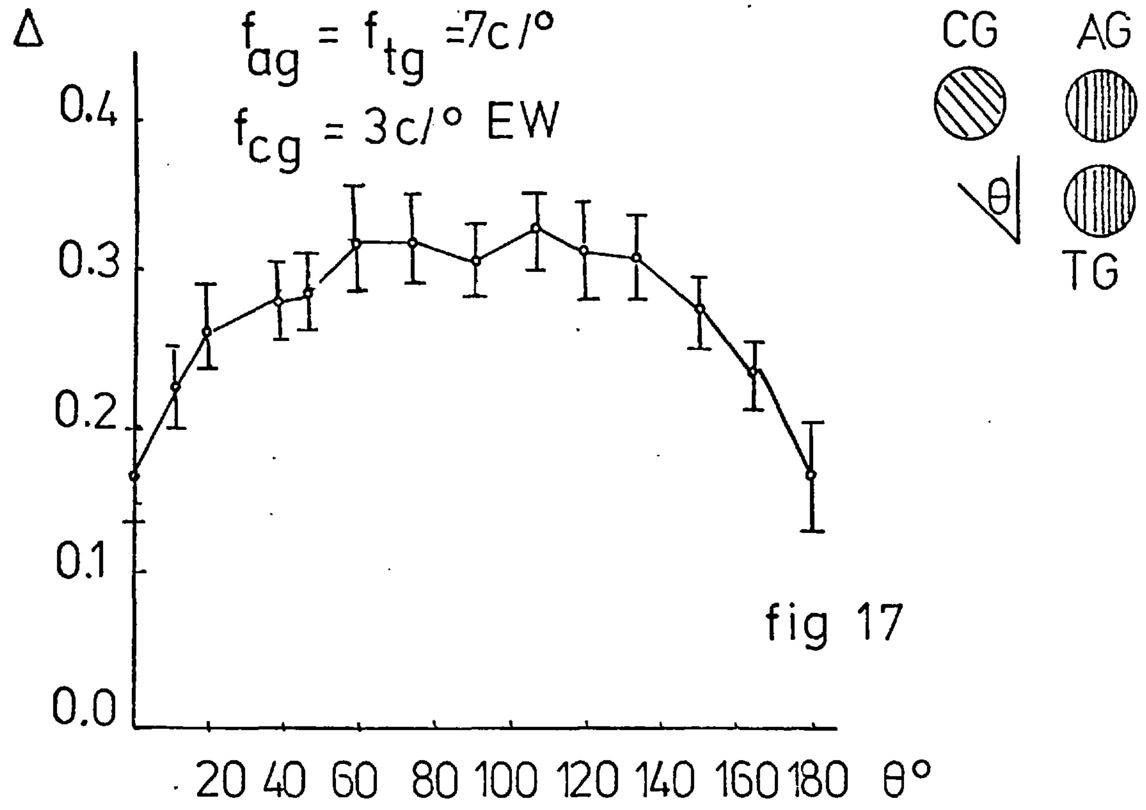

Δ
$f_{ag} = f_{tg} = 7c/°$
$f_{cg} = 3c/°$ EW
CG
AG
θ
TG
0.4
0.3
0.2
0.1
0.0
20
40
60
80
100
120
140
160
180
θ°

fig 17

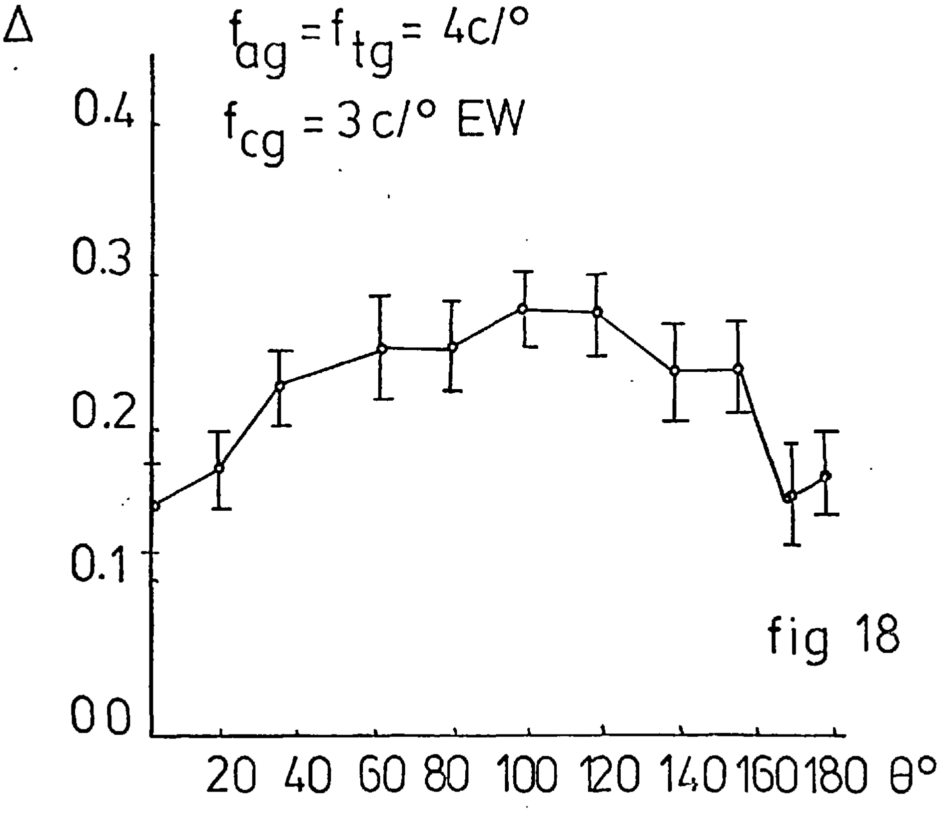

Δ
$f_{ag} = f_{tg} = 4c/°$
$f_{cg} = 3c/°$ EW
0.4
0.3
0.2
0.1
0.0
20
40
60
80
100
120
140
160
180
θ°

fig 18

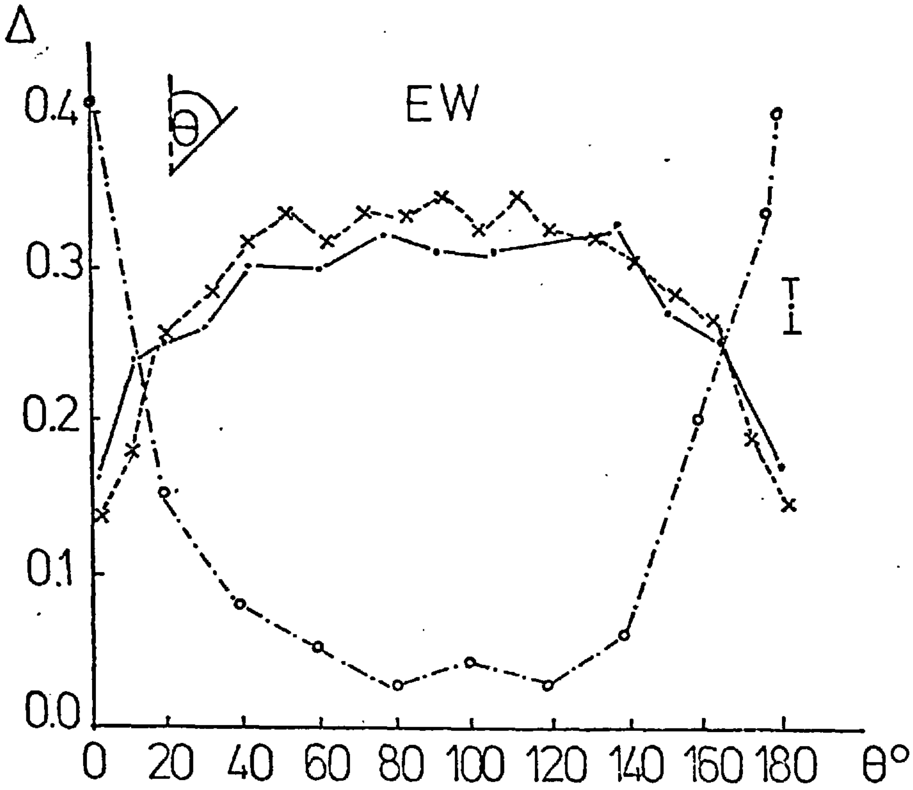


fig. 19

• $f_{cg} = 3c/°$ at θ° ; $f_{ag} = f_{tg} = 7c/°$ vertical
× " " " ; " " " at θ °
∘ no CG ; $f_{ag} = 7c/°$ at θ ; $f_{tg} = 7c/°$ vertical

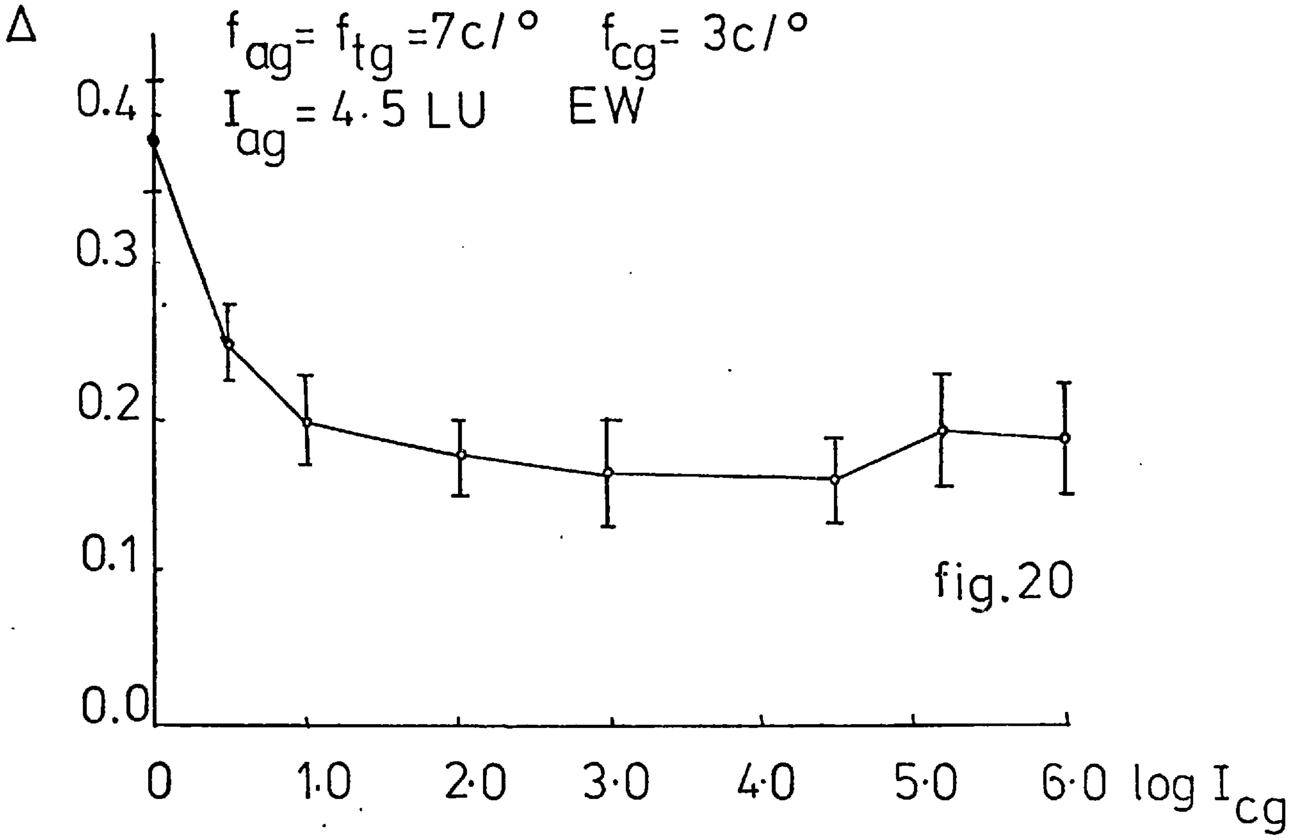


fig.20

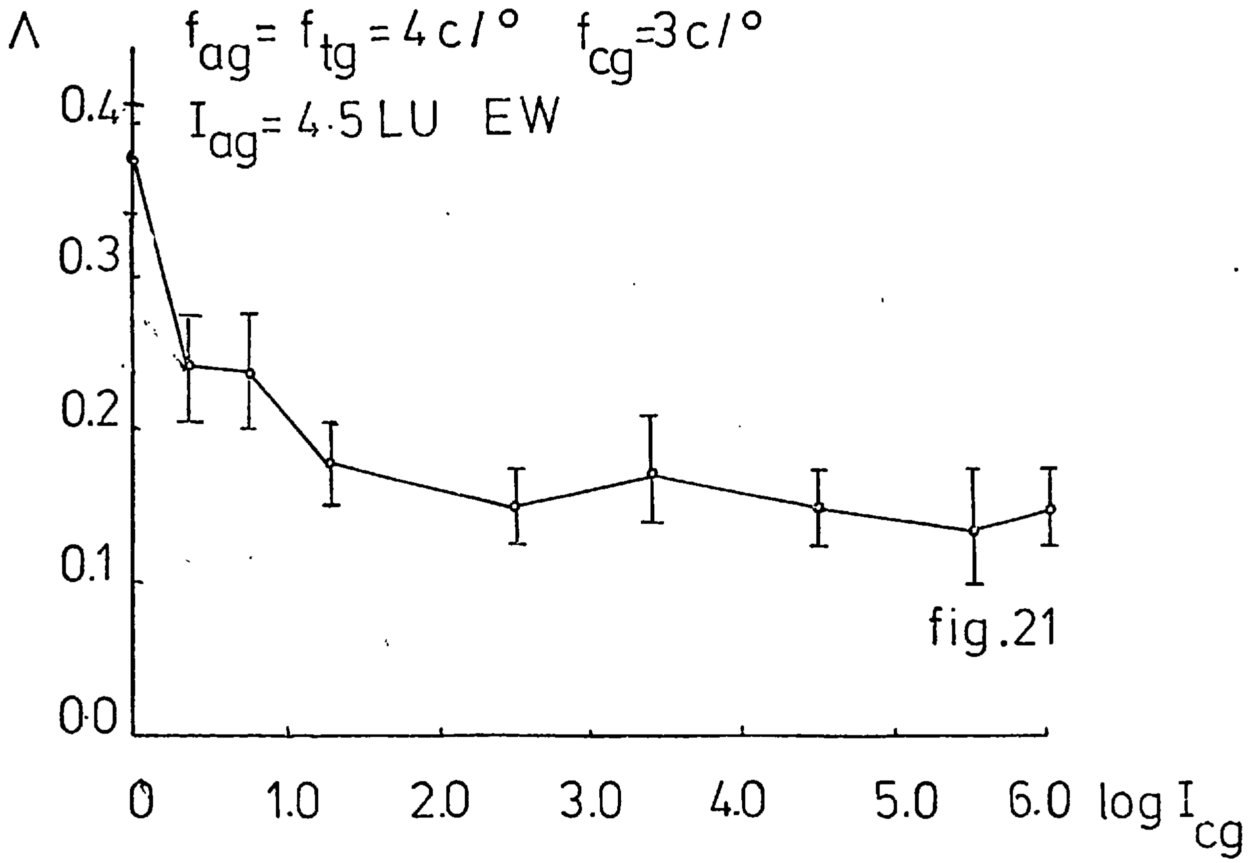


fig.21

blue conditioning grating
red adaptation and test

(e) Binocular rivalry and time course measurements

When the observer views two non-identical gratings, presented, one to each eye, it is generally impossible to fuse them in such a way that the two gratings are superimposed to form a single image. Rather, he will see the two gratings alternate perceptually with only one grating visible at any particular moment. This phenomenon is known as "binocular rivalry". The period during which one or other grating is perceived depends on the two spatial frequencies being observed and varies from 50% visibility of both gratings to complete perceptual domination by one or other of the gratings (one of the earliest reports was published by B.B. Breesein, 1899). In the present experiment, it was found that a 3 c/° conditioning grating is perceptually dominant in the presence of an adaptation grating, almost irrespective of the spatial frequency of this adaptation grating. In the case where a 7 c/° adaptation grating and a 3 c/° conditioning grating were used, the conditioning grating was visible for 83% ± 5% of a 5 minute period and adaptation grating for only 17% ± 5 %. The measurements were made by an observer viewing the two fields through the interferometer eyepieces and operating the pen recorder to mark the rotating drum only when the conditioning grating was visible. It appears possible, therefore, that the efficiency of the 7 c/° adaptation grating is reduced by binocular rivalry caused by the 3 c/° conditioning field as a result of which, it is not perceived by the observer for 85% of the adaptation period. There is, however, evidence that such rivalry is not the cause of the inhibitory interaction. Firstly Blake and Fox (1974) have carried out experiments into the relative locations within the visual system of the contrast elevation effect and binocular rivalry (see chapter 1). The build-up of the monocular and interocular contrast elevation effect from the unadapted to fully adapted levels is not instantaneous, but rather increases over approximately 20 secs. of adaptation with a well-defined time course

(Blakemore and Campbell, 1969b). Blake and Fox (1974) compared the magnitude of threshold elevation produced after approximately 6 seconds monocular adaptation with that produced after the same period of adaptation to the same stimulus, but with a totally unrelated pattern in the alternate eye, this latter being chosen so that the adaptation stimulus was perceptually suppressed for at least 50% of the adaptation period. They found no significant difference in the degree of threshold elevation in the two experiments and concluded that the adaptation stimulus functioned as such even during those periods when, because of rivalry, it was invisible to the observer. They suggested that the site of binocular rivalry was located centrally with respect to the site of the contrast elevation effect.

Further evidence that rivalry does not directly influence the degree of threshold elevation is provided by the present experiment. Measurements were taken of the alternation rates of the 3 c/° conditioning grating and the 7 c/° adaptation grating with the gratings presented horizontally instead of vertically. In this configuration, the suppression of the adaptation effect by a low frequency conditioning grating is not observed (fig. 11). It was found, however, that the binocular rivalry rates were approximately the same in the two set-ups (80% CG; 20% AG for horizontal bars, c.f. 83% CG; 17% AG for vertical bars). This result indicates, therefore, that the cause of the reduced elevation effect is not mechanistically related to the perceptual suppression of the adaptation grating.

Detailed time course measurements were made in order to determine whether the conditioning field influences the rate of induction of the contrast threshold elevation effect by the adaptation grating. It was reasoned that if the conditioning grating suppresses the detection of the adaptation grating prior to the site of the grating threshold adaptation effect, the time course of the effect would be modified. The experiments commenced with the observer fully adapted to two uniform fields, presented one to either eye. The uniform adaptation fields were then replaced for a chosen period of time, t_a, by an adaptation grating (right eye) and a conditioning grating (left eye). The uniform fields, adaptation and conditioning gratings were all set at an illumination level equivalent to a level 4.5. log units above the threshold level of the adaptation grating. The test and adaptation gratings were, in turn, replaced by the test grating, presented for 3 seconds to the right eye, during which time the observer attempted to set the illumination level of the grating to its threshold level. Thus values of Δ were determined for different periods, t_a, of adaptation. In practice, it was impossible for the observer to find the test threshold level in a single presentation cycle and a number of further presentation cycles were necessary. In this cycle, the duration of presentation of the uniform field was 30 secs. for a 5 sec. adaptation period, up to 2 mins. for a 30 sec. adaptation period, the uniform field presentation being in each case of sufficient duration to dissipate the effects of the preceding presentation of the adaptation grating. The variation of Δ with t_a was determined for a number of different field configurations and the experimental data are plotted in figs. 23 to 26. The time course for build up of the contrast threshold elevation effect was firstly determined. In this case, no uniform field or conditioning grating was presented to the left eye, which remained dark adapted throughout, the cycle of uniform adaptation and test field presentation being restricted to the right eye. The data for this configuration are plotted in fig. 23 and are in good agreement with the corresponding data of Blakemore and Campbell, (1969b). Results of experiments in which both eyes perceived a uniform field, and a conditioning grating was presented to the left eye are given in figs. 24 to 26.

It can be seen from these data, that although the maximum amount of

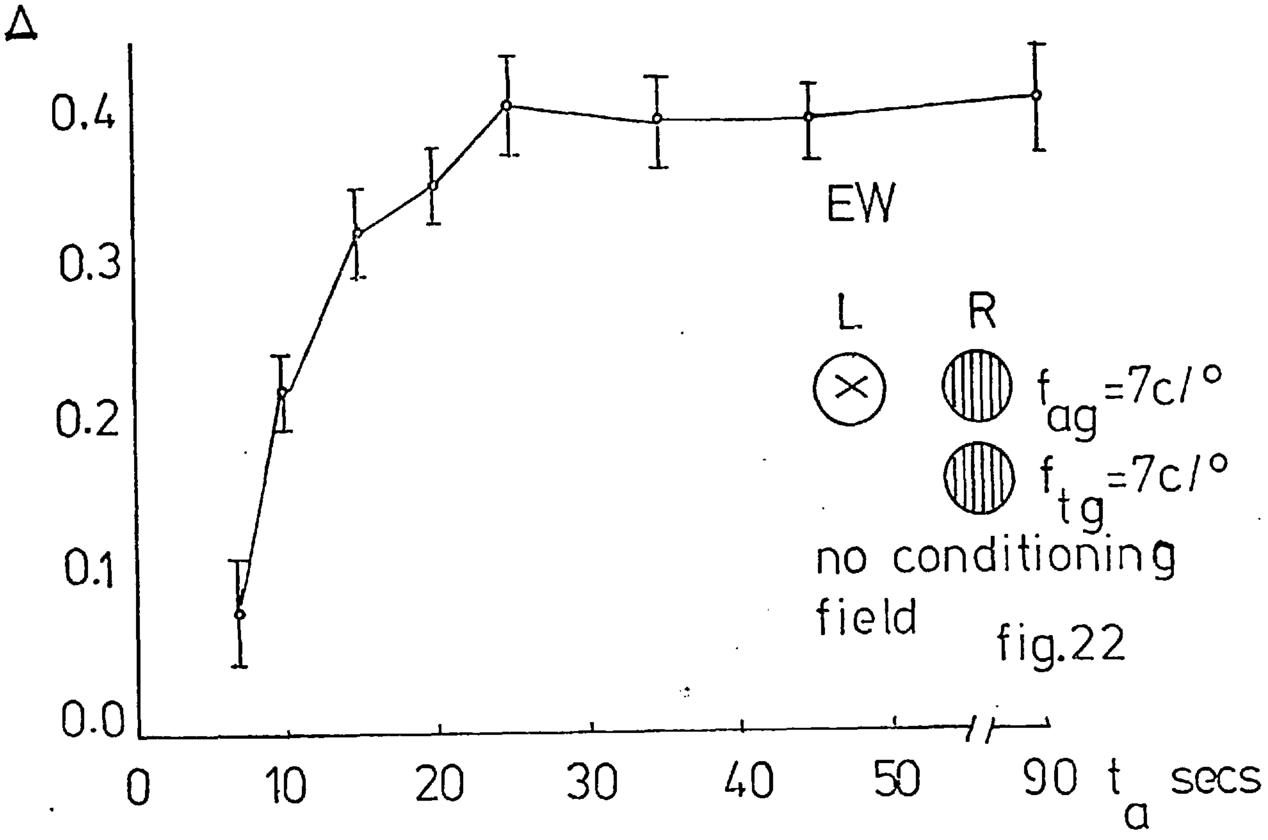

Δ
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
90
t_a secs
EW
L
R
f_{ag}=7c/°
f_{tg}=7c/°
no conditioning field

fig.22

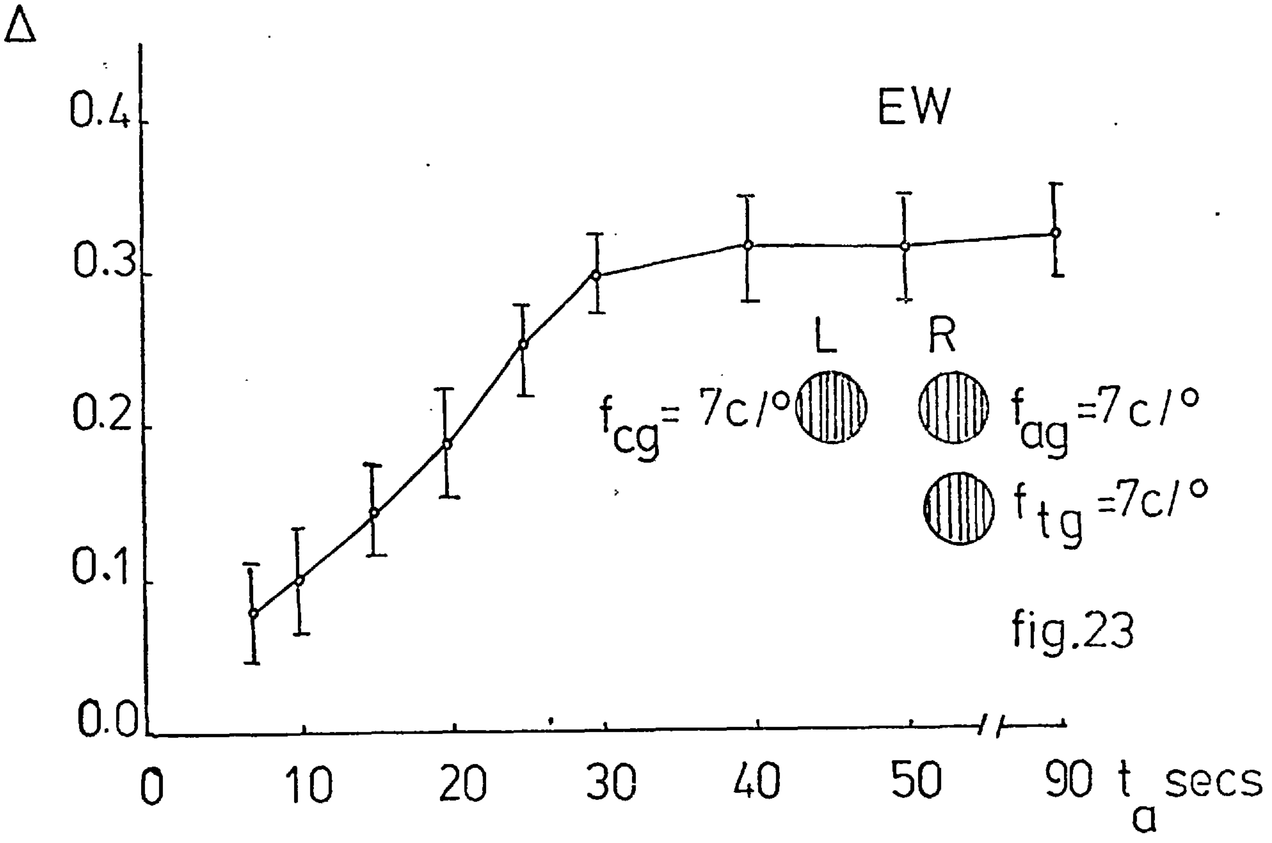

Δ
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
90
t_a secs
EW
L
R
f_{cg}= 7c/°
f_{ag}=7c/°
f_{tg}=7c/°

fig.23

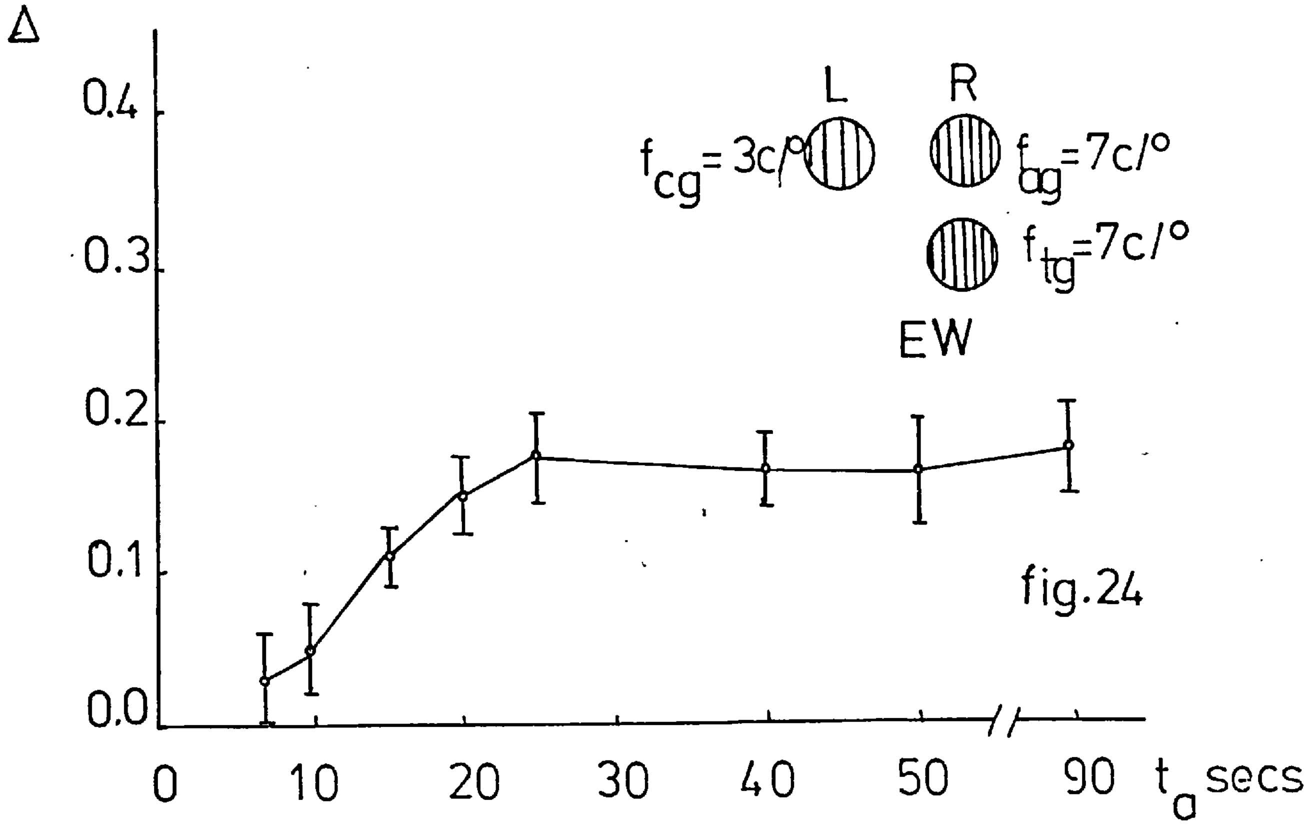

Δ
0.4
0.3
0.2
0.1
0.0
L
R
f_{cg}=3c/°
f_{ag}=7c/°
f_{tg}=7c/°
EW
0
10
20
30
40
50
90
t_a secs

fig.24

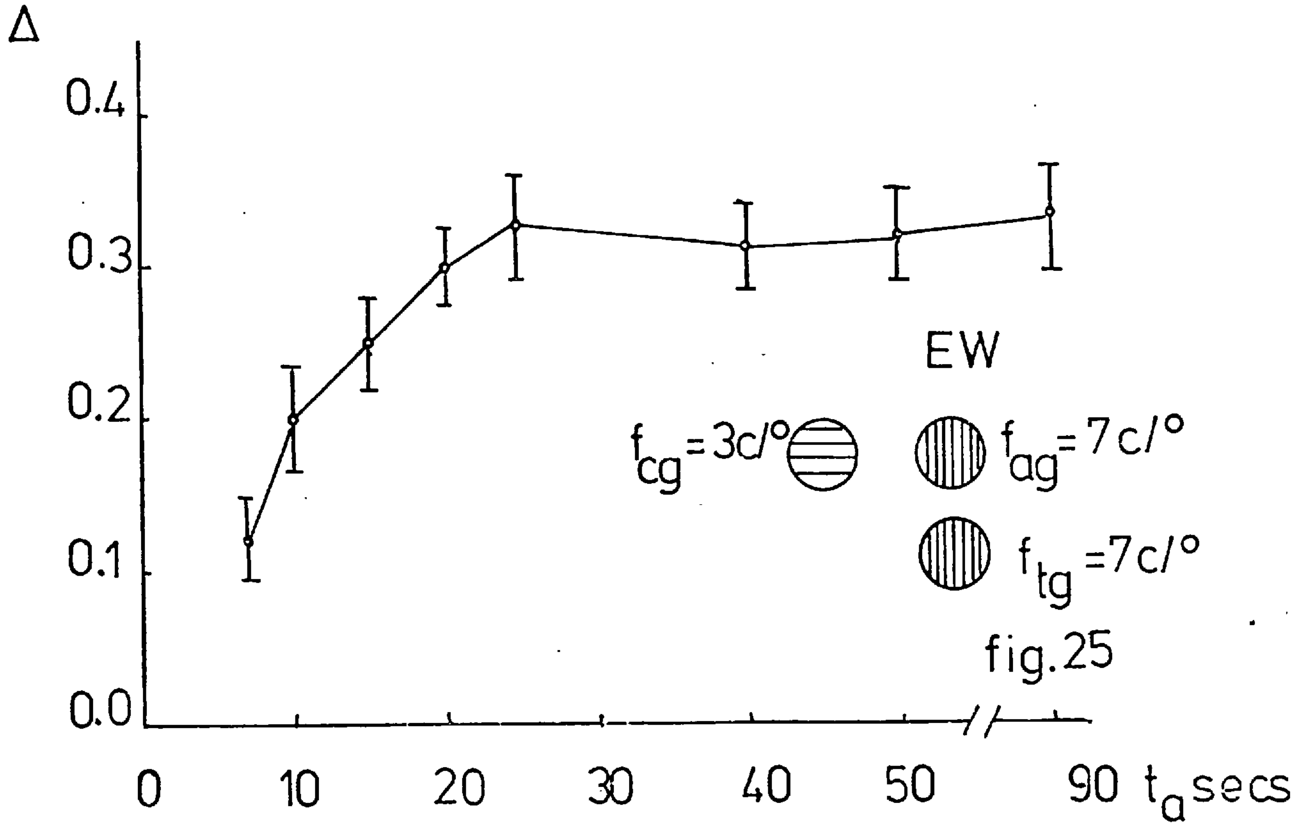

Δ
0.4
0.3
0.2
0.1
0.0
EW
f_{cg}=3c/°
f_{ag}=7c/°
f_{tg}=7c/°
0
10
20
30
40
50
90
t_a secs

fig.25

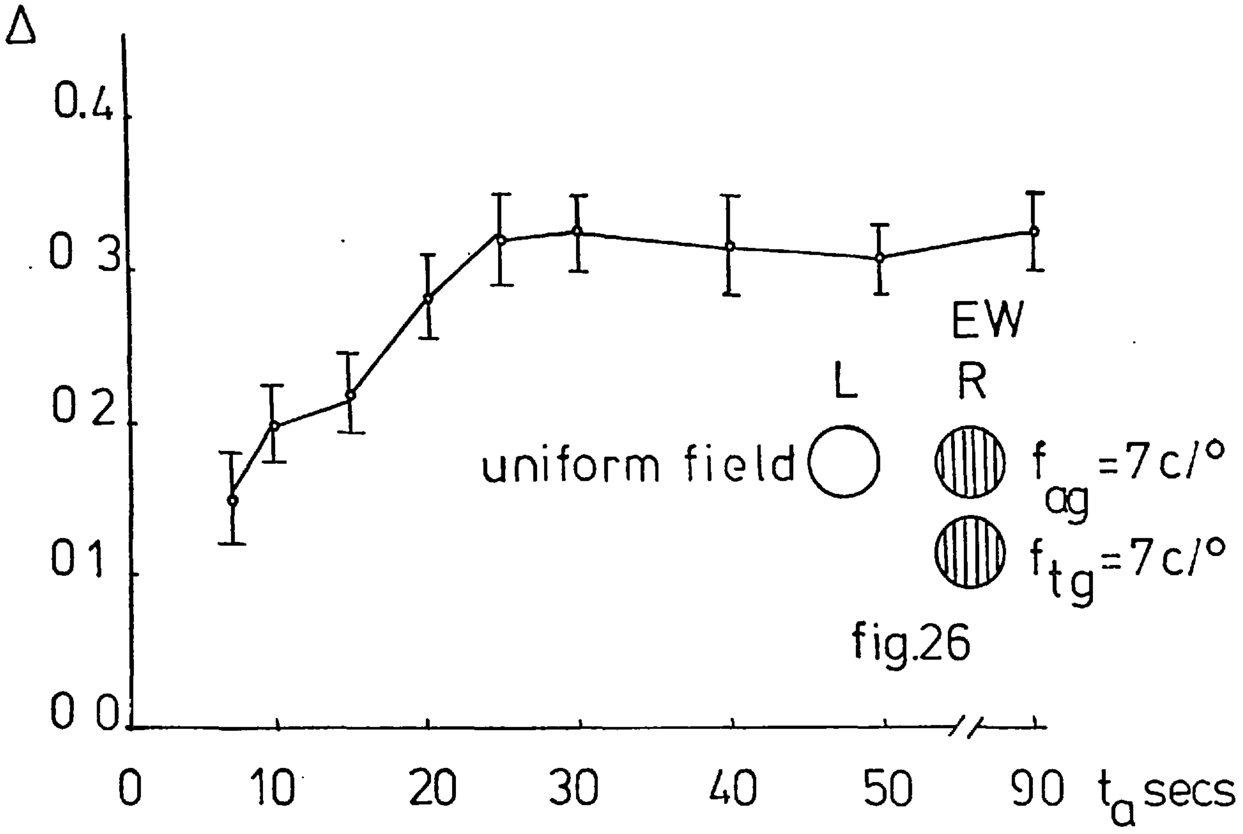

Δ
0.4
0 3
0 2
0 1
0 0
0
10
20
30
40
50
90
t_a secs
EW
L
R
uniform field
f_{ag}=7c/°
f_{tg}=7c/°

fig.26

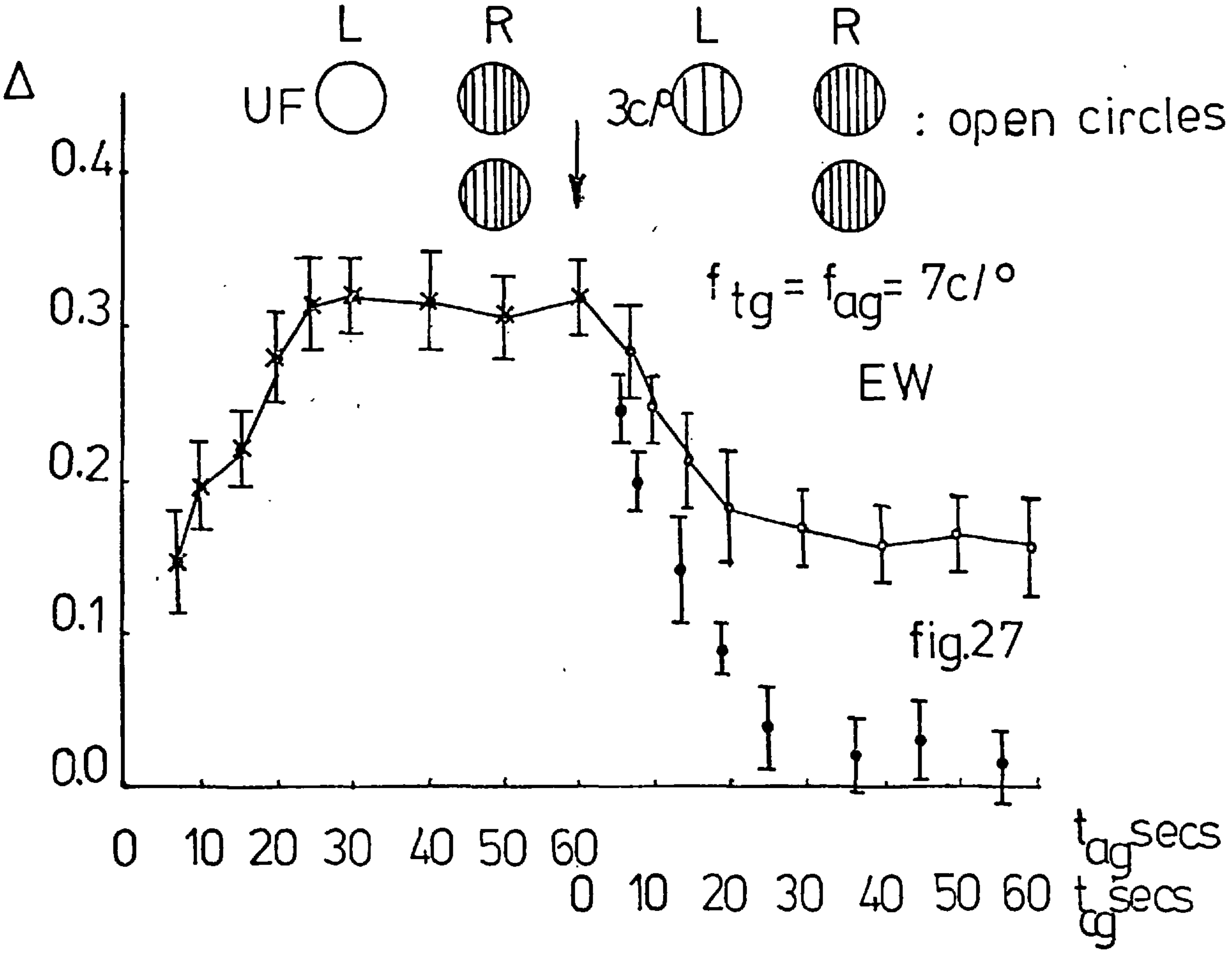

Δ
L
R
L
R
UF
3c/°
: open circles
f_{tg}= f_{ag}= 7c/°
EW
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
t_{ag} secs
0
10
20
30
40
50
60
t_{tg} secs

fig.27

contrast elevation is influenced by the nature of the conditioning field, the minimum period of presentation of the adaptation grating necessary to produce this elevation is not significantly influenced. It remains at about 30 seconds regardless of whether the conditioning field is the same as the adaptation grating (fig. 23), whether it is a 3 c/° vertical grating (fig. 24), a 3 c/° horizontal grating (fig. 25), a uniform field (fig. 26) or whether the conditioning field is not presented at all (monocular configuration, fig. 22). As was argued previously, if perceptual suppression of the adaptation stimulus through binocular rivalry with the conditioning field was responsible for the suppression effect associated with the conditioning field, some change in the time course would be expected. The data in figs. 23 to 25 show that this is not the case, thus confirming the previous conclusion that binocular rivalry does not give rise to the conditioning effect. The time courses for the different conditioning fields are redrawn in a single figure for comparative purposes in fig. 28.

The suppression effect following the presentation of a 3 c/° vertical conditioning grating is not instantaneous, but follows a well-defined time course similar to that observed for the contrast threshold elevation effect itself. The time course of the conditioning effect was determined in a similar fashion to the time course measurements previously described. The experiment commenced with a determination of the increase of Δ with increase in the period, t_{ag}, of adaptation (fig. 27) A uniform conditioning field was presented to the left eye (as in fig. 26) so that when the 3 c/° conditioning field was introduced later in the experiment, there was no sudden change in adaptation condition of the left eye. The space-average illumination level of both conditioning fields was, as before, equal to that of the 7 c/° adaptation grating, itself 4.5 log units above threshold level for detection of the adaptation grating. After some 60 secs. adaptation, by which time the value of Δ had settled to a steady maximum

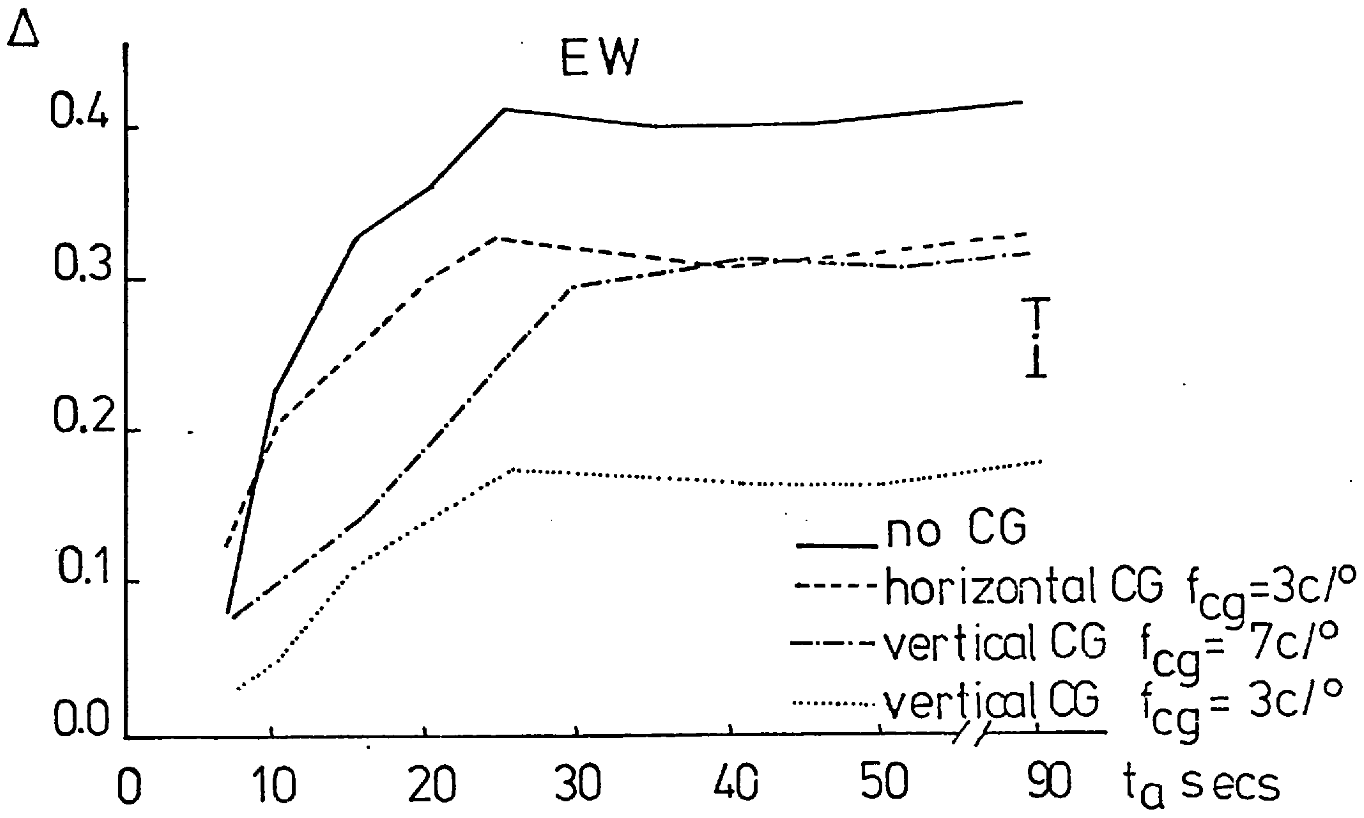

Δ
EW
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
90
t_a secs
no CG
horizontal CG f_{cg}=3c/°
vertical CG f_{cg}= 7c/°
vertical CG f_{cg}= 3c/°

fig . 28

value, the 3 c/° conditioning grating was substituted for the uniform conditioning field, and Δ measured as a function of t_{cg}, the duration of presentation of the 3 c/° conditioning grating. Each point corresponding to different values of t_{cg} was determined four times, and each determination necessitated a cycle of 60 secs. adaptation, followed by a conditioning period of duration t_{cg}. From the experimental data it can be seen that Δ reduces to a minimum value after a conditioning period, t_{cg}, of some 30 secs. which is comparable with the adaptation period t_{ag}, required to establish the maximum value of Δ. In a further series of measurements, the effect of introducing the conditioning grating was compared with the effect of removing the adaptation grating. In this case, the 60 sec. adaptation period was followed by a period of t_{cg} during which the adaptation grating was replaced by a uniform field of the same illumination level as the space-average level of the adaptation grating. In this case, the uniform conditioning field was presented to the right eye, throughout the experiment. The variation of Δ with different periods, t_{cg}, of presentation of the uniform field are plotted as filled circles in fig. 27. It is apparent that the time course of Δ after the adaptation grating was replaced by a uniform field is similar to that found when the 3 c/° conditioning grating was introduced into the left eye, although in the former case Δ falls to a minimum value of zero, whilst in the latter its minimum value is about 0.15.

It was shown by Blakemore and Campbell (1969b) that the contrast threshold elevation effect is short-lived, being significant for only some 60 secs. following removal of the adaptation grating. To complete the time course experiments, the effect of a conditioning grating field on the time course of Δ, following cessation of the adaptation field, was determined. After two minutes adaptation to a 7 c/° adaptation grating and 3 c/° conditioning grating, the 7 c/° test grating was presented continuously and the observer asked to adjust its illumination level during the two minute period immediately following adaptation. The observer operated the pen-drive which marked the recording paper mounted on the rotating recording drum (described in chapter 2) whenever he adjusted the wedge to give a satisfactory threshold. After two minutes, the observer re-adapted to the adaptation and conditioning gratings, and the recovery curve was measured again. Five such measurements were made and the sets of data collected by averaging the threshold readings over 2 sec. intervals, thus producing a single, average recovery curve. The values so obtained correspond to the overall change in threshold illumination level of the test grating following grating adaptation. In order to determine the corresponding change in Δ, it was necessary to repeat the experiment, but with the conditioning and adaptation gratings replaced by uniform fields of illumination level equal to the space-average illumination level of the grating fields. The difference between the threshold levels for the grating and uniform field adaptation conditions yield, by definition (chapter 1, page 32), the values of Δ.

Values of Δ plotted as a function of time for four different conditioning fields are shown in figs. 29 to 32. It is apparent that in all cases, including that where the conditioning field is most effective in suppressing the threshold contrast elevation effect (fig. 32) the time course of Δ following adaptation is approximately the same, requiring approximately 60 seconds to return to a zero value. This is consistent with Blakemore and Campbell's (1969b) data and indicates that the conditioning grating has little influence on the time course of recovery of Δ following adaptation.

The time course experiments show clearly that the temporal course of induction of the contrast threshold elevation effect and recovery from this same effect are not influenced by the conditioning field. This implies that the adaptation mechanism is unchanged by the conditioning field. The results also support the conclusion that the suppression of threshold contrast elevation arising from the conditioning grating is not due to the binocular

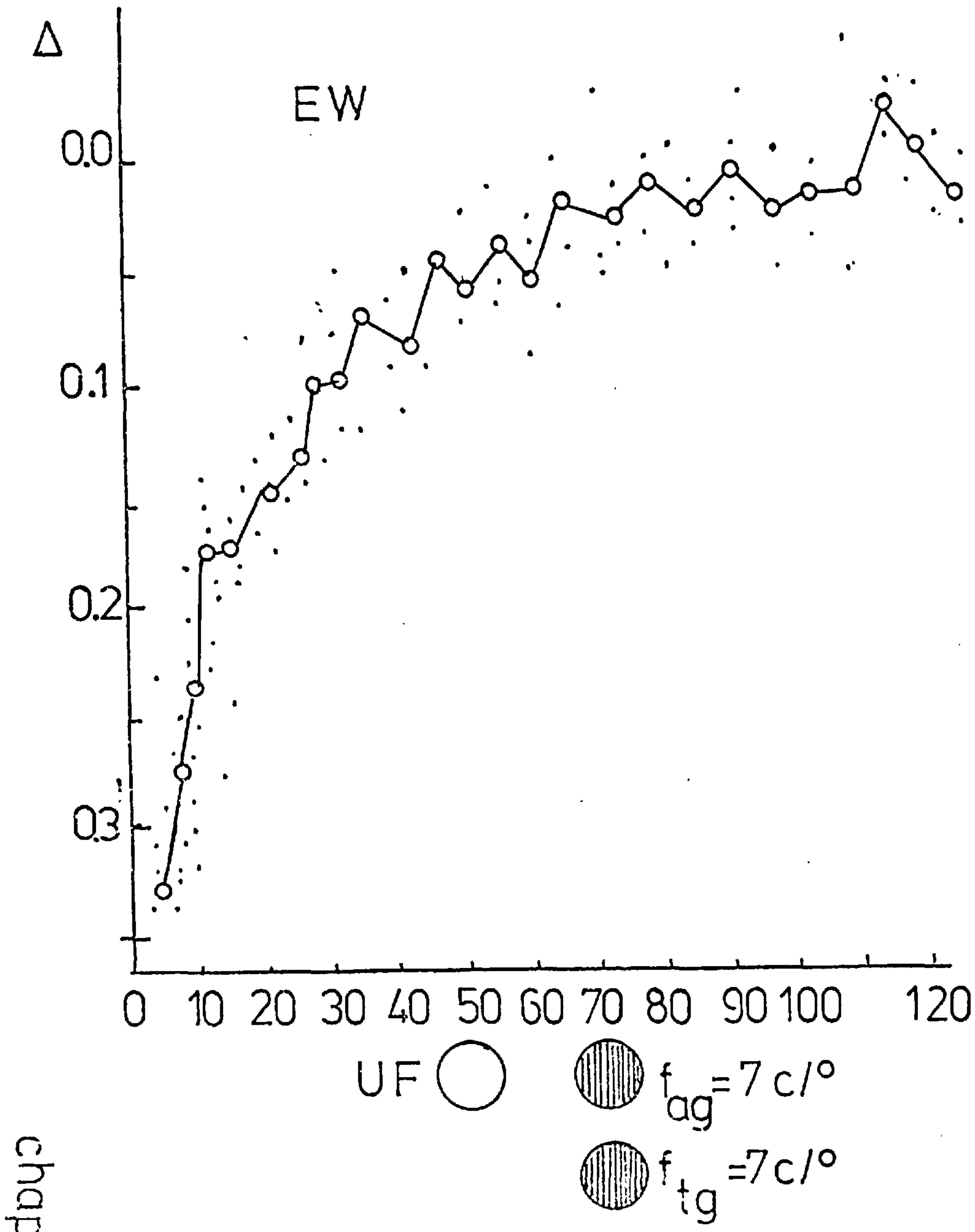

Δ
EW
0.0
0.1
0.2
0.3
0
10
20
30
40
50
60
70
80
90
100
120
UF
f_{ag}=7 c/°
f_{tg}=7 c/°

fig 29

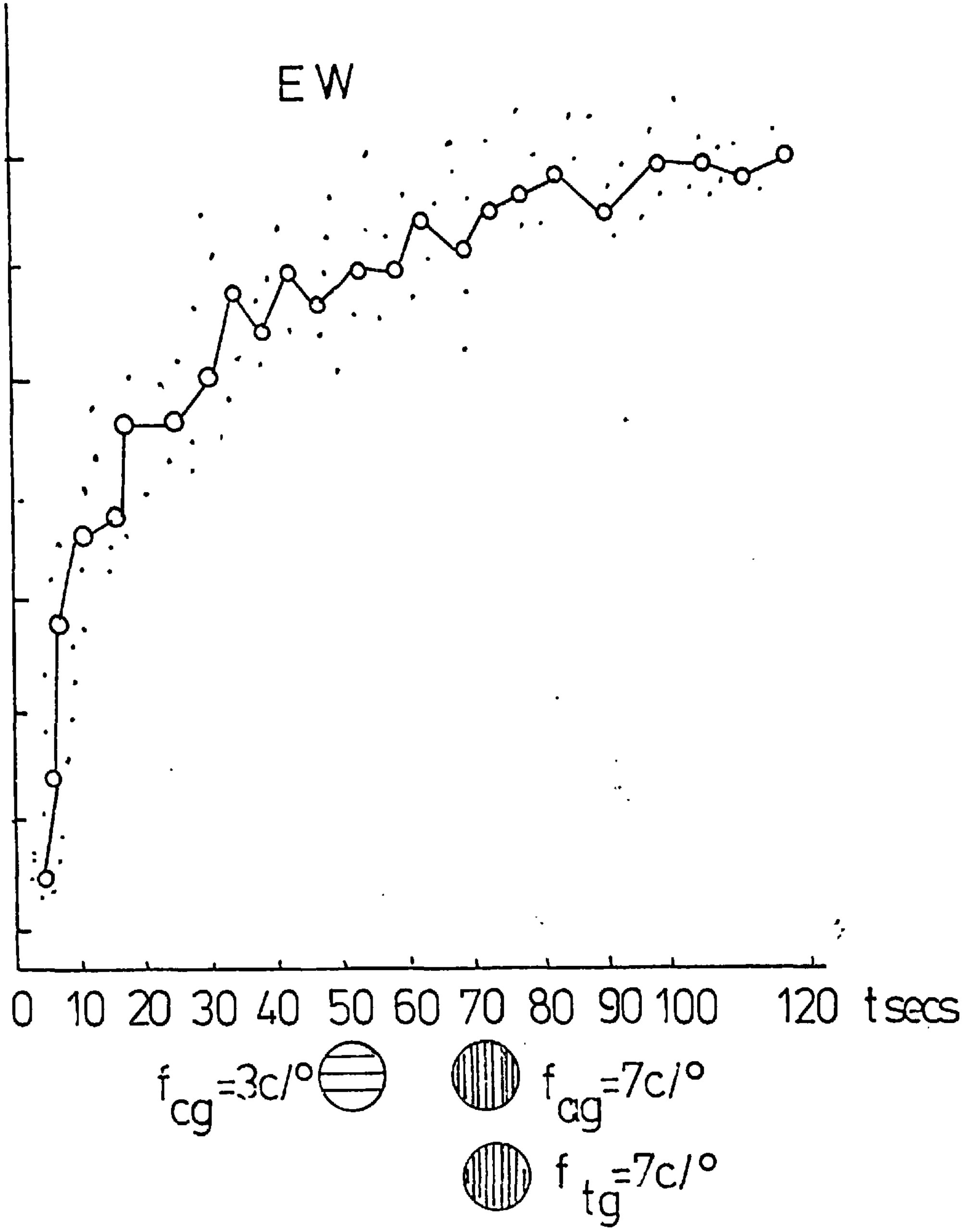

EW
0
10
20
30
40
50
60
70
80
90
100
120
t secs
f_{cg}=3c/°
f_{ag}=7c/°
f_{tg}=7c/°

fig 30

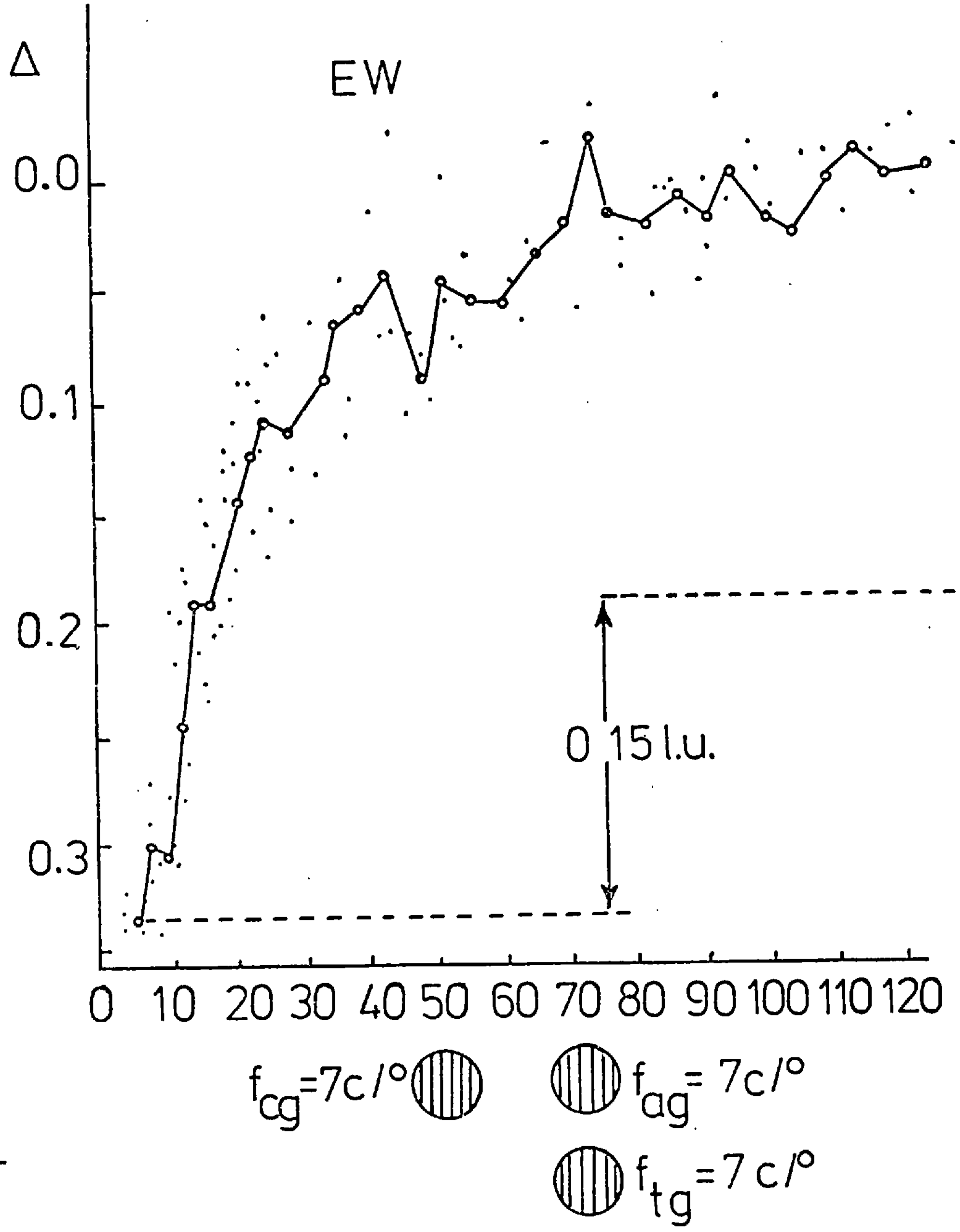

Δ
EW
0.0
0.1
0.2
0.3
0 15 l.u.
0
10
20
30
40
50
60
70
80
90
100
110
120
f_{cg}=7c/°
f_{ag}= 7c/°
f_{tg}=7 c/°

fig. 31

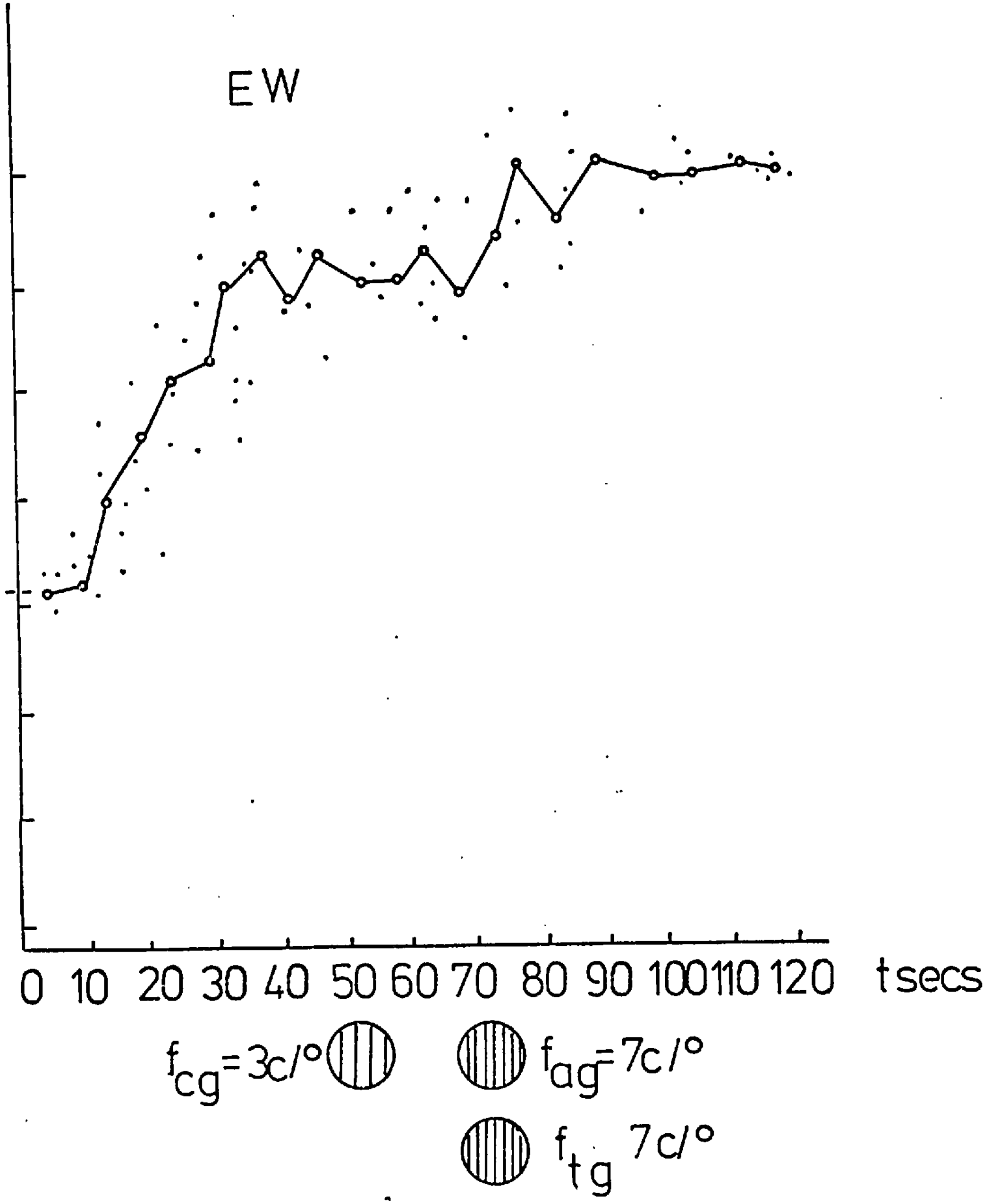

EW
0
10
20
30
40
50
60
70
80
90
100
110
120
t secs
f_{cg}=3c/°
f_{ag}=7c/°
f_{tg} 7c/°

fig.32

rivalry associated with the conditioning grating. Perhaps the most important information yielded by the time course experiments is that the time course of the suppression effect following the presentation of the conditioning grating is similar to that following cessation of the adaptation grating (fig. 27). This result shows that the action of the conditioning grating is equivalent to removing in part the input signals to the adaptation mechanism which arise from the adaptation grating. (The conditioning grating does not block these signals entirely, since Δ falls to a value of 0.15 rather than zero). For this reason it is considered that the action of the conditioning grating is inhibitory on the signals from the adaptation grating.

(f) Off-axis measurements.

All the measurements on the binocular interaction so far described were made with the adaptation fields completely filling the 30° objective eye pieces. The test, as presented to the right eye, was also 30° wide. By putting one of a series of stops in the back focal plane of the right eye objective, it was possible to present the test and adaptation gratings with variable off-sets from a central fixation point (see chapter 2 for details). A 5° adaptation grating of 7 c/° was presented in synchrony with the 30°, 3 c/° conditioning grating of earlier experiments. The observer fixated on a $\frac{1}{2}$° spot in the centre of the right eye piece. Measurements of Δ were taken for displacements of the adaptation grating to the left and to the right of the fixation spot in both the vertical (fig. 33) and the horizontal (fig. 34) directions. In each case, a comparison set of data is drawn where f_{cg} is set at the non-inhibitory value of 7 c/° instead of 3 c/°. Fig. 33 shows that the conditioning effect of the 3 c/° grating is not dependent on vertical displacements of the 7 c/° test grating (comparable with interocular measurements made by

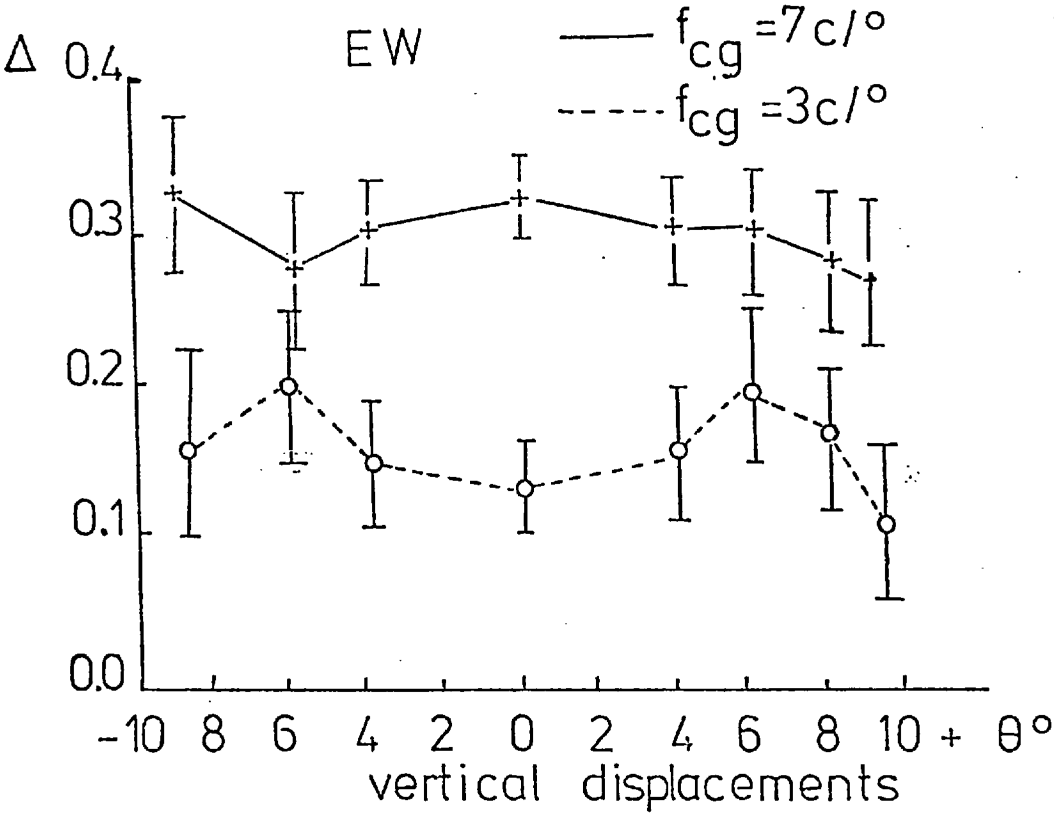

Δ
EW
fcg =7c/°
fcg =3c/°
0.4
0.3
0.2
0.1
0.0
-10 8 6 4 2 0 2 4 6 8 10 + θ°
vertical displacements

fig.33

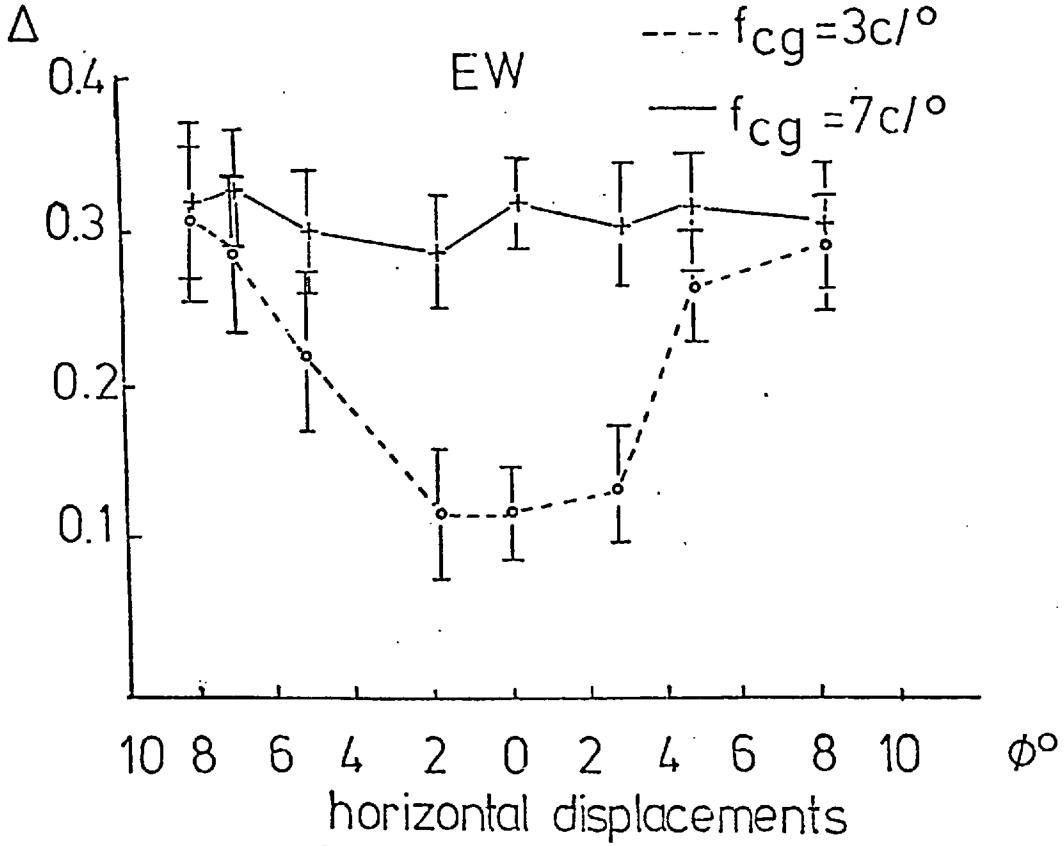
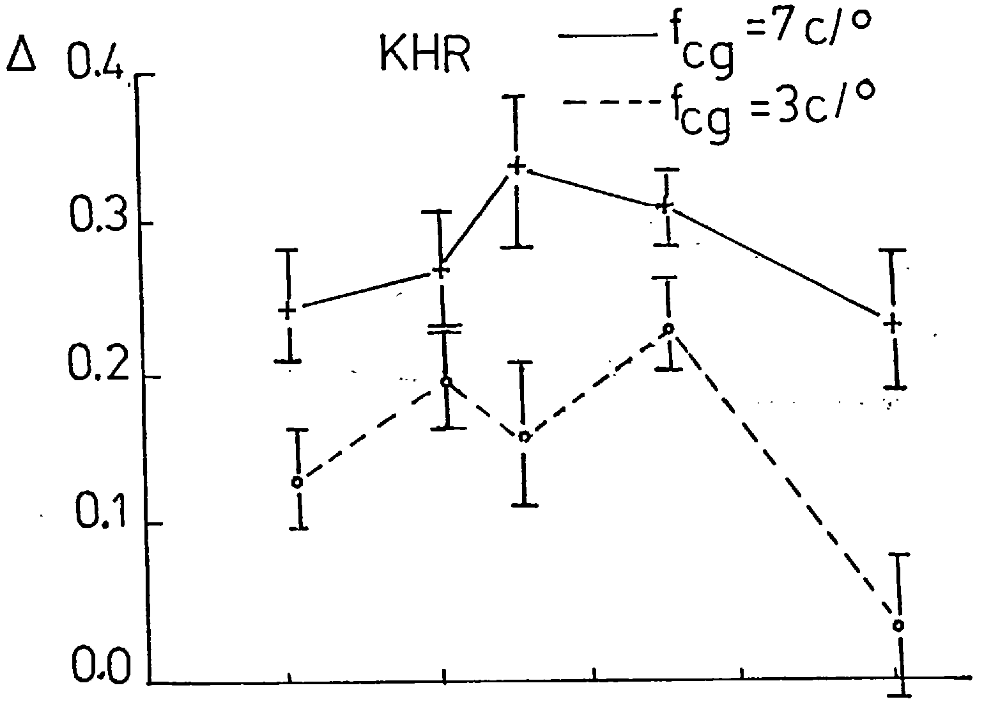

Δ
EW
fcg=3c/°
fcg =7c/°
0.4
0.3
0.2
0.1
10 8 6 4 2 0 2 4 6 8 10 φ°
horizontal displacements

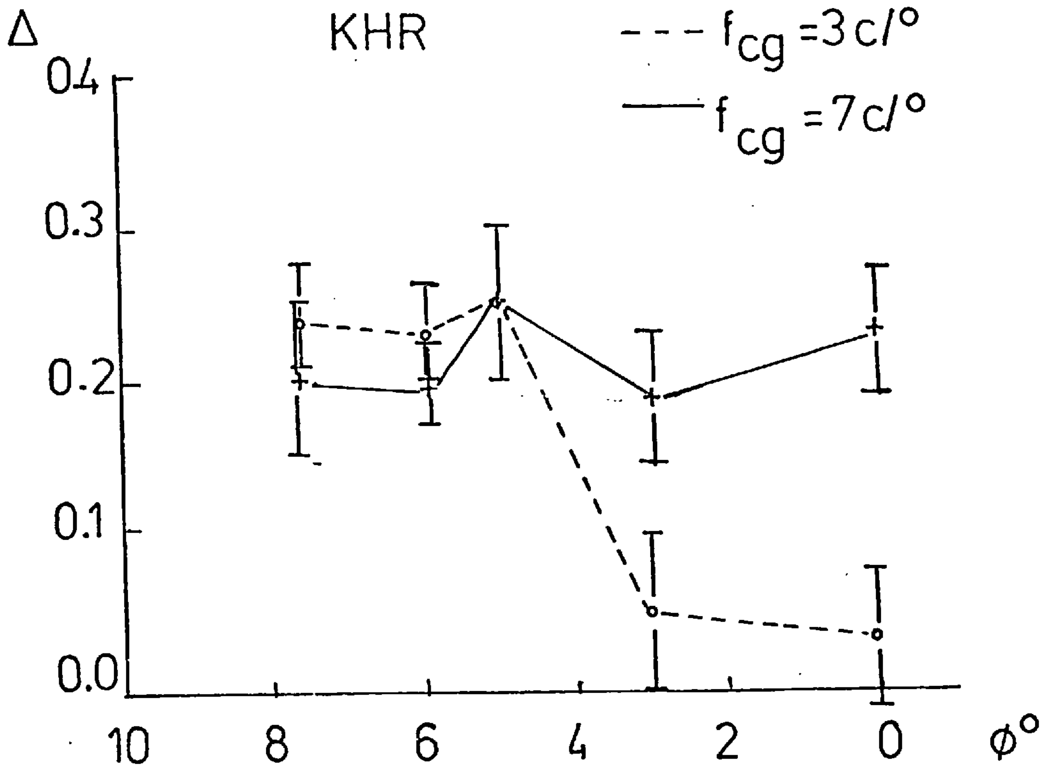
fig.34

Maudarbocus (1973)). It should be noted, however, that the threshold measurements off-axis in this direction were extremely difficult to take and the error bars are, therefore, larger than in previous experiments. Fig. 34 illustrates the effects of making horizontal displacements in the position of the test and adaptation gratings. Unlike fig. 33, the conditioning effect in this direction is dependent on retinal location, being restricted to the central region with Δ increasing as the test grating is displaced away from the fovea. With an offset of some 8°, Δ is approximately the same as that measured in the presence of a 7 c/° conditioning grating. In both figs. 33 and 34, the values of Δ found for the 7 c/° conditioning grating are independent of retinal location of the test and adaptation gratings.

Because of the difficulties experienced in performing these experiments, a second observer, KHR, repeated the observations for horizontal and vertical displacements between zero and 8° off axis. The results for both 7 c/° and 3 c/° conditioning gratings are shown in figs. 35 and 36. The error bars are again larger than in previous experiments but the general trends are the same. The difference in the values of Δ measured in the presence of a 7 c/° conditioning grating compared with that measured in the presence of a 3c/° grating is within the error, constant for increasing vertical displacements. The difference is not constant, however, for increasing horizontal offsets; again, the conditioning effect is restricted to the central region and Δ measured in the presence of the 3 c/° grating increases to the uninhibited value as the test is displaced horizontally.



vertical displacements
fig.35



horizontal displacements
fig. 36

Chapter 5.

SUMMARY AND DISCUSSION OF THE ~~DATA~~ RESULTS FOR THE SUPPRESSION OF THE THRESHOLD CONTRAST ELEVATION EFFECT

Summary

The experiments presented in chapters 3 and 4 have shown that a conditioning grating, CG, the spatial frequency of which lies in the range 1 to 4 c/°, presented to one eye, significantly reduces the threshold contrast elevation effect exerted by an adaptation grating on a test grating of the same spatial frequency. The principal parametric properties of the effect can be summarized as follows:-

1) A conditioning grating of spatial frequency in the range 1 to 4 c/° is effective in reducing the threshold contrast elevation effect for all spatial frequencies of the test and adaptation grating (Chapter 4, figs. 1 - 5). The conditioning effect is therefore markedly frequency specific, and this specificity is not determined by the adaptation and test gratings.

2) When the test and adaptation gratings are of spatial frequency, (f_{tg} equal to f_{ag}), in the range 1 to 4 c/°, the suppression effect does not occur if the spatial frequency, f_{cg}, of the conditioning grating is equal to f_{ag}. The fall of Δ as f_{cg} is changed from the value f_{ag} gives a tuning curve which is significantly sharper than that associated with the threshold contrast elevation effect itself (Chapter 4, figs. 1, 2 and 6)

3) The suppression effect is limited to binocular presentation of the adaptation and conditioning gratings (Chapter 4, fig. 7).

4) The suppression effect is maximal when the gratings are oriented vertically, and falls to an insignificant value for orientations greater than some 30° from the vertical (Chapter 4, figs. 11 - 16, and 19).

5) The suppression effect is selective for the angle of orientation of the conditioning grating, relative to the (vertical) test and adaptation gratings. This orientation selectivity is closely similar to that found for the contrast threshold elevation effect itself (Chapter 4, figs. 17, 18 and 19).

6) The variation of the conditioning effect with change in illumination level, I_{cg}, of the conditioning grating is of similar form to the variation of the threshold contrast elevation with change in the illumination I_{ag} of the adaptation grating (Chapter 4, fig. 10).

7) Blue and red conditioning gratings are equally effective in suppressing the contrast threshold elevation effect associated with a red adaptation grating (Chapter 4, figs. 20 and 21). Under binocular measurement conditions the contrast threshold adaptation effect is similarly independent of the wavelength of the adaptation grating (Maudarbocus and Ruddock, 1973a).

8) The time course of build up and decay of the contrast threshold adaptation effect is not influenced by the presence of a conditioning grating (Chapter 4, figs. 22 - 32). The time course of decay of Δ following onset of the conditioning grating is similar to that found when the adaptation grating is replaced by a uniform field (Chapter 4, fig. 27).

9) For 5° circular test and adaptation gratings, the conditioning grating is equally effective for displacements up to 10° off-axis in the vertical meridian (Chapter 4, fig. 33). For displacements in the horizontal direction, however, the effect of the conditioning grating falls away from the fovea, becoming insignificant for displacements greater than some 8° off-axis (Chapter 4, fig. 34).

Three aspects of the conditioning grating effect will be examined in relation to the data reviewed above. These are the identity of the visual pathways through which the signals from the conditioning grating propagate through the visual system; the neural correlates of the effect and the role of the effect in the overall visual response.

The Visual Pathways through which the Conditioning Grating Exerts the Suppression Effect

The experimental data reviewed above establish that the conditioning effect has certain parametric features which are closely similar to those found for the contrast threshold elevation effect. These are the lack of wavelength selectivity, orientation selectivity, the time course and the dependence on the illumination level of the conditioning grating. It seems probable, that these parametric characteristics are properties common to the neuronal pathways through which both the adaptation and conditioning effects are transmitted. It should be noted, however, that an adaptation grating presented contralaterally to a test grating can induce the threshold contrast elevation effect (Blakemore and Campbell, 1969b; Maudarbocus and Ruddock, 1973b). Thus there must be at least two kinds of signal pathway through which the signals from one eye can influence those from the other eye: one which gives rise to the conditioning effect and the other to the binocularly transmitted contrast threshold elevation effect. That there are two different pathways is confirmed by the fact that some properties of the conditioning effect differ from those of the threshold contrast elevation effect. These are its restriction to near vertical orientation of the gratings, the restricted spatial frequency range of conditioning gratings for which the effect is observed, its restriction to binocular interactions and its restriction to near foveal displacements along the horizontal meridian.

Two possible pathways exist through which the conditioning grating signals could be propagated through the visual system. The first possibility is that the conditioning signals, which, as was argued in the previous chapter, are inhibitory on those arising from the adaptation grating, are propagated along a special group of fibres in the optic nerve bundle. The alternative is that the signals may be carried by the trans-callosal fibres from one side of the brain to the other. It has been shown (von Bonin, Garol and McCulloch,1942; Myers, 1962) that in the cat, trans-callosal fibres synapse into area 18 of the visual cortex and from there establish short-axon connections into the region of area 17 (the striate visual cortex) which borders on area 18. It has further been shown that this border region of area 17 contains the cortical representation of the vertical meridian of the visual field (Choudhury, Whitteridge and Wilson, 1965; Hubel and Wiesel, 1967). Thus, the effects of such connections should be expected to be restricted to the retinal strip around the vertical meridian, which is true for the conditioning grating effect (item 8 above). The possible role in the overall visual function which may be associated with the conditioning effect will be discussed later, but in order to clarify this role, it is necessary to decide between the alternative pathways. This has not been possible, although experiments with a subject possessing a split brain (as in Mitchell and Blakemore, 1970) or with one optic nerve severed beyond the optic chiasma could provide evidence for one of the two possibilities.

Neural correlates of the Conditioning Grating Effect

The origin of the threshold contrast elevation effect is not entirely clear. The fact that is is orientation- and width-selective and can be transmitted interocularly suggests that it may arise in binocularly driven width- and orientation-selective neurones of the kind studied in the cat and monkey cortex by Hubel and Wiesel (1962, 1965a,1968). Indeed, Maffei, Fiorentini and Bisti (1973) have described adaptation properties in cortical neurones of the cat which are closely analogous to those observed in psychophysical experiments. Some properties of single neurones in the visual cortex are suggestive of the conditioning effect which has been described in the previous chapters. It has been shown that most simple neurones in the visual cortex are excited by signals from the ipsilateral eye, signals from the contralateral eye being almost exclusively inhibitory (Pettigrew, Nikara and Bishop, 1968; Henry, Bishop and Coombs, 1969). Scanning along the horizontal meridian of the receptive fields of these neurones, it was found that there was a small receptive field region, well-defined with respect to the horizontal meridian, which gave rise to excitatory responses when both eyes were stimulated. The inhibitory control exercised by the contralateral eye, and its sharp spatial tuning are similar to the properties of the conditioning effect and thus may constitute a neural correlate of the effect.

The Role of the Conditioning Grating Effect in the Overall Visual Performance

Because the conditioning grating effect is restricted to the vertical meridian, one possibility is that it is active in the stereoscopic visual function. Stereoscopy is achieved by detecting the disparity of visual images represented on the two retinae, due to the slightly different location of the two eyes. The disparities which arise are solely in the horizontal meridian, and thus it is only the displacement of vertical features in the two retinal images which permits intrinsic three dimensional vision. The neural basis for such visual function has been found in the responses of disparity sensitive cortical neurones in the cat (Barlow, Blakemore and Pettigrew, 1967; Nikara, Bishop and Pettigrew, 1968) and of neurones in area 18 of the primate visual cortex (Hubel and Wiesel, 1970a).

The low spatial frequency specificity of the adaptation effect suggests that it could aid the fusion of coarse detail in the binocularly viewed visual scene, and suppress rival signals from finer detail which exist in other regions of visual space. Psychophysical experiments (Tyler, 1973) have shown that a stereoscopic image can be formed by fusion of a sinusoidal line image and a straight line image presented one to each eye. It was found that the maximum frequency of the sinusoid for which depth could be perceived was 3 c/°. From this it was concluded that stereovision caters for coarse structure representing the larger, and thus, often the nearer and more relevant detail within the visual field. The low frequency specificity of this particular stereoscopic effect agrees with the low frequency specificity of the conditioning effect which has been investigated here.

An alternative possibility is suggested by Choudhury, Whitteridge and Wilson's (1965) hypothesis that the trans-collosal fibres are responsible for linking together the two halves of the visual field. If indeed the signals corresponding to the inhibitory effect of the conditioning grating are transmitted via the callosal fibres, their function may be to aid fusion of the two visual half fields by suppression of non-matching inputs into the visual cortex along the vertical meridian. Data to be described in the next chapter for subjects with anomalous vision show, however, that the conditioning grating effect may be absent, without giving rise to abnormal matching of the visual half-fields. These observations do not, however, exclude the possibility that the inhibitory signals from the conditioning grating are carried by the callosal fibres since it has been suggested that the callosal fibres may also be necessary for stereoscopy at the centra fovea (Mitchell and Blakemore, 1970; Blakemore, 1970c).

Chapter 6.

THE CONDITIONING GRATING EFFECT FOR OBSERVERS WITH ABNORMAL VISUAL CHARACTERISTICS

In this chapter, a number of the experiments carried out by observers with normal vision and described in the previous chapter were repeated by subjects with visual defects. The experiments chosen for these subjects were those which showed most clearly the action of a low frequency conditioning grating in suppressing the threshold contrast adaptation effect. The purpose of the experiments was to determine whether this conditioning effect was influenced by visual disorders. Two main categories of visual defect were studied. The first group consisted of two observers who had suffered as children from squints; although corrected cosmetically by surgery, neither of the subjects (DP, male, age 21 years, and AC, male, age 24 years) possessed any degree of stereovision as determined by Julesz patterns (Julesz, 1971). The second category was made up of astigmats; GA (22 years, male), MC (20 years, male) and TL (25 years, male), all astigmatic in the vertical meridian; RM (20 years, male) and DF (21 years, male) astigmatic in the horizontal direction.

1) Stereoblind Observers

The first experiment was carried out with a 7 c/° adaptation grating presented at 4.5 l.u. above its threshold to the right eye with a variable frequency conditioning grating matched in illumination level to the adaptation grating presented in synchrony with the adaptation grating to the left eye. Threshold measurements were made on a 7 c/° test grating presented subsequently to the right eye only. The test grating was presented for a 3 sec. period, alternated cyclicly with a 30 sec. presentation of the conditioning and adaptation gratings. The threshold elevation, Δ, (obtained by comparison of these measurements with those obtained after adapting both eyes to uniform fields of the same mean luminance as the gratings) was plotted as a function of the spatial frequency of the conditioning grating. The experimental arrangement is thus identical to that used previously for subjects with normal visual characteristics whose results were given in Chapter 3, figs. 35, 36 and 37. Data for the two stereoblind observers AC and DP, are given in figs. 1 and 2. In each case, comparable data for observer E.W. (who possessed normal vision) are given (dotted lines). It can be seen that neither of the stereoblind observers show the low frequency inhibition of the adaptation response by the conditioning grating displayed in the results of E.W.

The experiment was repeated by subject DP for test and adaptation gratings set at 2.5 c/° (fig. 3). Again, the sharply tuned inhibition apparent in the data of E.W. (dotted line) is not present in the data of DP. Superimposing a 7 c/° adaptation grating and a variable frequency conditioning grating, in the same (right) eye (fig. 4), however, produced results very similar to the monocular data of E.W. (broken line). Maximum elevation of threshold occurred when the conditioning and adaptation gratings (which were presented in phase) were of the same spatial frequency with a slight reduction in the value of Δ for other values of conditioning grating spatial frequency. As for the normal observer, the reduction in Δ observed for DP for adaptation to gratings other than two matched stimuli can be attributed to reduced contrast in the adaptation stimulus or to inhibition between spatial frequency channels such as that postulated by Tolhurst (1972). It is important to note, however, that there is, as in the case of observers with normal vision, no evidence of low frequency suppression by the conditioning grating presented monocularly with the adaptation grating.

A further series of experiments was undertaken in which Δ was determined

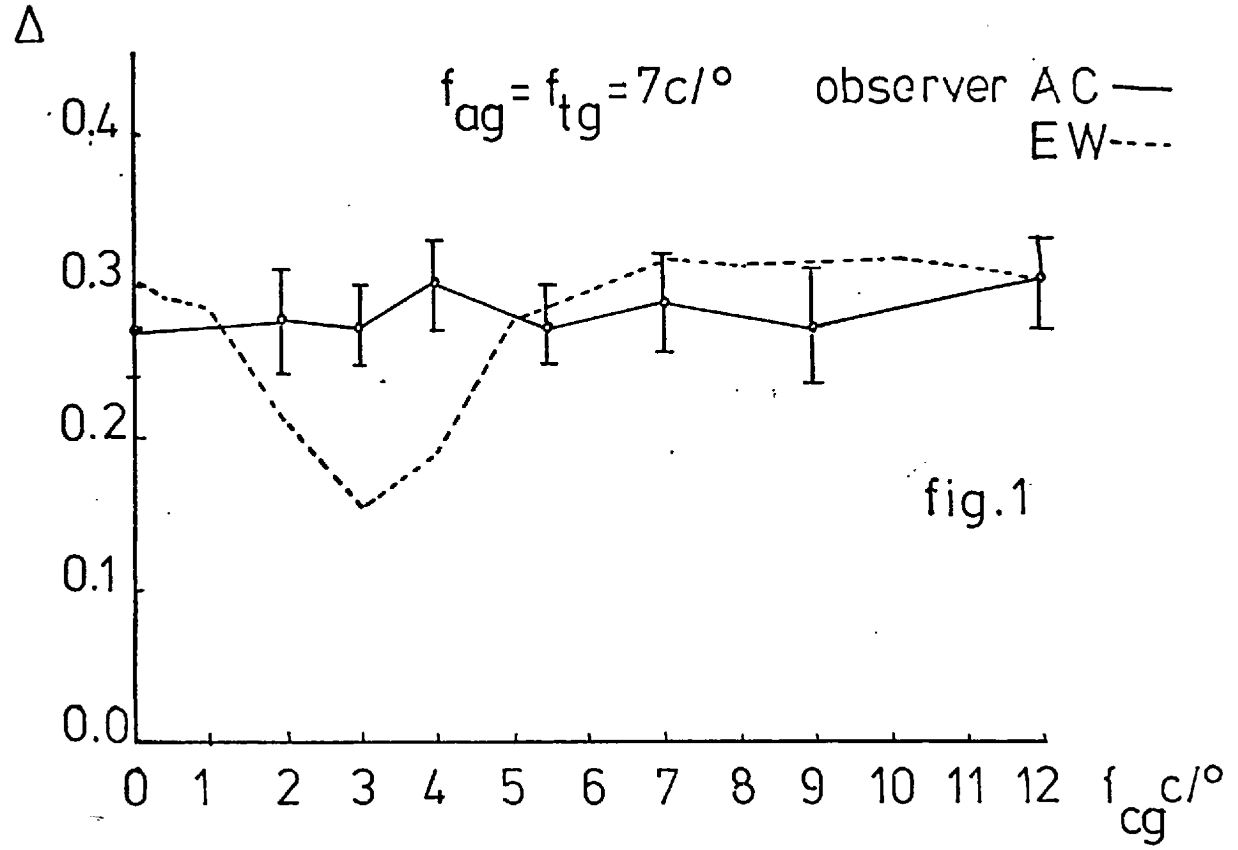


fig.1

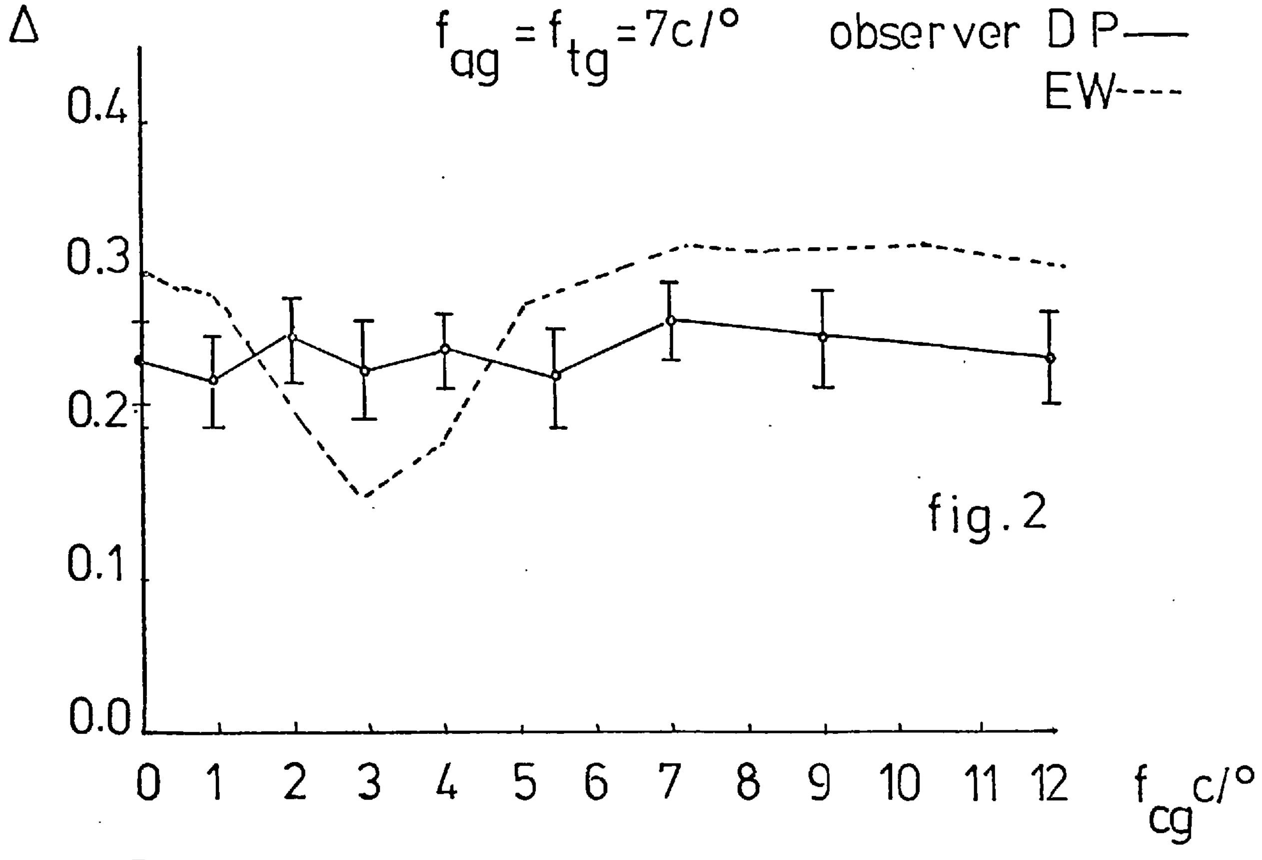


fig.2

TG in L eye

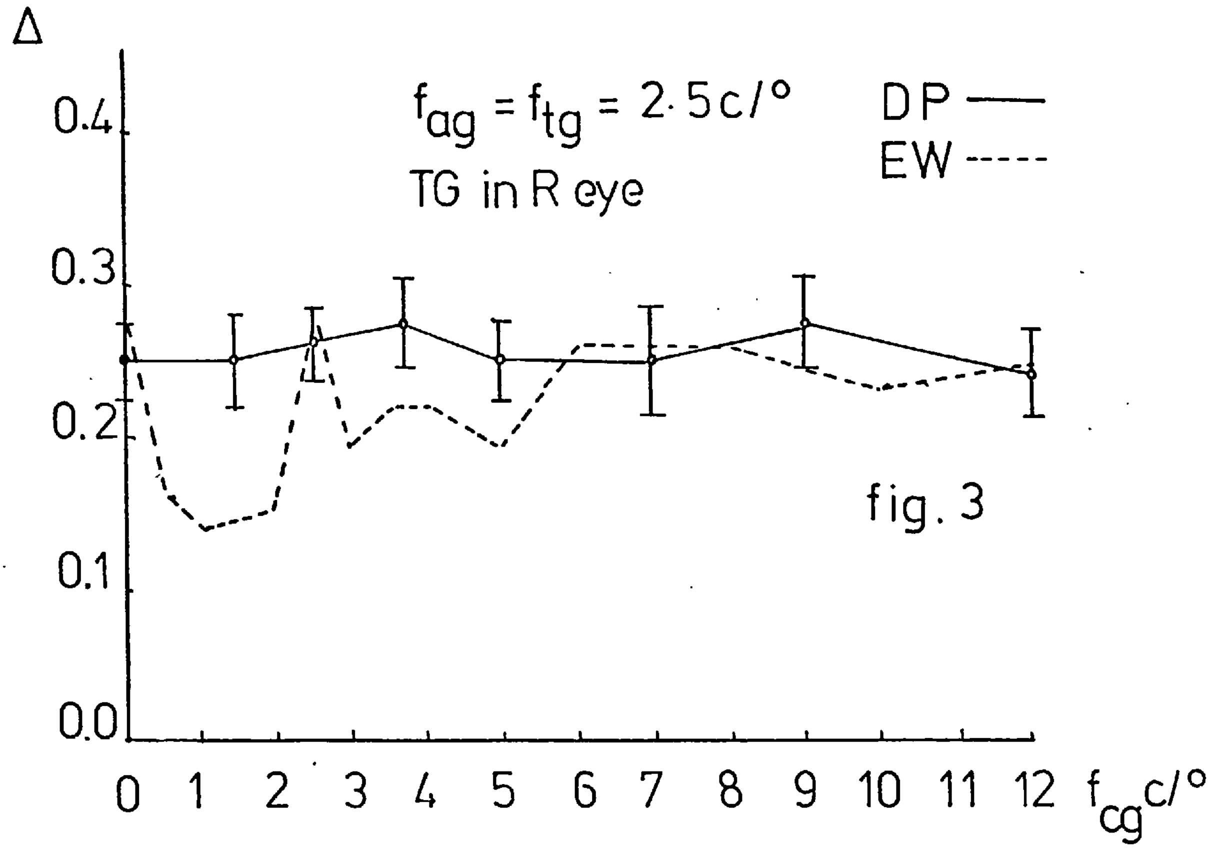


fig. 3

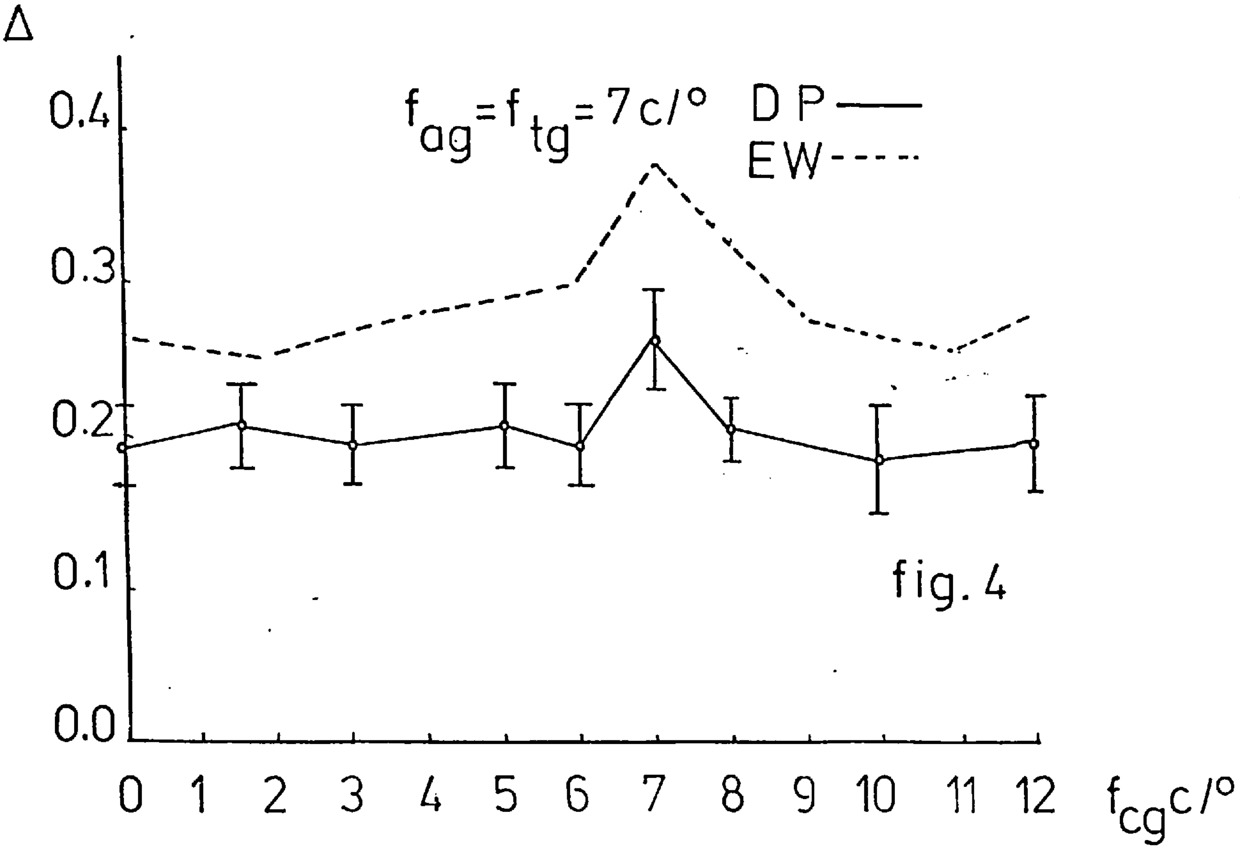


fig. 4

CG and AG superimposed in test eye : R eye as a function of the illumination level, I_{ag}, of the adaptation grating presented to the right eye and a 3 c/° conditioning grating, matched in intensity to the adaptation stimulus and presented, in synchrony with it, to the left eye. The test grating was subsequently shown to the right eye only. Two values of adaptation spatial frequency were investigated, 7 c/° (fig. 5) and 2.5 c/° (fig. 6); both sets of data were compared with that obtained with an identical right eye configuration, but no conditioning stimuli in the left eye, which remained dark adapted.

In both cases, the data obtained for the stereoblind subject in the absence of the conditioning grating are essentially the same as those for normal subject EW (fig. 4, chapter 3: 2.0 c/° adaptation and test gratings), with Δ increasing in an approximately linear fashion over the initial 2.0 - 2.5 l.u of adaptation grating illumination level, and then levelling off to a saturation value. A comparison between the results of DP where a conditioning grating was introduced and those of EW (continuous line in figs. 5 and 6) shows, however, that there is no suppression of adaptation by the conditioning grating in the case of DP. The similarity of these data obtained with and without the conditioning grating for the stereoblind observer, establishes that introducing a low frequency conditioning grating in no way affects the efficacy of the adaptation stimulus.

A final set of measurements on the conditioning effect was made with the stereoblind observer, DP, in which all the gratings were presented in the horizontal rather than in the vertical meridian. The test and adaptation spatial frequencies were set at 7 c/° and Δ plotted as a function of the spatial frequency, f_{cg}, of the conditioning grating. These data (fig. 7) can be compared with those taken previously where the gratings were set in the vertical meridian (fig. 2). It can be seen that the two sets are, within the error of the experiments, the same, indicating that the threshold elevation as measured by the stereoblind observer (DP) in

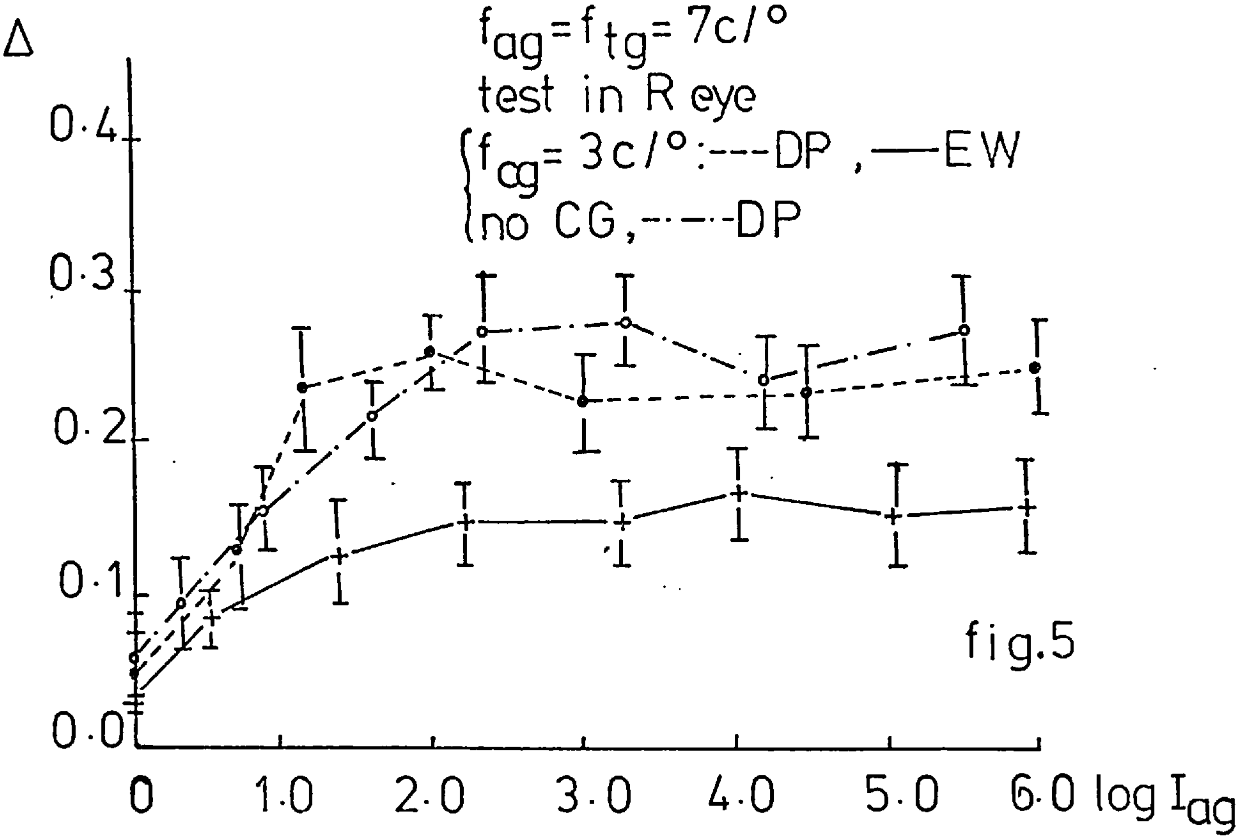

Δ
$f_{ag}=f_{tg}=7c/°$
test in R eye
$f_{cg}=3c/°$: ---DP , —EW
no CG, -·-·-DP
0·4
0·3
0·2
0·1
0·0
0
1·0
2·0
3·0
4·0
5·0
6·0
$\log I_{ag}$

fig.5

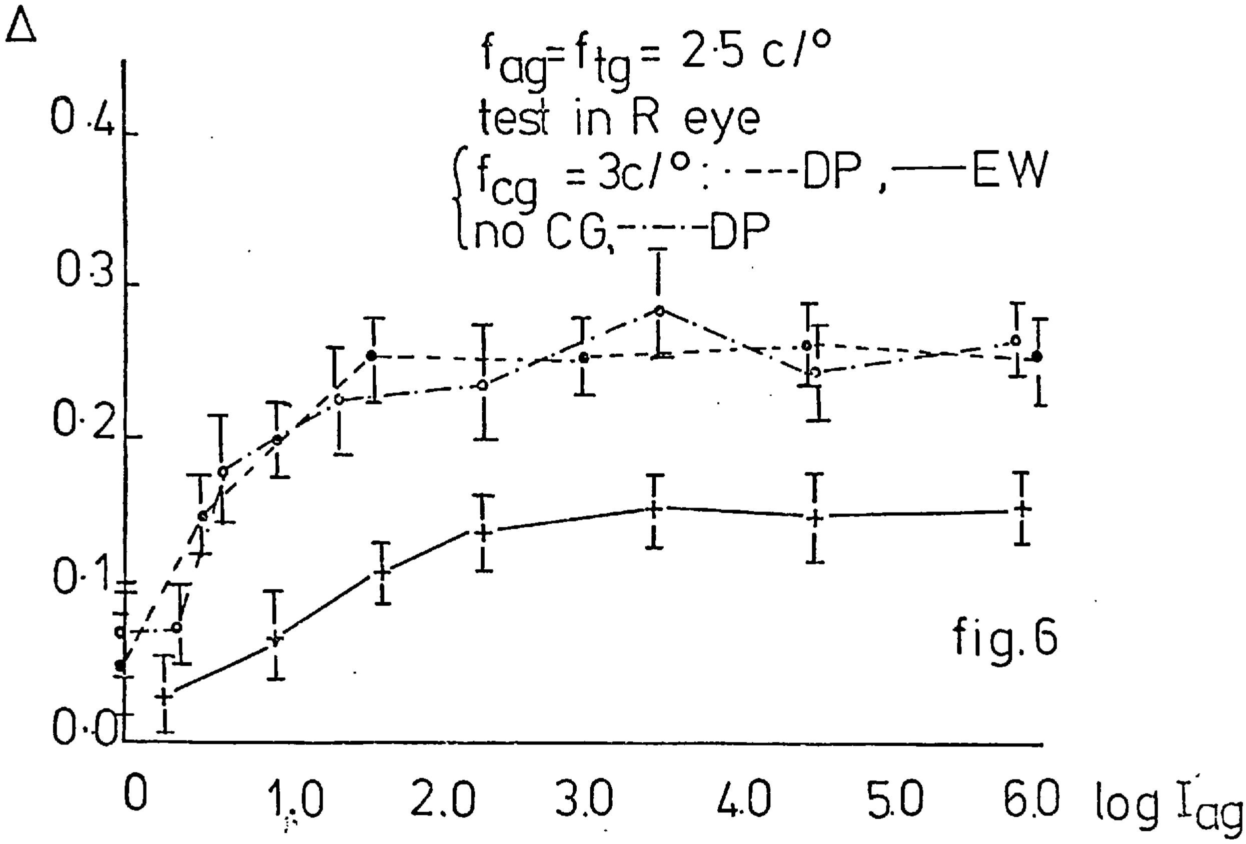

Δ
$f_{ag}=f_{tg}=2{\cdot}5\ c/°$
test in R eye
$f_{cg}=3c/°$: ---DP , —EW
no CG, -·-·-DP
0·4
0·3
0·2
0·1
0·0
0
1.0
2.0
3.0
4.0
5.0
6.0
$\log I_{ag}$

fig.6

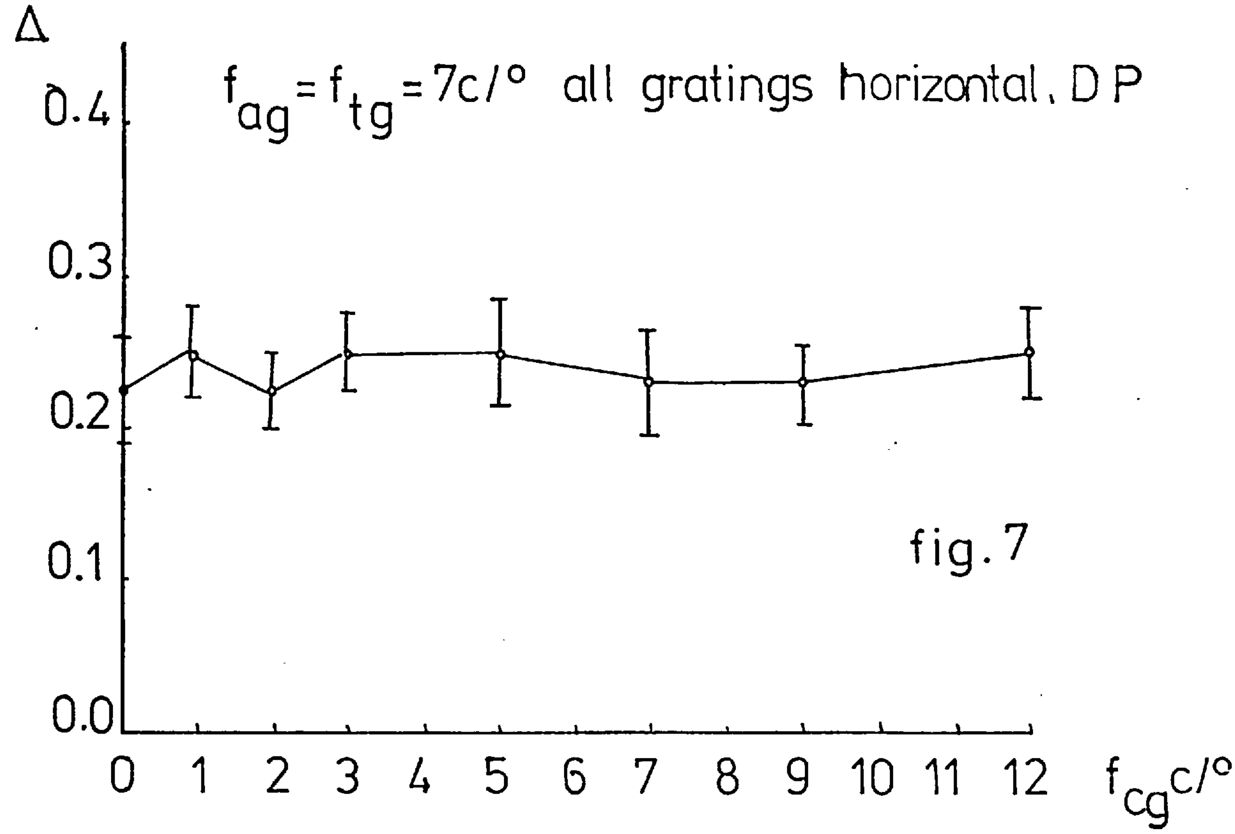

Δ
$f_{ag} = f_{tg} = 7c/°$ all gratings horizontal, DP
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
6
7
8
9
10
11
12
f_{cg} c/°

fig. 7

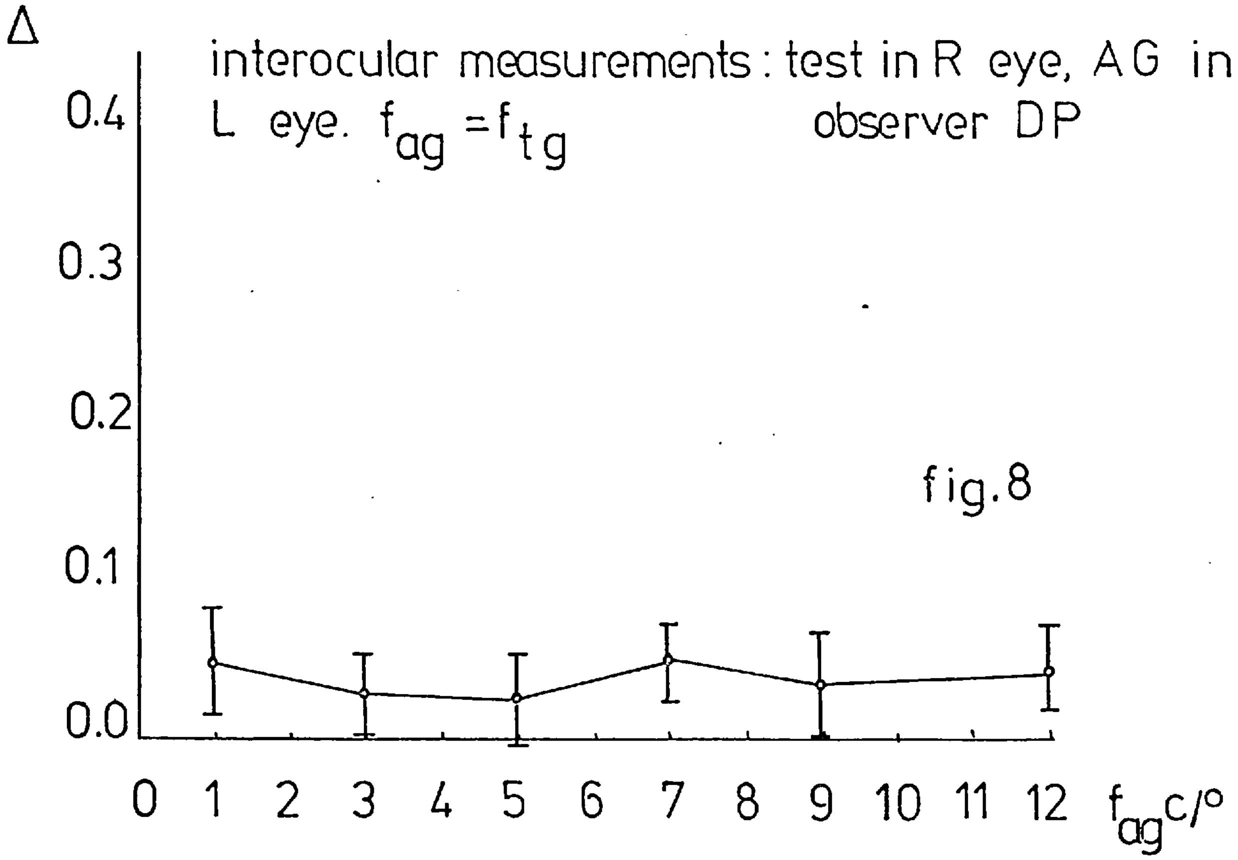

Δ
interocular measurements: test in R eye, AG in L eye. $f_{ag} = f_{tg}$ observer DP
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
6
7
8
9
10
11
12
f_{ag} c/°

fig. 8

his right eye is dependent neither on the orientation of the adaptation, test and conditioning gratings nor upon the spatial frequency of the conditioning grating.

The last experiment undertaken by observer DP was to measure the amount of interocular transfer of the contrast threshold elevation effect. In this experiment, the right eye was dark-adapted and the adaptation grating presented to the left eye only. After adaptation, the test grating, of the same spatial frequency as the adaptation grating, was presented to the right eye. The thresholds measured under these conditions were compared with those obtained after adapting the left eye only to a uniform field of the same mean luminance as the adaptation grating and a measure of the interocular Δ was thus determined. The experiment was repeated for a series of values of the adaptation grating spatial frequency, f_{ag}, and the results are given in fig. 8. It is apparent that the magnitude of the interocular transfer of the contrast threshold elevation is barely significant. In contrast, that recorded by other experimenters for observers with normal vision (Blakemore and Campbell, 1969; Gilinsky and Doherty, 1969) was about 70% of that measured monocularly.

Discussion

Experiments on the tilt after-effect (see Introduction) (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1973) have correlated reduced stereovision with reduced interocular transfer. Little work has been reported on the interocular aspects of the threshold elevation effect in stereoblind observers but it would appear likely that the basis for the reduction in transfer in the two adaptation effects is the same. Electrophysiological experiments on single cells in the visual cortex of the cat have shown that the binocularity normally observed in the responses of most cells is almost totally lost if one eye is covered or displaced to imitate a squint during a critical period in the early development of the kitten (Hubel and Wiesel, 1970b, Wiesel and Hubel, 1965; Hubel and Wiesel, 1965b). It is possible that these findings could account for the loss of stereopsis in human subjects who have suffered from a squint in terms of loss of matched binocular inputs from the two eyes. A more recent paper (Banks, Aslin and Letson, 1975) attempted to assess the period during which children were most susceptible to abnormal binocular experience in the form of a convergent strabismus (squint). Again, loss of binocularity was defined in terms of reduced interocular transfer of the tilt after-effect. Their results indicated that the sensitive period began during the first months after birth and peaked between 1 and 3 years of age. Since both DP and AC were five years old before operations for correction of the disorder were performed on them, it seems likely that the lack of binocular interaction evident in the experimental data is a consequence of having once had a congenital squint.

The experiments reported here show that neither of the two stereoblind observers exhibit the binocular inhibition associated with a low frequency conditioning grating which was found in observers with normal stereovision. It is not possible, however, to assume that this lack of suppression provides evidence for a causal relationship between the conditioning grating effect and stereoscopic visual function. It has been shown that stereoblind observers exhibit very little transfer of the tilt after-effect, possibly because of lack of binocularity in the cortical neurones (Movshon, Chambers and Blakemore, 1972). It would be unlikely, therefore, that any binocular inhibitory adaptation effect would be exhibited by these observers, no matter what the basis of the effect. These results do, however, imply that the conditioning grating inhibition effect does not underlie the proposed function of the callosal fibres (Choudhury, Whitteridge and Wilson, 1965) of joining together the two halves of the visual field. It was suggested in the last section that this was a possible role for the suppression. Neither of the stereoblind observers experienced any difficulties in lining up the two half fields in either eye such as would be expected if loss of suppression indicated loss of callosal fibre function. This does not preclude the possibility of the inhibition being transmitted in observers with normal vision through the callosal fibres since it has been suggested (Mitchell and Blakemore, 1970; Blakemore, 1970c) that these fibres also have a role in the mechanism of stereovision in the central region of the retina.

2) Experiments with Astigmatic Observers

The extent and axis of the astigmatism in five observers was determined both by use of Landholts Chart (Duke Elder (1949) p. 4408) and by spectacle prescriptions obtained from the subject's opticians. Details of ~~data of~~ noticeable onset of the disorder were also obtained from the latter source. These details are recorded in the chart given in Table 1. Astigmatism is a refractive anomaly in which, to quote Duke Elder (1949), no point focus is formed owing to the unequal refraction of the incident light by the dioptric system of the eye in different meridians. Often the refractive power changes gradually from one meridian to another and can easily be corrected for by a cylindrical spectacle lens. Generally the meridians of maximum and minimum refraction are at right angles to each other, and in 90% of cases, the section of least curvature is horizontal. Thus, an astigmatic observer will generally perceive one direction in which lines appear distinct and another in which lines appear blurred. Three observers in the present investigation, GA, MC and TL perceived clear horizontal lines and blurred vertical lines; the other two, RM and DF, saw clear vertical lines and blurred horizontal lines. The stereovision of all five observers was tested using Julesz patterns with increasing disparities (Julesz,1971) and the results of the tests are also presented in Table 1.

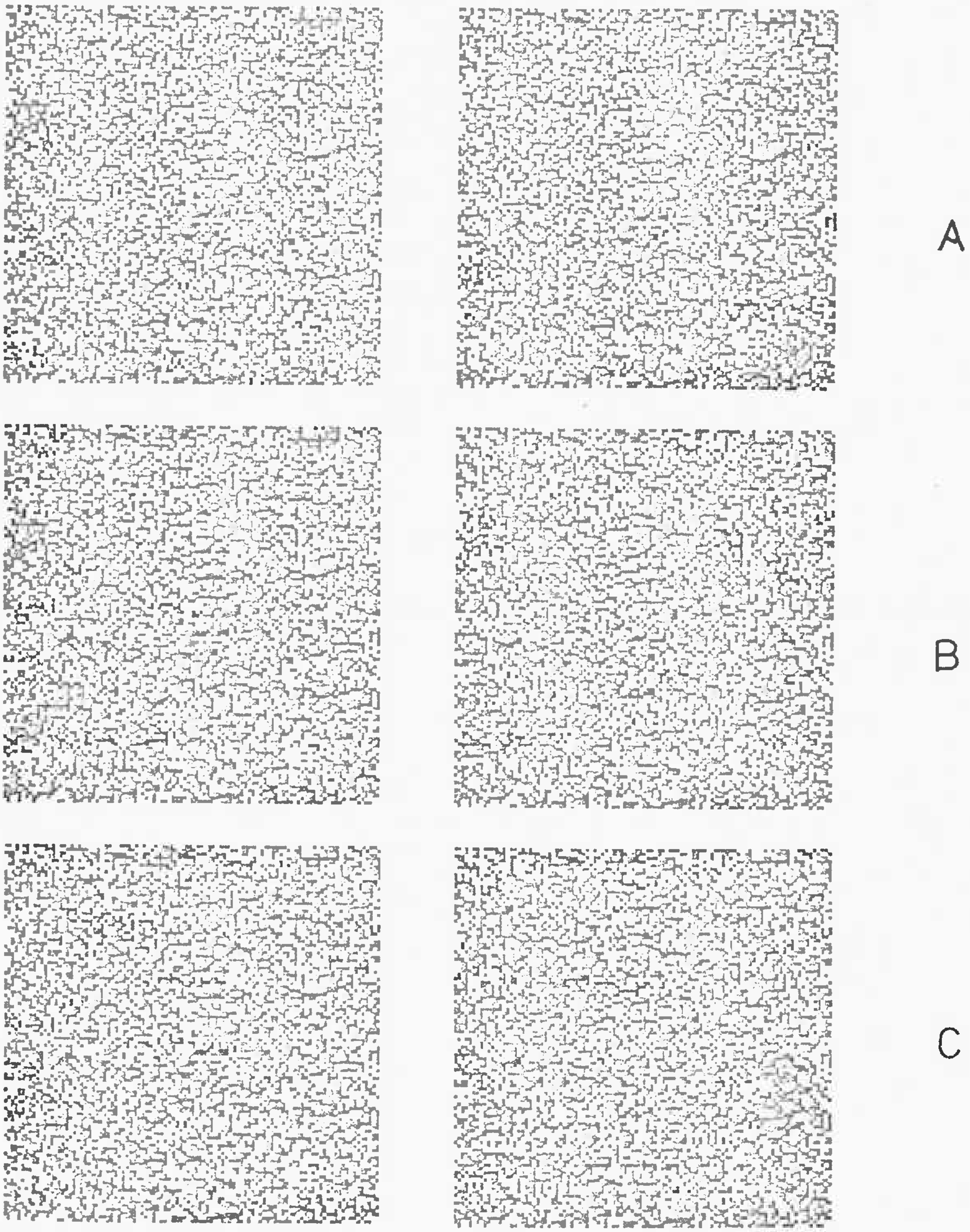
TABLE 1.

observer	age of onset yrs.	left eye	right eye	stereo-acuity*	f_{tg} in R $=7c/^{o}$ $\Delta_h-\Delta_v$	f_{tg} in L $=7c/^{o}$ $\Delta_h-\Delta_v$	f_{tg} in R $=2{\cdot}5c/^{o}$ $\Delta_h-\Delta_v$	f_{tg} in R $=12c/^{o}$ $\Delta_h-\Delta_v$
GA	3	sph.: -1·5 cyl.: -3·0 axis.: × 5	sph.: -1·5 cyl.: -3·5 axis: × 5	0	0·05±0·05	0·05±0·05	0·05±0·05	0·03±0·04
MC	6	sph.: plano cyl.: +2·0 axis.: ×10	sph.: +0·5 cyl.: + 3·0 axis × 170	2	0·09±0·04	0·06±0·04	0·07±0·04	—
TL	10	sph.: plano cyl.: -2·0 axis.: ×180	sph.: +0·25 cyl.: -2·0 axis: × 5	4	0·13±0·04	—	—	—
RM	6	sph.: +1·0 cyl.: +2·5 axis ×80	sph.: +1·5 cyl.: +3·5 axis: ×100	5	0·15±0·04	—	—	—
DF	8	sph.: -1·75 cyl.: +3·0 axis.: ×75	sph.: -1·5 cyl.: +3·5 axis.: ×105	4	0·15±0·05	0·16±0·04	0·09±0·04	—
EW	—	sph.: plano cyl.: — axis: —	sph.: +0·25 cyl.: — axis: —	5	0·15±0·04	0·17±0·04	0·15±0·04	0·1±0·04

sph.: spherical correction in dioptres
cyl.: cylindrical correction in dioptres
axis: axis of distinct meridian measured in degrees — clockwise from horizontal
*stereoacuity on a scale 0-7, 0 indicates no stereopsis, 4 indicates normal stereopsis

These tests gauged diminishing stereopsis through responses to seven random dot stereograms, designated A - G; the first, A, is 100% binocularly correlated, but the rest contain increasing numbers of complemented dots which cannot be fused - 10% for B and increasing in increments of 10% for the subsequent five patterns, to the last pattern, G, which contained 60% uncorrelated dots. The tests, when viewed through a stereoscope by a normal observer, showed a centre square with an impression of depth. The observers were asked to view these tests in a random sequence and indicate whether they could perceive the square. Each test was presented five times with the addition of a number of "dummy" tests to deter the observer from making arbitrary guesses. Thus stereopsis was gauged on a scale of zero, indicating no stereopsis, to seven, corresponding to the level of noise through which the 3-D square was still recognisable as such. The first three stereograms (A - C) in the series are illustrated in fig. 9. A normal observer with good stereopsis could achieve recognition down to stereogram E. The experiments undertaken by the five observers will be described, together with a brief description of their results. These results will be discussed in greater detail and in relation to the stereo-vision and astigmatism of the observers at the end of the chapter.

One basic experiment was performed by all the observers: a 7 c/° adaptation grating, with illumination level 4.5 log units above its threshold level was presented to the right eye in synchrony with a variable frequency conditioning grating, matched in space-average illumination level, which was presented to the left eye. The 7 c/° test grating was presented to the right eye only and Δ determined, as before, as a function of the spatial frequency of the conditioning grating. Because of the design of the apparatus and the interference fringes which make up the sinusoidal gratings (see Apparatus and Experimental methods chapter, page 55), no correcting lenses were needed for the



Test figures for determining stereopsis deficiency. Stereograms have diminishing binocular correlation : A, 100% ; B, 90% ; C, 80% .....down to G (not illustrated), 40%. Reprinted from Julesz (1971).

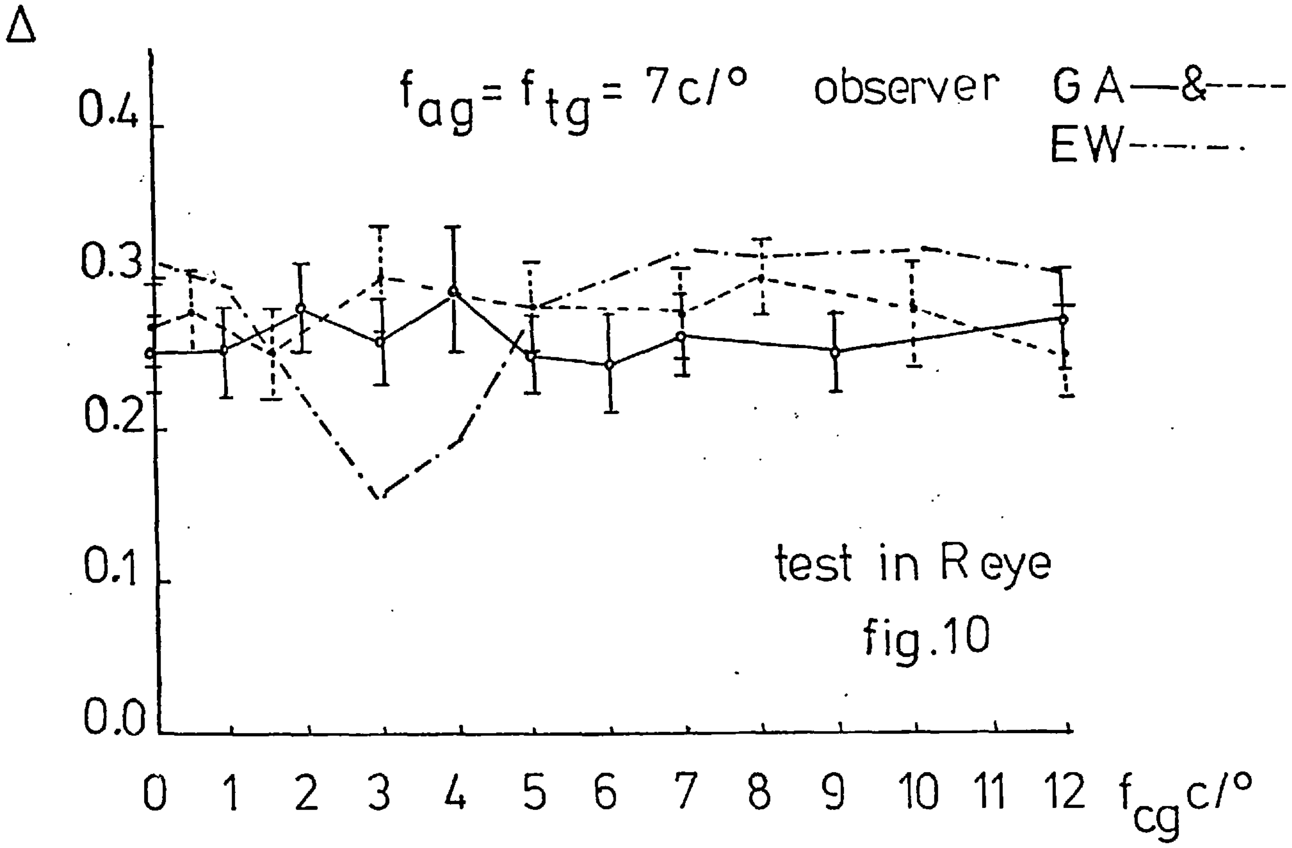
fig. 9

astigmats and the fringes were seen by them as being in focus for all orientations. Two series of experiments were carried out, one with the adaptation, conditioning and test gratings oriented vertically and the other with the gratings oriented horizontally. The two sets of data are presented together in figs. 10 - 14, one figure being plotted for each observer. Also plotted on the figures (designated by dot-dash lines, with no data points) are the results obtained by EW under the same experimental conditions for vertical orientation of the gratings.

Figs. 10 - 14 give the data for the five observers. GA (fig. 10) shows no low frequency suppression for a vertical conditioning grating of the sort observed in the data of EW. The results for vertical and horizontal gratings are, within experimental error, the same. Comparison, however, of the vertical with the horizontal grating data supplied by MC (fig. 11) indicates some low frequency inhibition by the conditioning grating Although this inhibition effect is less than that evident in the data of EW (minimum value of $\Delta = 0.22$ for MC, c.f. $\Delta_{min} = 0.15$ for EW), it is nonetheless, significant.

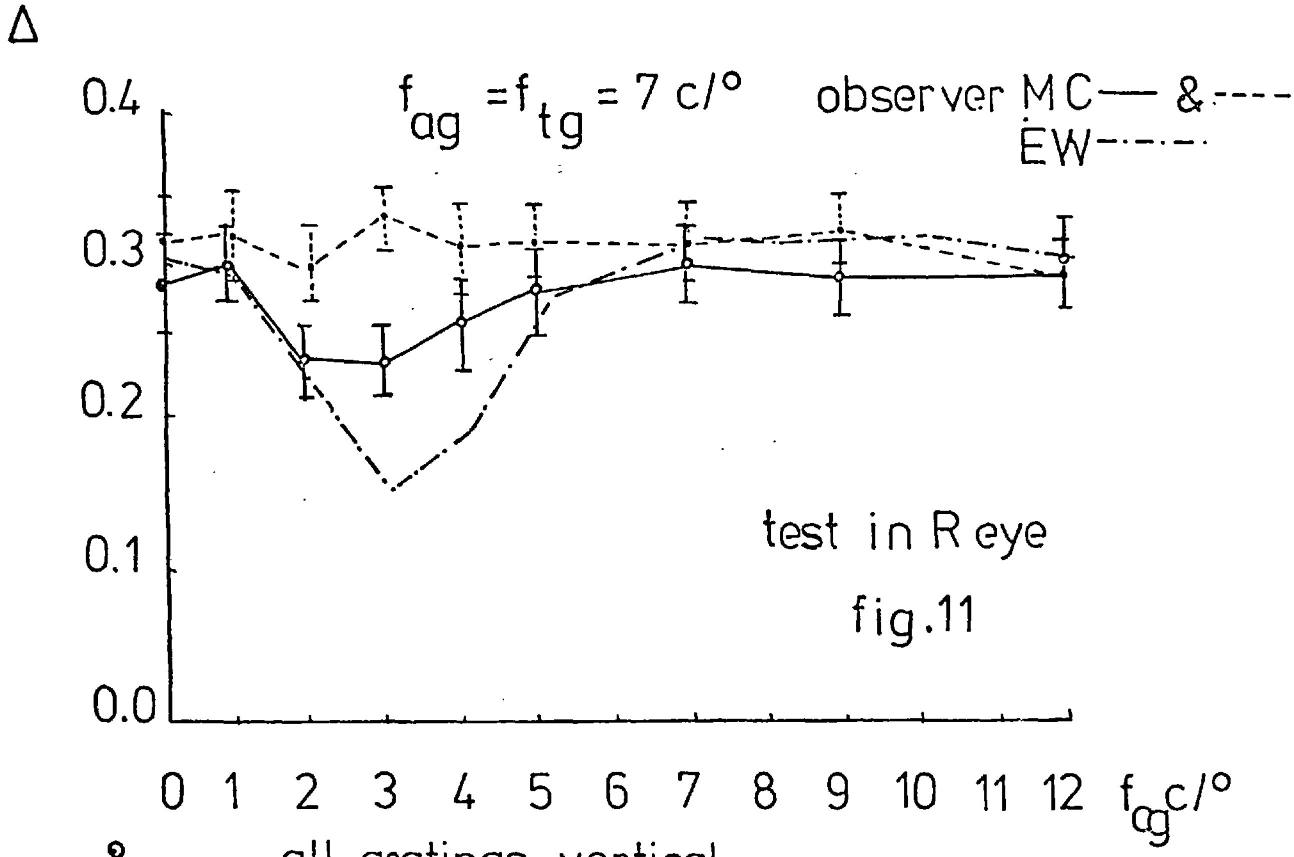
The results given by the other three observers, TL, RM and DF (figs. 12, 13 and 14) are not significantly different from those obtained from nonastigmats, e.g. those of EW, dot-dash lines. There are variations in the unsuppressed values of Δ and in the position and the extent of maximum suppression effect, but these differences are no greater than those which are found in comparing the results of different observers with normal vision (see figs. 35 - 38, Chapter 3).

The astigmatic properties of the left and right eyes in any subject are not generally identical. The severity and the meridian of the disorder can be different in the two cases (see table 1 for the five observers studied here). For this reason, the experiments were repeated for three observers (DF, GA and MC) with the test and adaptation gratings presented to the



test in R eye

fig.10



test in R eye

fig.11

-·-·- & —— all gratings vertical

---- all gratings horizontal

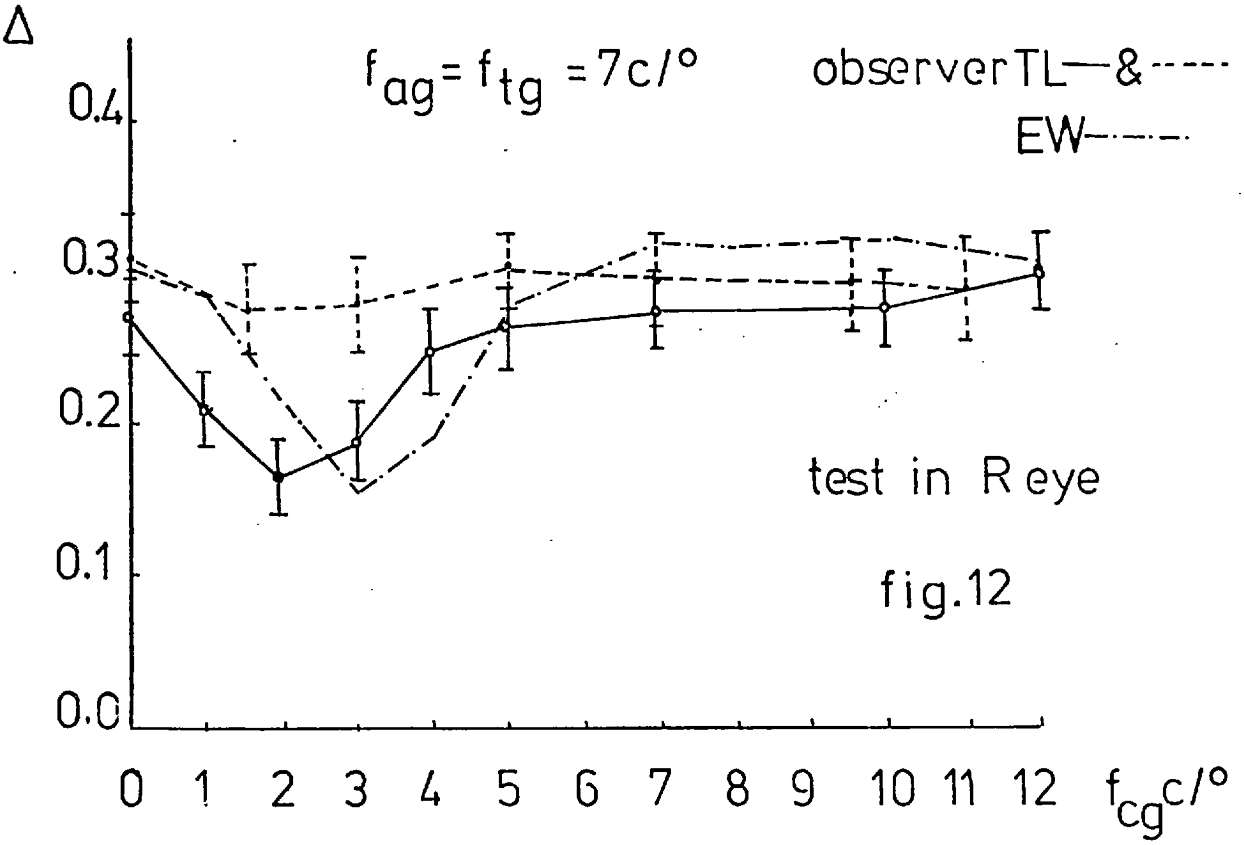


fig.12

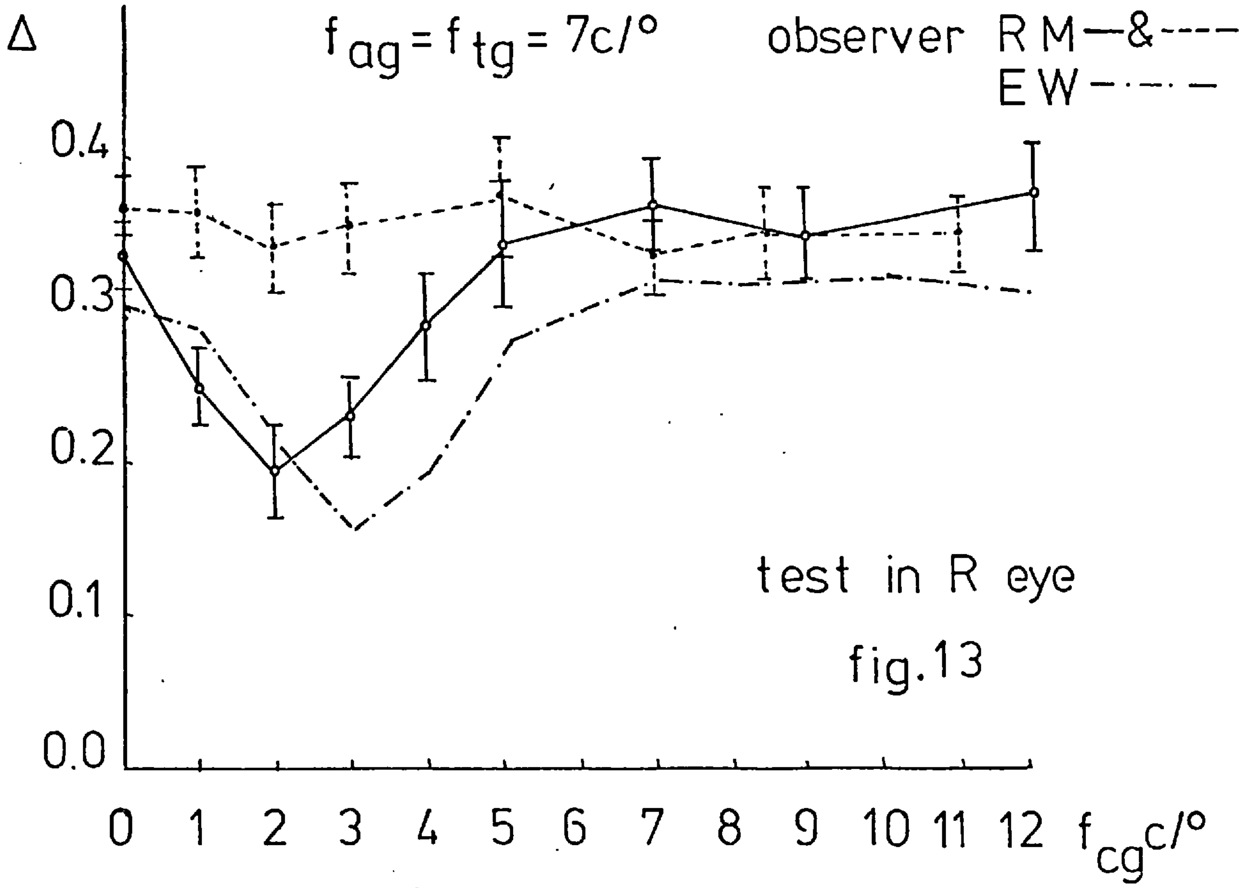


fig.13

-·-·-·& ——— all gratings vertical
----- all gratings horizontal

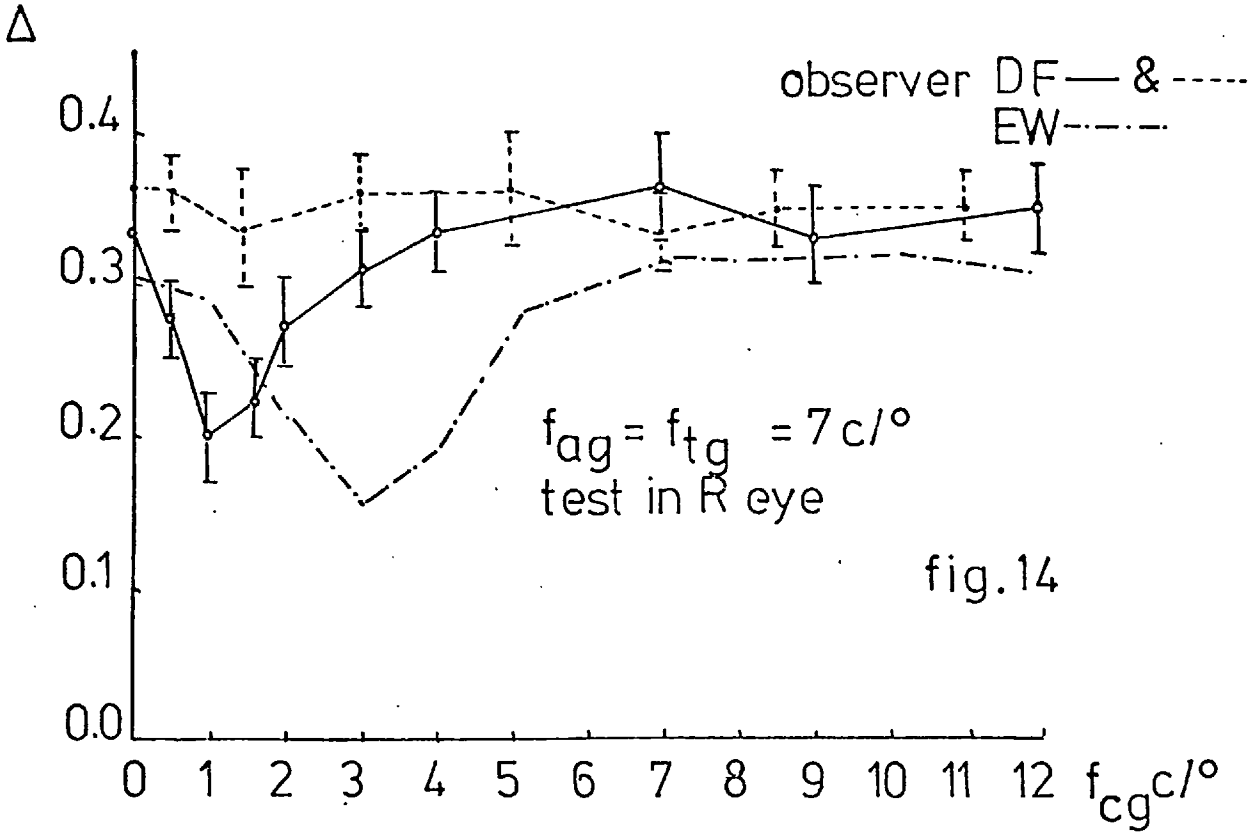


fig.14

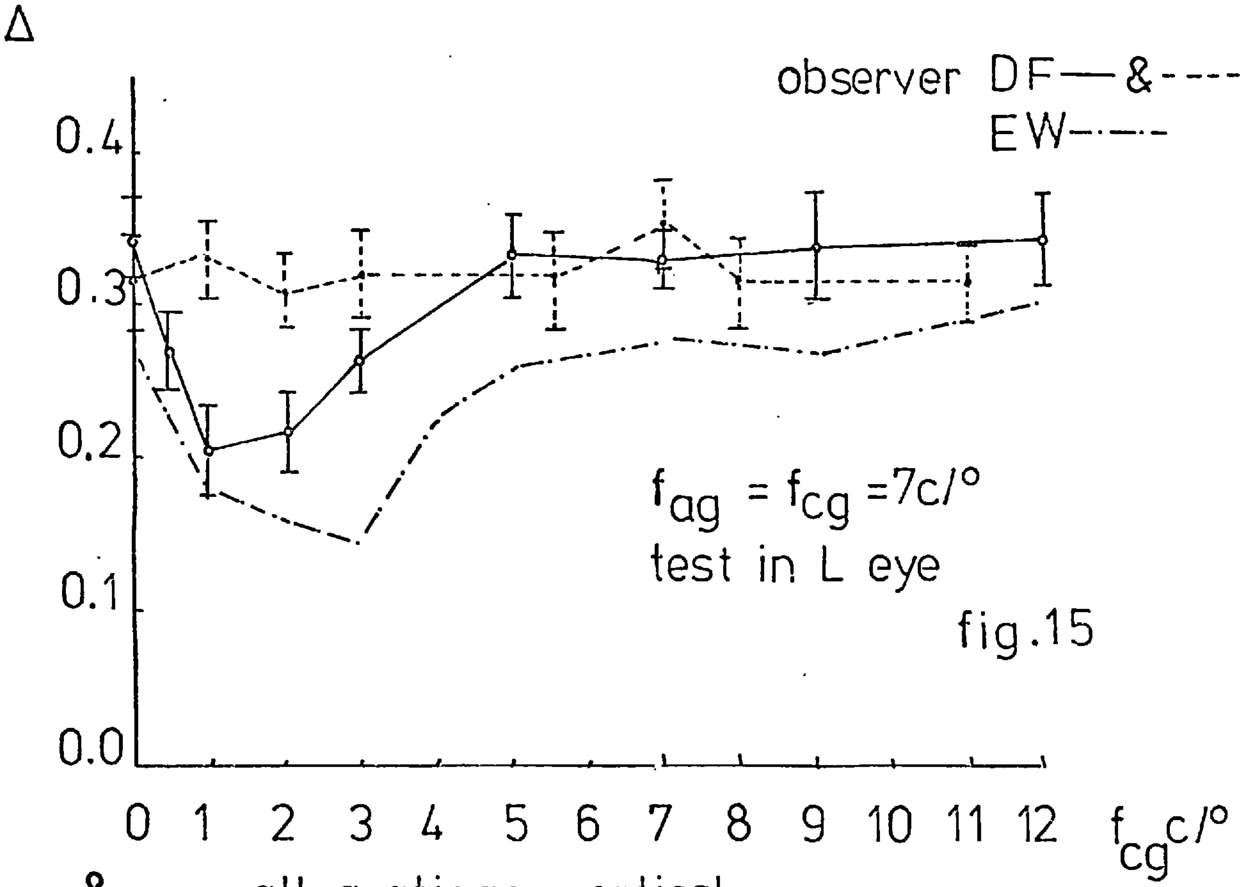


fig.15

-·-·- & —— all gratings vertical

---- all gratings horizontal

left eye rather than the right as before. The conditioning grating was presented in synchrony with the adaptation grating to the right eye. The results obtained from this new configuration are shown in figs. 15, 16 and 17. By comparing these figures with figs. 14, 10 and 11, it can be seen that the degree of suppression does not alter significantly with the interchange of the gratings. Observations from subject DF (fig. 15) show conditioning by low frequency vertical gratings of the same magnitude as shown previously (fig. 14). Observer GA (fig. 16) again shows no inhibition at all (c.f. fig. 10) and observer MC again obtains a small but significant reduction in Δ with a 3 c/° vertical conditioning grating compared with the value of Δ measured with a 3 c/° horizontal grating (c.f. fig. 11)

Observer GA performed two further experiments with adaptation and test gratings set at 12 c/° (fig. 18) and 2.5 c/° (fig. 19); Δ was again determined as a function of the conditioning grating frequency, f_{cg}. Neither of the two values of adaptation and test frequency give rise to the suppression effect, which is apparent in the comparison data for the normal subject, EW. Observers DF and MC repeated their experiments with 2.5 c/° test and adaptation gratings in the right eye and a variable frequency conditioning grating in the left eye for both vertical and horizontal grating stimuli. The sharp tuning of the suppression of adaptation by low frequency vertical gratings apparent in EW's results (dot-dash lines) is shown by both DF (fig. 20) and MC (fig. 21). The magnitude of the effect obtained by DF is very similar to that of an observer with normal vision, whereas that obtained by MC is considerably less, although the difference between the values of Δ obtained for vertical and horizontal gratings is still significant over the low frequency range of conditioning stimuli. A summary of the results of the experiments for both astigmatic observers and for EW is given in table 1.

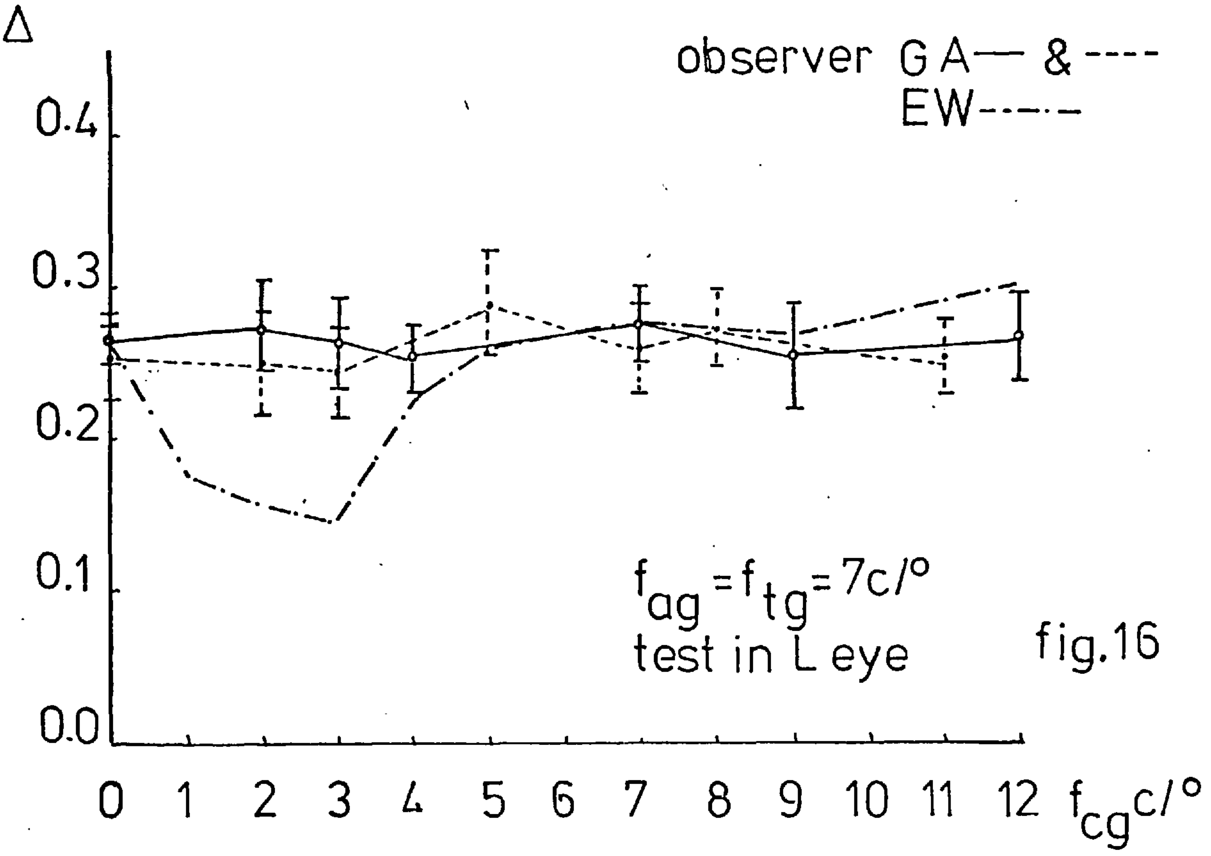


fig.16

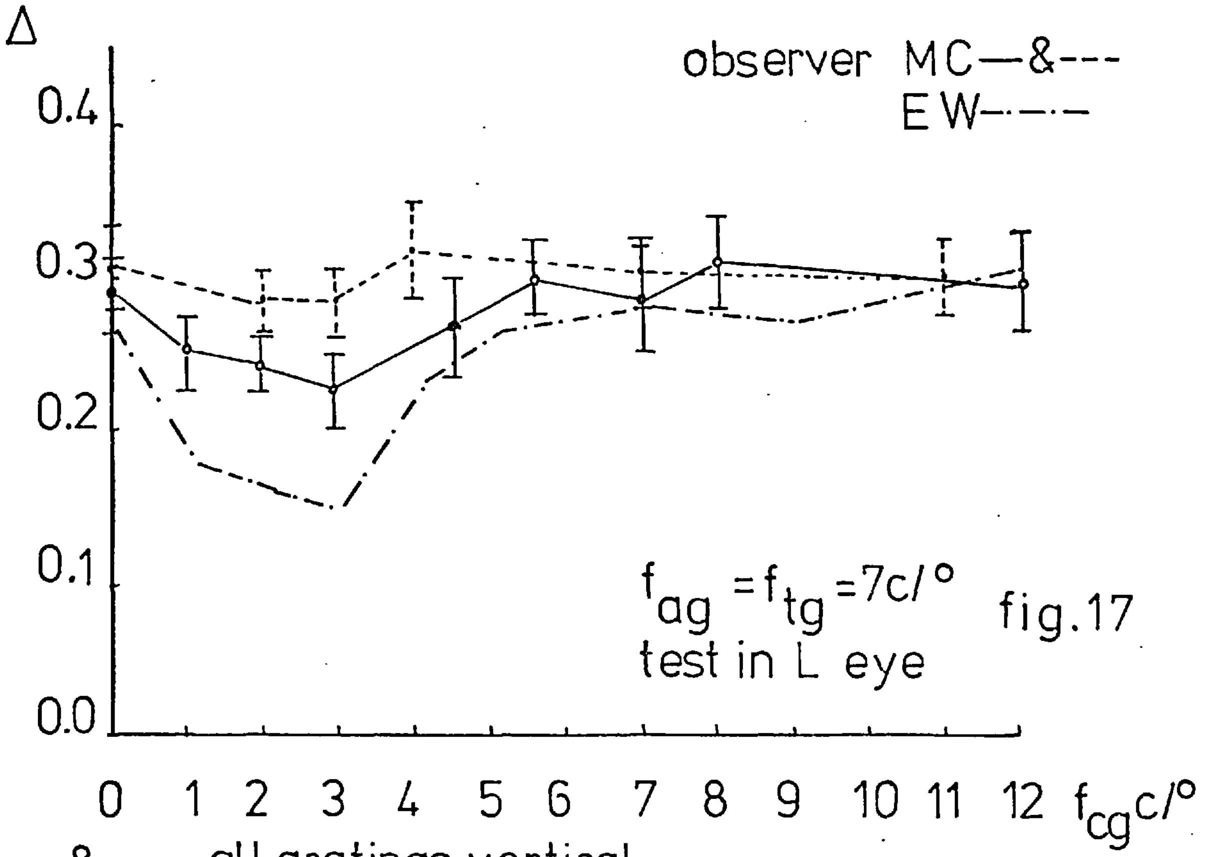


fig.17

-·-·- & —— all gratings vertical

---- all gratings horizontal

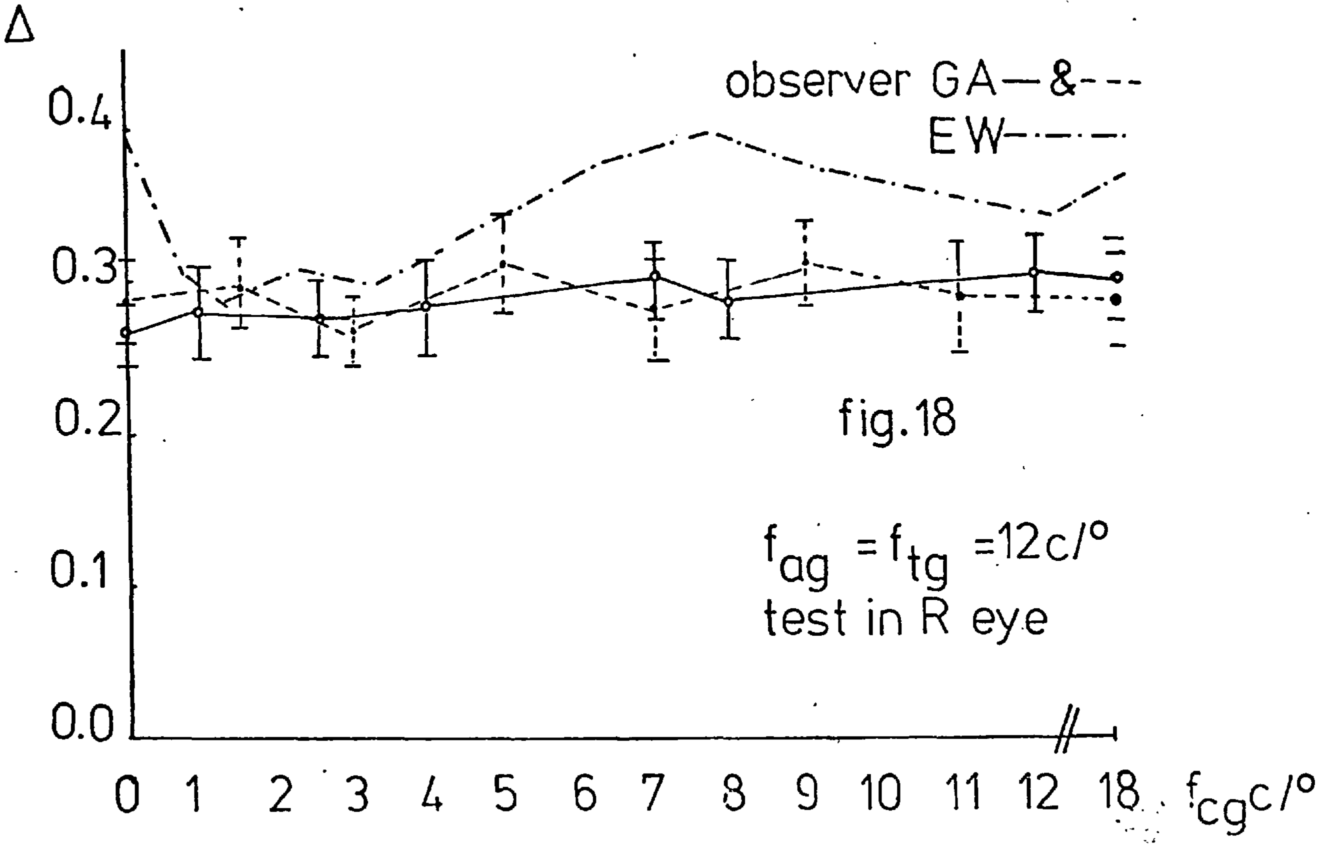


fig.18

$f_{ag} = f_{tg} = 12$c/°
test in R eye

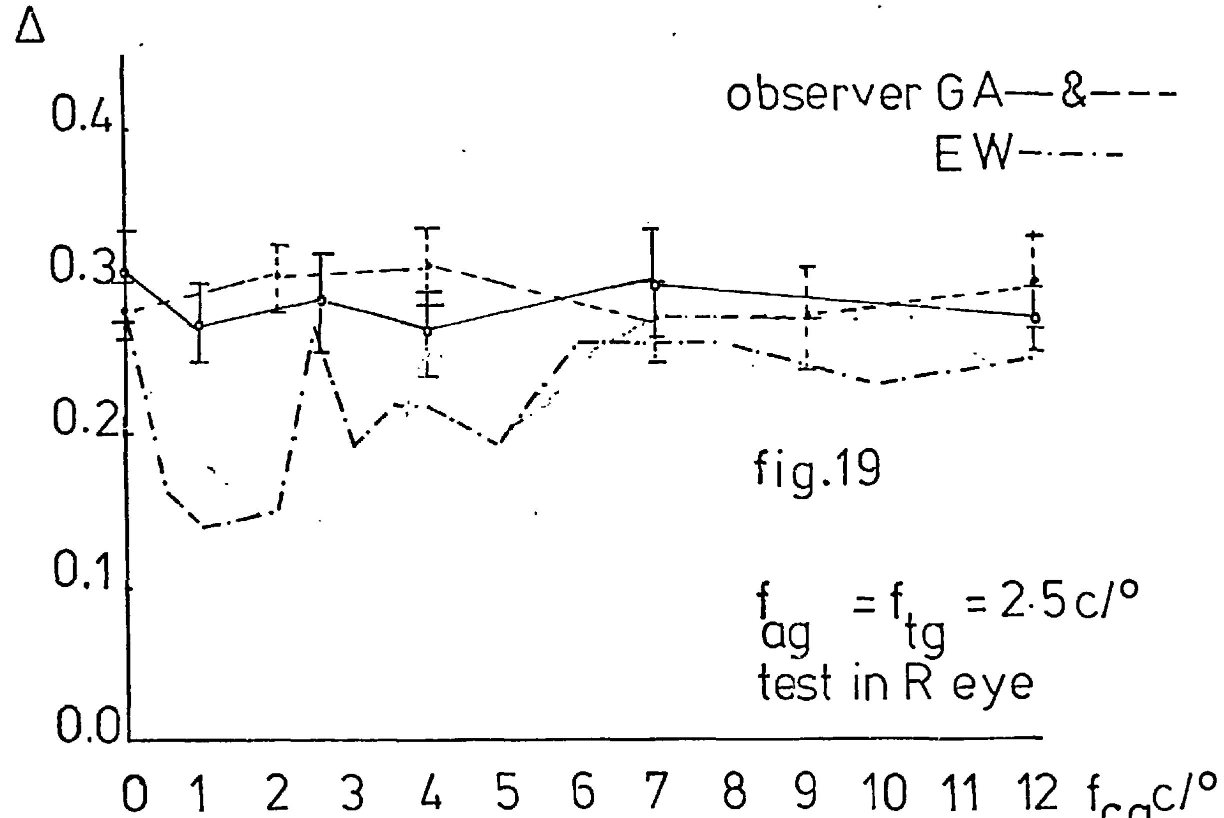


fig.19

$f_{ag} = f_{tg} = 2{\cdot}5$ c/°
test in R eye

-·-·- & —— all gratings vertical
---- all gratings horizontal

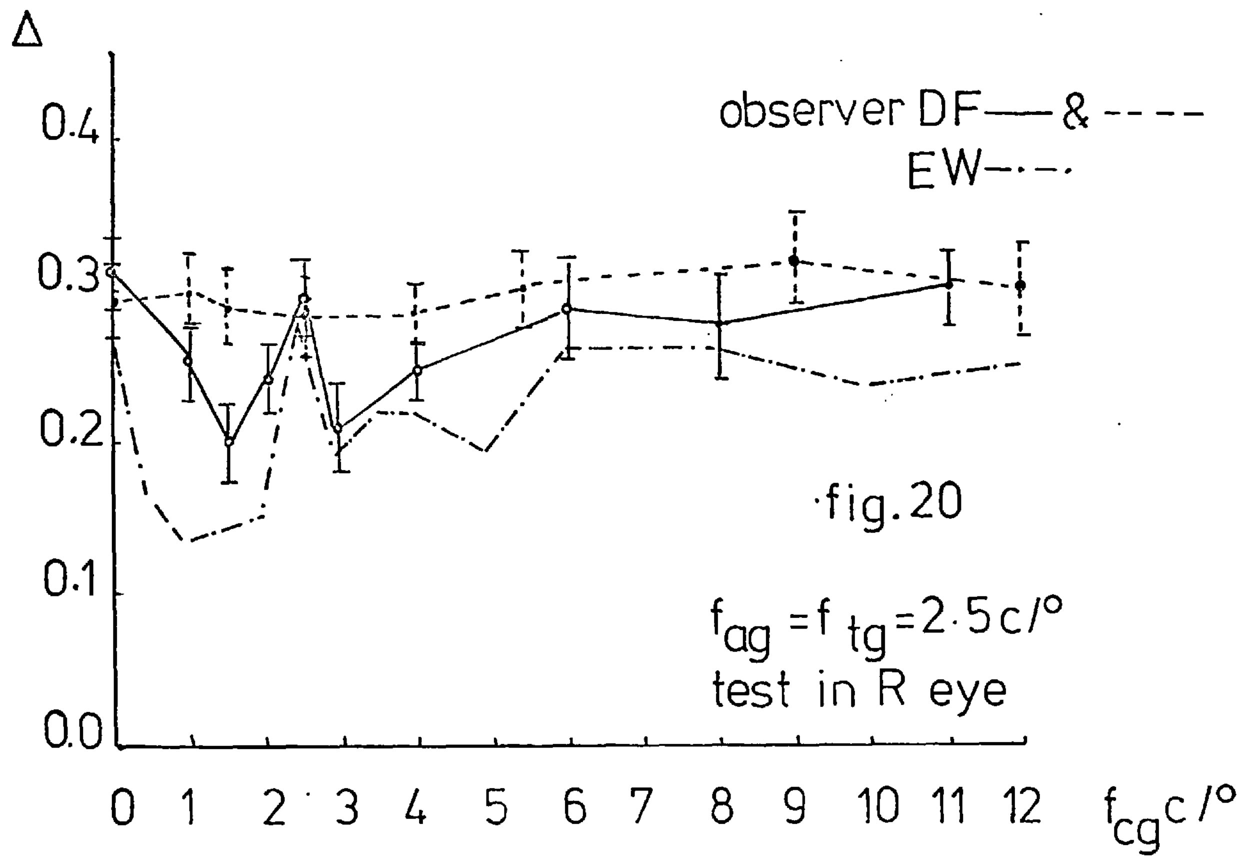


fig.20

$f_{ag} = f_{tg} = 2{\cdot}5\,c/°$
test in R eye

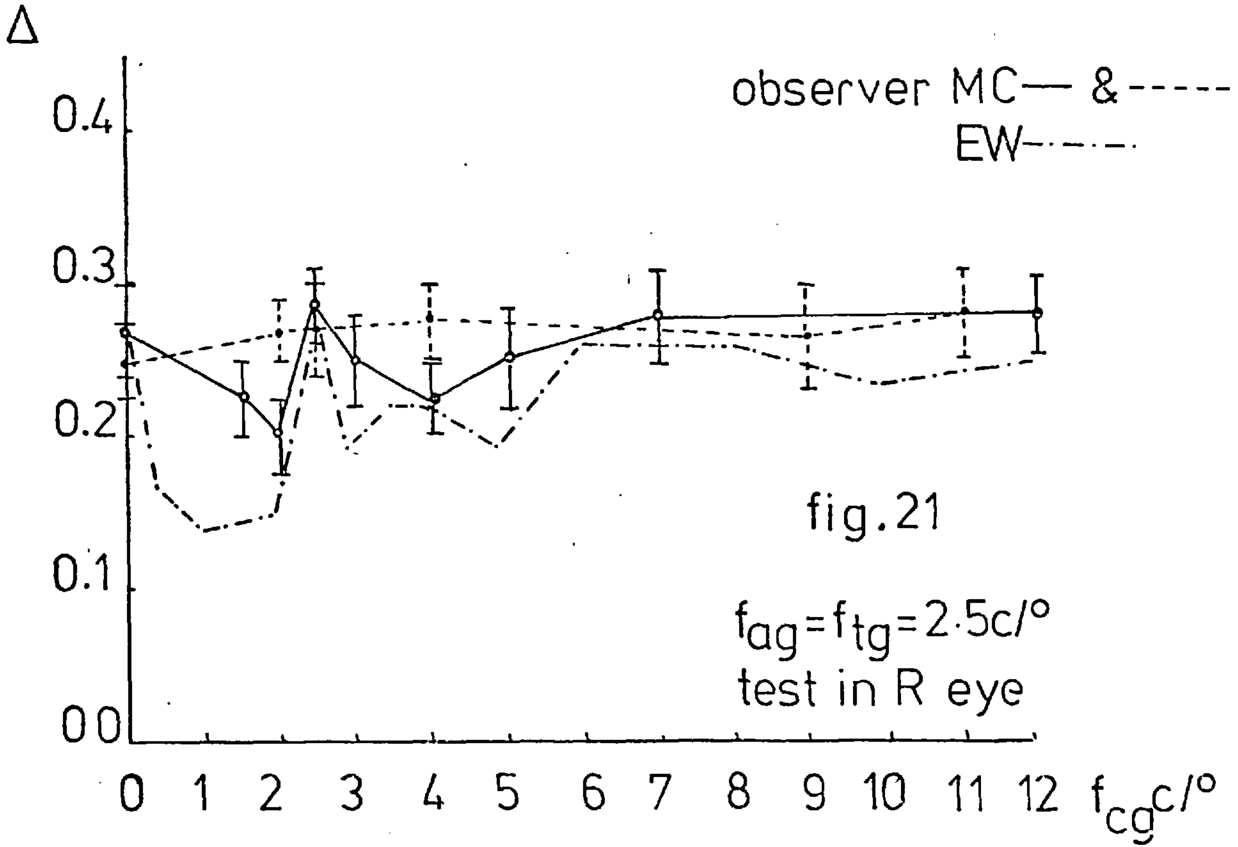


fig.21

$f_{ag} = f_{tg} = 2{\cdot}5\,c/°$
test in R eye

—·—·— & —— all gratings vertical
- - - - - all gratings horizontal

Δ_V in the table refers to the value of Δ, as measured for a vertical test grating spatial frequency, f_{tg}, in the presence of the vertical conditioning grating whose spatial frequency, f_{cg}, is such as to induce maximum suppression of response. Δ_H refers to the value of Δ obtained for a similar spatial frequency, f_{tg}, horizontal test grating in the presence of a horizontal conditioning grating of the same spatial frequency, f_{cg}. The quantity $(\Delta_H - \Delta_V)$ thus refers to the peak magnitude in log units of any suppression which a conditioning grating may exert on an adaptation grating presented to the alternate eye.

The results in table 1 can be divided into two sections: those given by astigmats who experience difficulties in the perception of approximately horizontal lines (horizontal astigmatism: RM and DF) and those given by observers with vertical astigmatism (GA, MC and TL). Comparison of the data in column 6 indicates that results for the first category of observer are very similar to those given by observers with normal vision, the magnitude of suppression of the threshold elevation effect by a low spatial frequency conditioning grating being, within experimental error, the same for both horizontal astigmats and non-astigmats. The stereopsis of these observers was also found to be normal.

The data for the second category of observers, the vertical astigmats, are not, however, so consistent. GA, who was not only the most severe astigmat, but has also suffered from the condition the longest, showed no significant suppression of Δ in any of the experiments which he performed, although these same experiments yielded suppression for non-astigmats. He also received no impression of stereopsis from even the most highly correlated stereogram (Julesz, 1971, and fig. 9). His results are, in these respects, very similar to those of DP and AC, the stereoblind observers considered earlier in the chapter. However, unlike these subjects, GA had no clinical history of strabismus.

Observer TL, although also a relatively severe vertical astigmat, gave results very different from those of GA. The magnitude of his suppression effect was found to be, within experimental error, the same as that displayed by non-astigmatic observers. His stereopsis was also at a normal level. His astigmatism, however, had developed at a relatively late stage (about ten years of age) unlike that of GA (about three years).

The results for the third astigmat in this category (MC) indicate a degree of low frequency suppression which is less than that shown by both non-astigmatic observers and by TL, but greater than that shown by GA. The suppression can be seen in fig. 21 where the very sharp tuning of Δ observed by EW (dot-dash line) around the point $f_{cg} = f_{ag} = 2.5$ c/° is clearly defined in the results of MC (continuous line). Although MC was able to obtain some impression of depth from the stereograms, his stereopsis was well below average. His astigmatism was severe and had first been diagnosed at about six years of age.

Considerable electrophysiological research has been carried out on single cells in the visual cortex of cats reared under conditions which induce artificial astigmatism (e.g. Hirsch and Spinelli, 1970; Blakemore and Cooper, 1970). These conditions generally consisted of environments composed totally of vertical or horizontal bars. The cortical neurones which were studied were found to have receptive fields which responded principally to the orientation of bar stimulus to which the eye had been exposed. There has recently been some discussion on the reliability of these results (Barlow, 1975). If they can be extended to humans, it would be expected that a subject who suffered from astigmatism during a critical period of development of the cortical neurones, if indeed, such a period exists for man, would be left with a type of residual 'neural' astigmatism which could not be compensated for by lenses, since the basis would be neural rather than optical. A study by Mitchell, Freeman, Millodot and

Haegerstrom (1973) indicates that abnormalities in acuity do remain for astigmats, even after the correction of the disorder. The acuity measurements were carried out with interference fringes similar to those used in the present experiments and thus the fringe formation by-passed the optics of the eye. They also performed experiments to gauge stereoacuity, although the configurations employed were not strictly comparable to those used here.

Four factors would seem to be important in any interpretation of the results shown in table 1: the nature of astigmatism, the age of onset of astigmatism, the magnitude of the conditioning effect and the degree of stereoacuity. Loss of stereoacuity could well be accounted for by the nature of the astigmatism; since stereopsis is based on the perception of horizontal disparities, a disorder which leaves the observer with reduced acuity for vertical lines might be expected to reduce stereopsis. However, reduction of acuity for horizontal lines would not similarly produce loss of stereopsis. It was found in the present experiments that RM and DF, horizontal astigmats, have normal stereopsis and that GA, a vertical astigmat, has none, which is in agreement with this proposal. The normal stereopsis displayed by TL and the partial stereopsis displayed by MC, both vertical astigmats, could be attributed to the age of onset of the disorder which, in both cases, is later than that of GA. If there is a "plastic" period of development during which cortical neurones can be modified (such as was proposed for the cat by Blakemore and Cooper (1970) and Hirsch and Spinelli (1970)), then it is possible that is occurs in the first five years after birth. A visual orientation disorder occurring outside the plastic period would not then be able to modify the characteristics of the neurones.

It is not feasible to suggest on the basis of these results when this plastic period might be likely to occur. The report on children suffering from strabismus cited earlier in the chapter (Banks, Aslin and Letson, 1975) indicated that it could occur between 1 and 3 years of age. There is a problem in the present investigation, however, in determining the exact age at which the astigmatism developed, since the dates supplied by the subjects' opticians refer only to the dates when spectacles were given for the disorder. There is evidence (Duke Elder, 1969) that subjects with severe astigmatism usually possess the defect at birth.

The magnitude of the conditioning effect exerted by a low frequency grating correlates with the degree of stereopsis which the observer possessed: no conditioning for an observer with no stereopsis, but 0.15 l.u. suppression of Δ for an observer with normal stereopsis. Again, this does not supply evidence that the two effects are directly related. If loss of stereopsis is taken as providing an indication of loss of binocularity in the cortical neurones (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1974), then the conditioning effect, being an essentially binocular interaction, might be expected to reduce accordingly. The experiments of Movshon, Chambers and Blakemore (1972) and Mitchell and Ware (1974) were concerned, however, with binocularity as measured by interocular transfer of the tilt after-effect in observers whose stereopsis was reduced through strabismus. Since GA and MC had no clinical history of strabismus, it seems likely that their loss of stereopsis can be attributed to their vertical astigmatism. If so, it is important to discover whether loss of stereopsis through astigmatism results in the same loss of binocularity that occurs with loss of stereopsis through strabismus. If it does not, more significance could be attributed to the correlation between the magnitude of the conditioning effect and the level of stereopsis. Part of the next chapter is concerned with this problem.

It has been observed that the conditioning effect is not affected by horizontal astigmatism, but can be affected by vertical astigmatism. This provides further evidence for the basis of the suppression mechanism being concerned solely with neural responses to lines which are of an approximately vertical orientation.

Chapter 7.

CHARACTERISTICS OF THE CONTRAST THRESHOLD ELEVATION EFFECT FOR ASTIGMATIC OBSERVERS

The experiments described in the first part of this chapter were carried out in an attempt to assess the extent and specificity of any reduction in the binocular response of astigmatic observers. The after-effect used to measure the binocularity was the interocular transfer of the threshold elevation effect rather than the transfer of the tilt after-effect which has been studied by previous experimenters (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1974). The visual field configuration consisted of an adaptation grating, of illumination level 4.5 l.u. above its threshold level, presented to the left eye with the subsequent presentation of a test grating of the same spatial frequency (7 c/°) and orientation as the adaptation stimulus to the dark-adapted right eye. Δ was computed by comparing the threshold for the test obtained after adaptation to a grating with that obtained after adaptation to a uniform field of the same mean luminance again presented solely to the left eye. Δ was determined for a series of orientations of the test and adaptation gratings (θ on the figures) measured from the vertical. Data for the five astigmatic observers studied in the last chapter are given in figs. 1 - 5. Comparative data for EW, a non-astigmat, are shown in fig. 6.

Fig. 1 illustrates the results obtained by GA, a vertical astigmat. It can be seen that there is no significant interocular transfer of Δ for any orientation of the test and adaptation gratings. Observer MC, fig. 2, also a vertical astigmat, did, however, obtain significant interocular transfer for all orientations, although transfer of adaptation for gratings made up of approximately horizontal bars was greater than transfer for approximately vertical bars (0.29 ± 0.025l.u., c.f. 0.19 ± 0.025l.u.). Observer TL, fig. 3, the third vertical astigmat in the group, again found transfer for all

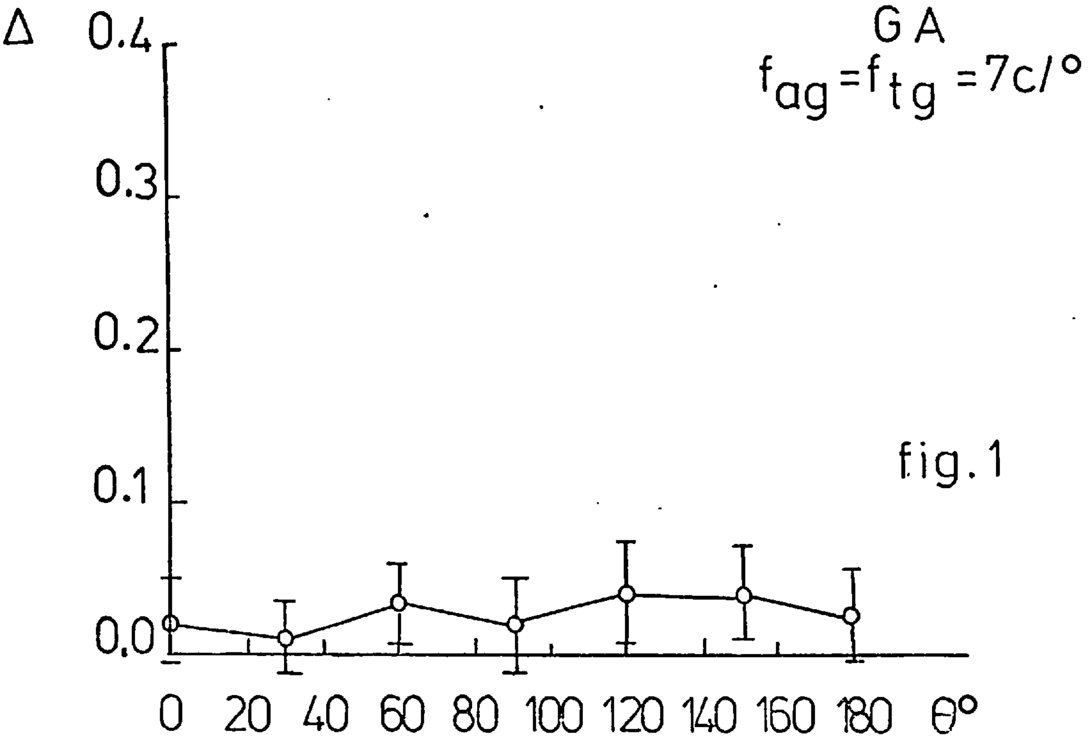


fig.1

test grating presented to R eye: adaptation to L eye. both gratings oriented at θ° to the vertical.

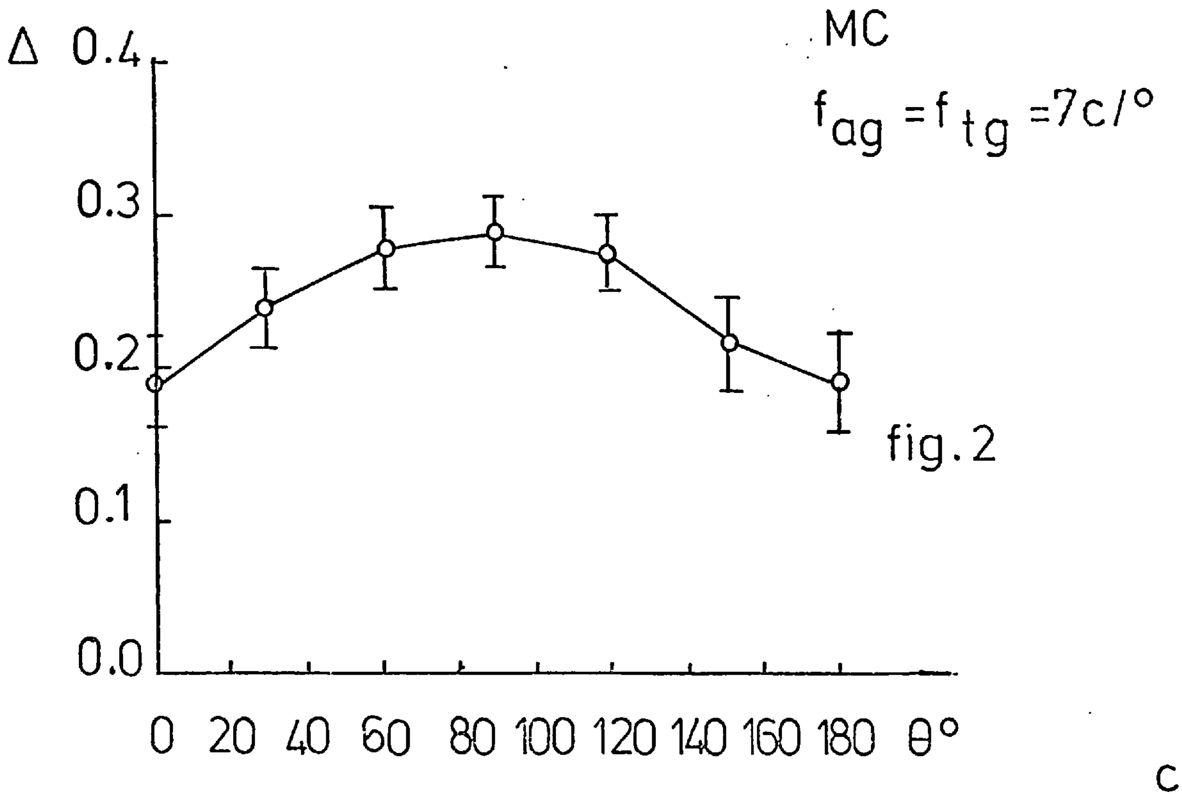


fig.2

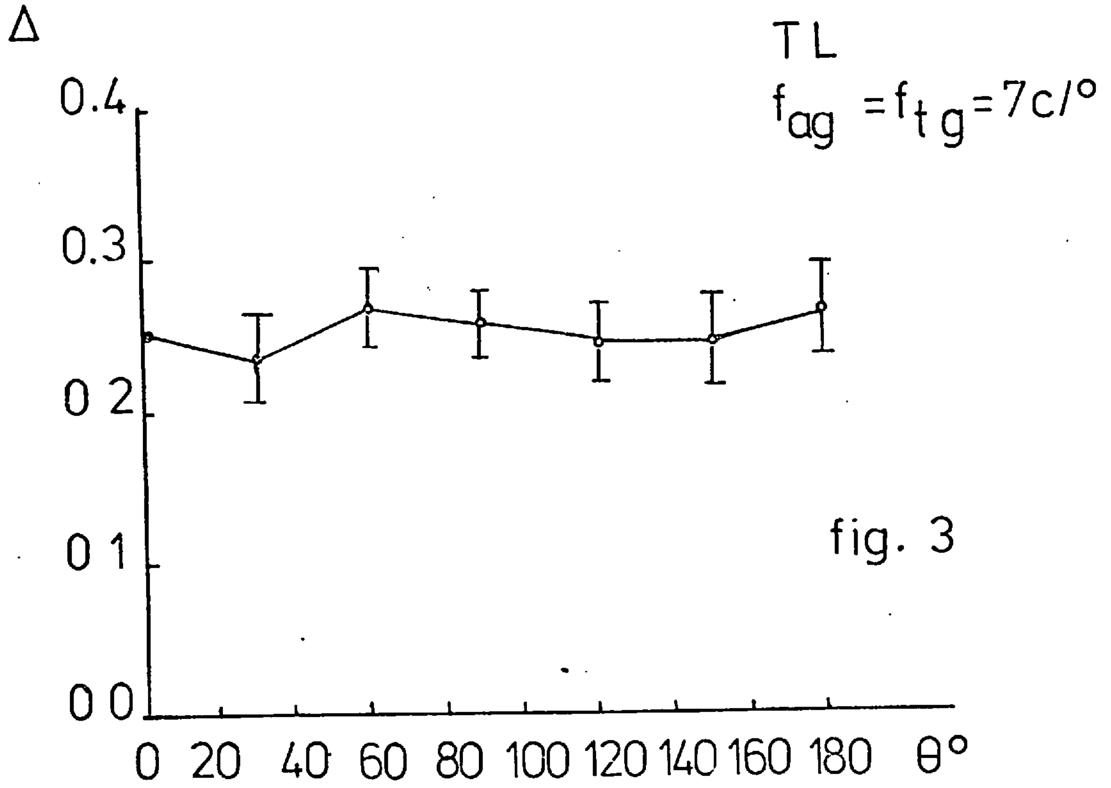


fig. 3

test grating presented to R eye: adaptation to L eye
both gratings oriented at θ° to the vertical

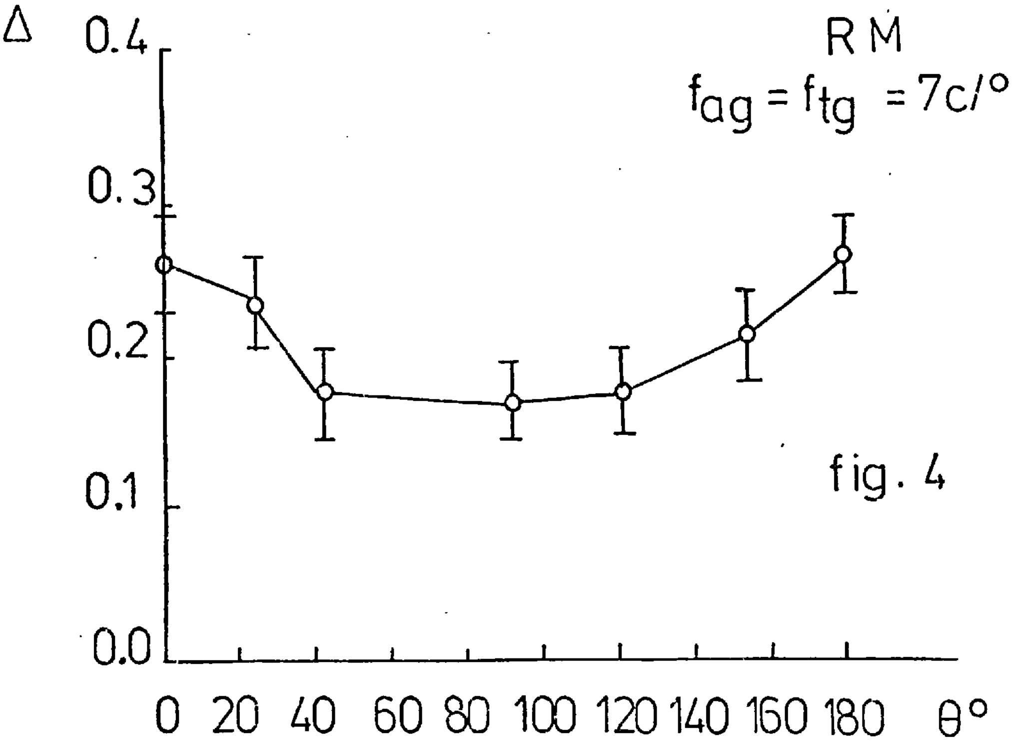


fig. 4

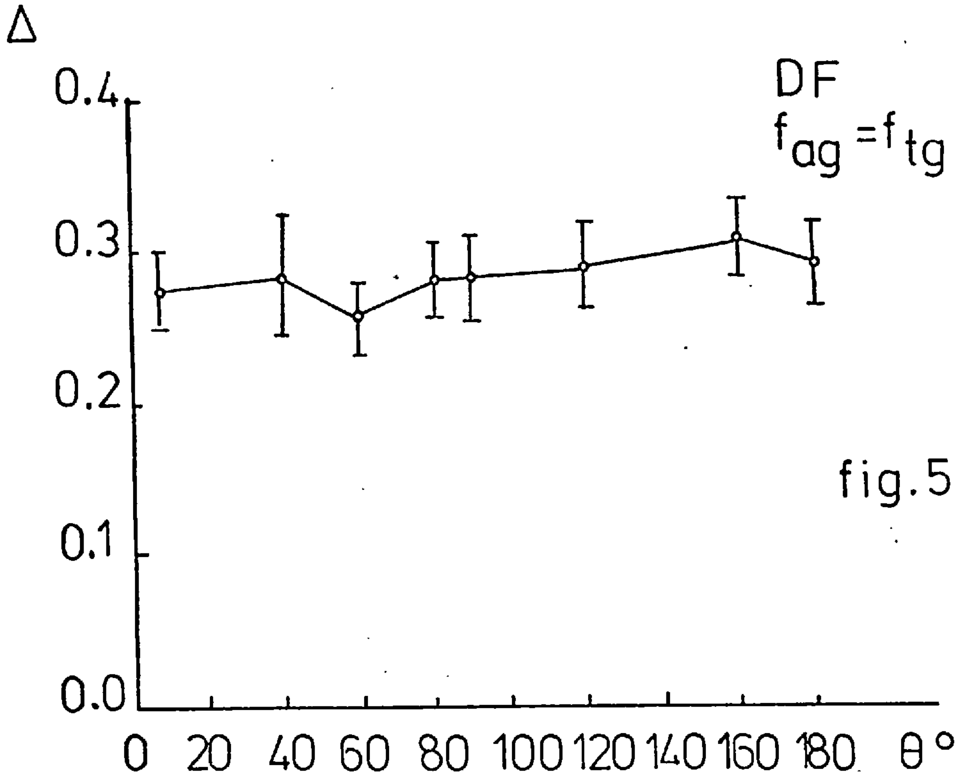


fig.5

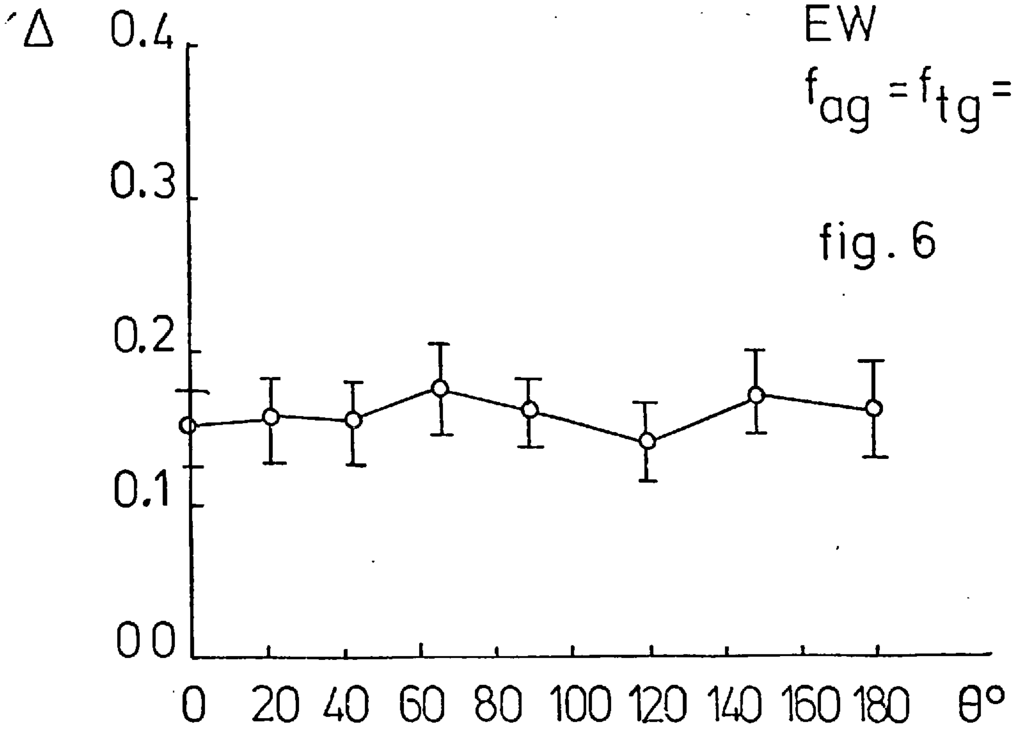


fig. 6

test grating presented to R eye : adaptation to L eye
both gratings oriented at θ° to the vertical

orientations of gratings, but there was no significant difference between the values of Δ measured for different meridians.

The remaining two observers were astigmatic in the horizontal direction. The results of RM, fig. 4, indicate significant transfer for all orientations of gratings, but as in the observations of MC, there was improved transfer for one meridian. Unlike MC, however, this meridian was in the vertical direction rather than the horizontal direction (0.27 ± 0.03 l.u., c.f. 0.17 ± 0.025 l.u.). DF (fig. 5) gave data similar to those of TL with approximately equal interocular transfer for all orientations. Although the threshold elevations obtained by EW (fig. 6) show a lower percentage of interocular transfer than that observed by previous experimenters (for discussion, see chapter 3, page 80), they are consistent with those of DF and TL in being, within experimental error, independent of grating orientation. These results indicate that astigmatism can suppress binocular response under certain conditions.

In the last chapter, it was shown that observers TL and DF displayed normal stereopsis and that they possess the same conditioning effect by a low frequency grating as is found for non-astigmatic observers. It has thus been established that the interocular transfer which they obtained is also consistent with that of observers with normal vision (e.g. that of Maudarbocus, 1973) in both degree and lack of orientation specificity. Although astigmatic in different directions (TL:vertical, DF: horizontal), it seems likely from the information supplied by their respective opticians (table 1, previous chapter), that the onset of the condition occurred at a comparatively late stage (10 years for TL; 8 years of age for DF).

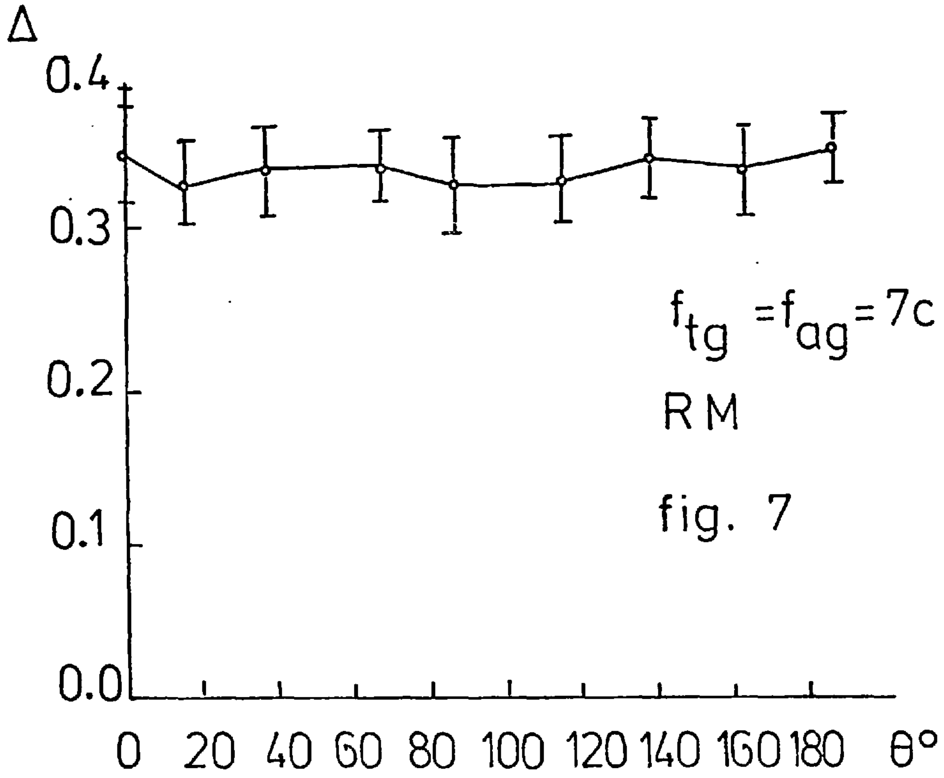
The results for subjects MC and RM can also be compared: the interocular transfer is greater in both cases for a particular meridian, the horizontal meridian for vertical astigmat MC and the vertical meridian for horizontal astigmat RM. This would suggest that the binocularity of the observer's cortical units concerned with lines presented to him with the same orientation as his astigmatic meridian is reduced if the onset of the astigmatism occurs at a relatively young age. For both MC and RM this was at some age before 6 years. Binocularity for other orientations would appear to be unimpaired. These findings are not wholly reflected in the amount of stereopsis displayed by the two observers. Although that shown by MC is well below average (see table 1, previous chapter) as might be expected from the reduced binocular response measured in this section, that shown by RM is quite normal. This can be correlated with the fact that depth perception necessitates the discrimination of horizontal disparities in the two visual fields. Thus, an observer who could not perceive adequately the vertical components of any image would not be able to perceive the disparities between these components and his stereovision would be consequently impaired. The stereovision of an observer, who could perceive the vertical lines, however, would not be reduced by his inability to discern horizontal lines, since these do not contribute directly to depth perception. These findings therefore indicate that stereoacuity alone is not a sufficient measure of binocular response since it is related principally to neurones which respond to lines in the vertical meridian.

Observer GA showed no interocular transfer for any orientation, just as he had shown no conditioning effect and no stereopsis. He acquired his astigmatism at a very young age (before three years). Interpreting his condition in the same way as that of MC, suggests that his lack of stereopsis and his lack of the conditioning effect can both be attributed to this early and severe vertical astigmatism. It might have been expected, however, that he would have shown some interocular transfer for horizontal bars, since the perception of these should not be reduced by vertical astigmatism. It is possible that GA suffered as a child, from some other visual disorder, perhaps horizontal astigmatism or extreme myopia which is now, no longer, quite so apparent. Alternatively, it is possible that his total lack of binocular response is caused by a congenital anomaly, although no clinical history is available.

Determination of the orientation specificity of the interocular transfer of adaptation is, necessarily, a binocular experiment. MC and RM (figs. 7 and 8) repeated the experiment with adaptation and test gratings both presented to the right eye. Again Δ was measured as a function of the orientation of the test and adaptation gratings. The results show that the monocular values of Δ, unlike the interocular values in figs. 2 and 4, are not influenced by the orientation of the gratings, indicating that the preferential adaptation for gratings in the non-astigmatic meridian is confined only to the interocular experiment.

The results obtained so far appear to correlate with the experiments performed on animals reared in environments consisting of lines of specific orientations (e.g. Hirsch and Spinelli, 1970; Blakemore and Cooper, 1970). Although it is possible to say that the binocular response of certain cortical units has been reduced for some of the astigmats, the results do not indicate whether other fundamental characteristics of these units, such as their orientation and spatial frequency tuning, have been in any way affected by the astigmatism, although experiments by Abadi (1974) have shown that the ability to perceive changes in orientation is not affected by astigmatism.

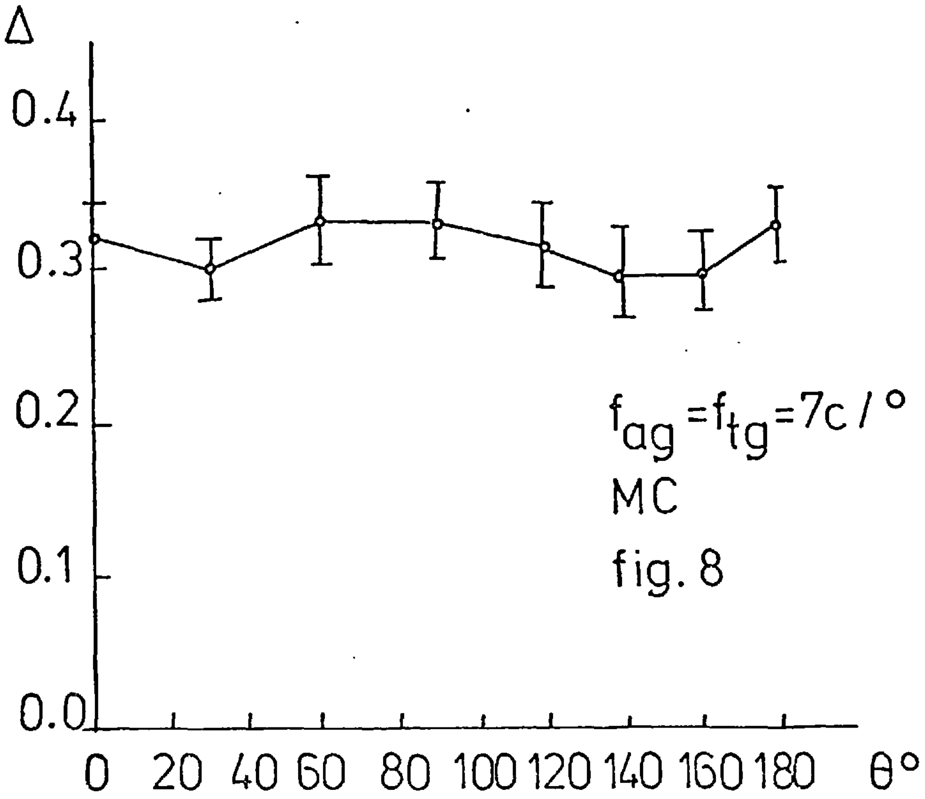
The orientation selectivity of the threshold contrast elevation effect, which is one of the basic properties of the effect, was determined for observers GA and MC (both vertical astigmats). In each case, the test grating was held vertical and Δ determined as a function of change in angle of an adaptation grating of the same spatial frequency (as discussed in Chapter 3). MC performed the experiment for both a monocular (test and



$f_{tg} = f_{ag} = 7c/°$

RM

fig. 7



$f_{ag} = f_{tg} = 7c/°$

MC

fig. 8

test and adaptation gratings both presented to R eye at θ° to the vertical adaptation presented to the same eye) and a binocular (test in right eye, adaptation in left eye) configuration. GA performed only the monocular experiment since he obtained none of the interocular transfer of Δ necessary for the binocular experiment.

Fig. 9, the data for GA, can be compared with data obtained by EW, a non-astigmat, in performing the same experiment (continuous line in fig. 11). Although the value of Δ for parallel test and adaptation gratings is less for GA than for EW, the characteristics of the curve in relation to the way in which Δ falls off for nonparallel test and adaptation stimuli, is very much the same. Fig. 10, the data obtained by MC for the two experiments, can similarly be compared with the results of EW (fig. 11). Again, the values of Δ for parallel gratings are different for the two observers but the nature of the orientation selectivity is similar in terms of the width of the curves. Since GA and MC were vertical astigmats and the test gratings in these experiments were also vertical, these data establish that although binocularity of certain cortical units may be reduced, the orientation specificity in terms of the tuning of these units is the same for both astigmats and non-astigmats.

Having checked the orientation specificity, the final group of experiments with astigmatic observers was designed to determine the spatial frequency tuning response as displayed by two of the astigmats, GA (a vertical astigmat) and RM (a horizontal astigmat). EW (normal vision) also repeated the experiments for comparison. The measurement of frequency tuning curves was discussed in Chapter 3 and involves maintaining the spatial frequency of the test grating constant and determining Δ as a function of change in the spatial frequency of the adaptation grating. The experiment was done initially with both gratings vertical and then repeated with both gratings horizontal. Although data are given for EW and RM for both interocular (test in right eye, adaptation in left eye) and monocular

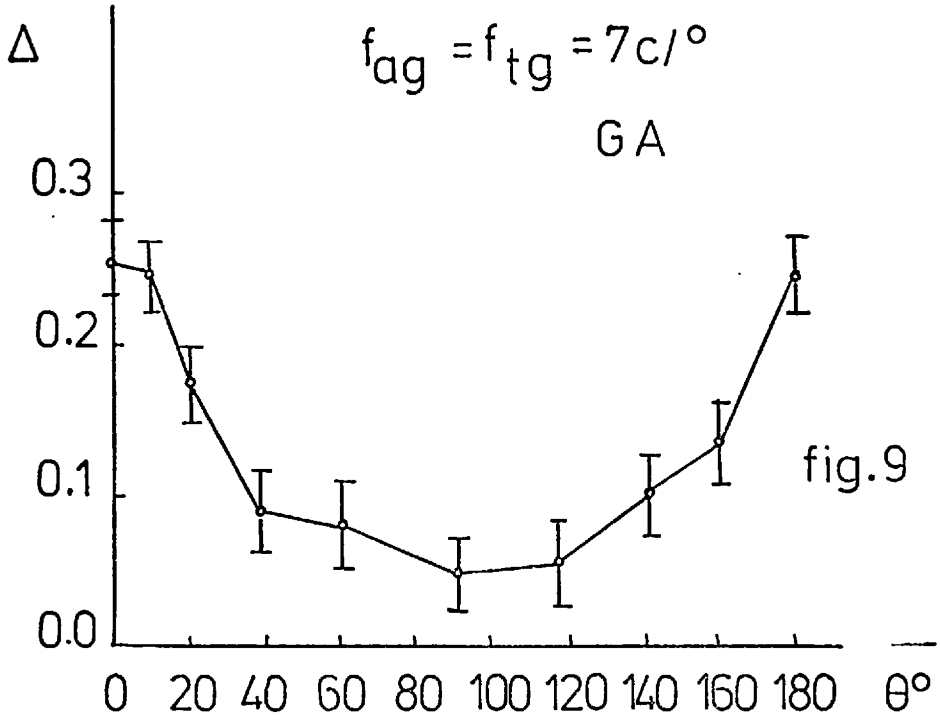


fig.9

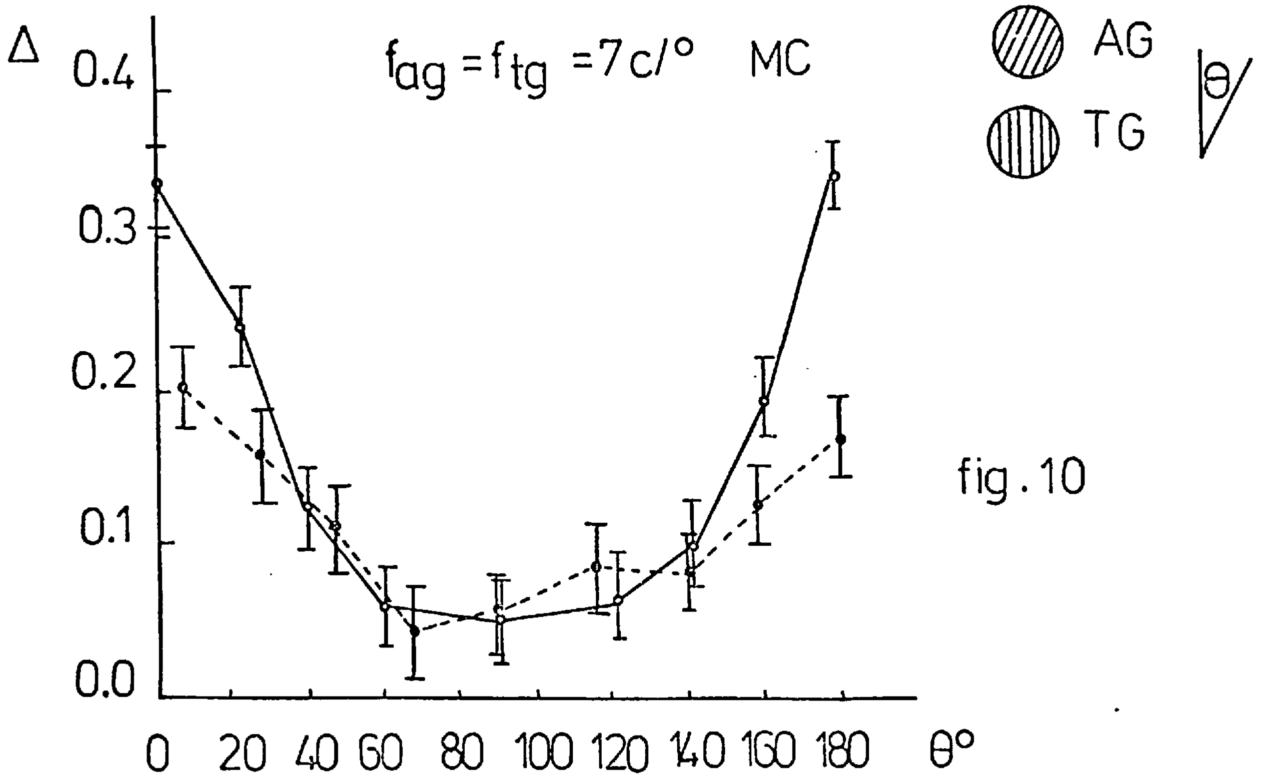
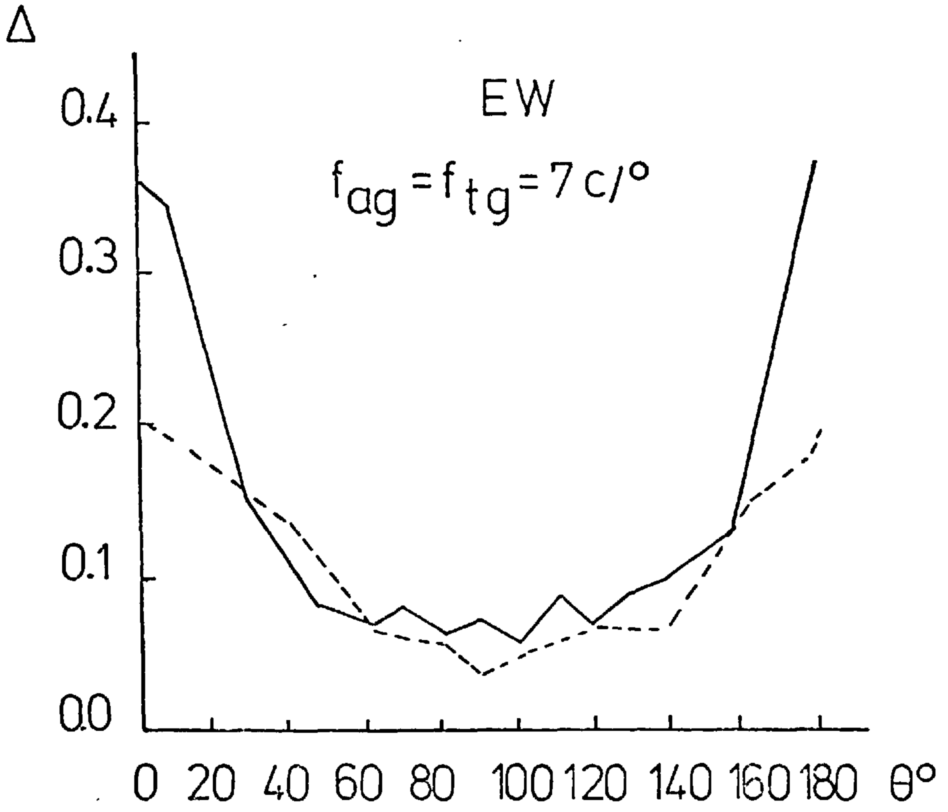


fig.10

test and adaptation in R eye : ——

test in R eye, adaptation in L eye: ----



test and adaptation in R eye : ——

test in R eye, adaptation in L eye : -----

fig.11

experiments, GA was unable to perform the interocular experiments, since, as before, he obtained no interocular transfer of Δ.

Figures 12 and 13 illustrate the results obtained monocularly by GA for vertical and horizontal gratings respectively. The dotted line represents the data obtained by EW in these experiments (represented in more detail in figs. 16 and 17). Although the value of Δ determined for test and adaptation gratings of the same spatial frequency is again higher for EW than for GA, the bandwidths of the horizontal and vertical tuning curves are, within the experimental error, the same in both cases.

Similarly, a comparison of the monocular and interocular curves, as determined in both horizontal and vertical meridians, obtained by RM (figs. 14 and 15) and EW (figs. 16 and 17) show no significant differences in the bandwidths. The differences in the interocular transfer of the effect at the peak of the tuning curves (figs. 14 and 15) can be attributed to the horizontal astigmatism of RM (as discussed earlier in this chapter), but it is important to note that the basic tuning characteristics displayed by the two astigmats are the same not only for horizontal and vertical gratings, but also the same as those of a normal observer, EW.

The conditioning effect of a low frequency grating was discussed in the previous chapter in relation to astigmats. It was correlated with the nature of their astigmatism and the level of their stereopsis. It was suggested that the reason why some observers with anomalous vision did not display the same conditioning effect as observers with normal vision was connected with reduced binocular response of certain cortical units. This chapter has attempted to discover more about this reduced binocular response. It has been determined that those two astigmatic observers who obtained interocular transfer of the grating threshold elevation effect for all grating orientations obtained a standard level of the conditioning effect. Two further observers obtained a larger percentage

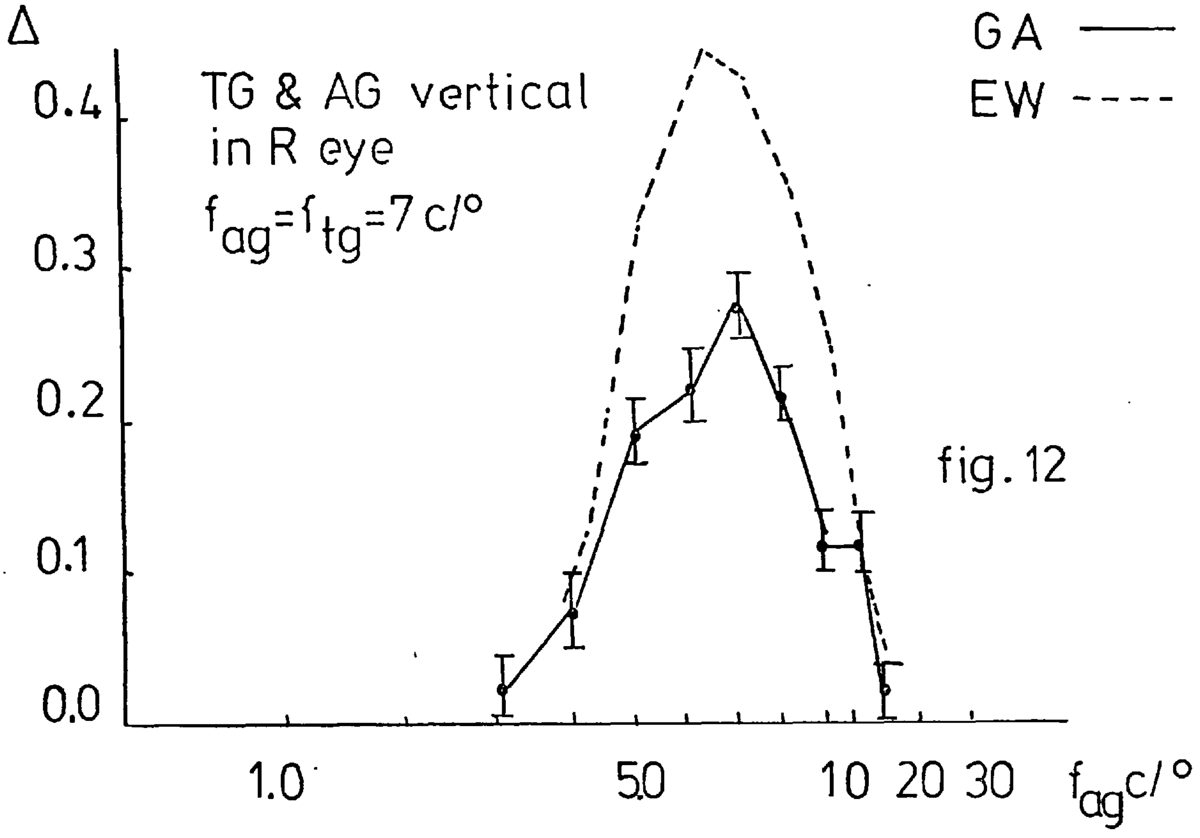

Δ
0.4
0.3
0.2
0.1
0.0
TG & AG vertical
in R eye
f_ag=f_tg=7 c/°
GA ——
EW - - - -
1.0
5.0
10
20
30
f_ag c/°

fig. 12

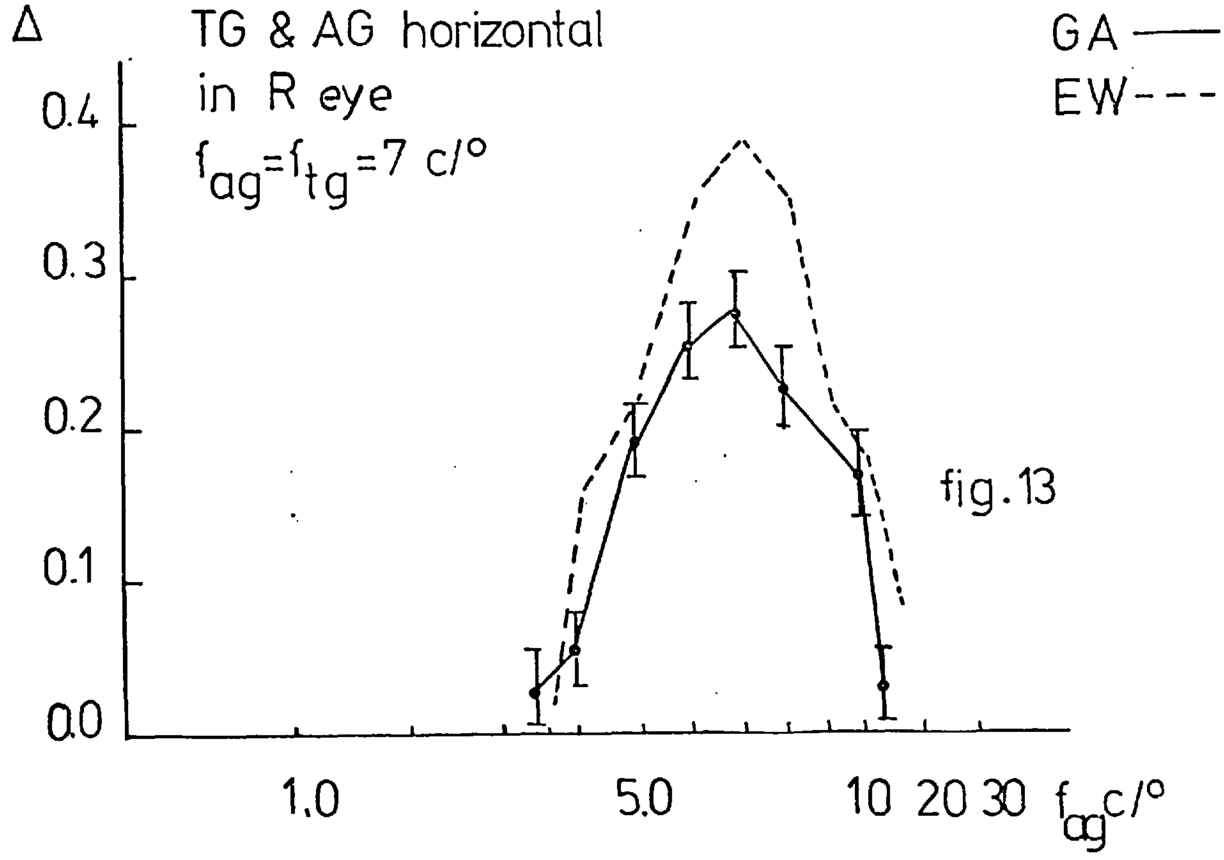

Δ
TG & AG horizontal
in R eye
f_ag=f_tg=7 c/°
GA ——
EW - - -
0.4
0.3
0.2
0.1
0.0
1.0
5.0
10
20
30
f_ag c/°

fig. 13

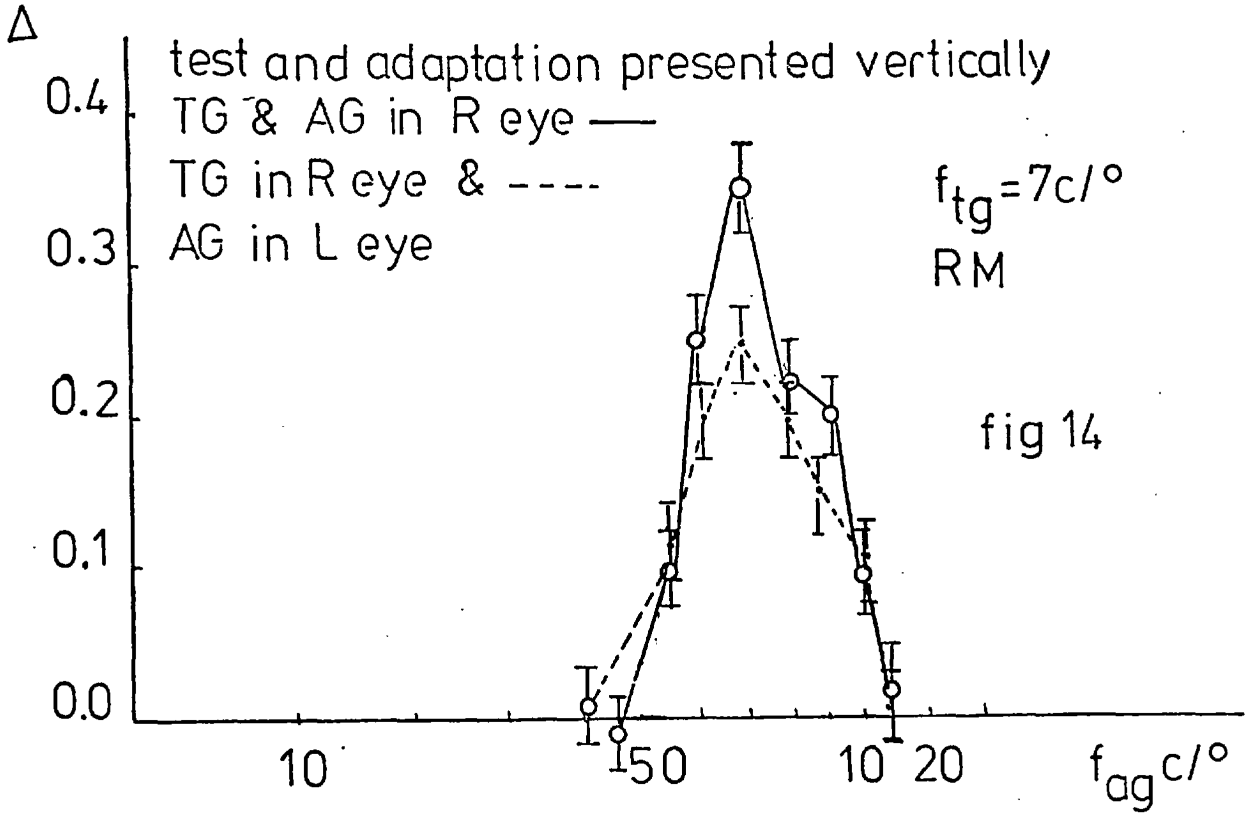

Δ
test and adaptation presented vertically
TG & AG in R eye ——
TG in R eye & ----
AG in L eye
f_tg=7c/°
RM
0.4
0.3
0.2
0.1
0.0
10
50
10 20
f_ag c/°

fig 14

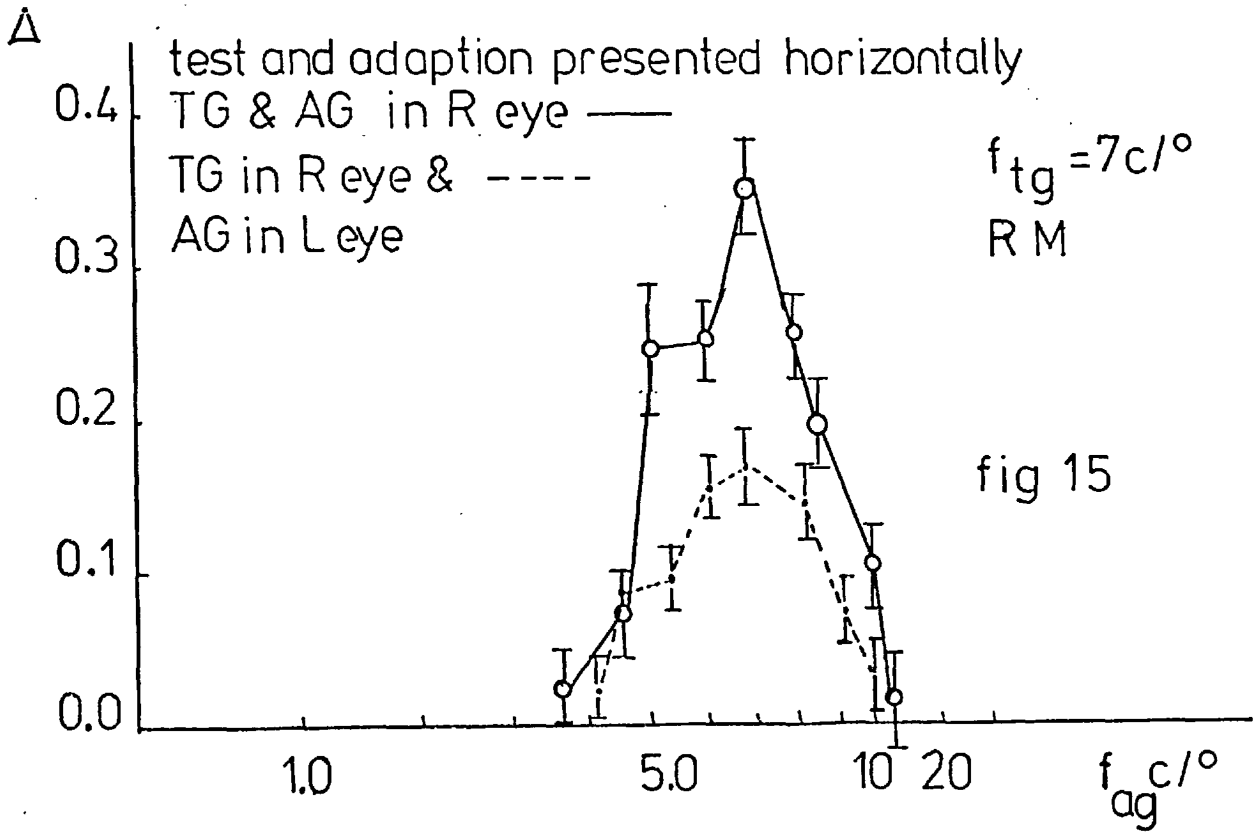

Δ
test and adaption presented horizontally
TG & AG in R eye ——
TG in R eye & ----
AG in L eye
f_tg =7c/°
R M
0.4
0.3
0.2
0.1
0.0
1.0
5.0
10 20
f_ag c/°

fig 15

test and adaptation presented vertically

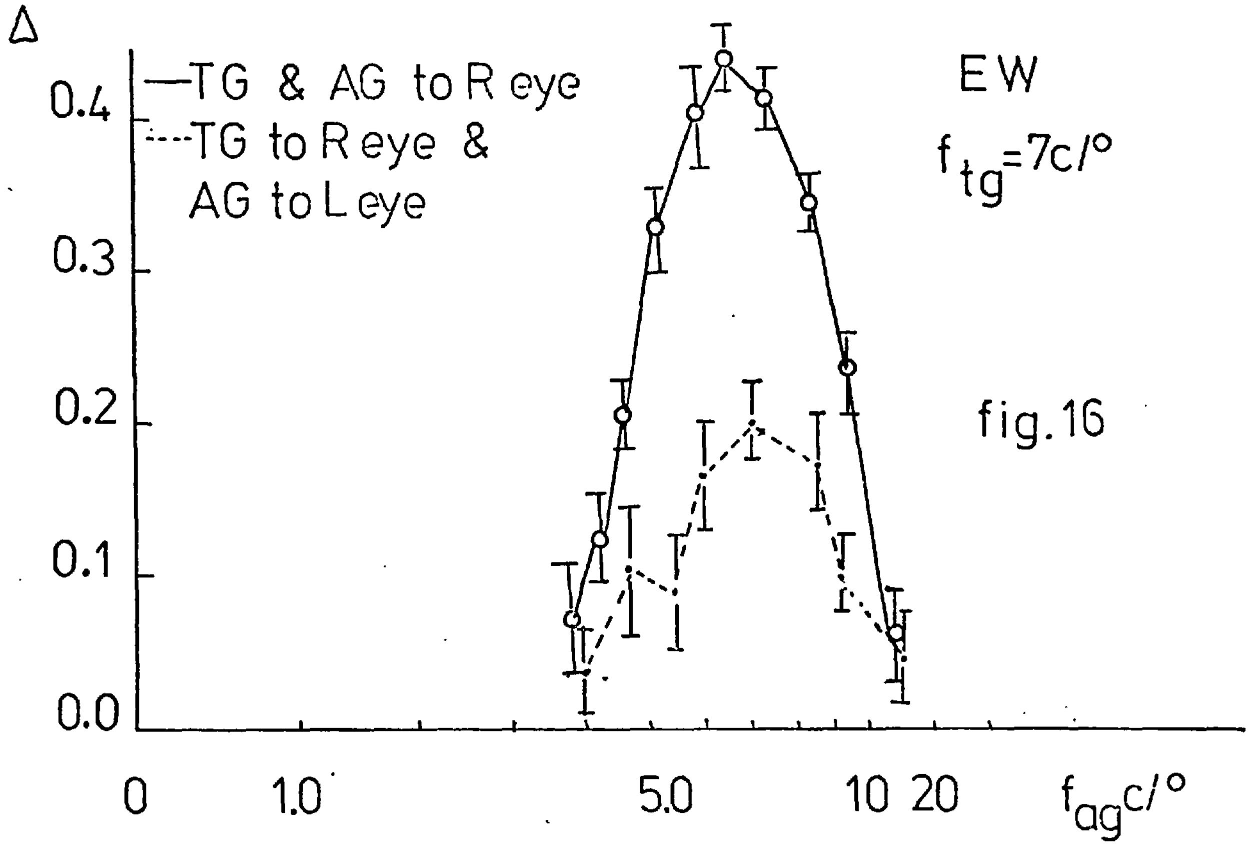


fig.16

test and adaptation presented horizontally

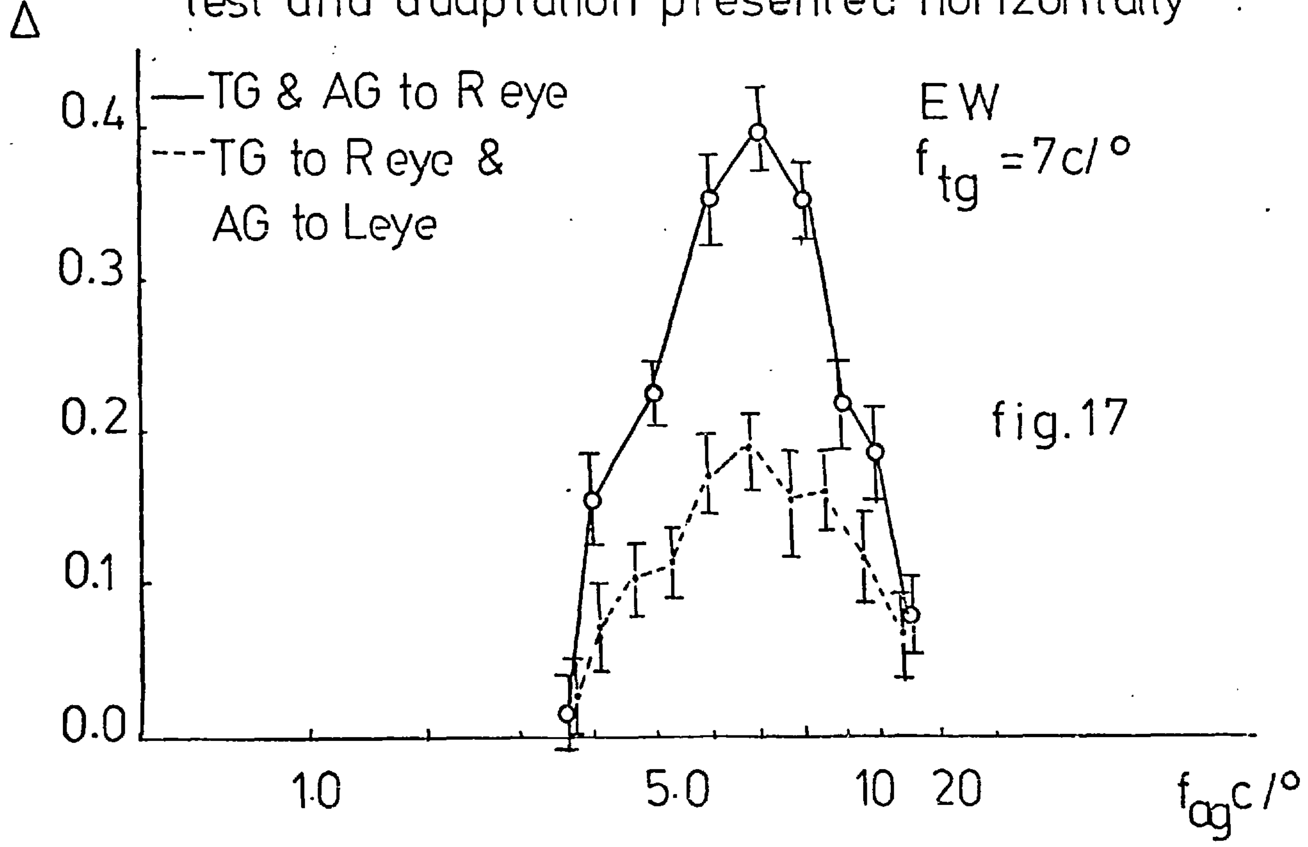


fig.17

of interocular transfer for gratings oriented in their non-astigmatic meridians. The reduced response to vertical gratings shown by vertical astigmat, MC, is in accord with the lower level of binocular conditioning which he obtained (described in the previous chapter) and also with his reduced stereopsis. The reduced response to horizontal gratings, however, shown by RM is not reflected in his results for the conditioning effect, nor in his level of stereopsis, which are both similar to those of non-astigmats. This provides further evidence that the basis of the suppression of adaptation produced by a low frequency conditioning grating is concerned only with vertical components within the visual field, since reduced binocular response in the horizontal direction is not accompanied by a reduction in conditioning effect. The orientation selectivity and spatial frequency selectivity of the contrast threshold elevation effect measured for the astigmatic observers establish that these properties of the adaptation mechanism are normal.

It is suggested that the results obtained by an astigmat depend not only on the type of astigmatism, but also on the age at which the condition developed. A considerable number of subjects would be required, however, before a reliable estimate of any critical period could be determined.

Chapter 8.

SUMMARY AND GENERAL CONCLUSIONS

The initial aim of the work reported here was to determine whether a particular adaptation phenomenon, the elevation of grating threshold following adaptation to a spatially identical grating presented at a high illumination level and with high contrast could be shown to summate when two eyes, rather than just one, were adapted. No summation was found; rather, presenting identical adaptation gratings to both test and non-test eyes was found to produce slightly less elevation of test threshold than that which had previously been obtained when an adaptation grating was presented to the test eye only. This reduction was found to be independent of the wavelength of the stimulus presented to the non-test eye (the "conditioning grating" as it has been termed) and also independent of the orientation of its constituent sinusoidal bars. It is possible that the inhibitory control produced by stimulation of this eye has an electrophysiological correlate in the properties of cortical simple cells (Henry, Bishop and Coombs, 1969); by using independently applied stimuli to both eyes, it was found that the response of a simple cell to stimulation within the receptive field in its dominant eye could be much reduced by stimulation of particular regions of the non-dominant eye. In fact, an inhibitory receptive field could be determined for the non-dominant eye.

Although independent of wavelength and orientation, the reduction in the level of adaptation response produced by the addition of a conditioning grating was not totally independent of its spatial frequency. If the conditioning grating, the test-eye adaptation grating and the test grating itself were all set vertically at a spatial frequency of 7 c/°, the value of threshold elevation, Δ, observed for EW was 0.32 ± 0.03 log units. If, however, the adaptation and test gratings were kept at 7 c/°, and the spatial frequency of the conditioning grating reduced to 3 c/°, Δ dropped to 0.15 ± 0.03 log units. Further reduction in the spatial frequency of the conditioning grating resulted in a rise in Δ to the original value of approximately 0.32 log units. This significant and frequency specific reduction in adaptation response was termed "the conditioning effect". Although the magnitude of the inhibition became rather less pronounced for higher values of test and adaptation spatial frequency, the conditioning grating frequency which gave rise to maximum inhibition did not shift significantly from 3 c/°. The parametric properties of the conditioning effect were reported in detail in chapter 4. Two alternative neural pathways for transmission of the inhibitory signals found to be associated with the conditioning effect were discussed in chapter 5. The two possibilities outlined consisted of either transmission ~~either~~ by fibres of the optic nerve bundle or transmission across the interhemispheric connection made via the callosal fibres. Further investigation into these experiments as undertaken by observers with a relevant and clinically documented anomaly, such as a split brain, could well provide evidence as to which proposal is the more likely. Possible functional roles for the conditioning effect, in terms of both stereovision and a mechanism responsible for lining up the two halves of the visual field were also discussed in chapter 5.

Further experiments were carried out by two observers who, through having once had congenital strabismus, were completely stereoblind. Neither of these observers showed any conditioning effect. This cannot, however, be taken as direct evidence that the two phenomena are related since stereoblindness has been found to reduce or remove other binocular interactions not specifically associated with stereovision (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1974).

If the mechanism for the conditioning effect was associated solely with the lining up of the two halves of the visual field, as suggested earlier, it would be expected that observers, such as the two stereoblind subjects, who obtained no conditioning effect, would also experience difficulties in lining up visual images which lay across the vertical midline. No such difficulties, however, were encountered.

The conditioning experiments were also performed by a second group of anomalous observers: five astigmats, three of whom perceived vertical lines with difficulty and two who were astigmatic in the horizontal direction. The horizontal astigmats obtained a level of conditioning effect equivalent to that of non-astigmatic observers: of the vertical astigmats, one obtained no suppression at all, one showed conditioning at a level about half that of non-astigmats, whilst the results of the last observer showed the full conditioning effect. These observations suggest that the conditioning effect is dependent on binocular response of cortical units to lines only in the vertical meridian. Horizontal astigmatism does not seem to affect this vertical response. The different results shown by the vertical astigmats can possibly be attributed to the age of onset and the severity of the astigmatism; the earlier age at which the anomaly developed, the less the conditioning effect which that subject showed.

The experiments were extended to assess the binocular response of the astigmats in more detail. Interocular measurements were taken by each observer on the transfer between the two eyes of the threshold elevation effect. The experiments were repeated for pairs of test and adaptation gratings presented at different orientations. Again the results were found to correlate with both the nature of the astigmatism and the age of onset. One observer whose horizontal astigmatism developed at a comparatively late age showed the same degree of interocular transfer over all angles. The second horizontal astigmat showed preferential transfer in the vertical direction (the direction he perceived most clearly) whilst one of the vertical astigmats showed more transfer in the horizontal direction. Both these subjects had been diagnosed as being astigmatic at the same age - about

6 years. A second vertical astigmat who had apparently not needed optical correction until he was 10 years old, showed interocular transfer at approximately the same level over all orientations. The third vertical astigmat showed no interocular transfer at all; this subject had worn cylindrical lenses since he was three years old.

The measure of binocular response provided by these experiments was closely related to the results of the conditioning experiments. It was not possible, however, to assign a definite limit to any critical period of visual development, such as that which has been indicated by electrophysiological experiments in kittens (e.g. Blakemore and Cooper, 1970; Hirsch and Spinelli, 1970) because of a lack of accurate clinical data and also because of the limited number of observers. A correlation was made, however, between the binocular responses, as measured by both the conditioning effect and the interocular transfer of the threshold elevation effect, and the level of stereopsis which the subjects displayed for a series of random dot stereograms (Julesz, 1971).

Although two of the astigmats have shown preferential interocular transfer of adaptation for gratings oriented along their respective non-astigmatic meridians, no such preferential adaptation was found in a series of monocular experiments, where both adaptation and test gratings were presented to the right eye, and Δ determined as a function of the orientation of the gratings. This would indicate that only binocular response is affected by astigmatism, whilst monocular response, determined in relation to adaptation phenomena, remains unimpaired. Monocular acuity measurements have shown, however, that astigmats can acquire residual astigmatism which results in reduced acuity for lines oriented along the relative meridian which cannot be compensated for by optical means (Mitchell, Freeman, Millodot and Haegerstrom, 1973). This would imply that the basis for the reduced acuity was neural.

In addition to the experiments concerning the conditioning effect, an investigation was made into the orientation and spatial frequency characteristics of the threshold elevation effect as displayed by the astigmats. These characteristics have been shown to be extremely selective for observers with normal vision (Blakemore and Campbell, 1969a and b; Gilinsky and Doherty, 1969) and thus provide evidence for shape-sensitive cortical units. It seemed possible that astigmatism might impair the orientation or frequency selectivity, perhaps making the tuning response characteristics broader than those of observers with normal vision. Results of the experiments showed, however, that although the maximum threshold elevation obtainable for spatially identical gratings, presented either monocularly or interocularly, was subject to observer differences, the widths of the spatial frequency tuning curves and the orientation specificity data were not fundamentally different either from those of other astigmats, or, indeed, from observers with normal vision.

Chapter 9.

SPATIAL FILTERING EXPERIMENTS

In the following chapters, a series of experiments are described which utilize spatial filtering of the images of a series of visual stimuli. The purpose of the experiments was to determine how modification of the spatial frequency composition of the different images affects an observer's ability to recognize and differentiate these different images. The experiments were performed with the aid of two Fourier transform lenses mounted on a spatial filtering bench and a number of concentric binary filters, which were introduced into the diffraction plane of the image.

Fourier Theory as applied to Optical Systems

In 1946, Duffieux showed that the Abbé theory of the image formation of coherently illuminated objects could be restated in terms of Fourier analysis. He also developed a corresponding theorem for incoherently illuminated objects. His only assumption was that the diffracting aperture was the Fourier transform of its Fraunhofer diffraction pattern. Subsequently, a general theory of image formation was produced (Hopkins, 1951, 1953). Before Fourier theory can be applied to a particular system, the relationship between the input and output of the system must be linear. The two main conditions of linearity are: (i) superposition, and (ii) stationarity.

(i) superposition:

If the input to a system varies with location (x) and is denoted by $g_1(x)$, and the output is denoted by $a_1(x)$, then the relationship between these quantities may be represented by:-

$$g_1(x) \longrightarrow a_1(x)$$

If a different input, $g_2(x)$ gives rise to an output $a_2(x)$:

$$g_2(x) \longrightarrow a_2(x)$$

then superposition states that:-

$$g_1(x) + g_2(x) \longrightarrow a_1(x) + a_2(x)$$

(ii) stationarity:

A displacement x' of an input variable results only in a corresponding displacement in the associated output variable, i.e.

$$g(x - x') \longrightarrow a(x - x')$$

The superposition requirement is satisfied by an optical system since superimposing intensities in the image plane has the effect of linear addition of the intensities. The principle of stationarity requires the image of a point source to be the same for all points within the object. In practice, a small region of the image is considered and the aberrations of the entire image are taken as being the same as for this small region; this approximation has been shown to be justified for corrected optical systems (Hopkins, 1962).

A schematic two-dimensional optical processing system in which the spatial frequency content of an image can be modified is shown in fig. 1. The object transparency Ob located in the object plane of lens fl_1 is illuminated by a collimated coherent beam. The spatial frequency content of the object is displayed in the diffraction pattern located in the Fourier plane fp of lens fl_1, situated at a distance of f_1, the focal length of this lens, away from it. It is in this plane that filters are introduced to modify the final image. A second lens fl_2, distance f_2 (focal length of the second lens) away from the Fourier plane, refocusses the diffraction plane to form the image, which is located in the plane ip (see fig. 1).

The two-dimensional amplitude distribution in the Fourier plane is defined by the spatial frequency coordinates l and m, and is denoted by U(l,m). Similarly, the amplitude distribution in the object plane is defined by distance coordinates x and y, and is denoted by A(x,y). These two quantities are related by an inverse Fourier transform such that:-

$$U(l,m) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} A(x,y) \exp\left\{-2\pi i(lx + my)\right\} dxdy \qquad (1)$$

The spatial frequency coordinates l and m can be defined in terms of their respective true distance coordinates, α and β, by the relations:-

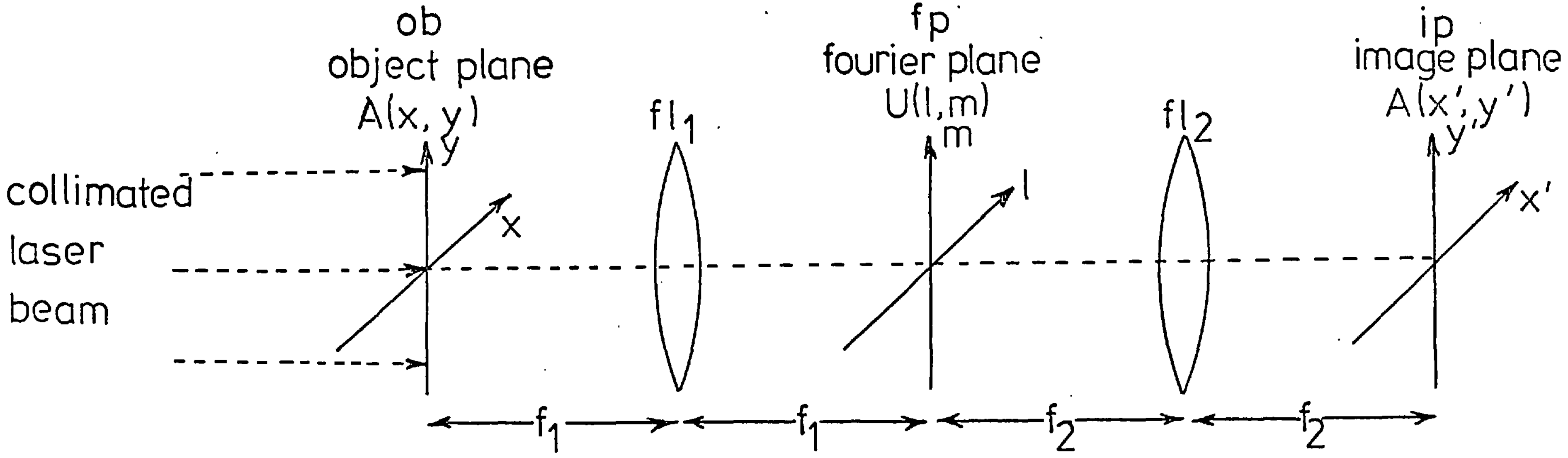
$$l = \alpha/\lambda f_1 \qquad \text{and} \qquad m = \beta/\lambda f_1 \qquad (1a)$$

where λ is the wavelength of the monochromatic illumination and f_1 is the focal length of lens fl_1 (fig. 1).

Consider now that the amplitude distribution in the spatial frequency plane is modified by a spatial filter located in this plane with amplitude transmittance defined by t(l,m). The amplitude distribution U'(l,m) over this plane after filtering is given by:

$$U'(l,m) = U(l,m).t(l,m) \qquad (2)$$

The final filtered image formed by lens fl_2 (fig. 2) is located in the back focal plane of this lens and its amplitude distribution A'(x'y') in terms of the distance coordinates, x' and y', in the image plane, is given by the Fourier transform of the filtered amplitude distribution in



Schematic diagram of a two-dimensional spatial filtering system

fig.1

the spatial frequency plane U'(l,m), i.e.

$$A'(x',y') = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} U'(l,m)\exp\left\{2\pi i(x'l + y'm)\right\}\, dl dm \qquad (3)$$

Substitution of equation (2) into equation (3) gives:

$$A'(x',y') = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} U(l,m)t(l,m)\exp\left\{2\pi i(x'l + y'm)\right\} dl dm \qquad (4)$$

If after modification by a spatial filter, a point source were imaged by this system the image amplitude distribution T(x',y') of the point source can be defined in terms of the filter function t(l,n), i.e.

$$T(x',y') = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} t(l,m)\exp\left\{2\pi i(lx' + my')\right\} dl dm$$

This distribution can be used to rewrite equation (4) in terms of spatial coordinates which is expressed by the convolution integral:

$$A'(x',y') = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} A(x'_0,y'_0)T\left\{(x' - x'_0)(y' - y'_0)\right\} dx'_0 dy'_0$$

where x_0 and y_0 are dummy integration variables. (A rigorous description of the convolution theorem is given in Bracewell (1965), chapter 3). The ratios of the variables x and y in the object plane and x' and y' in the image plane are directly proportional to the magnification of the optical system. This is defined by the ratio $-f_2/f_1$ of the focal lengths of two lenses fl_1 and fl_2 respectively (fig. 1). In the apparatus used in the present experiments, the focal lengths of the two lenses are equal. Thus:-

$$x'/x = y'/y = -f_2/f_1 = -1.$$

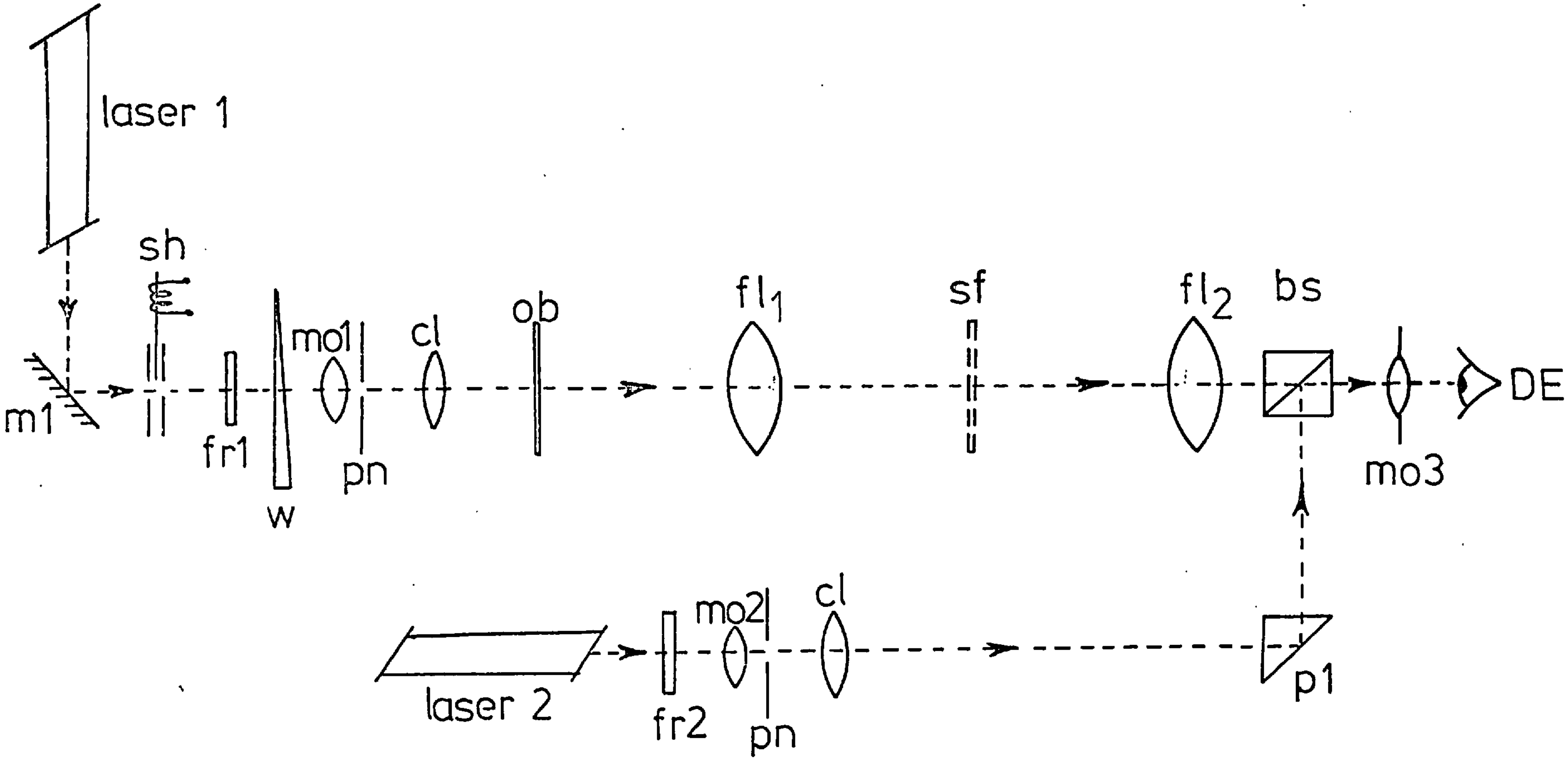
The intensity distribution I(x'y') in the image plane is given by the square of the modulus of the image amplitude distribution A'(x',y'), i.e.

$$I(x',y') = |A'(x',y')|^2$$

Apparatus

A schematic diagram of the experimental apparatus is given in fig. 2. The choice of the spatial filtering lenses, fl_1 and fl_2, is very critical, since these lenses must have a very high level of correction of aberrations. Lens systems with up to six elements for use in optical data processing have been described (e.g. Blandford, 1970). The main disadvantage of a system with such a large number of elements is the increased amount of "speckle" which arises from interference and scatter from both dust particles and the optical surfaces when illuminated by coherent light. Wynne (1974, a and b) described a number of Fourier transform lenses, consisting of only two elements which give a level of aberration correction comparable to that of the multi-element system. The two lenses fl_1 and fl_2 (fig. 2) which were used in these experiments were identical and of the cemented doublet type described by Wynne (1974b). The aberration curves for these lenses are reported in the same paper. In order to reduce the overall length of the apparatus, the lenses were constructed by I.C.OS to have a focal lengths of 50 cms. rather than one metre as specified in the original design.

Two helium-neon lasers (wavelength = 632 nm) (Spectra-Physics, type 120) are used as light sources for the equipment; laser 1 (see fig. 2) provides the spatial filtering channel and laser 2, the background channel. The beam of laser 1 is focussed by a x10 microscope objective, mo1 on to a



Schematic diagram of spatial filtering bench

fig. 2

pinhole pn (25 µm diameter). The emergent beam is collimated by the lens cl, thus providing uniform illumination over the object transparency, ob, which is located in the back focal plane of the Fourier transform lens, fl$_1$. The object transparencies themselves are discussed in more detail later in the chapter. The back focal plane of lens fl$_1$ and the front focal plane of lens fl$_2$ are arranged so as to be coincident and thus provide the Fourier transform plane where the diffraction pattern can be modified by the introduction of a filter, sf, as shown in fig. 2. The filters took the form of a series of mounted transparencies which will be described later in the chapter. The filtered diffraction pattern is refocussed by transform lens fl$_2$ and the final image is viewed by the observer through a x10 microscope objective, mo3.

All the experiments were performed monocularly with the observer viewing the images through his dominant eye (DE in fig. 2). This is defined by the eye the individual observer would choose to perform monocular detection tasks. The reason for using this eye alone arose from the discomfort experienced by the observers if they were obliged to use their non-dominant eye for prolonged detection experiments. The observer's head was stabilized by means of a dental bite bar attached to the bench.

A uniformly illuminated background field was superimposed on the final image; this was supplied by laser 2 (a helium-neon laser). The beam from laser 2 was focussed by a x10 microscope objective, mo2 (see fig. 2), on to a 25 µm pinhole pn. The beam was then collimated by the lens cl and after reflection from prism p1, superimposed on the image channel by beam splitter bs. The observer viewed the image and the background field through the microscope objective mo3. The microscope objective was mounted on a transverse slide by means of which fine lateral adjustments could be made by the observer to focus ~~precisely~~ the final image precisely.

The background field was presented to the observer throughout the course of the experiment. The filtered image, however, was presented for a period of $\frac{1}{2}$ second only, the presentation period being controlled by an electromagnetic shutter, sh, (fig. 2) attached to a time switch operated by the experimenter.

The illumination levels of the image and background channels were controlled by neutral density filters (fr1 and fr2 respectively in fig. 2). Fine adjustments of illumination level in the image channel were made by means of a neutral density wedge, w. Details of the calibration of both the wedge and the neutral density filters were given in chapter 2. The light levels at the exit objective, mo3, were monitored by the photocell attachment constructed by Burton (1973) and again described in chapter 2.

All the optical components were mounted in metal saddles which were, in turn, fastened securely to a rigid optical bench.

Experimental Methods

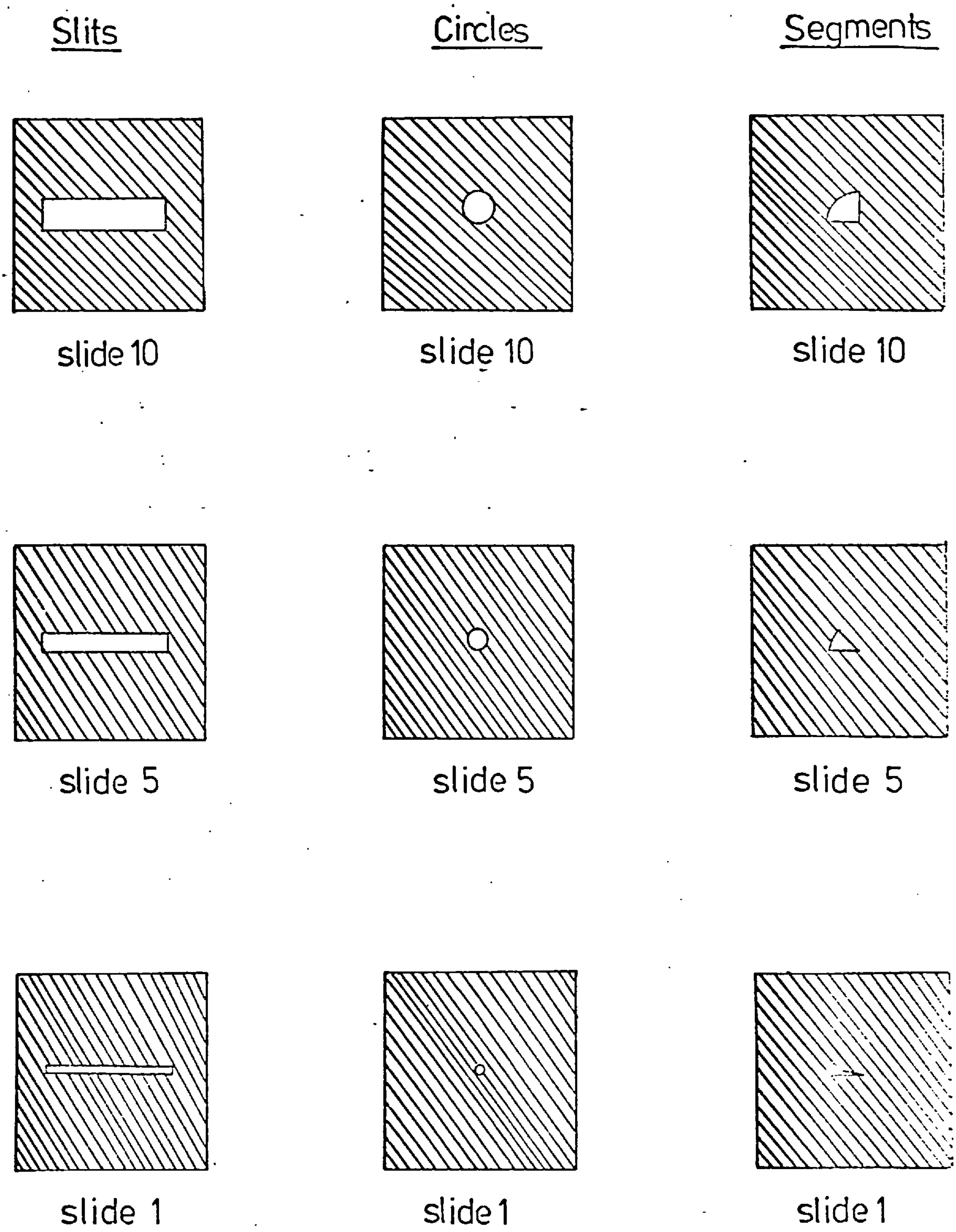
The experiments which were undertaken can be divided into two categories: (a) those performed with image stimuli presented at suprathreshold illumination levels and (b) those where the images were presented at threshold.

(a) Suprathreshold experiments

In these experiments, the object slides belonged to one of three series, each based on a particular geometric shape. Each series consisted of ten slides formed by parametric variation of the basic shape. The three geometrical shapes were:

(i) a slit of a constant length but variable width,

(ii) a circle of variable diameter,



Examples of object transparencies
fig. 3

(iii) a segment of a circle of constant radius, but variable angular subtense.

The object slides were produced photographically using "Kodalith", a very high contrast film which registers only binary information. A sheet of exposed Kodalith placed in the object plane (ob, fig. 2) was found to be sufficiently dense to prevent the collimated laser beam from being detected by the observer. The transparencies were carefully centred in the holders and mounted between two sheets of glass with a film of microscope oil introduced either side of the transparency. This "oil-gating" technique is designed to reduce phase differences which may arise across the surface of the transparency if it is left as an air interface.

The narrowest of the slit slide series was 0.15 mm wide and 25 mm long, and designated no. 1. The other nine slides consisted of slits whose widths changed in increments of 0.05 mm, whilst remaining constant in length. Thus the widest slit, slide no. 10, measured 0.6 mm x 25 mm. The series of circular slides covered the same range with slide no.1 representing a circle of diameter 0.15 mm and slide no. 10, a circle of diameter 0.6 mm. The third slide series showed ten segments of circles, all with a radius of 0.6 mm. The smallest segment, slide no. 1, had an angular subtense of 9°; the largest segment, slide no. 10 had an angular subtense of 90°. The intermediate slides displayed segments where the angular subtense changed in increments of 9°. In each slide series, the objects were shown as unexposed regions on completely exposed backgrounds. Slide nos. 1, 5 and 10 in each series are illustrated approximately to scale in fig. 5.

Filters

The spatial frequency filters consisted of a number of circular discs and apertures of different radii (0.15 mm - 8 mm). These were generated on microfilm using the Imperial College CDC 6400 computer. Because of the low optical density of the dark regions of the microfilm, the films were contact-printed onto Kodalith which has a much higher optical density 2.5 log units for microfilm, c.f. 4.0 log units for Kodalith). All the filters were binary, that is, the transmittance function of the filters at any point was either zero or unity. These filters were centred and then oil-gate mounted in the same way as was previously described for the object slides.

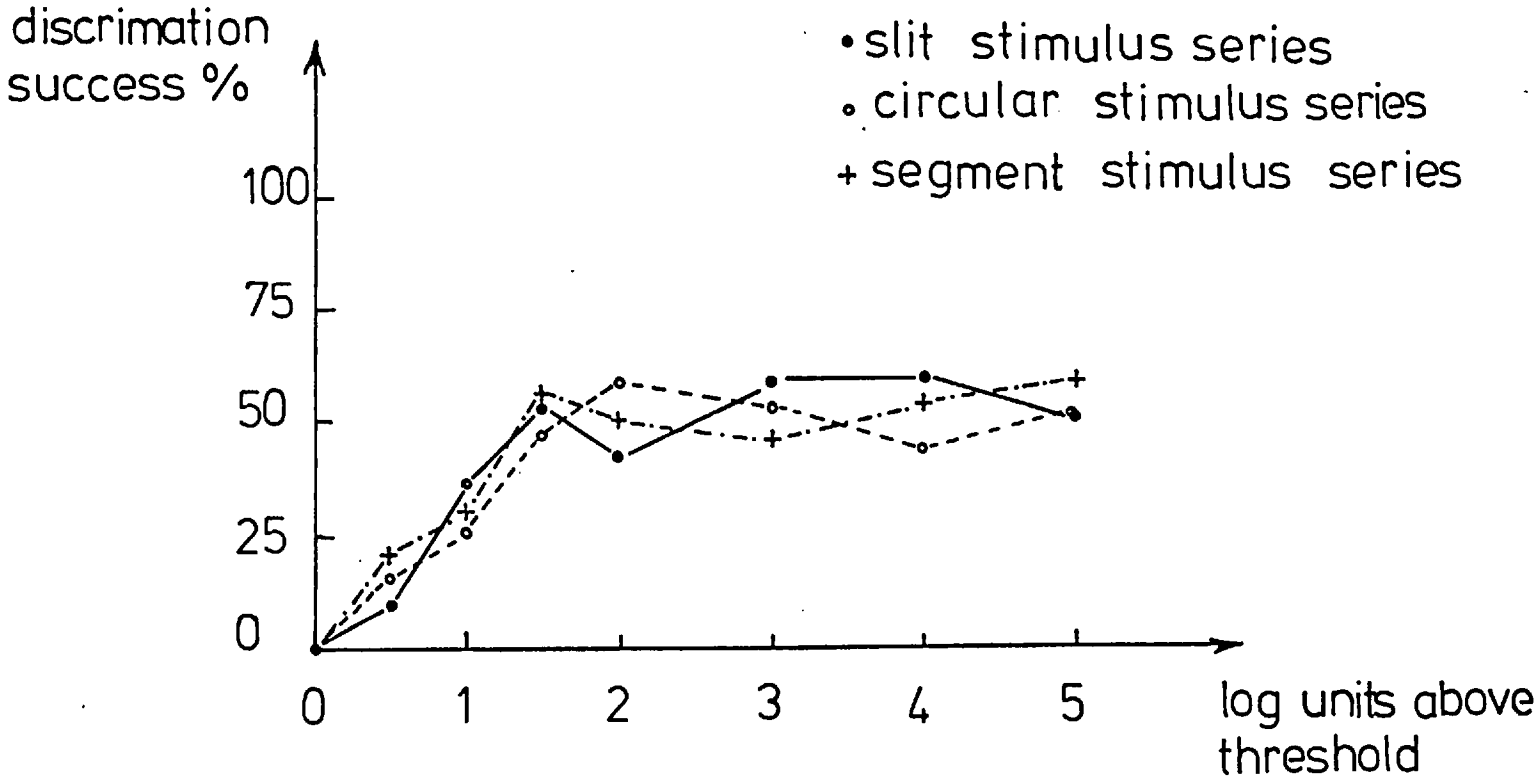
Procedure

The experimental task which the observer was asked to perform was one of discrimination between objects of a single series. The three series of objects were studied separately, although the basis of the experiment was identical for all three. The observer was shown the narrowest and the widest slit, circle or angular segment. All ten slides of a particular series were then shown to him in a random sequence of twenty presentations per slide - 200 presentations in all. The observer was asked to judge on a scale of 1 to 10, which particular slide he was being shown. The presentation time was varied in a preliminary experiment in order to determine the duration of presentation for which the observer obtained a 50% success rate, over 200 presentations, in classifying correctly the unfiltered images of the slides. A presentation time of $\frac{1}{2}$ second was found to meet this requirement. With this level of success, it was anticipated that filters inducing either enhancement or degradation of overall visual performance could be identified. After performing the experiment with no filter present, the observer repeated the 200 trials with one of the spatial filters, either disc or circular aperture, centred on the diffraction pattern located in the transform plane (sf in fig. 2).

A problem arises from filtering in this manner - the different filters are found to reduce the mean illumination level across the final image compared with the illumination level across the same image in the unfiltered configuration. For this reason, a preliminary experiment was undertaken to determine how the discrimination success rate varied as a function of the illumination level of the images. Since these illumination levels are measured in terms of log units above threshold of the image, it was necessary firstly to determine the thresholds of the ten slides in all three series. These thresholds are defined as the illumination level of the image, in the absence of spatial filtering, where the observer could just no longer see the structure of the image. The appropriate adjustments were made by inserting neutral density filters (fr1 in fig. 2) into the imaging channel. All images were presented against a constant uniform background field of illumination level 2.0 log trolands (as measured with a Holophane lumeter) provided by laser 2 of fig. 2. The threshold for the smallest object in each series (slide no. 1) was found to be not significantly different from that of the largest object (slide no. 10). 200 slide presentations of each of the three series were subsequently made with all the slides presented at the same illumination level. The experiment was repeated for a number of illumination levels and the results are given in fig. 4. These results suggest that as long as the images, filtered or unfiltered, are presented to the observer at an illumination level greater than 1.5 log units above their respective threshold levels, the results of the discrimination experiments will reflect only the quality of the images and not their mean illumination levels.

(b) Threshold measurements

This series of experiments was undertaken (in conjunction with John Barbur, an M.Sc. research student) in order to compare the results obtained for recognition of the specific geometric shapes described in the



unfiltered images ; presentation time = 0.5 secs

fig.4

previous section with those found for recognition of more general visual stimuli. The objects in this series consisted of ten photographic transparencies taken of members of Imperial College's Optics Section. All the faces were well known to the observer. Three main problems arise from the use of these more generalized objects. In the previous section, the observer was asked to discriminate between related images presented at illumination levels well above their threshold. When the slides described in this section were presented at the same illumination levels, however, the observer was able to discriminate between them with a 100% success rate, since he was able to ascribe a name to each of the faces on the slides. Thus, although a particular filter, when introduced into the diffraction plane of the images, could be shown to detract from the recognition success rates (as measured without a filter), it was not possible to identify a filter which would improve recognition. To overcome this difficulty, the measurements were carried out at approximately threshold illumination levels where the unfiltered success rates were less than 100% and would therefore allow the spatial filtering to indicate improvement as well as impairment of performance.

A second problem arises from the criterion of the threshold illumination level of a stimulus as "just-not-see", measured after the illumination has been reduced from a level where the stimulus is clearly visible. In the experiments described here, the observer was asked to apply the threshold not to the level where a general facial structure was visible, but to the level where the face was positively identifiable. It was found to be extremely difficult to make this distinction if the illumination was lowered from a level where the face was clearly visible. A much more consistent threshold was obtained by beginning with the image invisible and increasing the illumination until the observer could correctly identify the face which was being presented to him. Thus a "just-see" rather than a "just-not-see" criterion for threshold has been adopted. All the images in these threshold measurements were presented without filtering on a uniform background field of 2.0 log trolands and appropriate threshold settings were made by adjusting the neutral density filters and wedge (fr1 and w in fig. 2). The presentation period of the images at this stage was two seconds.

The third problem arises from the introduction of filters into the diffraction plane. It was shown in the previous section (fig. 4) that discrimination of a series of slides is unaffected by the illumination levels of the slides, unless these are less than 0.15 l.u. above threshold. If the slides are presented at approximately threshold levels, reductions in mean illumination levels, such as those introduced by the filters, result in considerable changes in recognition performance. Thus it was necessary to ensure that the filtered images were always presented to the observer at the same mean illumination level as their respective unfiltered thresholds. This was achieved by measuring the mean threshold illumination levels in the absence of the background field using the photocell described in chapter 2 (and Burton, 1973). Since these recordings were made only for comparison with equal light levels no calibration of the photocell was required. In the subsequent experiments when filters were introduced into the diffraction plane, the neutral density wedge (w in fig. 2) was adjusted for each of the ten slides to increase the illumination level, as recorded by the photocell, up to the level previously measured as corresponding to the threshold value. The appropriate wedge settings for the ten slides in the presence of each of the filters were noted by the experimenter.

The experimental procedure was comparable to that described in the previous section. Each run consisted of five presentations of each of the ten slides, making 50 presentations in all, arranged in a random sequence and each superimposed on a background field of 2 log trolands. The neutral density wedge was set before each presentation to the value corresponding to the threshold of the particular slide due to be presented. The presentation period of each slide was adjusted until the observer was obtaining a success rate for correct identification of approximately 50% for the 50 presentations. These presentations were made with the images at their respective threshold illumination levels (as measured for a 2 sec. presentation period) and in the absence of a filter. The duration of presentation for which the observer obtained approximately 50% successful identifications was found to be ½ second.

The unfiltered results were compared with those obtained with one of the series of filters centred in the diffraction plane (sf in fig. 2). It was therefore possible to determine how modification of the spatial frequencies of the images affected recognition performance. The filters themselves were taken from the range described earlier in this chapter (transmitting apertures and nontransmitting discs). Before each of the 50 presentations in all filtered trials, the neutral density wedge was set to the predetermined value which increased the mean illumination level of the slide due to be presented up to the level which corresponded to its threshold as measured in the absence of a filter.

Chapter 10.

SPATIAL FILTERING: RESULTS AND DISCUSSION

(i) Suprathreshold experiments

The observer in these experiments, CD, male and 20 years old, had normal vision. The experimental procedure was described in detail in Chapter 9; essentially observer discrimination of a series of ten object transparencies was determined for a number of symmetrical binary filters centred in the diffraction plane. The results were compared with those obtained for the same objects in two trials without filters, one made before and one after the measurements with the filters and for three separate series of objects. The three series of objects consisted of: (i) ten slits of systematically increasing widths and constant length, the observer being asked to judge the width of the object on a scale 1 - 10: (ii) ten circles of increasing diameters, the observer being asked to judge the diameter on a scale 1 - 10: (iii) ten segments of sircles of constant radius and systematically increasing angular subtense. The observer was asked to estimate this subtense, again on a scale 1 - 10.

200 random presentations were made in every trial, in both filtered and unfiltered configurations, 20 presentations of each slide in the series. All images were presented at 3.0 log units above their individual threshold illumination levels. Two classes of filters were tested for each series. The first class was made up of circular non-transmitting background; the radii of the discs in the filters used were: 0.15 mm, 0.17 mm, 0.20 mm, 0.25 mm, 0.32 mm, 0.35 mm, 0.5 mm, 1.0 mm, 1.5 mm, 2.0 mm, 2.5 mm, 3.0 mm, 4.0 mm, 5.0 mm, and 8.0 mm.

The second class consisted of transmitting circular apertures on a nontransmitting background; the radii of the apertures of the filters tested were: 0.25 mm, 0.5 mm, 1.0 mm, 1.5 mm, 2.0 mm, 2.5 mm, 3.0 mm, 4.0 mm, 5.0 mm and 8.0 mm. Certain limitations were placed on the filters as the laser power available in the spatial filtering channel was restricted (laser 1 in fig. 2, chapter 9). With nontransmitting disc filters of radii greater than 8 mm, or transmitting aperture filters of radii less than 0.25 mm, it was not possible to provide sufficient illumination across the final images to bring them to 3.0 log units above their respective threshold illumination levels.

During the course of each trial, the experimenter noted the size estimate given by the observer after each of the 200 presentations. At the end of the trial, the experimenter determined the number of correct responses for each of the ten slides. The procedure, as stated earlier, was to carry out one unfiltered trial before and after a filtered trial. The mean of the number of correct responses for each slide was evaluated for the two unfiltered trials, and these values compared with the corresponding values in the filtered trials. Performance was determined as the difference between the number of correct responses for each slide in the two configurations, expressed as a percentage of the twenty presentations of each of the ten slides. Thus, in the data graphs, the dotted line through the zero performance ordinate point represents the mean of the unfiltered trials. All points above this line indicate an improvement in performance in the 'filtered' trial for a particular object slide, points below the line indicate reduced performance in the 'filtered' trial. Where significant or unexpected changes in performance were found to result from the introduction of a filter, the unfiltered-filtered-unfiltered trials were repeated and a second set of data obtained.

Figs. 1a to 1j and 2a to 2o, illustrate the results of introducing the transmitting apertures and non-transmitting discs respectively into the images of the ten segment objects. Figs. 3a to 3j and 4a to 4o illustrate the results of introducing the two classes of filters into the slides of the circle series and figs 5a to 5j and 6a to 6o, the corresponding results for the slit series. Presented in this way, general trends in improvement and deterioration of performance are apparent.

For example, small transmitting apertures (radii less than 1.5 mm) are found to reduce discrimination performance for most of the objects in the three series (figs. 1a to 1d, 3a to 3d and 5a to 5d). When these experiments were repeated, notably bad discrimination performances associated with a particular slide in the first trial were not always found in the second trial, e.g slide no. 4 in fig 5c: 1st run (solid line), -40%, 2nd run (dotted line), -10%. Larger apertures (radii 2.0 to 8.0 mm) produced performances both better and worse than the unfiltered results across the ten slides in the three series (figs. 1e to 1k, 3e to 3k and 5e to 5k). It was not possible, however, to isolate specific trends in the data away from the unfiltered results for any one of the three series.

Deterioration of performance was found to result from introducing large non-transmitting discs (radius $\geq$ 4 mm) into the images of the three series (figs. 2m to 2o, 4m to 4o and 6m to 6o). This deterioration, like that resulting from introducing small apertures, is consistent with removing a large part of the spatial frequency content of the images. A series of non-transmitting disc filters (radii in the approximate range 0.15 - 1.0 mm) have been identified which, when introduced in the spatial filtering plane, resulted in consistently improved performance over the range of objects (figs. 2a to 2h, 4a to

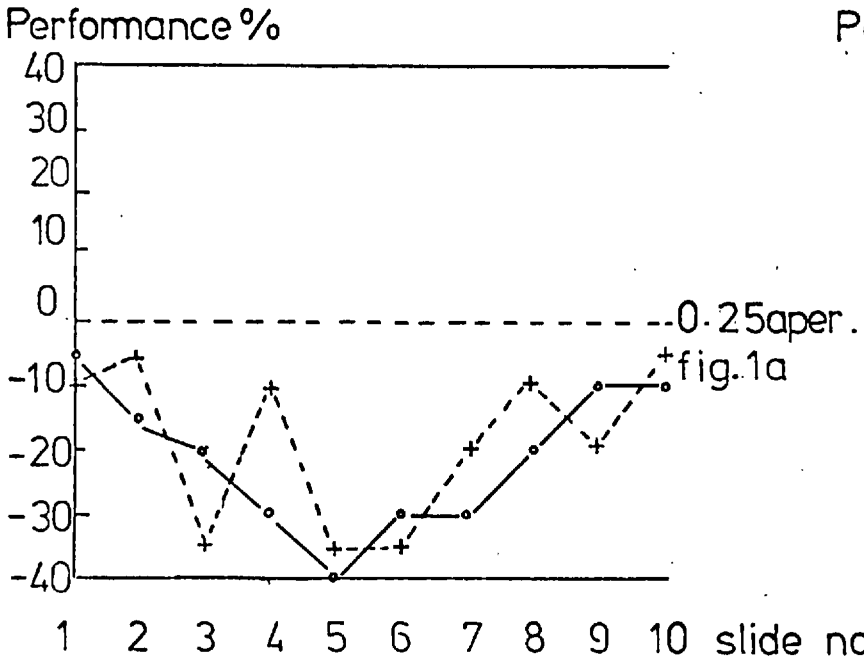


fig.1a

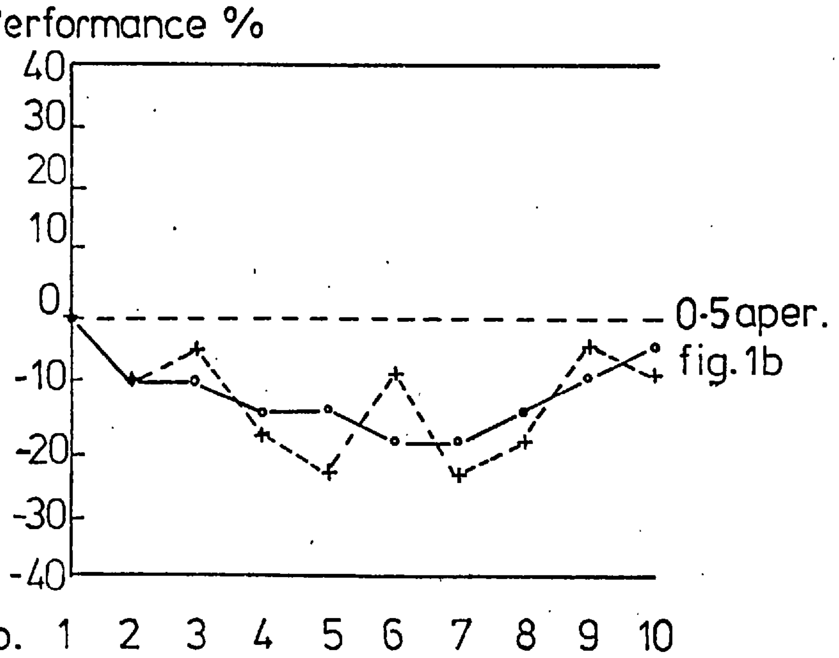


fig.1b

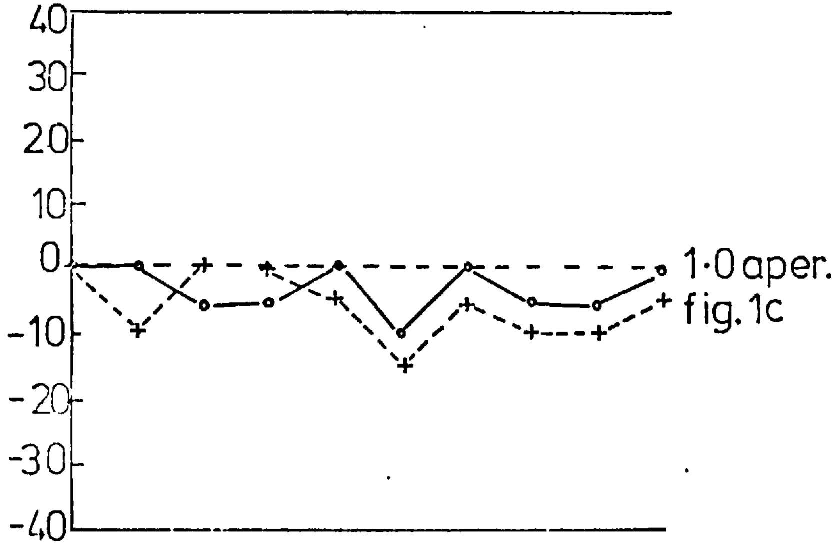


fig.1c

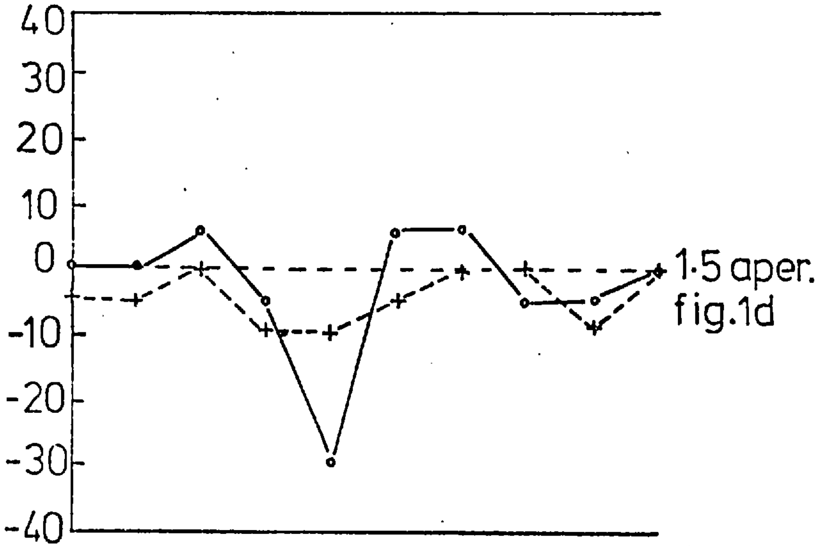
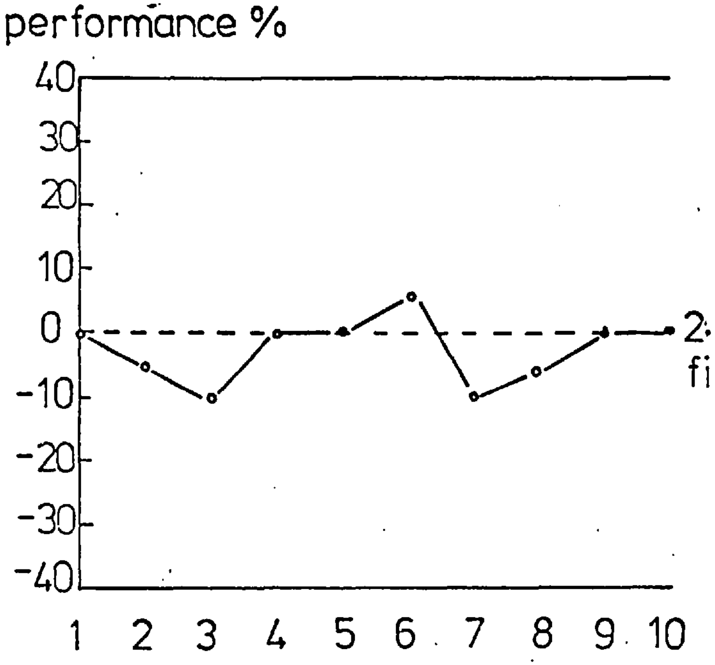
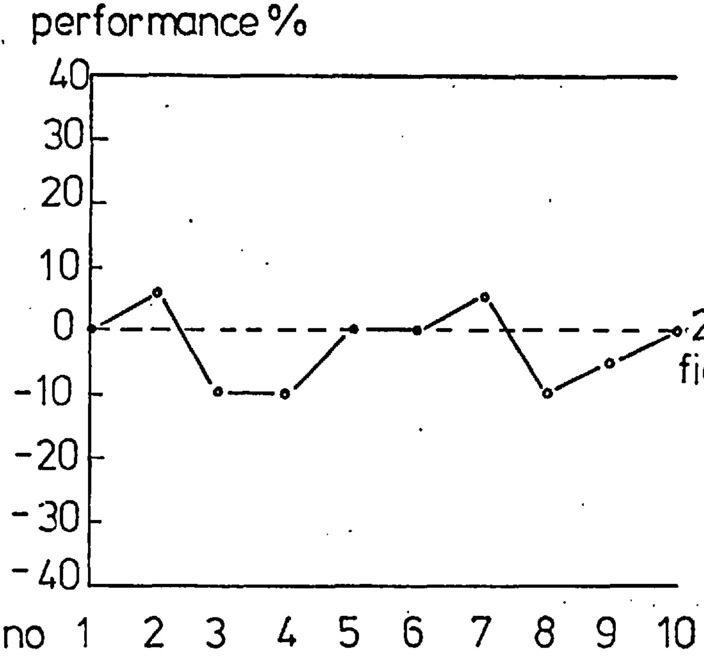


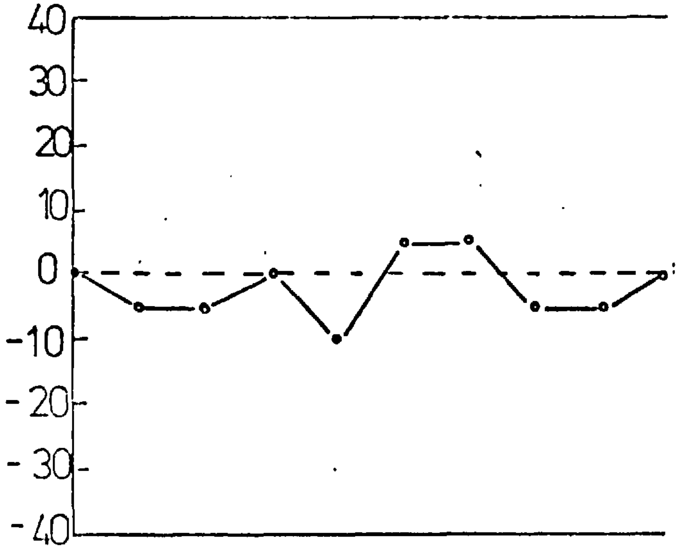
fig.1d



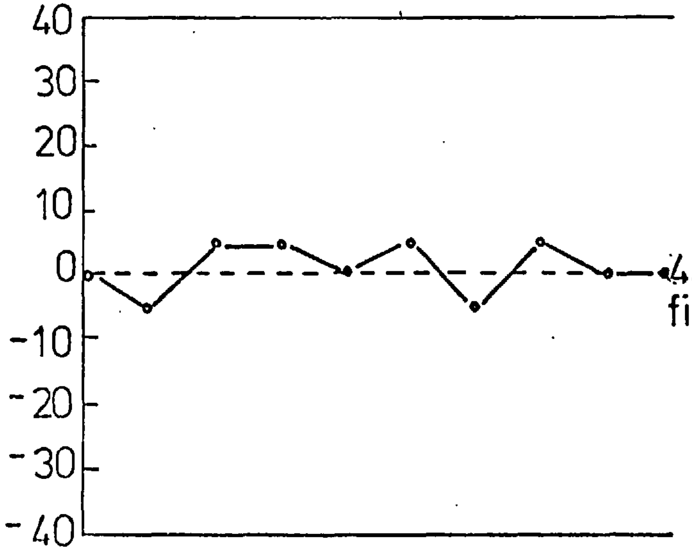
2·0. aper.
fig:1e



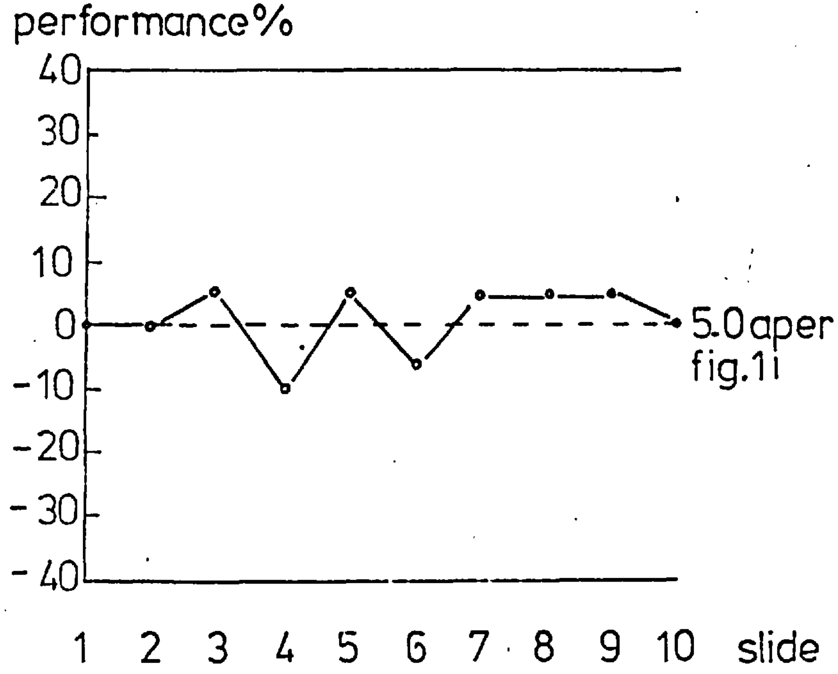
2·5aper.
fig.1f



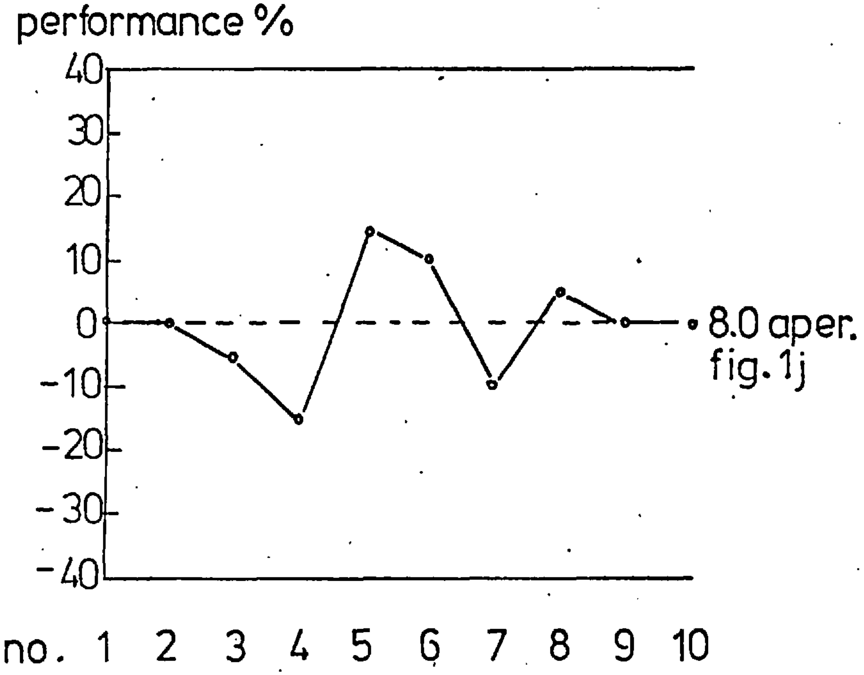
3·0 aper.
fig.1g



4.0aper.
fig.1h

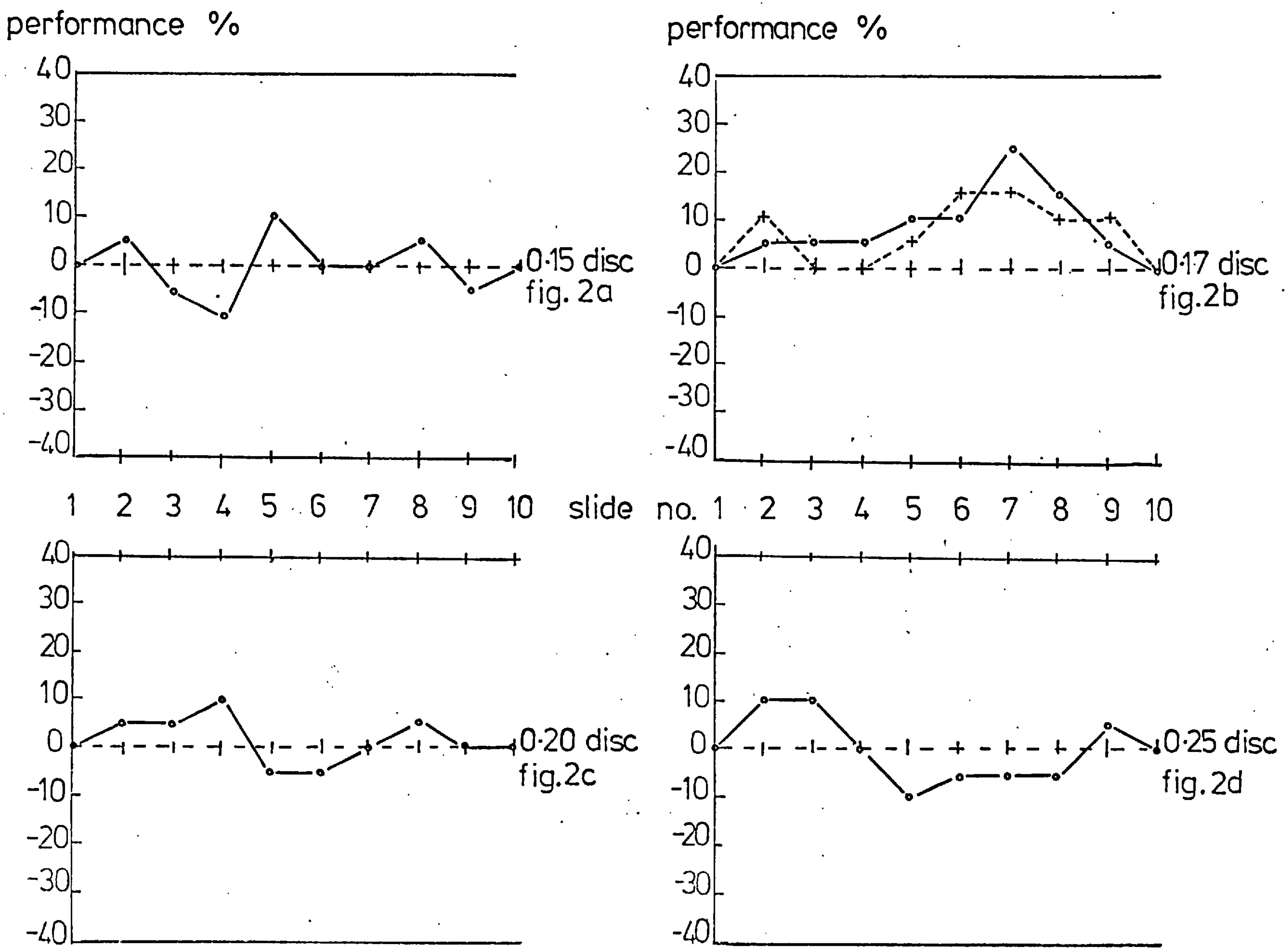


5.0 aper
fig.1i



8.0 aper.
fig.1j

Segments series



Segment series

Segment series

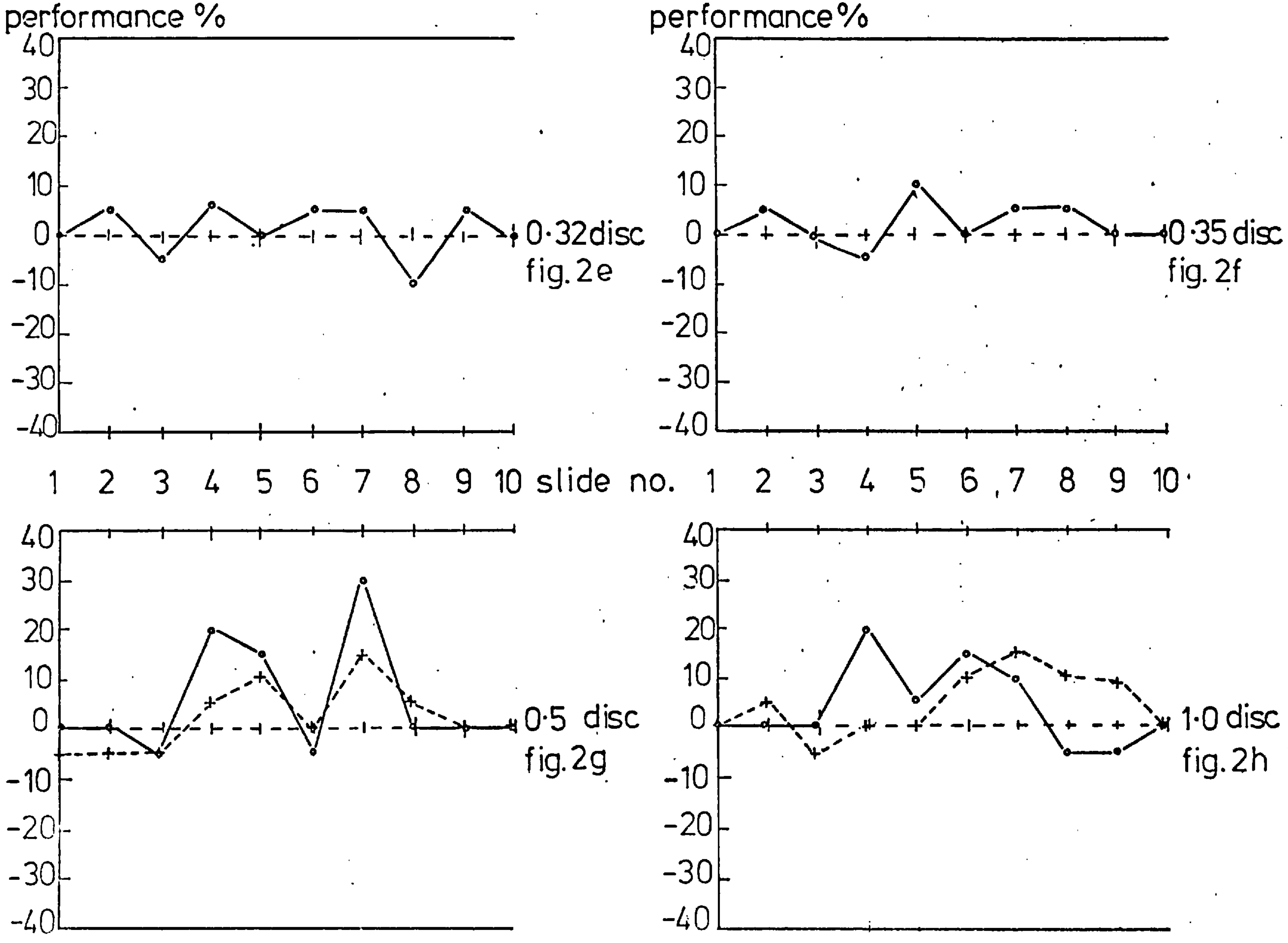
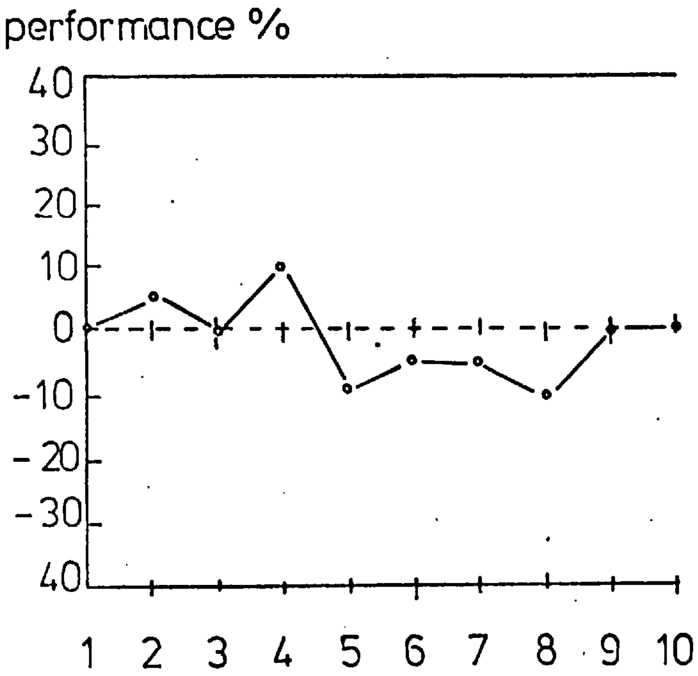


fig. 2e

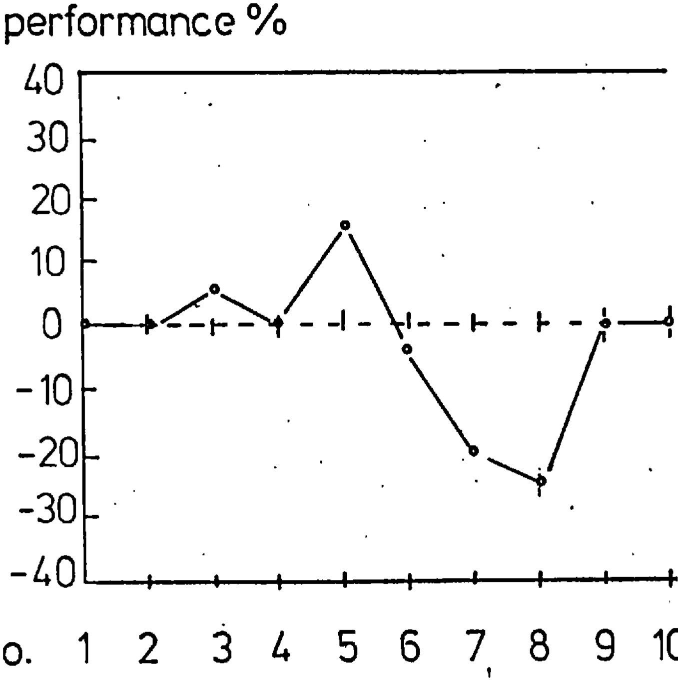
fig. 2f

fig. 2g

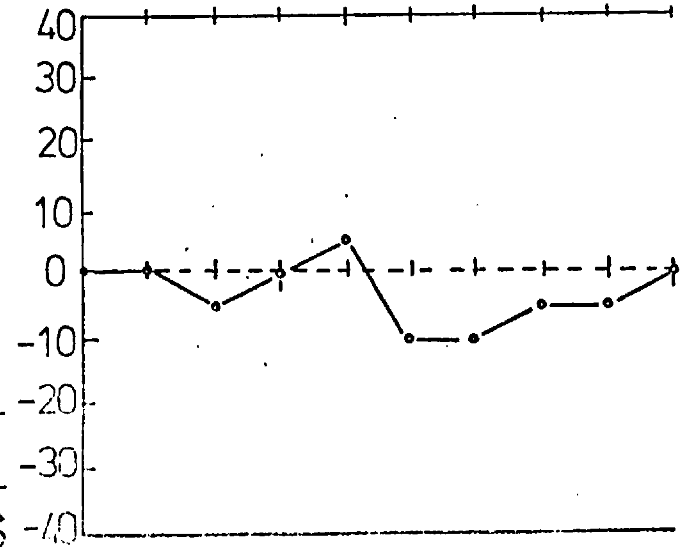
fig. 2h



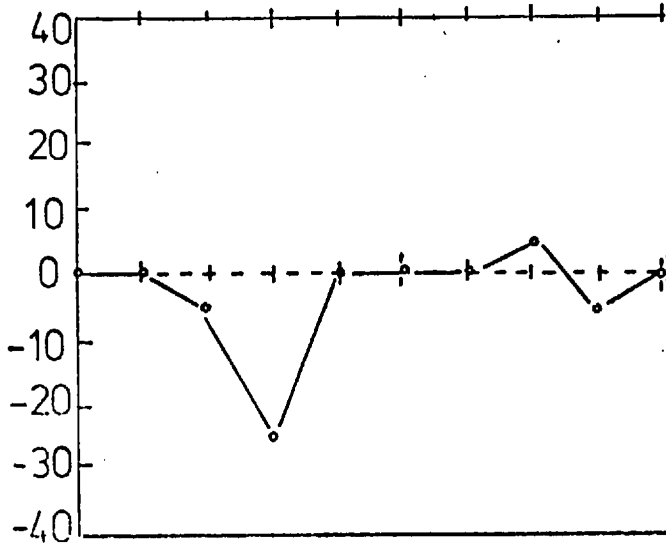
1.5 disc
fig.2i



2.0 disc
fig.2j



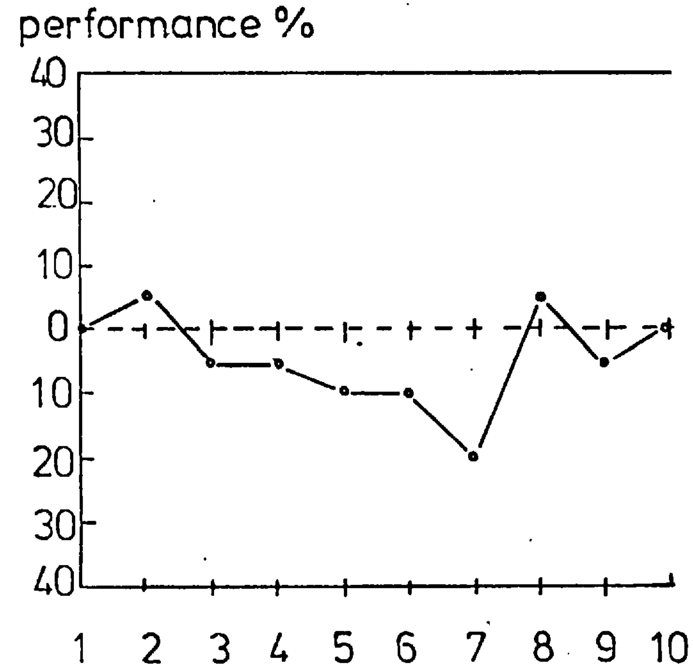
2.5 disc
fig.2k



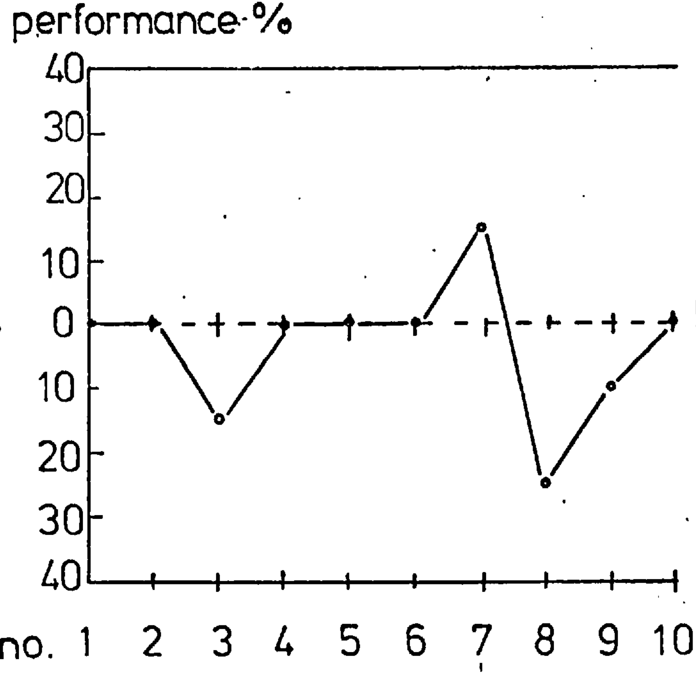
3.0 disc
fig.2l

Segment series

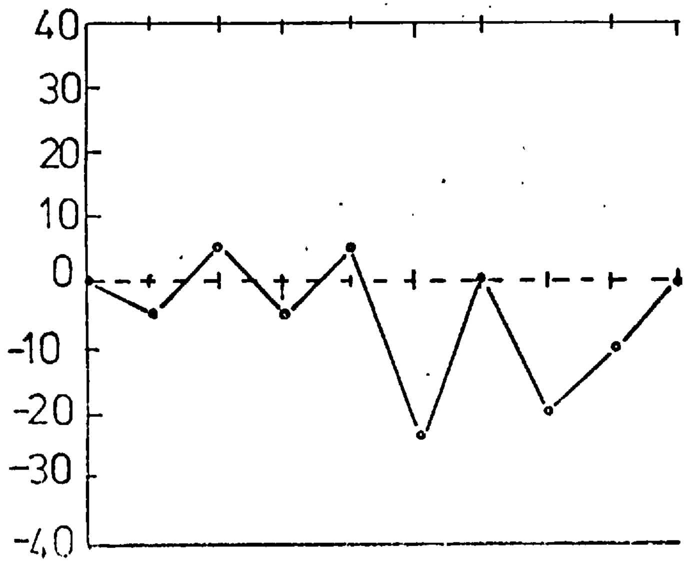
chapt.10



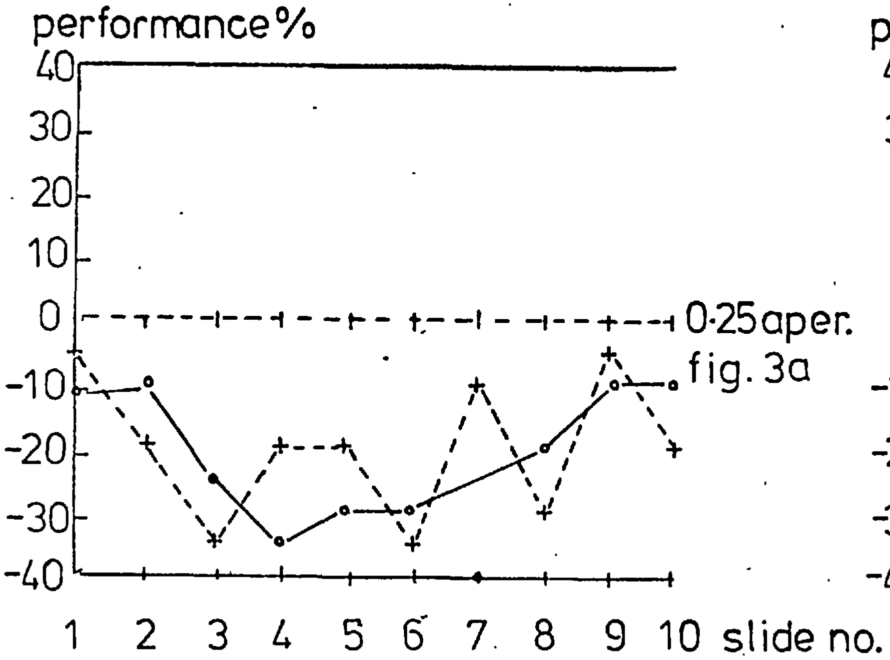
4·0 disc
fig. 2m



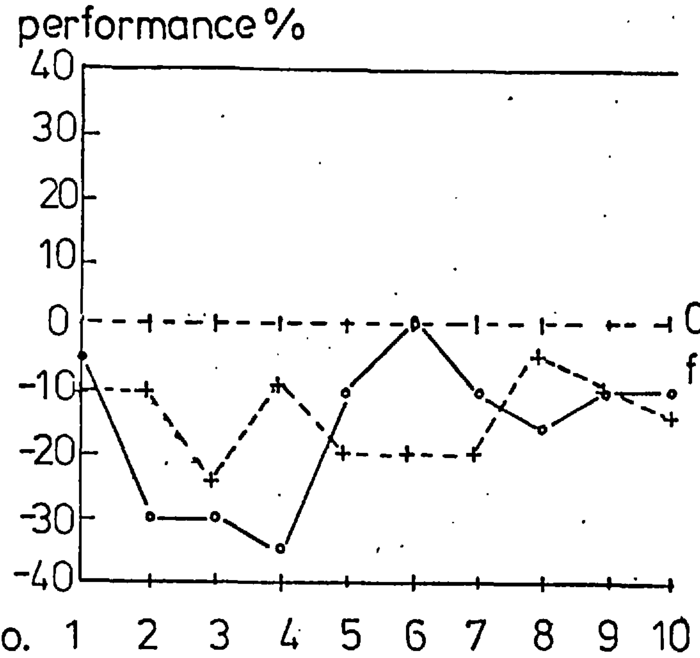
5 0disc
fig.2n



8·0 disc
fig.2o

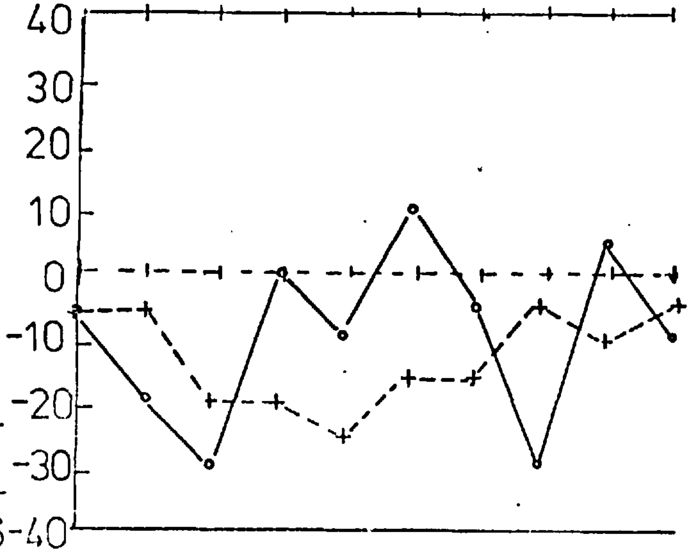


0·25 aper.
fig. 3a

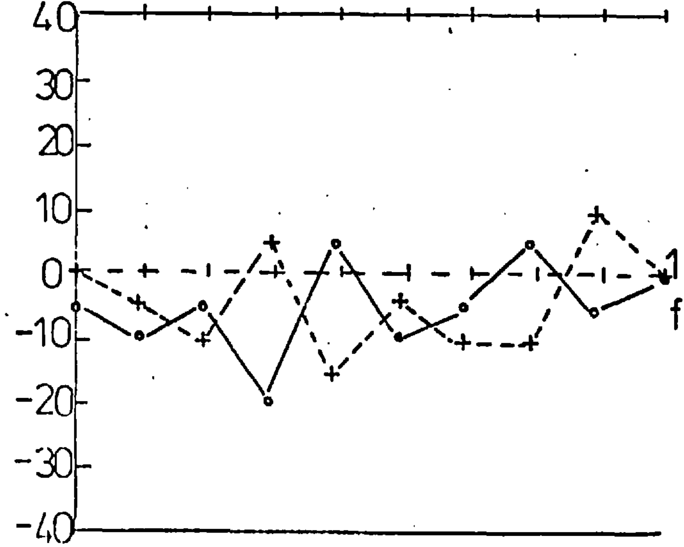


0·5 aper.
fig. 3b

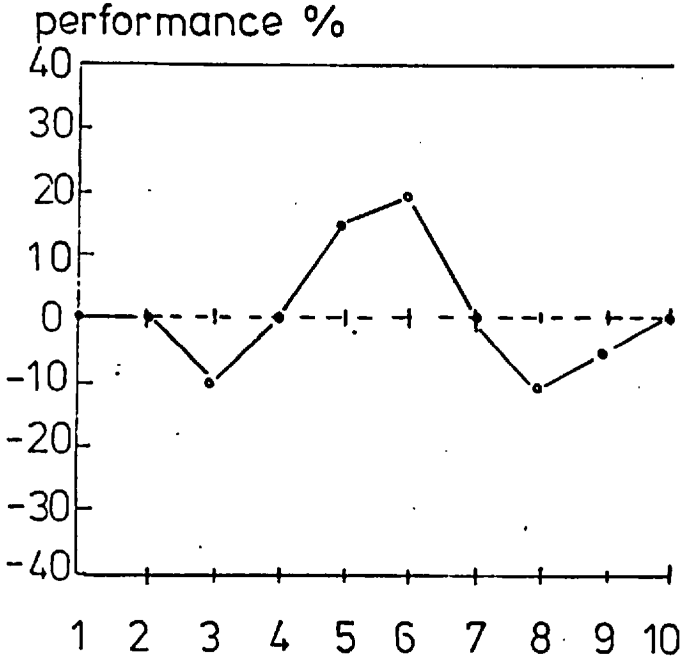
Circle series



1·0 aper.
fig. 3c

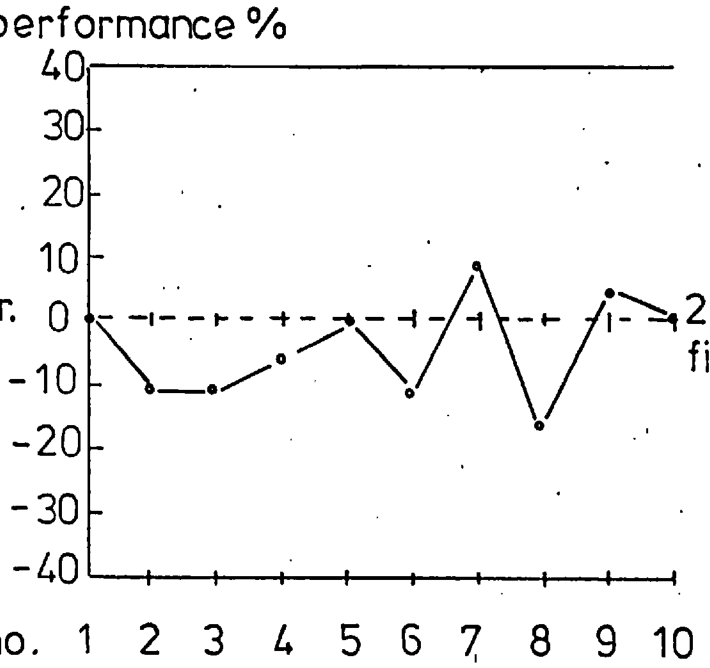


1·5 aper.
fig. 3d

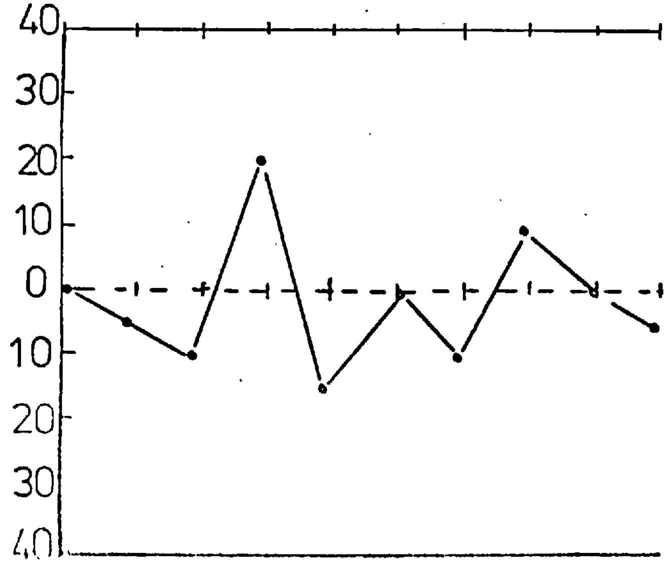


2.0 aper.
fig. 3e

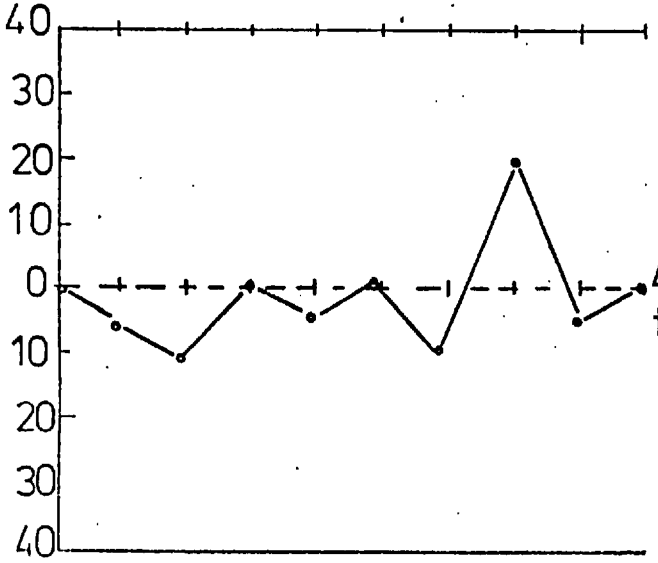
slide no.



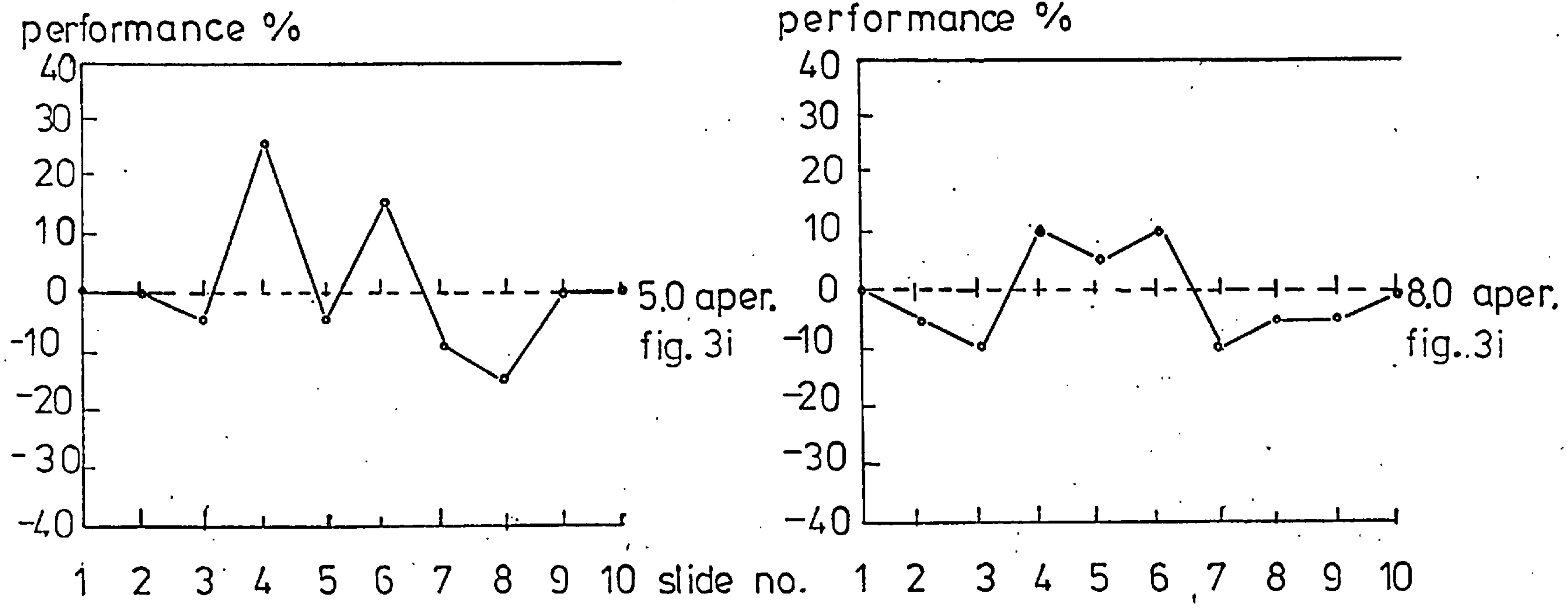
2.5 aper.
fig. 3f



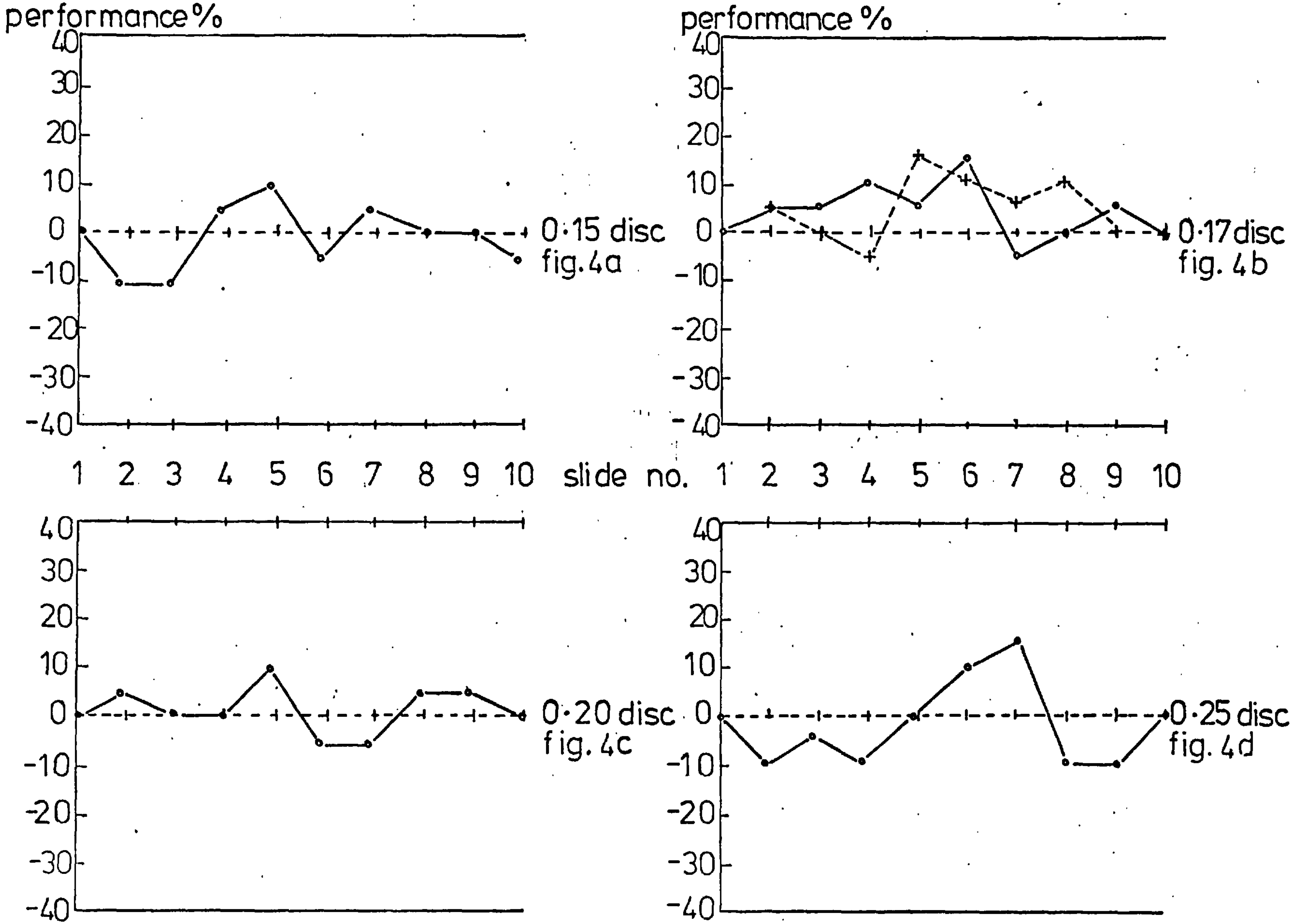
3.0 aper.
fig. 3g



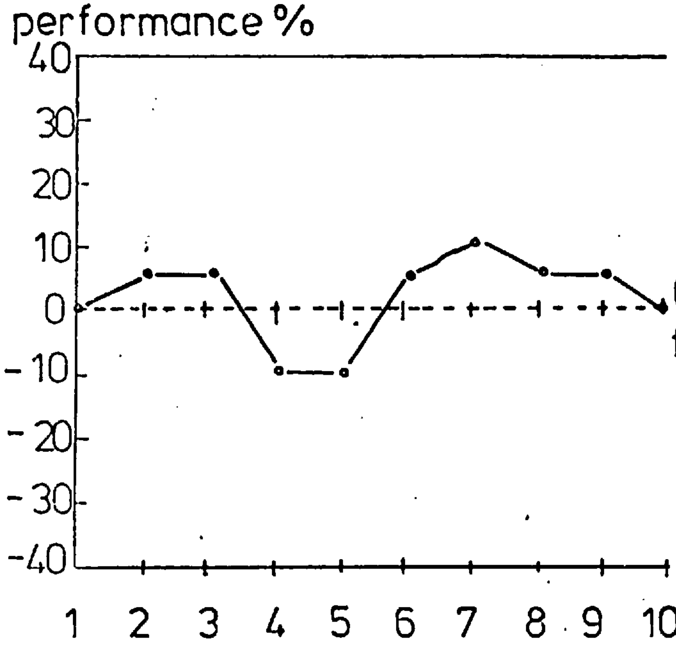
4.0 aper.
fig. 3h



Circle series

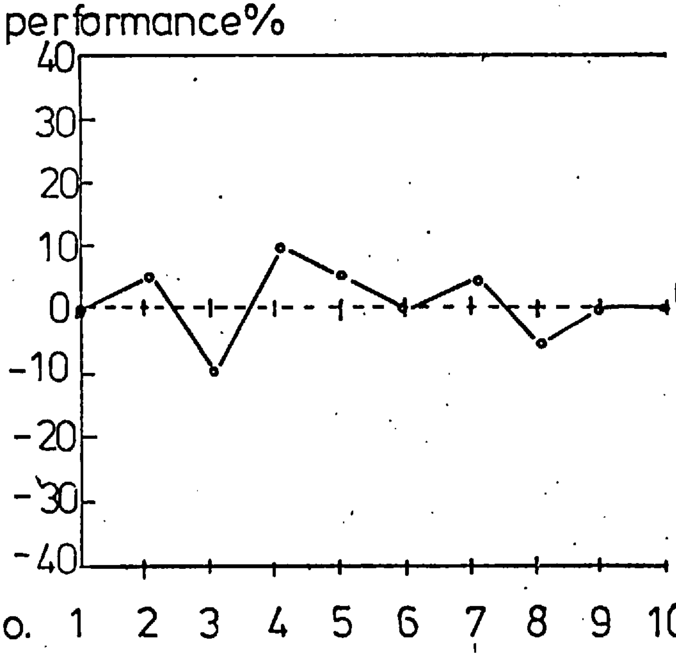


Circle series

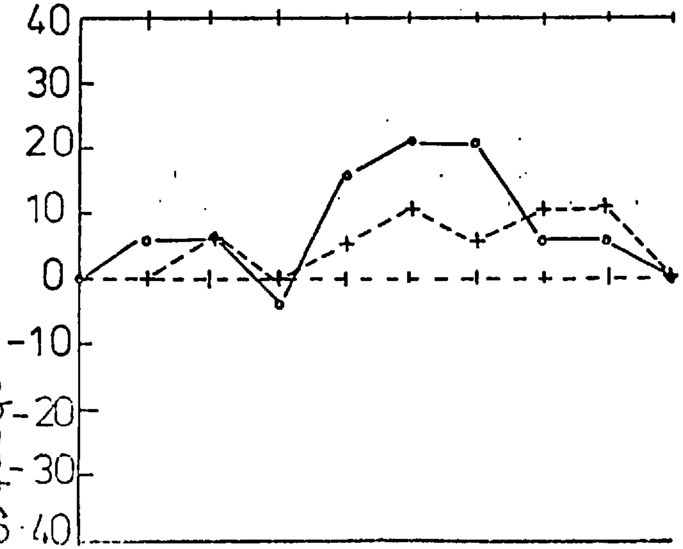


0·32 disc
fig. 4e

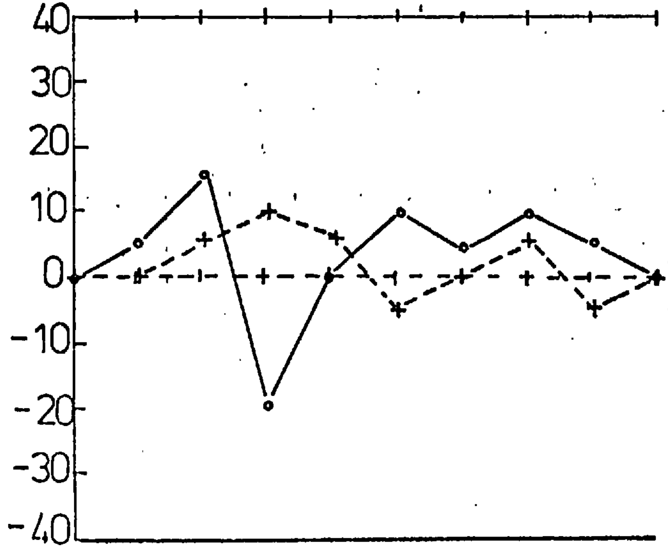
slide no.



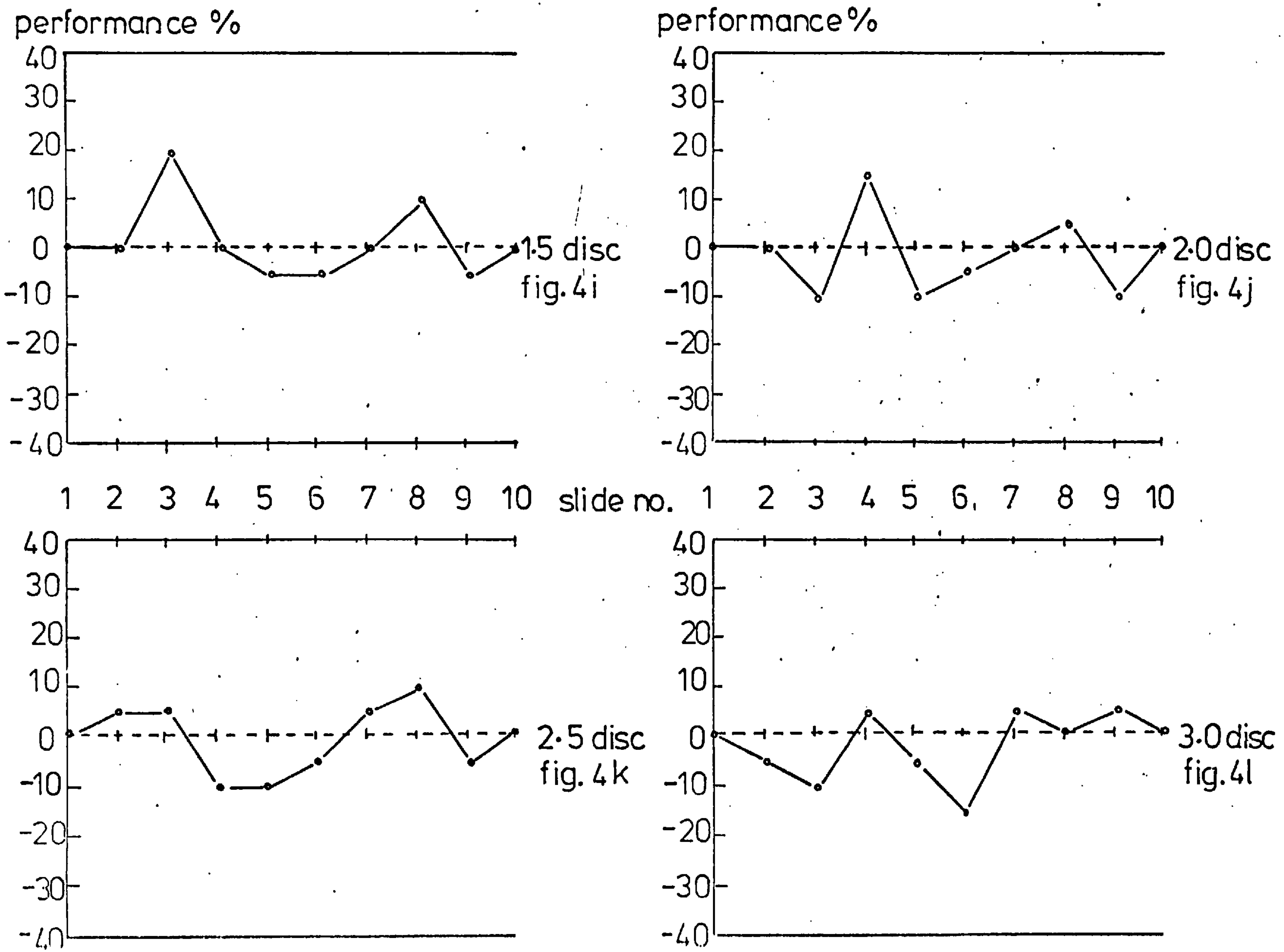
0·35 disc
fig. 4f



0.5 disc
fig. 4g

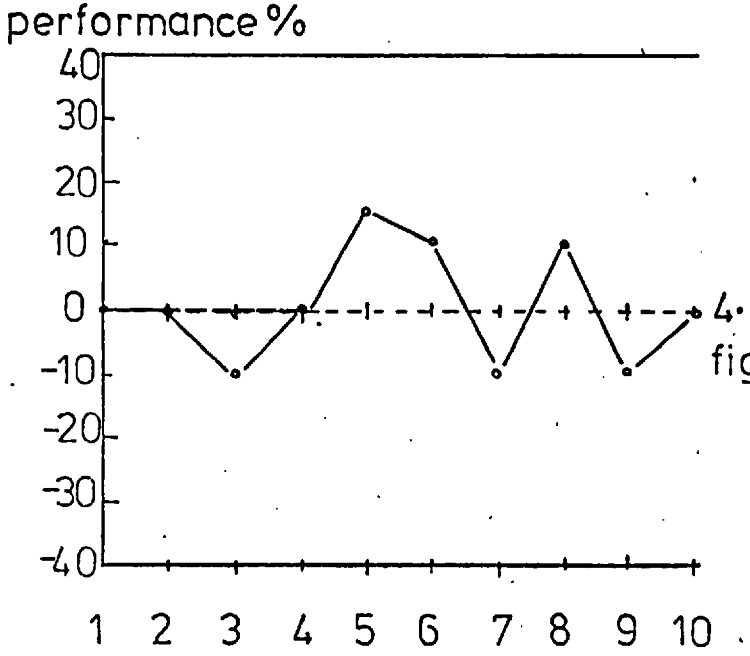


1·0 disc
fig. 4h

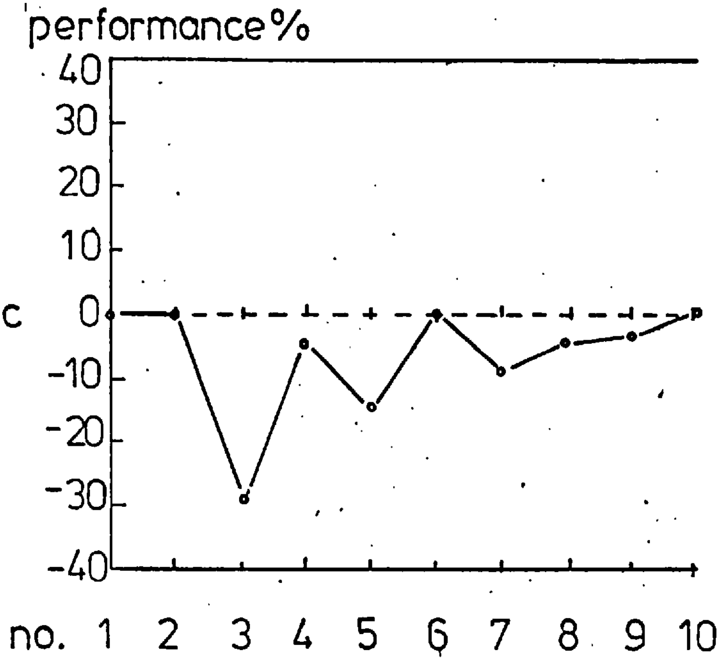


Circle series

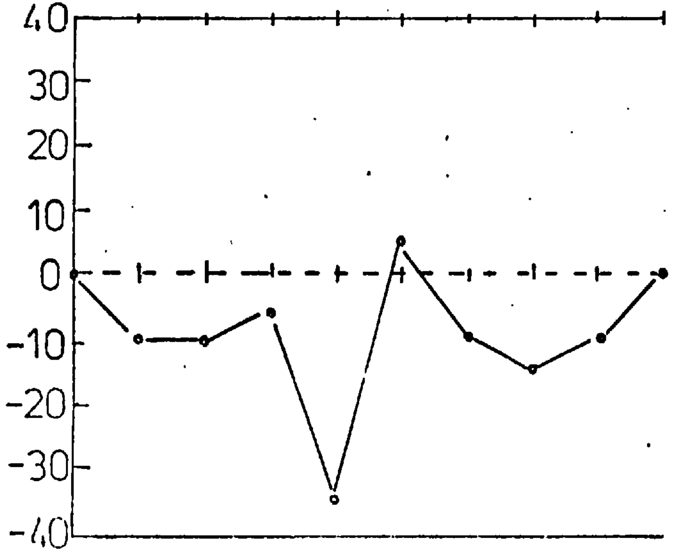
Circle series



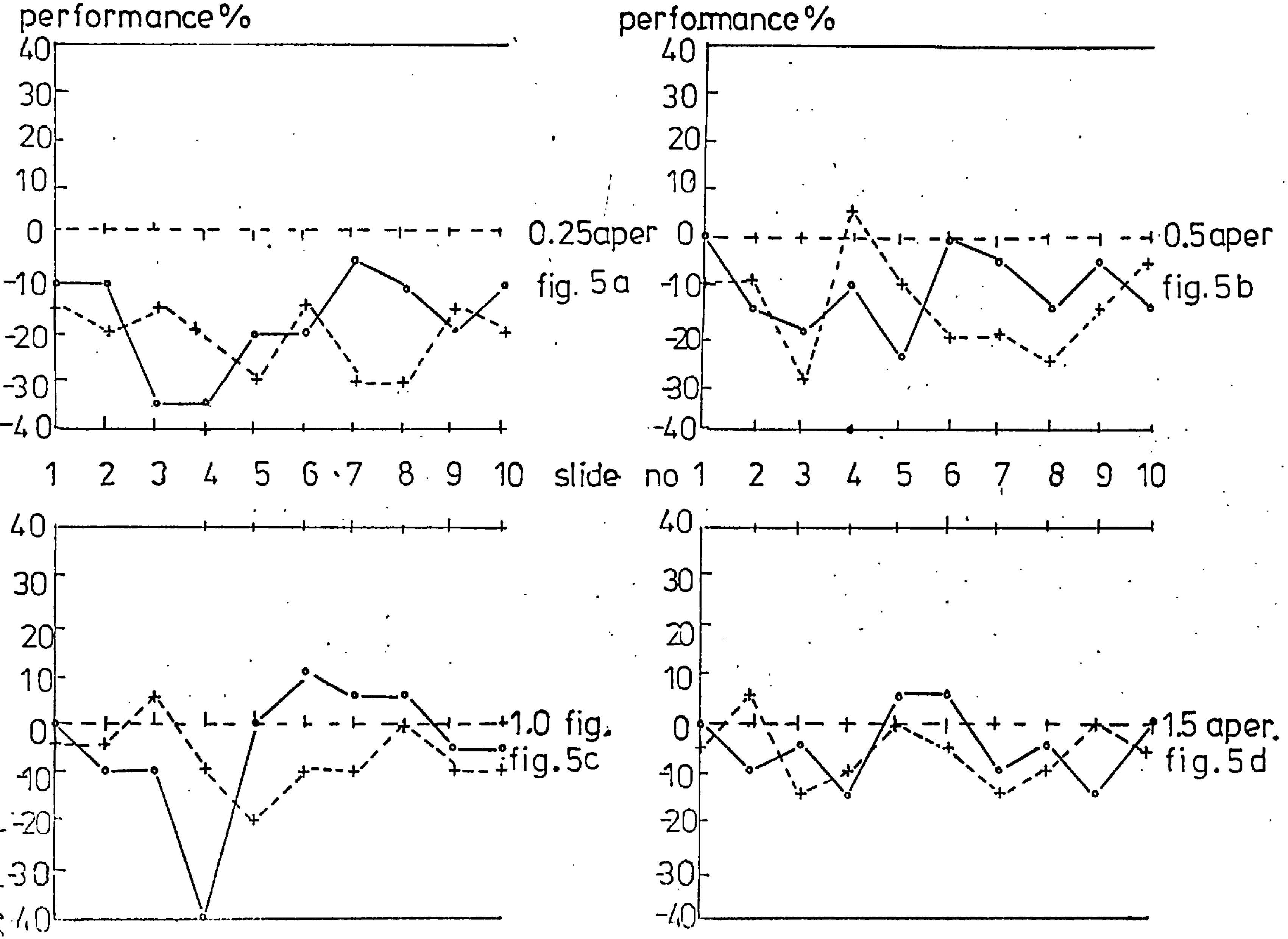
4·0 disc
fig. 4m



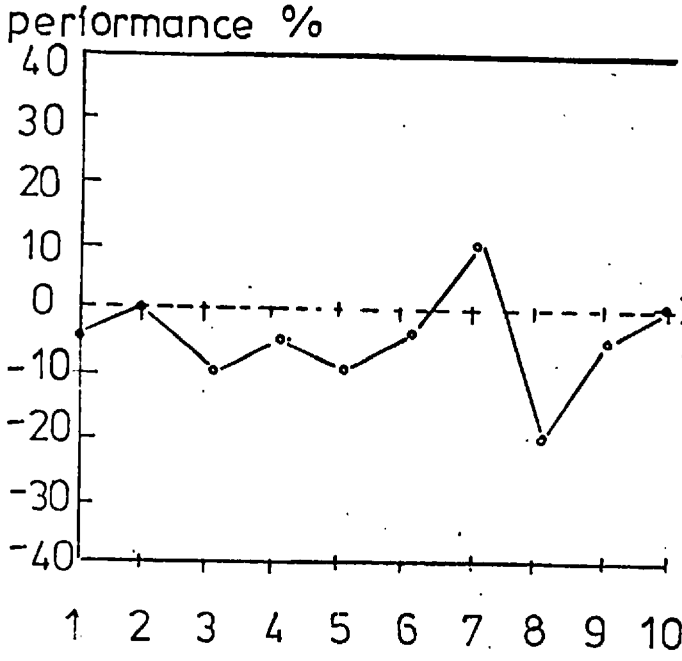
5·0 disc
fig. 4n



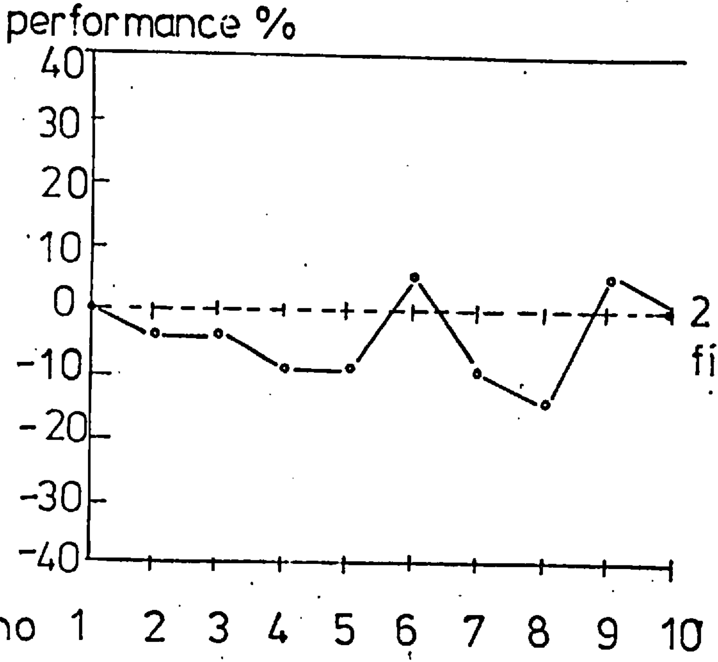
8·0 disc
fig. 4o


performance %
40
30
20
10
0
-10
-20
-30
-40
0.25aper
fig. 5a
0.5aper
fig. 5b
1 2 3 4 5 6 7 8 9 10 slide no 1 2 3 4 5 6 7 8 9 10
1.0 fig.
fig. 5c
1.5 aper.
fig. 5d

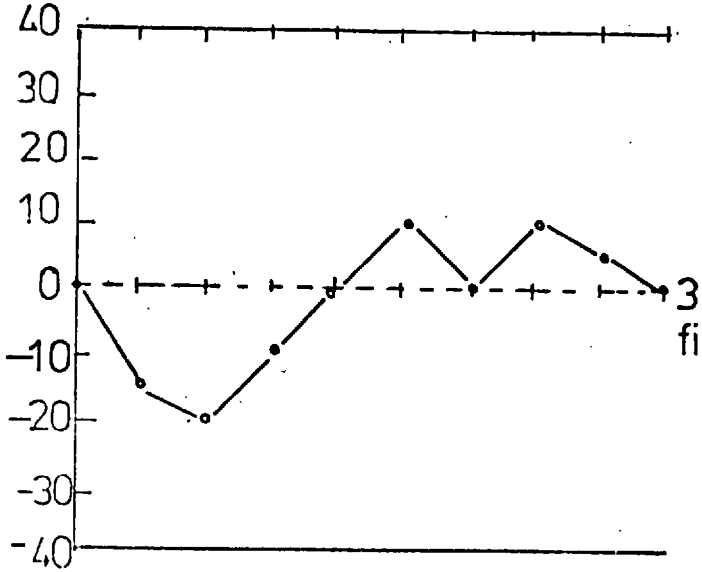
Slit series



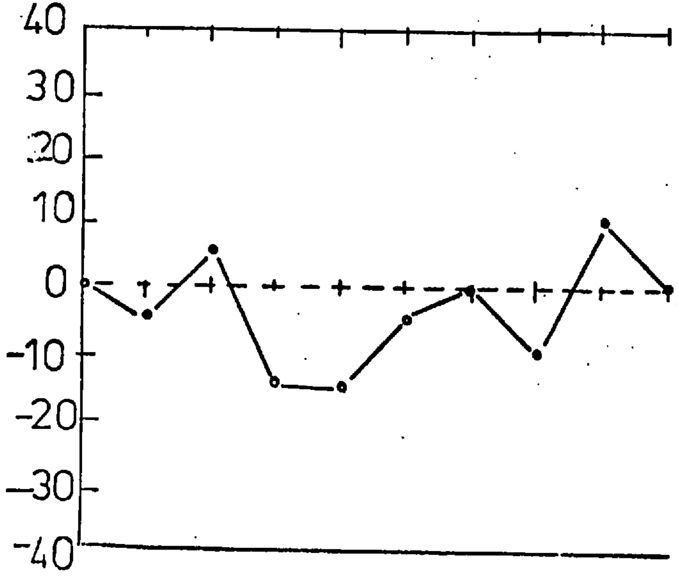
2.0 aper
fig. 5e



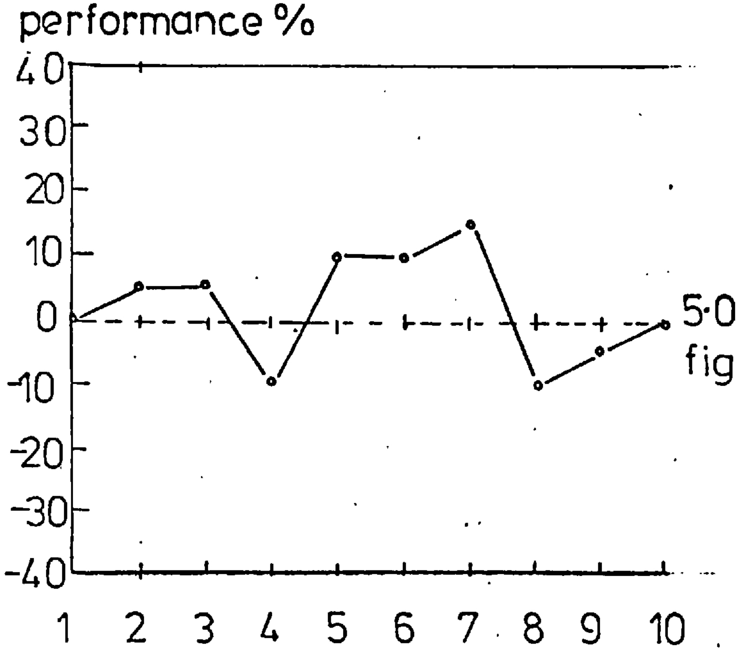
2.5 aper.
fig. 5f



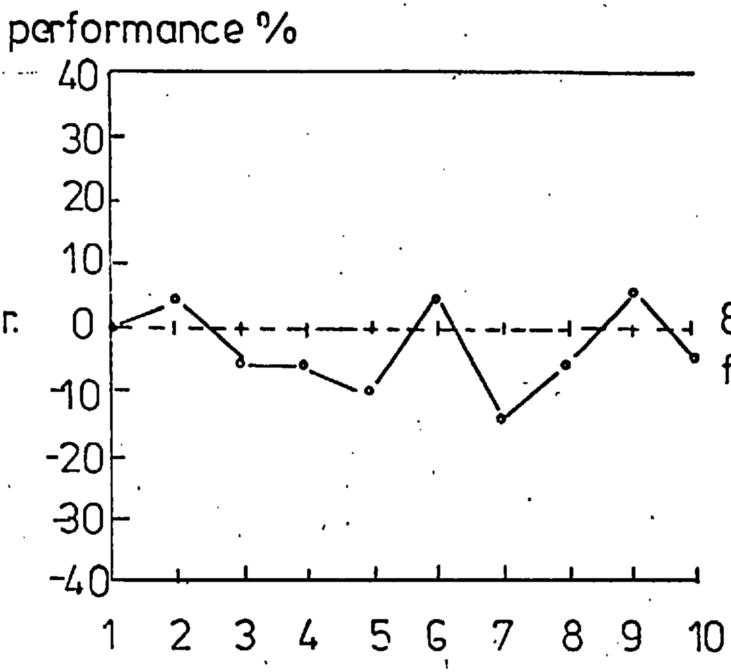
3.0 aper.
fig. 5g



4.0 aper.
fig. 5h

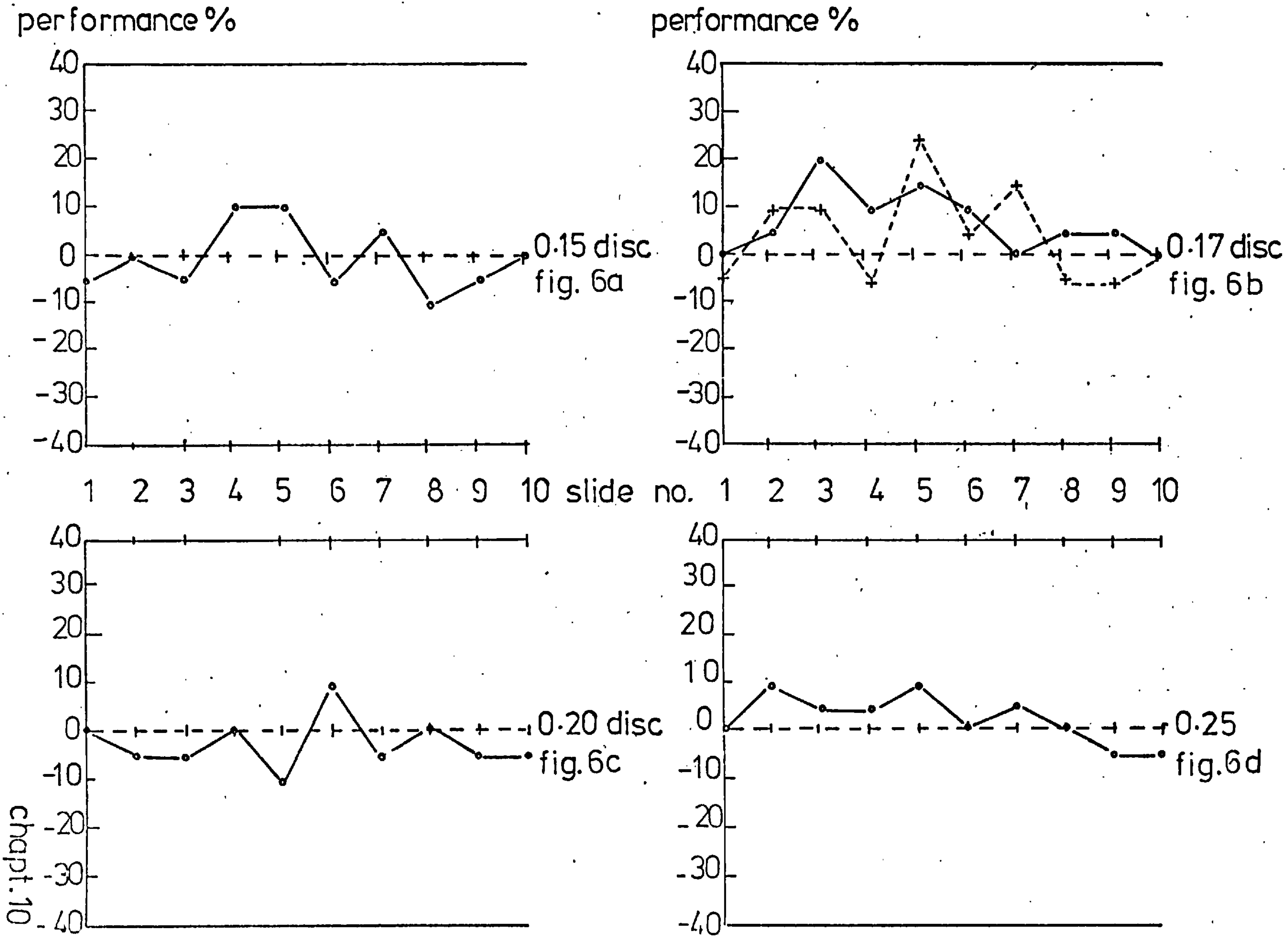


5·0 aper.
fig. 5 i



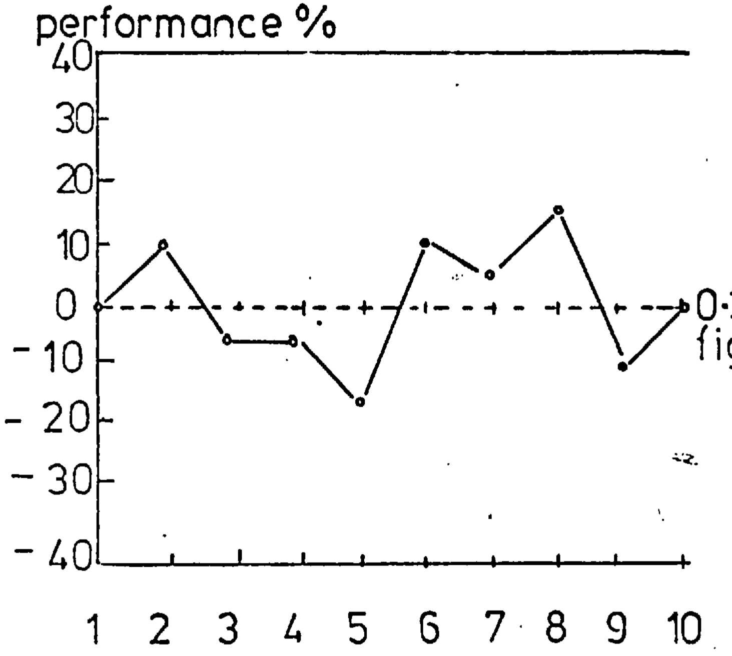
8·0 aper.
fig. 5 j

Slit series

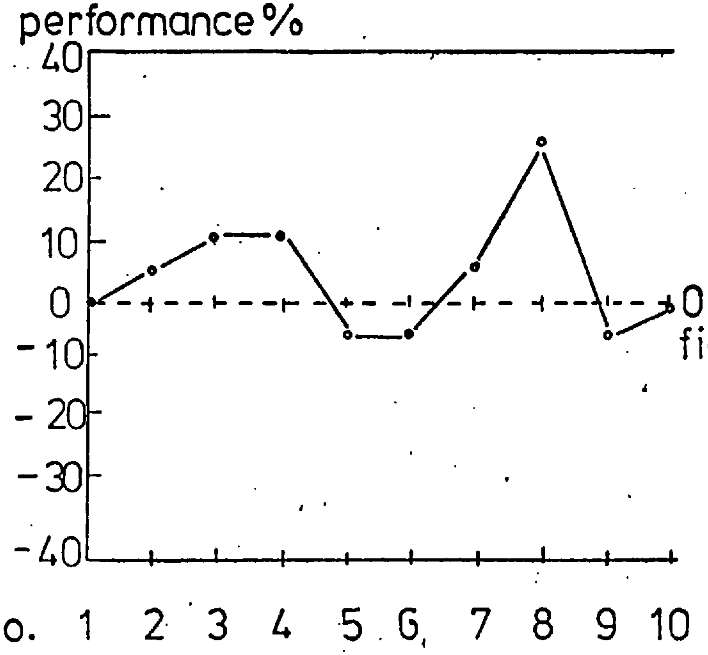

performance %
40
30
20
10
0
-10
-20
-30
-40
0.15 disc
fig. 6a
0·17 disc
fig. 6b
1 2 3 4 5 6 7 8 9 10 slide no. 1 2 3 4 5 6 7 8 9 10
0·20 disc
fig.6c
0·25
fig.6d

Slit series

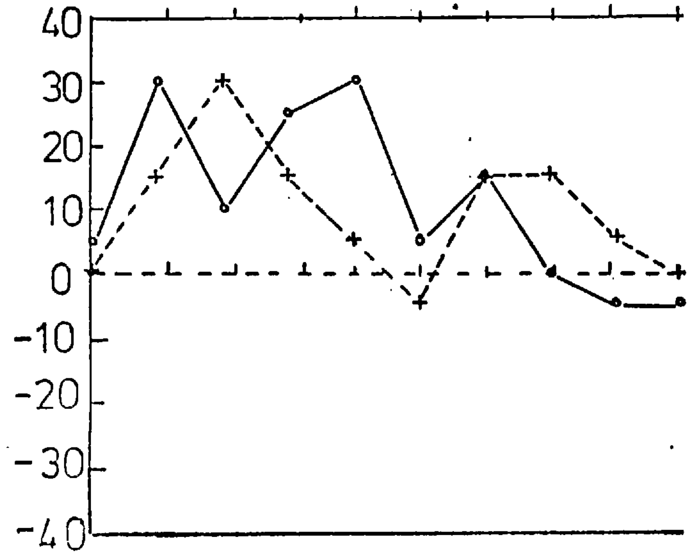
Slit series



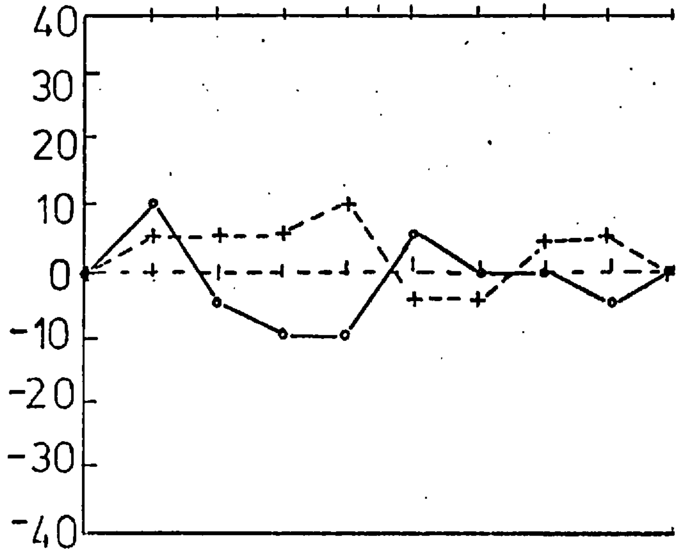
0·32 disc
fig.6e



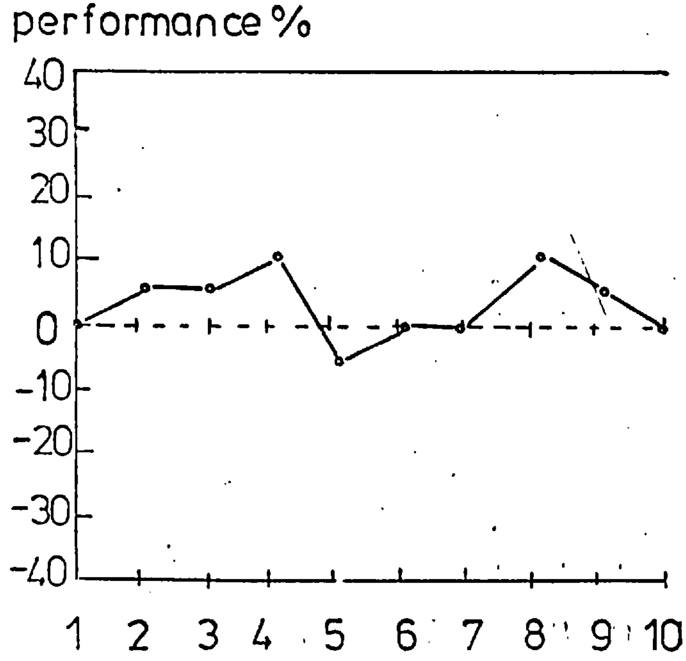
0·35 disc
fig.6f



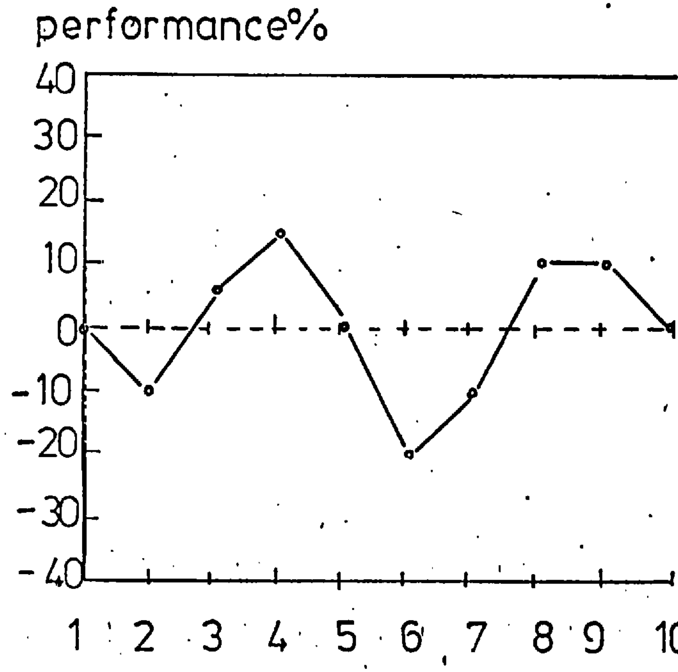
0·5 disc
fig.6g



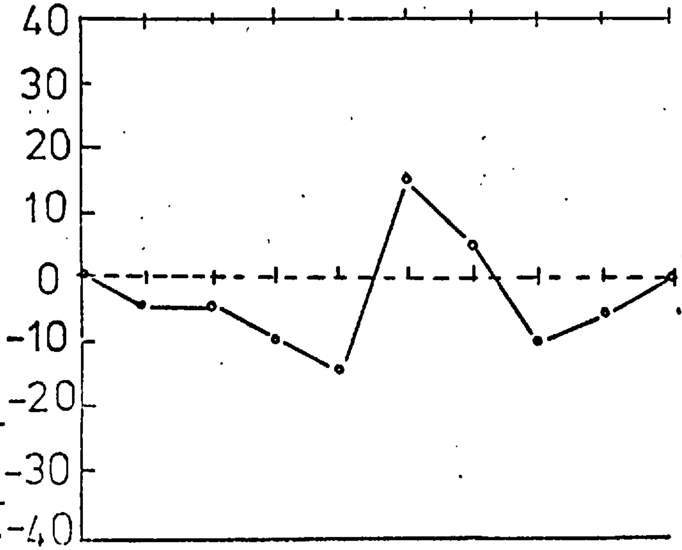
1·0 disc
fig.6h



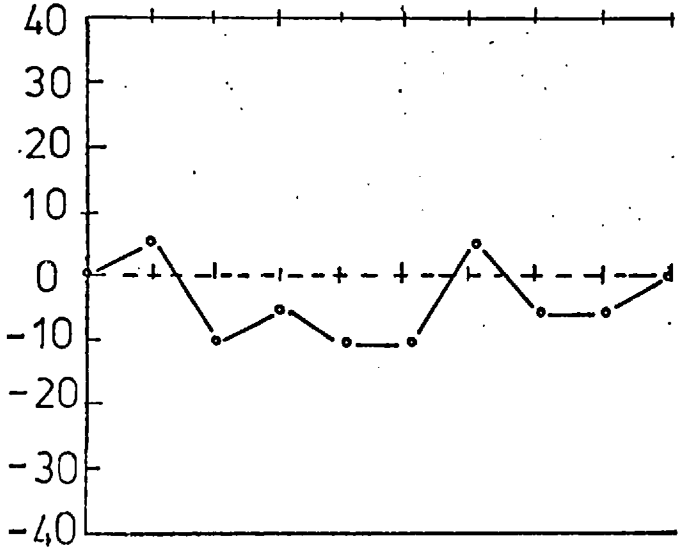
1·5 disc
fig. 6i



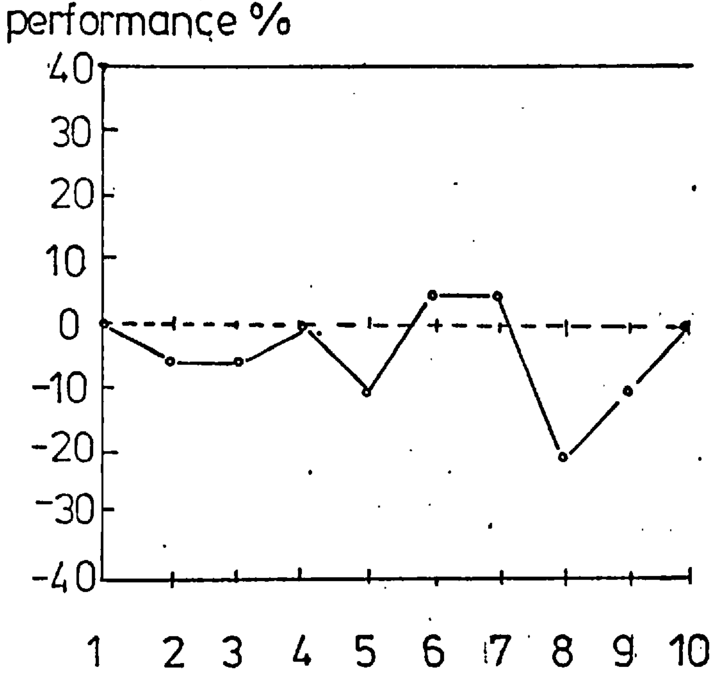
2·0 disc
fig. 6j



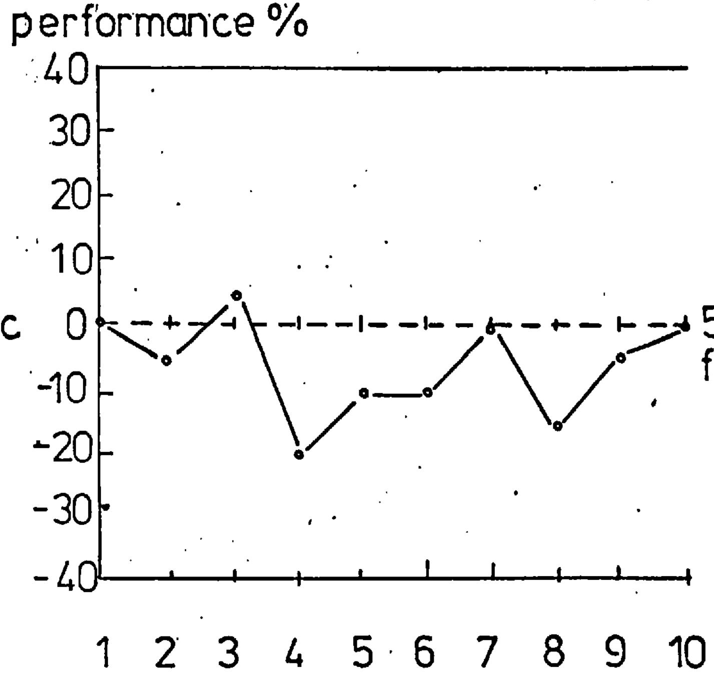
2·5 disc
fig. 6k



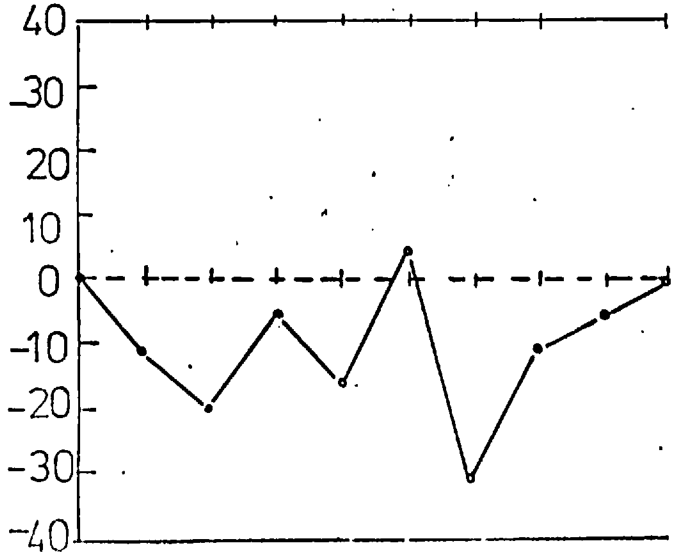
3·0 disc
fig. 6l



4.0 disc
fig. 6m



5.0 disc
fig.6n



8.0 disc
fig. 6o

4h and 6a to 6h). This improved performance was particularly marked for two filters, a 0.17 mm radius disc (fig. 2b, 4b and 6b) and a 0.5 mm disc (fig. 2g, 4g and 6g). It was found, as was the case in repetitions of the previous experiments, that a particularly good discrimination of one slide in the series following the introduction of one of these two filters would not necessarily be shown to the same extent if the trials were repeated. For example, fig. 4g, first experiment, discrimination performance for slide seven (solid line), was equal to +20%; in the second experiment, performance for the same slide (dotted line) was +5%. The general trend, however, of improved discrimination across the ten slides in a series was observed when these experiments (0.17 mm and 0.5 mm discs) were repeated. Measurements taken following the introduction of disc filters in the intermediate radius range of 1.5 to 3.0 mm (figs. 2i to 2l, 4i to 4l and 6i to 6l) did not indicate any consistent differences in performance between the filtered and unfiltered configurations.

A particular filter removes the same range of spatial frequencies from the diffraction pattern of all the objects, regardless of shape or size. The spatial frequency content, however, of all these different objects must necessarily be unique. For this reason, it might be expected that a filter which improved the discrimination of one object would not necessarily improve the discrimination of its neighbours in the series which, because of their different sizes, would have different spatial frequency contents. Where specific improvements or deteriorations in performance for particular slides have been noted and the experiment repeated, the variations have not always been found to be the same for the two runs (as discussed earlier). General trends in performance, however, over all ten slides in all three series, following the introduction of the same filters have been found to remain constant when the experiment was repeated. There appears to be justification, therefore, for determining a performance quotient which relates only to the type of object and the filter used, and not to the particular object within the series. A quotient for each filter was obtained by summing the performance percentages for all ten objects within a series in the presence of the same filter and dividing by the total number of slides - ten in all these experiments.

Fig. 7 shows the change in performance quotient with increasing radius of the non-transmitting discs for all three types of object. The same data for filters of radius less than 2 mm are superimposed and plotted on an expanded scale in fig. 8. The quotients obtained for the three types of objects after filtering by transmitting apertures are shown in fig. 9. The trends of improvement introduced by the small radius, non-transmitting, disc filters (radius less than approximately 1.0 mm), and in particular, trends associated with the 0.17 mm and 0.5 mm radius filters (fig. 8), appear to be not only significant, but independent of which of the three series of objects is being filtered. Deterioration of performance, following filtering by larger non-transmitting discs (fig. 7) and small (radius less than 5.0 mm) transmitting apertures (fig. 9) also appears to be approximately independent of the object type.

Significance tests have been carried out to quantify the apparent improvements in discrimination of the slides within the three object series induced by spatial filtering with either a 0.17 mm or a 0.5 mm radius disc. These tests have shown that the discrimination performances for both filters are significantly better (on a 0.05 level) than that for the unfiltered test objects. This applies to all three object series. A detailed analysis of the significance testing of one of these points (0.5 mm filter, segment series) is given in Appendix 2.

Non-transmitting disc filters

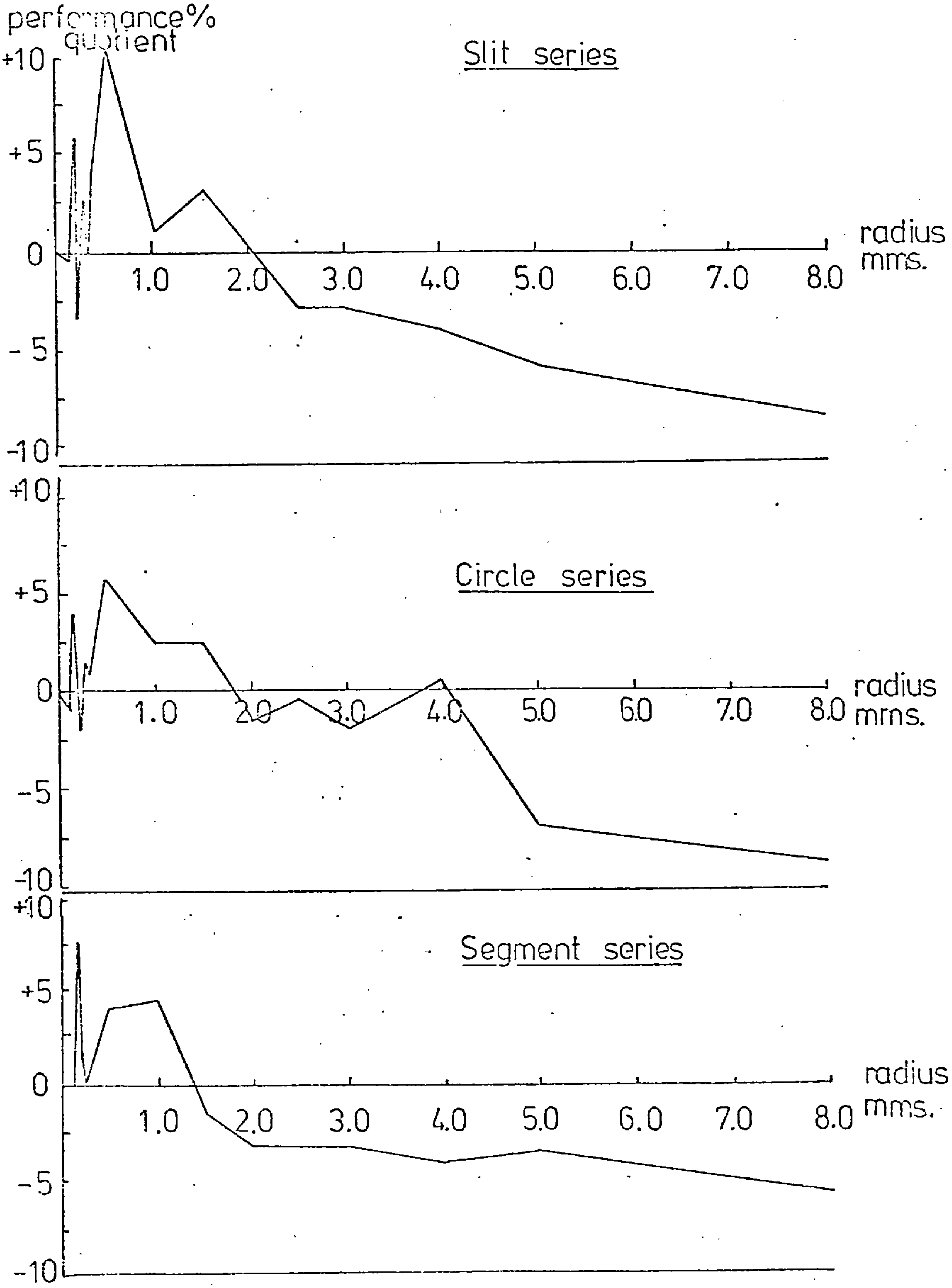
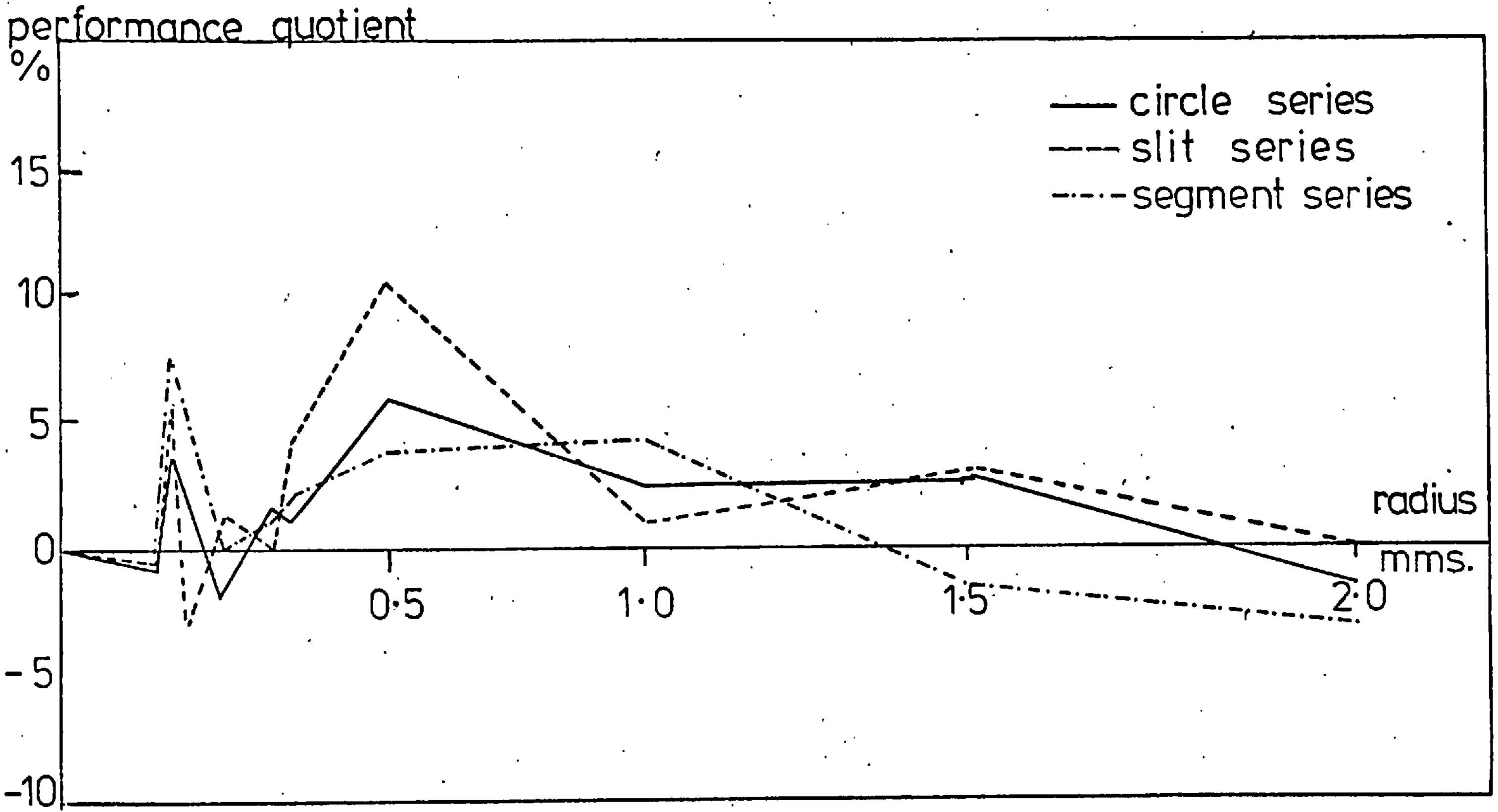
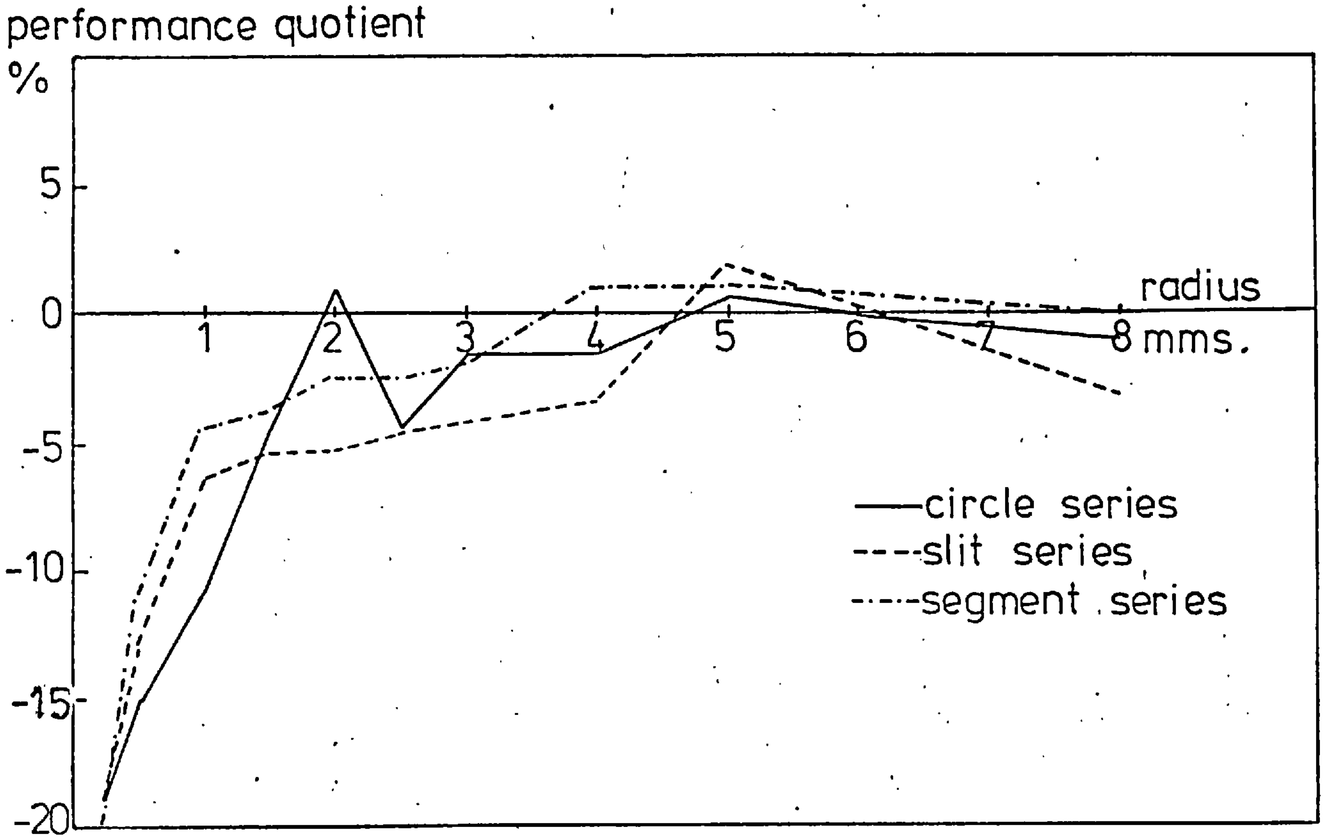


fig.7



Expanded data for non-transmitting disc filters

fig.8



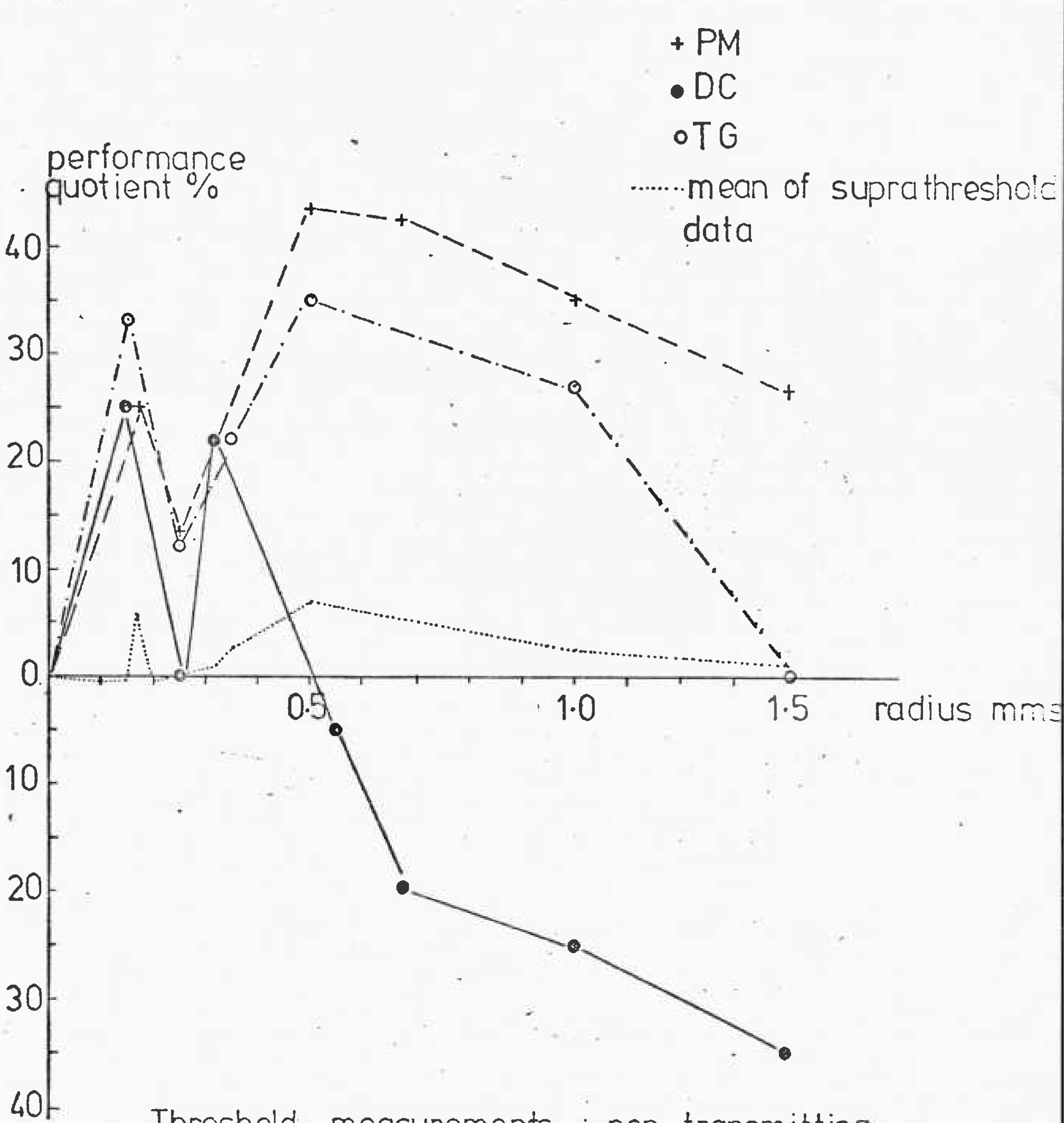
Data for transmitting aperture filters.

fig. 9

(ii) Threshold experiments

Three observers performed these experiments: PM, male, age 21, with normal vision; DC, male, age 22, with myopic vision (corrected) and TG, male age 21, with normal vision. The details of the experimental procedure were discussed in Chapter 9. To summarize, the observer was asked to identify a series of photographs of familiar faces, presented at approximately threshold illumination levels. Ten different transparencies were used, each one being shown five times in a series of 50 random presentations. The total number of correct responses for the unfiltered configuration was compared with that obtained with one of a series of filters in the diffraction plane of the transparencies. The difference between the two values was expressed as a percentage of the total number of presentations (50), to give a performance quotient comparable to that derived for the suprathreshold experiments in the previous section. The main aim of these threshold experiments was to study the effect on generalised pattern recognition of introducing into the diffraction plane those filters which had been shown to improve discrimination performance for specific geometrical shapes (previous section). For this reason, only non-transmitting disc filters with radii less than 1.5 mm were investigated. The results of these experiments for the three observers, PM, DC and TG, are given in fig. 10. Also superimposed on this figures is the mean of the suprathreshold data obtained for the three series of objects over the same filter range (shown previously in fig. 8).

The threshold data obtained by observer DC (fig. 10) is different from those of the other two observers in that a reduction in performance follows the introduction of filters with radii greater than 0.5 mm, whereas observers PM and TG obtain improvement in performance for



Threshold measurements : non-transmitting disc filters

fig.10

filters up to a radius of 1.5 mm. There is, however, marked improvement for all three observers when filters of below 0.5 mm radius are used. Although the improvement is much more pronounced for the threshold experiments, the general pattern of the data following the introduction of these filters is much the same as that found for the suprathreshold experiments (dotted line in fig. 10).

Discussion

The experiments employing spatial frequency filtering techniques can be viewed in two ways. Firstly, they can be seen as a practical demonstration of possible improvements in visual discrimination and recognition resulting from modification of the spatial frequency spectrum of the test objects. Secondly, the results of the experiments can be examined for possible evidence which they may yield regarding the visual mechanisms which subserve the recognition and discrimination of spatially structured stimuli. From the practical viewpoint, the experimental results can be interpreted as showing that it is possible to improve visual performance by the introduction of certain filters into the transform plane of the spatial filtering bench. Such improvement generally occurs with non-transmitting disc filters of radius less than 1.0 mm. These filters improve both the recognition of near threshold stimuli (faces) and the discrimination of suprathreshold geometrical targets (fig. 10). This improvement can, therefore be considered of potential practical application in observer assessment of photographic records such as those obtained in medical scanning, geophysical surveys, etc.

The results are, however, more difficult to analyse in terms of the underlying visual mechanisms, although five main observations can be made.

(i) The improvement which follows the introduction of certain filters is not a function of the nature of the target stimulus nor of the illumination level at which the stimuli are presented (as long as these levels are constant over any two experimental trials which are being compared) (figs. 8 and 10).

(ii) The application of Fourier Analysis to visual performance is currently popular (e.g. Campbell and Robson, 1968), although such analysis, even if theoretically justified, is not directly applicable to the data obtained in these experiments. The main problem in applying Fourier analysis to the data lies in the assessment of the spatial frequency content of the final modified image intensity distribution. Equation 1a of Chapter 9 relates the spatial frequency coordinates, l and m, to their respective true distance coordinates α and β:

$$l = \alpha/\lambda f_1 \quad \text{and} \quad m = \beta/\lambda f_1$$

where f_1 is the focal length of the transform lens (fl_1 in fig. 1, chapter 9 = 50 cms) and λ is the wavelength of the coherent illumination (632.8 nm).

Since the filters are symmetric they can be simply described in terms of the spatial frequencies they remove from the pattern rather than their radii in the true distance coordinates. The spatial frequencies corresponding to the cut-off radii of the filters are given in Table 2. (The values in cycles/degree of visual angle are obtained from the cycles/cm value using a conversion factor. This factor is derived from the number of degrees of visual angle which a 1 mm x 1 mm object subtends at the eye (2.3° in this apparatus)). It is not possible to assume, however, that removing certain spatial

Table 2 filter characteristics.

radius mm	frequencies removed c/cm	frequencies removed c/°	
0·15	0 — 4·74	0 — 0·21	non-transmitting disc filters.
0·17	0 — 5·37	0 — 0·23	
0·20	0 — 6·32	0 — 0·27	
0·25	0 — 7·90	0 — 0·34	
0·32	0 — 10·11	0 — 0·44	
0·35	0 — 11·06	0 — 0·48	
0·50	0 — 15·80	0 — 0·69	
1·00	0 — 31·60	0 — 1·37	
1·50	0 — 47·39	0 — 2·06	
2·00	0 — 63·19	0 — 2·75	
2·50	0 — 79·00	0 — 3·43	
3·00	0 — 94·79	0 — 4·12	
4·00	0 — 126·38	0 — 5·49	
5·00	0 — 158·00	0 — 6·87	
8·00	0 — 252·76	0 — 11·00	
0·25	7·90 — ∞	0·34 — ∞	transmitting aperture filters
0·50	15·80 — ∞	0·69 — ∞	
1·00	31·60 — ∞	1·37 — ∞	
1·50	47·39 — ∞	2·06 — ∞	
2·00	63·19 — ∞	2·75 — ∞	
2·50	79·00 — ∞	3·43 — ∞	
3·00	94·79 — ∞	4·12 — ∞	
4·00	126·38 — ∞	5·49 — ∞	
5·00	158·00 — ∞	6·87 — ∞	
8·00	252·76 — ∞	11·00 — ∞	

frequency components from the diffraction pattern of an object removes these same components from the final image distribution. Consider an object which consists of three sinusoidal grating frequency components (unit amplitude): 0.1, 0.9 and 1.0 in arbitrary units. The object distribution, A(x), is defined as:

$$A(x) = \cos 0.9\,x + \cos 1.0\,x + \cos 0.1\,x$$

In visual terms, it is necessary to consider the intensity distribution, I(x), of the object:

$$I(x) = \left| A(x) \right|^2$$

In the Fourier plane, the filtering operation is performed on A(x). Consider that a filter is introduced which removes all frequencies in the range zero to 0.2, leaving a modified amplitude distribution A'(x):

$$A'(x) = \cos 0.9\,x + \cos 1.0\,x$$

In the image plane, the visual system responds to the intensity distribution I'(x):

$$I'(x) = \left| A'(x) \right|^2$$

$$= \cos^2 0.9\,x + \cos^2 1.0\,x + 2(\cos 0.9\,x \cos 1.0\,x)$$

$$= 1 + \tfrac{1}{2}\cos 1.8\,x + \tfrac{1}{2}\cos 2.0\,x + \cos 1.9\,x + \cos 0.1\,x$$

Thus, a term (cos 0.1 x) lying in the frequency cut-off range specified by the filter reemerges in the image intensity distribution. The improvement in performance introduced by the small non-transmitting disc filters cannot, therefore, be correlated directly with the consistent removal of certain spatial frequencies other than the D.C. component from the intensity distribution of the final image. For the same reason, it is not possible to correlate the removal of certain ranges of spatial frequencies from the Fourier plane of the image with the M.T.F. of the observer's visual system.

(iii) It has not been possible to correlate visual performance with some artefact arising within the spatial filtering bench itself. It is necessary in any spatial filtering experiment to ensure that all significant spatial frequencies within the diffraction patterns of the objects studied, are passed by the transform lenses. The upper spatial frequency limit of the Wynne (1974 a and b) lenses used in this optical bench is given as 63 c/mm at 633 nm (the wavelength of the laser used in these experiments). This corresponds to a circular transmitting aperture filter of radius 19 mm, centred in the transform plane. The experiments described here, however, show that there is no significant loss of performance for transmitting aperture filters of radius greater than 4 mm (fig. 9) for any of the three series of geometrical shapes. Therefore, any high frequency attenuation derived from limitations of the transform lenses does not affect the recognition of the final images in any measurable way.

(iv) A computer programme was devised which generated the theoretical intensity profiles of the final images of the slit series after the spatial frequency content had been modified by filtering. Examples of these intensity distributions are shown in Appendix 1. These computed distributions show that the filters which gave rise to improved performance certainly removed the D.C. component, but showed no obvious correlation between this improved performance and pattern structure. The improvement is probably related in some way to increased edge information, but is not general in all patterns with edge enhancement. The observers themselves were unable to suggest intuitively why the images became more readily identifiable to them.

(v) Recognition and discrimination of complex patterns are only partially controlled by visual function; memory and the ability to compare different stimuli are also being tested. Therefore, it is not reasonable to expect to derive any total explanation of particular aspects of visual function from such an experiment.

In conclusion, it would seem that these recognition and discrimination experiments are not well suited for analysis of the visual mechanisms which subserve the perception of spatially structured stimuli. From the practical viewpoint, the experiments have shown, however, that significant improvement of recognition and discrimination performance can be obtained by spatial filtering methods.

Appendix 1

In chapter 10, the problems encountered in attempting to identify the cause of improved discrimination of a series of objects when certain spatial filtering operations were performed on their diffraction patterns, were discussed. One approach (Chapter 10; discussion, point (iv)) was to obtain computer-generated intensity profiles equivalent to the object intensity profile after appropriate spatial filtering had been performed. The profiles were generated on Imperial College's CDC 6400 Computer for the slit object series only. The programme required the slit to be set up as a one-dimensional array. Since only binary information was present in the original slide, the array contained zero terms, representing non-transmitting regions of the object and unity terms, representing the transmitting regions. The inverse Fourier transform of this array (equivalent to the diffraction pattern of the object) was generated by calling up the appropriate algorithm from the computer library and applying this to the input data. By superimposing a binary array equivalent to a circular filter (either transmitting or non-transmitting) on the Fourier transform of the input distribution,an operation equivalent to optical spatial filtering was performed. The elements in the resulting modified array were transformed again by a second computer algorithm to give an array equivalent to the filtered amplitude distribution of the object. A plotting routine was used to trace out on microfilm the square of the amplitude distribution thus generating a theoretical intensity profile of the filtered image as seen by the observer after spatial filtering had been performed on the object slide.

Figures 1 - 6 show computed intensity profiles across a transmitting slit equivalent to slide 10 as described in Chapter 9 (suprathreshold experiments). The width 'S' is equivalent to 0.61 cms; its length l is taken appendix 1.

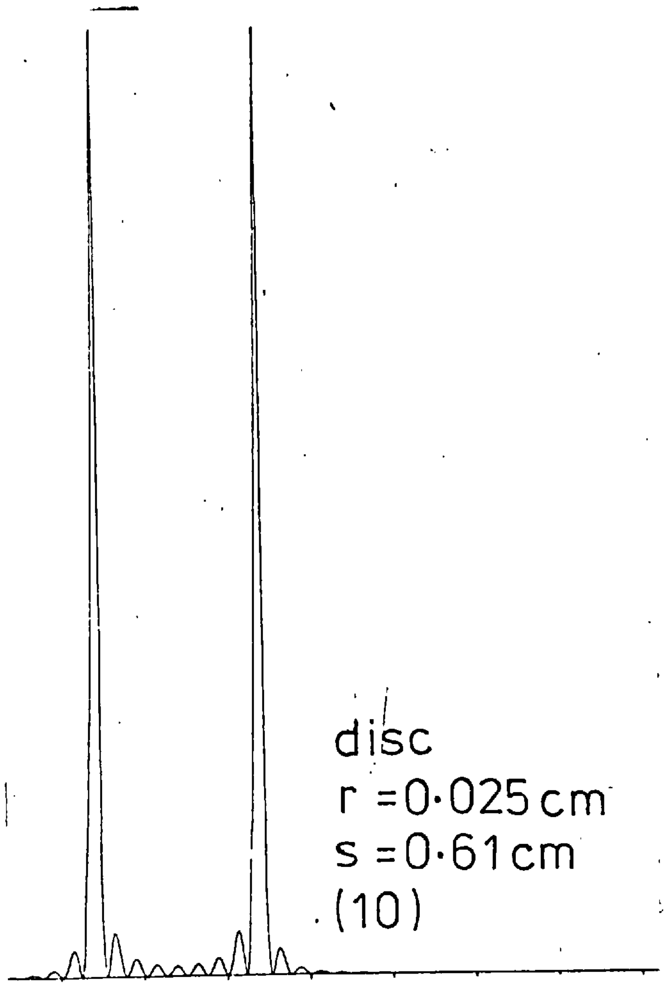


fig. 1

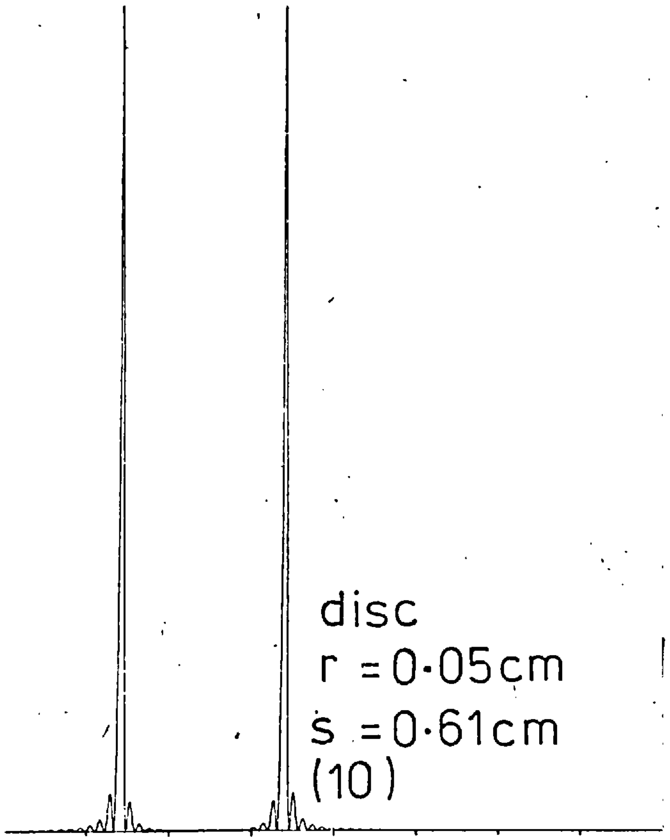


fig. 2

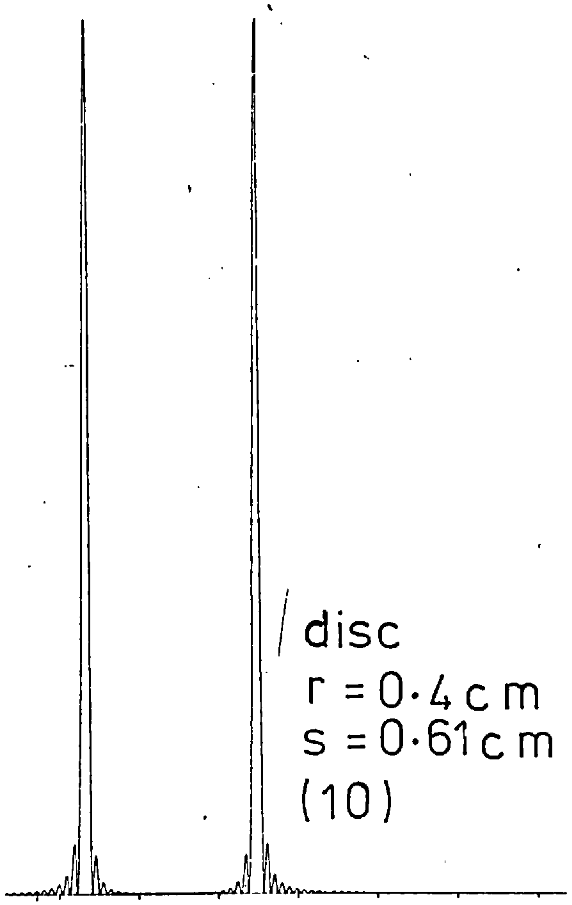


fig. 3

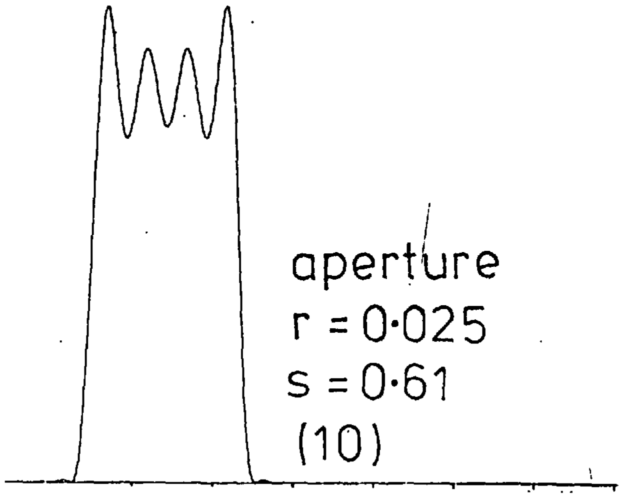


fig. 4

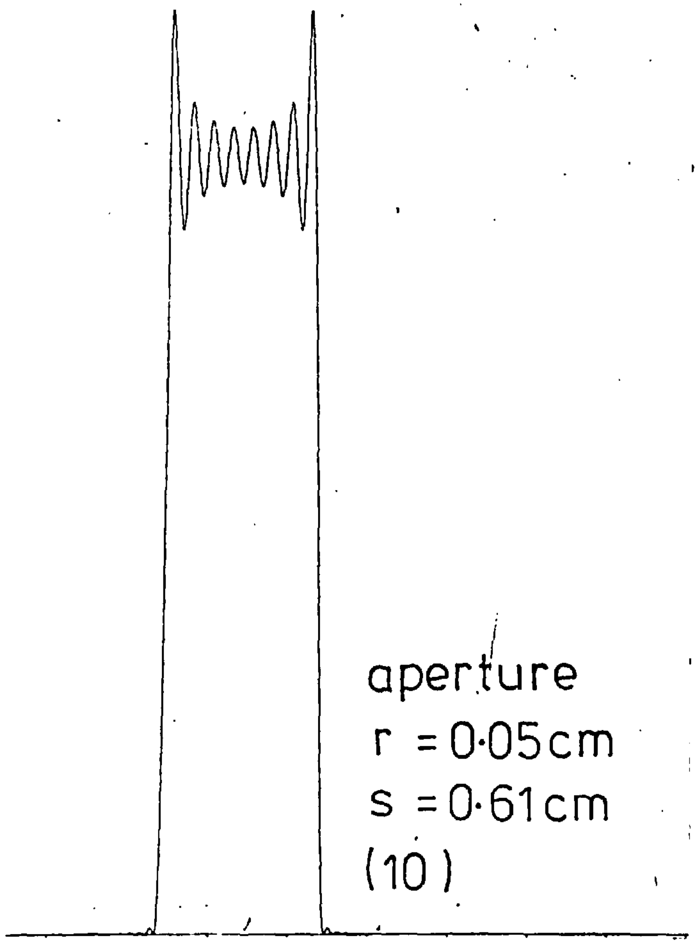


fig. 5

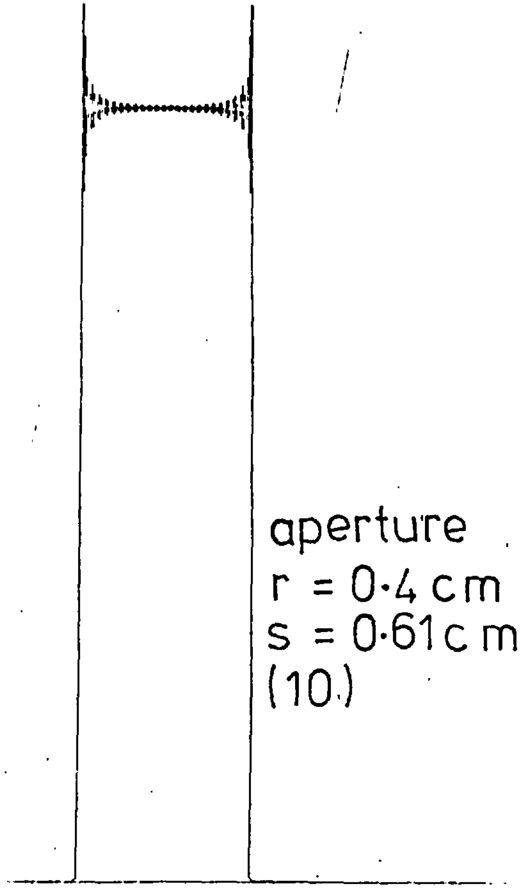


fig. 6

as infinite (justified on the experimental basis of $l \gg s$). In each of the six figures, an operation equivalent to spatial filtering by a circular filter of radius r has been carried out in the transform plane of the object slit. In figures 1 - 3, the filter is a non-transmitting disc on a transmitting background; in figures 4 - 6 the filter is a transmitting aperture on a non-transmitting background.

These figures are examples taken from an extensive set of computed profiles representing all ten slit objects after filtering by the complete range of circular discs and apertures described in chapter 9.

Appendix II

This appendix is concerned with testing the significance of the apparent improvement in discrimination performance which follows the introduction of certain spatial filters (see Chapter 10) into the transform plane of the three object series. Although all the relevant filtering experiments have been tested for significance using the technique described, the analysis of only one trial is given here: the discrimination of the segment object series as measured before and after spatial filtering by a 0.5 mm radius disc.

During the course of the suprathreshold experiments described in Chapter 9, the observer was asked to discriminate between ten slides based on the same geometrical shape, each of which was presented twenty times, a total of two hundred presentations in all. The experimenter recorded not only whether the observer correctly identified a particular slide, but also the actual response he gave when the guess was not correct. In this way, ten distributions of guesses, one for each of the ten slides, were obtained. These distributions are given in numerical terms in Tables 3a and 3b, where 3a represents the results obtained with no spatial filtering and 3b, the results obtained for the corresponding experiment following the introduction of a 0.5 mm disc into the transform plane of the objects. The observer's response to a particular object is described on a scale where zero indicates a correct identification, a minus value indicates underestimation of size (e.g. a response denoted -2 for slide number seven means that it was identified as slide number five), and a positive value, an overestimation. It is apparent that each distribution centres around the zero point of the scale which denotes the true identity. The responses have been summed to give two distributions of the 200 estimates, one distribution for the unfiltered experiment, the other

Table 3a

estimate →

slide ↓

UNFILTERED	-3	-2	-1	0	+1	+2	+3
1	0	0	0	19	1	0	0
2	0	0	2	16	1	1	0
3	0	1	4	10	3	2	0
4	0	2	4	8	4	2	0
5	0	1	6	8	4	1	0
6	0	3	4	8	3	2	0
7	0	1	6	6	5	2	0
8	2	3	3	6	4	2	0
9	0	1	1	16	2	0	0
10	0	0	1	19	0	0	0
	2	12	31	116	27	12	0

Table 3b

estimate →

slide ↓

FILTERED	-3	-2	-1	0	+1	+2	+3
1	0	0	0	19	1	0	0
2	0	0	1	16	1	2	0
3	0	0	6	9	4	1	0
4	0	0	5	12	3	0	0
5	0	0	5	11	4	0	0
6	0	0	7	7	5	1	0
7	0	0	4	12	4	0	0
8	0	0	8	6	5	1	0
9	0	0	1	19	0	0	0
10	0	0	1	19	0	0	0
	0	0	38	130	27	5	0

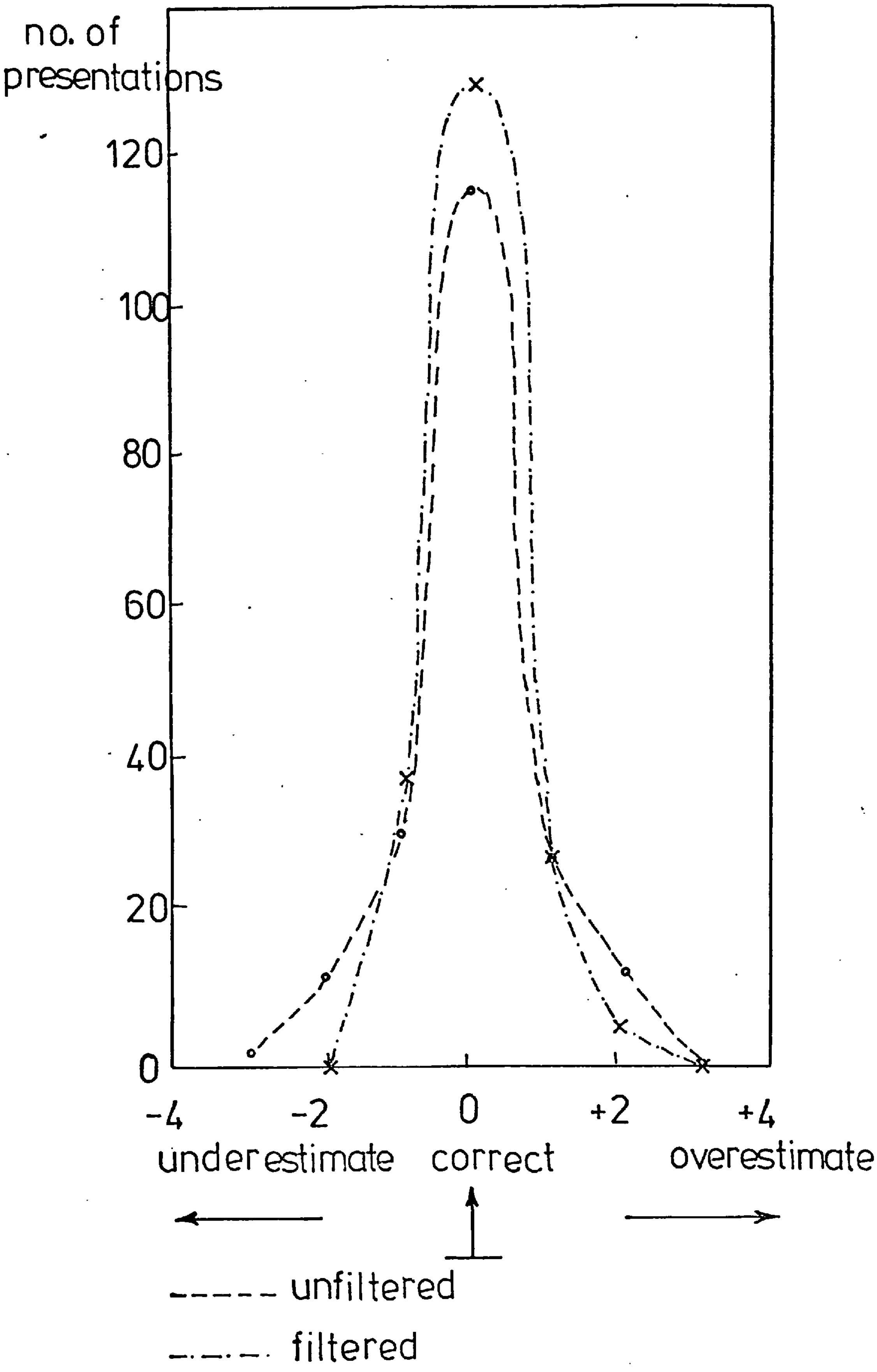


fig.1

appendix 2

for the filtered experiment. The distributions are plotted in figure 1.

The totals (N_{uf}: unfiltered; N_f: filtered) are set out in Table 4. The significance testing is based on the null hypothesis that spatial filtering does not affect overall performance. χ^2 values, as defined in Table 4, were calculated for each estimate. The rejection region for such a hypothesis with seven degrees of freedom and a 5% significance level is given as:

$$p(14.07 < \chi^2 < \infty) = 0.05$$

(using the appropriate χ^2 tables)

According to Table 4:

$$\chi^2 = 18.6$$

$$\therefore \; \chi^2 > 14.07$$

and the hypothesis that filtering does not affect performance must be rejected. Therefore on a 5% significance level, filtering by a 0.5 mm radius disc improves the discrimination of the segment object series compared with the corresponding unfiltered experiment.

estimate	N_{uf}	N_f	χ^2
-3	2	0	1·13
-2	12	0	11·02
-1	31	38	1·36
0	116	130	1·57
+1	27	27	0·0
+2	12	5	3·52
+3	0	0	0·0
	200	200	18·6

$$\chi^2 = \frac{(|N_{uf} - N_f| - 1/2)^2}{N_{uf}}$$

Table 4

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