A COMPARISON OF THE EFFECTS OF ACTIVE AND PASSIVE IMAGE-DISPLACEMENTS ON VISUAL THRESHOLDS

by

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ABSTRACT

The effects on visual thresholds of active displacement of the peripheral retinal image (produced by saccadic eye movement) and passive displacement of the peripheral retinal image (produced by field rotation) were compared. The purpose of this comparison was to investigate whether it is necessary to invoke a saccade-locked central inhibition of visual sensitivity in order to account for the elevation of threshold associated with saccadic eye movement.

It was found that active image displacements of six degrees extent were associated with a mean threshold elevation of 0.5 log units, whereas closely similar passive displacements of the same retinal image were associated with a mean threshold elevation of 0.3 log units.

It is possible that some of the difference between the threshold elevation associated with active and passive displacement of the retinal image may have been produced by a small difference between the image displacement in the extreme periphery under the two conditions. Whether this is so or not, the maximum threshold elevation associated with a saccade rather than with the retinal image displacement caused by the saccade, was shown to be 0.2 log units. This is considerably smaller than the 0.5 log units threshold elevation previously believed to be associated with saccadic eye movement. It is possible that even this slight threshold elevation is not a corollary of the programming of a saccade but rather reflects a disturbance of visual processing by the shearing of the retina believed to occur during a saccade.

In other experiments the elevation of threshold associated with small passive displacements of the peripheral and parafoveal retinal image (similar in extent and timecourse to those caused by micro-

saccadic eye movements) was studied. It was shown that there was no significant elevation of threshold associated with passive pseudo-microsaccadic displacements of the retinal image under conditions in which threshold elevation has been reported to occur in association with microsaccades. This discrepancy may, however, reflect a deficiency of the experiments with microsaccadic eye movements rather than a true difference between the effects of active and passive micro-displacements on visual thresholds. It was shown that small displacements of large high-contrast peripheral and parafoveal patterns can produce elevation of threshold for foveal flashes, and the form of this effect was investigated as a function of displacement magnitude.

The variation of the threshold elevation associated with three degree passive displacements of the retinal image as a function of the eccentricity of the displaced contour was studied and it was shown that even contours more than 40 degrees eccentric to the test flash produced clear threshold elevation.

The possible relation of the psychophysical threshold elevation associated with displacement of peripheral contours and the physiological periphery effect is discussed. Although there are similarities between the two effects, it is by no means certain that the two are correlates.

Subsidiary experiments showed that elevation of threshold could be produced by peripheral stimuli involving no displacement of contour, but only tachistoscopically presented pattern appearance or pattern change, and that flicker thresholds as well as flash thresholds were raised by peripheral stimulation. Scalp-evoked-potentials were recorded to investigate whether an electrophysiological correlate of the psychophysical threshold elevation associated with peripheral image displacement existed. No such effect was found.

Substantially independent experiments concerned with the control of human rapid eye movements are reported in appendices six and seven.

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CHAPTER ONE

Visual sensitivity during saccadic eye movements and pseudosaccadic displacements of the retinal image

1.1 Introduction

It is a curious but easily verified fact, apparently first reported by Javal (1878), that in reading the eyes move in a series of jumps or saccades, separated by pauses during which the eyes are stationary. Dodge and Cline (1901) showed that this pattern of eye movement is typical of all visually guided eye movement in stationary surroundings, and found that the saccades have stereotyped timecourses with peak velocities of several hundred degrees/sec. Thus movements of 5 degrees are accomplished in rather less than 30 msec and even movements of 40 degrees last only 100 msec.

Several authors noted that during saccades in a normal, lighted environment one cannot detect any momentary blurring of the perceived world, and considered that this was contrary to what would be expected if vision during saccades was a function only of the retinal stimulation received.

Erdmann and Dodge (1898) found that if a letter or simple figure was placed between two fixation points so as to be unrecognizable from both, then no eye movement which was not broken by a pause made it possible to recognise the character. They suggested that under normal conditions no visual impressions were gained during eye movements.

These and other peculiarities of vision associated with saccadic eye movement prompted Holt (1903) to suggest that saccades are accompanied by a transient 'central visual anaesthesia'. A similar suggestion had been made earlier by Exner (1890) in order to account for the disappearance of after-images during saccades.

Dodge (1900, 1905) and Woodworth (1906) considered that the inability to see stimuli presented during saccades could for the most part be explained by retinal factors i.e. smearing of the image, the brief duration of the stimuli, and masking of the stimuli by the stationary patterns normally present on the retina before and after a saccade. Woodworth claimed that all the effects reported by Holt could be produced without eye movement at all, by a displacement of the field of view which mimicked the retinal image motion produced by a saccadic eye movement. Dodge considered that some central factors (i.e. attention) might play a role in the lack of perception of visual stimuli falling on the saccadically moving eye, but was able to show that any central inhibition of vision that occurred in saccades was small. He found that when the same brief retinal stimulus was presented to the stationary and saccadically moving eye, the thresholds for visibility of the stimulus were approximately equal.

Volkmann (1962) repeated this experiment with a more carefully controlled stimulus than was available to Dodge. The test stimulus was a flash lasting 20 microsec and so was insignificantly blurred even if it occurred in the middle of a saccade. The retinal location and timing of the flash were also carefully controlled. Under these conditions the threshold for visibility of a test flash delivered during a saccade was about 0.5 log units above that for a flash delivered to the stationary eye. It was found that elevation of threshold occurred for stimuli presented up to 50 msec _before_ the onset of the saccade (Volkmann et al., 1968) and this discovery of 'anticipatory' threshold elevation was widely accepted as proof that the elevation of threshold was due to some central inhibitory process associated with saccades.

In 1968 Richards showed that threshold elevation could be produced by a sudden _passive_ displacement of the eye. He found that equal magnitudes of threshold elevation were produced by similar active and passive displacements of the eye, and suggested that the threshold elevation might in both cases be attributed to mechanical shearing of the retina.

MacKay (1970a, b) raised the question of whether either central inhibition or mechanical shearing need be invoked to explain the reported elevation of threshold during saccades, since he showed that a passive displacement of the peripheral retinal image alone, without any eye movement, raised the threshold for visibility of a test flash, even when the test flash was presented up to 40 msec before the onset of the image displacement. This experiment revealed a logical flaw in the previous investigations of vision during saccades, namely the failure to control for the possible masking effects of the motion of the peripheral image over the retina which necessarily occurs during saccades in a non-uniform visual environment.

The main aim of the present experiments was to compare the threshold elevations associated with active displacement (by saccadic eye movement) and passive displacement (by field displacement) of the peripheral retinal image, and so determine whether the effect demonstrated by MacKay is the entire explanation of the elevation of threshold during saccadic eye movement, or whether after all other factors must be invoked to explain some aspects of 'saccadic suppression'.

1.2 Early observations and experiments

Holt (1903) reported two main observations on which he based his hypothesis of central visual anaesthesia during saccadic eye movements. The first was that when a saccade was made away from a bright light, two streaks were seen, one darting out from the light in the opposite direction to the saccade (which he referred to as the falsely localised streak), and the other appearing between the light and the final fixation point (which he referred to as the correctly localised streak). The effect was best seen with large (i.e. 40 degree) saccades. The 'correctly' localised streak is much fainter than the 'falsely' localised streak. This phenomenon was apparently first noted by Mach (1886). Following Schwartz (1892), Holt claimed that the 'correctly' localised streak appeared a discernible interval later than the 'falsely' localised streak. Holt further claimed that when the falsely localised streak appeared it 'darted out' from the light whereas when it disappeared it 'suffered a sudden eclipse'. The correctly localised streak, however, 'flashed out suddenly in situ', but 'faded away very slowly'. He argued that the temporal discontinuity of the perceived intensity of the streaks was due to an intervening 'central anaesthesia' of vision.

Holt's second observation was made by an ingenious method designed to present identical retinal stimuli to the stationary and saccadically moving eye. A lighted aperture became transiently visible when a second aperture, cut in a card mounted on a pendulum, passed across the first aperture. The illumination of the stationary aperture was adjusted so that the aperture was just clearly visible when momentarily exposed during a pendulum swing. Holt then studied the visibility of the aperture during eye movements timed to cross the aperture at the same moment as the aperture in the pendulum. Under these conditions the lighted aperture was frequently invisible. Holt considered that the velocity of the eye movements matched that of the pendulum, in which case the retinal stimulation received by the stationary and saccadically moving eye would have been identical. As Dodge (1905) pointed out, however, a single saccade between fixation points placed 40 degrees apart (as in Holt's experiments) would have had a mean velocity of 400 degrees/sec

(Dodge and Cline, 1901), whereas the velocity of the pendulum transit was only 80 degrees/sec. The non-visibility of the lighted aperture during a saccade was thus explicable by retinal blurring alone, without any assumption of central anaesthesia.

Dodge (1900) had considered that the hypothesis of central inhibition of vision during saccades was disproven by the simple observation that only when a saccade of suitable size (i.e. of suitable velocity) was made across a rotating disc with holes punched near the edge and dimly lit from behind, could the holes be seen clearly.

Holt's form of the central inhibition hypothesis could not, however, be disproven by this simple observation, since he considered that the 'anaesthesia' of vision was due to 'muscle sensations of present movement streaming to consciousness, to form the basis of the new post-motum localization' (i.e. proprioceptive signals from the eye muscles) (Holt, p. 44). Holt considered that the anaesthesia should last only as long as the duration of the saccade, and argued that the percept seen in Dodge's experiment could be mediated by a positive after-image still visible after the end of the anaesthesia. Holt realised that this form of the central inhibition hypothesis implied that the latency of onset of the inhibition would depend on the time of conduction of proprioceptive signals from the eye muscles, and pointed out that some of his observations implied that anaesthesia did not begin until some tens of milliseconds after onset of a saccade.

Dodge (1905) showed that Holt's criticism of his previous observations could not be sustained since even threshold stimuli could be made visible to the saccadically moving eye. He balanced the illumination reflected from and transmitted through a perforated disc so that the perforations were just visible during a saccade whose velocity matched that of the holes in the disc, but were otherwise completely invisible. He then compared the effective duration of the retinal stimulation in this case with the duration of exposure of the same perforations necessary for the perforations to be seen with the eyes stationary. The times were approximately equal (30 and 25 msec respectively), ruling out the possibility of any substantial central inhibition of vision during saccades.

Dodge also pointed out that Holt's suggestion that proprioceptive signals 'streaming to consciousness' created a visual anaesthesia was weak on several counts, in that there does not seem to be a conscious impression of eye muscle activity, and that even if there were, then it would be unreasonable to expect anaesthesia as a consequence since no anaesthesia occurs in the tactile domain as a result of sensations of movement of the hand, and neither is there any anaesthesia as a result of slow eye movements. Dodge also suggested that Holt's hypothesis was unlikely to be able to explain the inability to see stimuli presented <u>during</u> a saccade since the latency of transmission of visual impulses was probably sufficiently long that visual signals would reach the higher centres responsible for perception only after the end of a saccade i.e. mostly if not entirely after the period of effect of any signals from the eye muscles.

Woodworth (1906) claimed that vision during a saccade 'does not differ essentially from vision with the resting eye, or with the eye which is making a pursuit movement - given only the same retinal stimulation in the three cases'. He briefly mentioned several observations to support this generalization, but did not supply sufficient experimental details for the reader to be able to assess this evidence. The only point not already covered is that he claimed that the reaction time to stimuli presented during saccades was approximately normal - certainly not great enough to permit even a 100 msec period of central anaesthesia. The type of anaesthesia envisaged by Holt, however, would have lasted as long as 100 msec only for large eye movements of 40 degrees or more, so without further details this was hardly a significant point.

The conclusion from this early work was that any centrally mediated alteration of visual sensitivity during saccadic eye movement is small.

1.3 Quantitative studies of threshold elevation associated with active and passive image displacements

The main purpose of the following review is to examine critically the quantitative data, published before or during 1971, concerning threshold elevation associated with saccadic eye movement or pseudo-saccadic image displacement.

The question that will continually be asked of these data is whether they undermine the 'null hypothesis' that 'saccadic suppression' is entirely caused by a visual masking effect of the kind reported by MacKay (1970a, b). Suggestions are then made for further experiments to resolve the remaining uncertainties.

The term 'null hypothesis' is here used (following R. A. Fisher, 1935) to mean that explanation of the data which does not require the conjecture of any novel effect, but only the assumption than an already known effect is operative under the particular conditions in hand. An example of a null hypothesis in this sense would be the suggestion that the responses of single neurones in the inferotemporal cortex of anaesthetized monkeys to silhouettes of hands (Gross et al., 1972) can be accounted for by the sensitivity of the neurones to grating patterns of the appropriate spatial frequency, without assuming any response specific to the meaning of the pattern.

To approach the data in this way is not to be biassed in favour of any one of a number of equally viable explanations of the phenomena, but rather to adopt the conceptually conservative attitude expressed by

Newton when he wrote: 'We are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances.' (Principia Mathematica, Bk. III, 1686.)

In the case in hand it would be unreasonable to give equal weights to the conjectures of Volkmann and Richards on the one hand, and the hypothesis of MacKay on the other hand, regarding the origin of the elevation of threshold associated with saccades, since at least in photopic surroundings with contours in the near-periphery, MacKay's effect alone is sufficient to explain the effects reported. The hypotheses of oculomotor inhibition of the visual pathway and mechanical disturbance of retinal signal processing are thus redundant. Even if there were direct evidence for the existence of either of these effects, which there is not (see below and Chapter Two for a discussion of these questions), these hypotheses would be less logically attractive than MacKay's since they could explain only the threshold elevation occurring in association with _active_ image displacements (i.e. saccadic eye movements), whereas MacKay's effect can account for the elevation of threshold associated with both active and passive image displacements.

1.3.1 Elevation of threshold associated with active image displacement in photopic surroundings

In 1962 Frances Volkmann published the results of what has since been acknowledged to be the classic quantitative study of saccadic suppression. Subjects made 6 degree saccades over a uniform photopic background (75 cd/m^2) of unspecified extent, but certainly less than 28 degrees in diameter, since the components of a corneal reflection eye-movement monitoring system were mounted at an eccentricity of 14 degrees. The test stimuli (a matrix of four 7' 31" diameter dots, 33' apart; or one of 16 common three letter words (letters 30' 42" high and 3' 40" wide)) were presented for 20 microseconds, at the midpoint of the saccades. Blurring was negligible with such short flashes. In control observations the test stimuli were presented foveally with the eyes stationary at the left and right fixative points.

Both 'yes-no' and 2-epoch forced choice paradigms were used and found to give similar results. (This finding appears not to have been noticed by Pearce and Porter (1970), who devoted an entire experiment to showing that saccadic suppression cannot be due to a shift of criterion for identifying flashes which are presented during a saccade.) Three subjects were used. Threshold elevations of 0.6, 0.5 and 0.4 log units were found for the three subjects.

In the light of MacKay's (1970a) observations, it is possible that the displacement across the retina of the image of the mounting of the corneal reflection system, and other peripheral objects, was sufficient to produce the threshold elevation observed. The mounting of the corneal reflection system, rather than the light from it, must be suspected, since Volkmann et al. (1968) were able to show that the threshold elevation persisted when the visible light originally used to provide a corneal reflection was replaced by ultraviolet light. Since it is not known how the magnitude of MacKay's effect varies as a function of the eccentricity of the peripheral contour, this suggestion is somewhat speculative. (See Chapter Four for the results of experiments on this subject.)

1.3.2 Parametric investigation of elevation of threshold associated with active image displacements

Also in 1962, Latour published a brief communication on the time-course and magnitude of the threshold elevation associated with 15 degree saccades. The full results were published in 1966 (and incidentally do not bear out the details of the earlier report, notably not confirming the large magnitude of threshold elevation reported in 1962). Latour's experiments were all made with a uniform background of 60 degrees in diameter. Eye movements were monitored by an infra-red reflection system. The lamp and infra-red sensitive diodes used were mounted on spectacle frames at an incompletely specified angular position. From Latour's sketch of the experimental arrangement the position appears to have been about 30 degrees lateral to the line of sight of the left eye. The effects were investigated of varying the background luminance from 0.007 to 7.8 cd/m^2, of varying the size of the saccades from 6 to 20 degrees, and of using smaller (7 min arc diameter) or larger (40 min arc) flashes. The test flashes (of duration 0.8 microseconds) were presented 4 degrees above the midpoint of the fixation lights, to avoid interaction with the fovea and blind spot. The method by which the experiments were conducted is rather neat, and worth describing. The test flash was presented at a number of intervals after the alternation of fixation light illumination which indicated when the subject was to saccade, and at two intensities differing by 10 per cent. When the flash intensity was correctly set, the experiment yielded two 'dip' curves when flash visibility was plotted as a function of time between the flash and onset of the saccade, one dip curve for each flash intensity. By constructing a staircase between the two curves and plotting the number of steps as a function of the time of the test flash the timecourse of the threshold elevation was obtained. Latour showed that the maximum overall error incurred by this method (for a typical number of steps) was about 30 per cent.

Latour's main result was that the maximum elevation of threshold associated with saccades was not 0.5 log units, but 0.25 log units. This is an amazingly overlooked finding. One can only assume either that researchers have not read Latour's monograph, or that like the author of the present work they failed to notice that Latour plots his data on a linear not a log scale, and so misinterpreted the numbers on the ordinates of Latour's graphs. The magnitude and temporal extent of threshold elevation decreases as saccades decrease in size. With 15 degree saccades (for which most data were collected) the timecourse of the threshold elevation is from 100 msec or so before the saccade onset until 40 msec or less after saccade onset. Maximum threshold elevation occurred for flashes presented during the saccade or slightly before saccade onset, and thereafter flash visibility increased, often rapidly so, with time. It was shown that the size of the test flash was a major factor governing the form and magnitude of threshold elevation. With the larger test flash roughly comparable magnitudes (0.2 to 0.25 log units) and timecourses of threshold elevation were found at all levels of background luminance (2 subjects). With the smaller test flashes, on the other hand, there was almost no elevation of threshold at higher background intensities. For flashes presented during (or in one case just before) the saccade a <u>depression</u> of threshold was observed. This depression of flash threshold was, with one subject, as much as 0.8 log units in one condition. At lower background intensities, elevation of threshold by up to 0.25 log units was observed (2 subjects). According to Latour this result cannot be explained by a variation of sensitivity to the 7 min arc flash with retinal image position, since sensitivity was measured and found to vary negligibly (no data presented).

Latour also showed that threshold elevation occurred in association with the rapid phases of optokinetic nystagmus.

In conclusion, Latour's data are consistent with the hypothesis that the elevation of threshold associated with saccadic eye movement is caused by the peripheral retinal image displacement produced by a saccade. It is noticeable that Latour obtained much smaller elevations of threshold than many other workers, and this may be related to the large size of his background field (although under some conditions Mitrani (see below) obtained large threshold elevations with a large background field). Also, it is to be noted that Latour found that the timecourse and magnitude of threshold elevation depended greatly on the diameter of the test flash used. It is hard to see why a central inhibition of vision should act selectively to impair the visibility of stimuli of one size rather than another, whereas it is conceivable (though not something that one would have predicted) that a masking effect might exhibit this strange behaviour.

1.3.3 Elevation of threshold and reduced pupillary light response associated with active image displacement

Zuber and Stark (1966) reported a similar timecourse for saccadic suppression to that obtained by Latour. They used twenty degree saccades made in a scotopic environment. The twenty microsecond flash, one degree in diameter, was always presented midway between the fixation points. Eye movements were monitored by infra-red light reflection from the iris-sclera boundary. In addition to plotting the dip in frequency of seeing of the test flash, they also compared the threshold for perception of flashes presented either just after the onset or just after the offset of the saccade, finding that the threshold for perception of flashes presented during the saccade was about one log unit higher than that for perception of flashes presented just after the saccade. They pointed out that in both cases the flashes were about ten degrees from the fovea, and so variation in retinal sensitivity was unlikely to have seriously undermined the finding (the flashes were not sufficiently far from the fovea ever to fall on the blind spot). In a second paper Zuber, Stark and Lorber (1966) reported the finding that the pupillary light reflex to a twenty degree diameter flash was much diminished, if not abolished, when the flash was presented during eight degree saccades in a 'dimly lit field', and they compared the timecourse of this effect with the timecourse of dip in the frequency of seeing of the same flash. The timecourses were somewhat similar but by no means identical, the pupil reflex effect tending to last longer than the perceptual effect.

They also presented data suggesting that flashes delivered during microsaccades were not seen, and that the threshold for the perception of flashes was raised when the flashes were delivered at about the same time as the fast phases of vestibular nystagmus.

The size of the threshold elevation reported by Zuber and Stark is larger by a factor of about two than that reported by Latour using saccades of similar size in similar conditions. There is no obvious explanation for the discrepancy, and lacking more evidence one must keep an open mind. It is worth pointing out. however, that Latour's experiments were, as far as one can judge from the data presented by both sets of authors, much more extensive than Zuber and Stark's. For example, Zuber and Stark twice publish a figure showing data obtained with one subject, in which frequencies of seeing are estimated from the presentation of only ten flashes. There is no remark that this experiment was repeated with similar results, either in the same or other subjects.

It is no surprise to find that there is no pupillary response to stimuli which are not seen. The attenuation of pupillary reflex found by Zuber et al. could equally well be explained by any of the hypotheses which have been put forward to explain the elevation of visual thresholds associated with saccades. It is of interest that Zuber et al. showed that there is also a diminished pupillary response to the second (weaker) flash of a flash pair, when the second flash is less visible than the first flash.

1.3.4 Elevation of threshold associated with microsaccades

Beeler (1967) reported a 0.4 log unit elevation of threshold for flashes delivered within 75 msec of microsaccades in a scotopic environment (10^{-3} cd/m^2). Krauskopf, Graf and Gaarder (1966) found that there was no detectable elevation of threshold for flashes delivered during microsaccades in darkness. (Their experiment was sensitive enough to have revealed an effect with magnitude rather less than 0.1 log unit.) These data raise no conclusive evidence against our null hypothesis that the threshold elevation associated with all saccades, even microsaccades, can be attributed to MacKay's effect. It is, however, clearly worth studying whether MacKay's effect does in fact occur with pseudo-microsaccadic image displacements. (See Chapter Three for the results of experiments on this subject. In that chapter it is pointed out that Beeler's experiment may be subject to an artefact which could well undermine the validity of the data.)

1.3.5 Timecourse of elevation of threshold associated with active image displacements

Volkmann, Schick and Riggs (1968) studied the timecourse of the elevation of threshold associated with saccades made under similar conditions to those used by Volkmann (1962). As was mentioned previously, they found that the visibility of flashes presented up to 50 msec before a saccade was decreased, with flashes presented during the saccade being least visible (three subjects). The drop in visibility of the test flash occurred for flashes presented earlier before right-ward saccades. This effect occurred regardless of which eye was used to view the stimulus. It could not be accounted for by a difference in the speed of right-ward and left-ward saccades, nor by the asymmetrical position of the corneal reflection light source, since it persisted when the experiments were repeated using ultra-violet reflected light.

1.3.6 Elevation of threshold associated with passive eye displacement

In the same year Richards (1968) demonstrated an elevation of threshold of about 0.5 log units associated with passive displacements of the eyeball, achieved by tapping the eyeball (only the return phase of the eye movement was used). In the following year, he published the results of an extensive study (Richards, 1969) claiming to show that saccadic suppression was the result of an impairment of retinal signal processing produced by shearing of the retina occurring during a saccade. He showed that the light from a flash presented just after a five degree saccade is most easily detected not when the light passes through the centre of the pupil but when it passes slightly eccentrically, so as to fall on the retina at an angle of some two degrees to the normal i.e. an aberrant Stiles-Crawford effect was obtained, suggesting a two degree tilt of the cones.

Richards also investigated the variation of threshold elevation (for flashes presented 40 msec after the onset of a five degree saccade i.e. just after the end of the saccade) with luminance of the background (varied from 0.03 to 300 cd/m^2). In this and in other experiments, the method of adjustment was used.

The test flash was a square of side one degree and always appeared in foveal view on a background of diameter 11 degrees. It was found that elevation of threshold decreased with decreasing luminance, to non-significant values at the lowest luminance used (0.03 cd/m^2). The form of the decrease suggested that the occurrence of the saccade effectively increased the background luminance by a constant proportion (of between 0.5 and 1.0 log units for the two observers used).

Following up this finding Richards investigated the effect of the colour of the flash and background on the magnitude of the threshold elevation obtained. He found that the thresholds for longer wavelength light (580 nm) were more elevated than for shorter wavelength light (460 nm) with a background of 3 cd/m^2 and colour temperature 2,500 degrees K. For the shorter wavelength flashes the elevation of threshold began earlier. If the background wavelength was altered, the test flash wavelength at which maximum threshold elevation occurred shifted to match the background.

Richards therefore argues that the background is the critical factor in saccadic suppression. The weakness of this argument, as Richards mentions, is that he did not investigate the timecourse of threshold elevation as a function of background luminance.

In a final experiment Richards made a fascinating observation, never to this author's knowledge commented on by later workers. He showed that the transient peaks of threshold elevation associated with the lighting and extinction of a background field (Crawford, 1947 and many others) did not occur when the test flash was preceded by a saccade. In the latter case, the extent of the threshold elevation associated with the presence of the background field was of course greater, but there were no 'on' and 'off' peaks, and furthermore the recovery of sensitivity upon extinction of the background was more rapid than without a saccade. Richards suggested that these phenomena might reflect the opening of the Dowling (1967) feedback loop mechanism in retina, on Richards hypothesis caused by mechanical shearing of the retina. There is, however, no evidence at all that mechanical shearing of the retina has any such effect, and Richards' effects could equally well be attributed to the displacement of the boundary of the background field over the peripheral retina.

1.3.7 Timecourse of threshold elevation as a function of retinal position

Mitrani (1970) studied the timecourse of the threshold elevation associated with 13 degree saccades as a function of the retinal location of the test flash (duration 2 msec). He claimed to show that the timecourse varies in such a way with retinal location that the locus of maximum flash sensitivity is fixed in space, not on the retina, at least during the course of a saccade. The test stimulus was a vertical column of five 50 min arc diameter spots, separated by gaps 60 min arc high. This stimulus could be presented 130, 260, 390, 520, 650 or 780 min arc to the right of the left fixation point, and in each case could be presented 10, 15, 20, 25, 30, 35, 40, 45, 50 or 55 milliseconds after the onset of the saccade, whose duration was approximately 55 msec. Mitrani's finding was that at any time during the saccade, stimuli presented further to the right (in space, not on the retina) are more easily seen, except that at the rightmost stimulus position, the flash is less well seen than when it is presented at the position immediately to the left of that point. Having obtained this result, he then plots the position of maximum retinal sensitivity as a function of time, and of necessity finds that it exactly parallels the timecourse of the saccade itself. For some entirely mysterious reason Mitrani used Yarbus' (1965) data on saccade timecourses to accomplish this transformation of his data, but then compares the transformed data to a saccade timecourse measured in his own i.e. Mitrani's experiments. The only significant effect of this is to shift the absolute retinal position of the point of maximum sensitivity at any time to the right about two degrees, since Yarbus' and Mitrani's timecourses are approximately parallel during the part of the saccade with which Mitrani is concerned.

The question which the data raise and which Mitrani does not answer, is whether the flashes would have been equally visible at all positions to the stationary eye. Without this control the results could possibly be accounted for by a slight non-homogeneity of the background field luminance, or by a slight imbalance of the flash intensities at the different flash positions, without having recourse to some complex spatio-temporal variation of saccadic suppression across the retina.

Even if Mitrani's effect proved genuine, it is possible that such an effect could be produced by a retinal masking effect of the kind discovered by MacKay, since another way of saying that the position of maximum flash sensitivity remains fixed in space during a saccade is to say that the position of maximum flash sensitivity remains fixed relative to peripheral contours. If the displacement of these peripheral contours over the retina during a saccade is the source of the elevation of visual thresholds associated with saccades, then it is quite possible that the least affected retinal region should sweep across the retina in phase with the peripheral contour during a saccade.

1.3.8 Elevation of threshold associated with passive image displacements

In MacKay's experiments (1970a, b) the stimulus parameters were chosen to be similar to those of Richards (1968), except that in MacKay's experiments the subject's eyes remained stationary and the field was displaced pseudosaccadically by means of a mirror mounted in the beam of the projector providing the illumination of the field (10 degrees in diameter, 30 cd/m^2 luminance). The displacement (3.2 or 4 degrees to the left) was accomplished in 10 msec or so, or in the later experiments 40 msec. The test flash was two degrees in diameter and of duration less than 100 microseconds, not milliseconds as printed in MacKay (1970a). In the first series of experiments the subjects fixated a point midway between the positions of the centre of the background field before and after the displacement. Flashes were delivered periodically, once per second, and the time of occurrence of the flash relative to the field displacement was varied haphazardly from trial to trial. The flash was presented either at the fixation point, or 1.6 degrees to the left or right of the fixation point i.e. at the initial or final position of the background field centre. MacKay found that the flash was frequently not seen if presented at about the same time as the displacement of the field. The drop in frequency of seeing of the test flash began for flashes presented some forty milliseconds before the onset of the displacement, and lasted until eighty milliseconds after the displacement onset, or longer. It should be noted that the boundary of the displaced field never approached closer than 2.4 degrees from the margin of the central test flash, or 0.8 degrees from the margin of the eccentrically presented test flash. This finding showed that it was not necessary to invoke either the concept of central inhibition or mechanical disturbance of retinal signal processing in order to account for the retroactive nature of saccadic suppression.

Neither is it necessary to violate the concept of causality in order to explain the retroactive nature of saccadic suppression, or of MacKay's effect, since Levick and Zachs (1970) have shown that even in retinal ganglion cells the signals generated by faint flashes may last for up to 70 msec.

MacKay found that the retinal position of the test flash influenced the magnitude of threshold elevation, the central test flash being more visible than the eccentrically viewed flashes. The central flash is of course at the greatest mean distance from the displaced contour.

In a second series of experiments the flash was presented in a fixed position relative to the displaced field (at its centre). The retinal image sequence was in this case closely similar to that produced by a saccadic eye movement. Subjects fixated either the central point or points 1.6 degrees to the left or right of that point. Results were similar to those obtained with the flash fixed in space, except that the flash was less visible in central fixation than in eccentric fixation.

When the experiments were repeated with a less rapid displacement, lasting about 40 msec, similar results were obtained when the flash was fixed in space to those obtained with the 10 msec displacement, but when the flash was fixed relative to the field, a transient recovery of flash visibility was consistently obtained for flashes presented between 20 and 60 msec after the onset of the displacement.

In a second communication (MacKay, 1970b), it was shown that some elevation of threshold persisted when the stimuli were presented dichoptically, the flash being presented to the left eye and the displaced field to the right eye. Again, visibility of the test flash began to fall for flashes presented up to 40 msec before the onset of the displacement. An interesting feature of the findings was that the drop in visibility of the test flash was greater for fixation to left than for fixation to the right of the mean centre of the displaced field (the drop was greater still for central fixation but this was to be expected from the previous experiments). This result was not explicable by variation of retinal sensitivity, which was negligibly assymetric.

In none of these experiments was MacKay concerned to make precise quantitative measurements of the threshold elevation, but rather to demonstrate that retroactive elevation of threshold could be generated by the retinal image displacement consequent on a saccade in illuminated surroundings, and that this effect may well not be retinal in origin. MacKay (1970b) noted merely that 'the maximum elevation of threshold measured was of the order of 3 dB'. It cannot be concluded from MacKay's experiments that the dichoptic effect is as strong as the monocular effect, although it seems to be of comparable magnitude.

The main point to be remembered from the details of MacKay's experimental results is that the magnitude and timecourse of threshold elevation vary with the position of the test flash and the speed of the displacement, so one should be wary of comparing the results of experiments in which these variables were not matched.

1.3.9 Elevation of threshold as a function of luminance and contrast

In 1971 Mitrani et al. published a paper with the delightfully clear and compact title 'Is saccadic suppression really saccadic?'. Flashes of unspecified size (perhaps one degree in diameter, as in the later papers) and of seven milliseconds duration, were presented on a uniform background of diameter fifty-three degrees, both with the eyes stationary and 10 msec after the onset of an eight degree saccade. The test stimulus position was linked to the output of the photoelectric eye position monitor in such a way that the test stimulus moved with the eye and was not blurred, in spite of its long duration. The experiment was performed at three levels of background luminance: 4×10^{-2}, 2 and 4 cd/m^2, and in a fourth condition in which large irregularly-shaped black figures were superimposed on the 4 cd/m^2 background, except in the region between the fixation points. At the scotopic background luminance, no elevation of threshold was found for flashes presented during a saccade. With the 2 cd/m^2 background the elevation of threshold was 0.2 log units, with the 4 cd/m^2 background 0.45 log units and with the structured 4 cd/m^2 background the elevation of threshold was 0.7 log units.

The main criticism of this experiment is that the timecourse of threshold elevation was not studied, and so it is not possible to discount the suggestion that the failure to find threshold elevation at the lower luminance level is because the latency of the threshold elevation was altered at that luminance.

It will be noted that Mitrani's data differ from those of Latour (1966), obtained under similar conditions in respect of the size and luminance of the background field. While Mitrani finds a variation of threshold from 0 log units at a background luminance of 4×10^{-2}cd/m^2 to 0.45 log units at a background luminance level of 4 cd/m^2, Latour finds threshold elevation of from less than 0.2 to 0.25 log units at background luminance levels from 1×10^{-2} cd/m^2 to 8 cd/m^2, with no clear relation between background luminance and the magnitude of threshold elevation. There is no obvious reason for this discrepancy.

1.4 Suggested function of saccadic suppression

Much has been written about the possible function of saccadic suppression, chiefly by those attempting to relate the phenomenon to the stability of the perceived world during saccadic eye movement.

It has often been thought that in order to account for visual stability all evidence of the occurrence of a saccade must be eliminated from the visual pathway, and a central inhibition of vision during saccades would certainly be one way of partially achieving this object. This principle is, however, a mistaken one, as our experience in the tactile domain shows: it is possible to be simultaneously aware of the 'brushing' signals generated when one's hand moves across a surface, and also to perceive the surface as stable in space. MacKay (1973) has argued that for stability it is not logically necessary that the consequences of self-induced movement should be eliminated from the afferent inflow, but rather that the characteristics of this inflow should match those of the prescribed movement, within evaluative limits which are probably adjustable. Evaluation could be quite separate from the pattern recognition system, and its anatomical substrate might, for example, not be in the cortex at all but in the superior colliculus. (See MacKay (1973) for a full discussion of visual stability.)

Even if one were to grant the necessity of saccadic suppression for visual stability, it can easily be seen that saccadic suppression would not be sufficient to stabilize the perceived world, since account has also to be taken of the change of retinal location of objects which occurs after a saccade has been made. Probably in most normal visual conditions it is this change of location of stimuli which is the major event to be accounted for. For example, if one views a regularly patterned field of large angular extent which is suddenly displaced with a pseudosaccadic timecourse, a powerful impression of displacement occurs only if the displacement is not an integral multiple of the spatial period of the pattern. If the displacement is, for example, one period exactly, there is no sensation of displacement; although one is aware of some brief event as the displacement occurs, it has no clear directionality to it. This observation shows that there are conditions in which vision during a saccadic image displacement is irrelevant to whether the displacement is perceived as a displacement of the world or not, and thus shows that saccadic suppression could never completely account for the perceptual stability of the world when saccadic eye movements are made.

1.5 Conclusions from review: outline of experimental work

No published evidence was discovered which requires one to reject the null hypothesis that saccadic suppression is caused by the visual masking effect discovered by MacKay. There are, however, two further experiments which need to be done before one can be sure that MacKay's effect can account for the reported elevations of threshold associated with saccades of small amplitude, and saccades in environments uniform to large eccentricities. The results of experiments with small passive image displacements similar to those produced by microsaccades are reported in Chapter Three below, and an experiment examining the variation of MacKay's effect with the separation of test flash and displaced contour in Chapter Four below.

Having considered the question of whether MacKay's effect can account qualitatively for the elevation of threshold associated with saccades of all amplitudes, and in all field conditions used in experiments concerning 'saccadic suppression', a quantitative study was undertaken to examine whether factors other than MacKay's effect contribute to the elevation of threshold associated with voluntary saccades in illuminated surroundings. In these experiments (reported in chapter five below) the elevations of threshold produced by active and passive displacements of the retinal image were compared both in timecourse and magnitude. The experiments were performed in a nearly uniform visual environment, so as to minimize MacKay's effect.

Chapter six is concerned with some experiments examining what kinds of peripheral stimuli, other than displacement of a contour, will produce elevation of threshold for perception of central test flashes.

In chapter seven experiments are described which investigated whether MacKay's effect has an evoked potential analogue.

Chapter eight reports some experiments in which the effect of peripheral contour motion on central flicker sensitivity was examined.

Chapter two is a review of the literature describing physiological effects which may be related to saccadic suppression and MacKay's effect.

The final chapter of the thesis summarises the findings of the above experiments, discusses the papers on this subject which have appeared since the work was begun, and makes some suggestions for further work.

CHAPTER TWO

Possible physiological correlates of 'saccadic suppression' [1]

There are two categories of physiological literature directly relevant to the 'saccadic suppression' controversy. The first category describes experiments examining whether the excitability of the visual system is modulated concomitantly with saccades or other rapid eye movements in darkness or other conditions where the eye movements do not result in any retinal image displacement. These reports provide a direct test of the central inhibition hypothesis. The second category describes experiments examining whether displacement of objects in the periphery of the visual field modulates the excitability of visual units whose classical receptive fields are restricted to the unstimulated area in the centre of the visual field. These experiments bear on the physiological basis of MacKay's effect.

2.1 Modulation of visual excitability concomitant with rapid eye movements

The physiological experiments made under conditions most closely comparable to those in psychophysical studies of saccadic suppression are those employing alert intact animals. The results of experiments with primates should carry more weight than those with lower animals.

It is worthwhile keeping the results of experiments using spontaneous saccades (analogous to voluntary saccades in humans) separate from those of experiments in which the rapid eye movements were induced

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[1] This review was originally written in 1974. Papers which have appeared since then are discussed in Appendix 3, with the exception of those cited in section 2.2.1, which has been rewritten to take account of the rapid developments in research on this topic since 1974.

by vestibular stimulation, since the latter occur involuntarily, and so may have perceptual consequences different from those of voluntary saccades. The evidence for perceptual threshold elevation during rapid phases of nystagmus is rather scanty. No physiological experiments have been made with microsaccades. It is doubtful if either cats or monkeys normally make true microsaccades, since the smallest saccades observed in the untrained animal are about one half of a degree in amplitude (Pritchard and Heron, 1960; Steinman et al., 1973).

2.1.1 Modulation of excitability of LGN associated with saccadic eye movements

Non-retinal influences on the lateral geniculate nucleus have been briefly reviewed by McIlwain (1972).

2.1.1.1 Experiments with alert intact animals

There have been several studies of LGN excitability during rapid eye movements of the alert intact animal (Cohen, Feldman and Diamond, 1969; Malcolm, Bruce and Burke, 1970; Ogawa, 1972; Adey and Noda, 1973; Büttner and Fuchs, 1973; Noda and Adey, 1974; Doty, Lee, Bartlett and Sakakura, 1974; Noda, 1975). In only one of these experiments (Doty et al., 1974) was any significant modulation of LGN excitability found concomitant with rapid eye movements in darkness or uniform visual environments, either at the single unit or gross potential level. In several of these experiments it was shown, however, that modulation of excitability does occur in association with saccades in patterned visual environments.

No conclusion on this point can be drawn from Ogawa's experiments (1972) with alert squirrel monkeys, since his only comment on the visual condition of the animal is that the 'experiments were carried out with the animal in a light-adapted state'. The absence of any clear statement that the experiments were performed in darkness suggests that the experiments were carried out in illuminated surroundings to which the animal was adapted.

Cohen, Feldman and Diamond (1969) also studied LGN transmission in the alert animal (rhesus monkey). For the most part the rapid eye movements in these experiments were induced by stimulation of the mesencephalic or paramedian pontine reticular formation; but the authors also studied the effects associated with spontaneous saccades and rapid phases of caloric nystagmus. They reported that 'in alert animals in darkness, orthograde potentials induced in LGN by optic tract shocks were not significantly affected by reticular stimulation, saccadic eye movements, or quick phases of nystagmus'. Retrograde optic tract potentials evoked by LGN stimulation were enhanced by reticular stimulation only when the monkey was not fully alert, and were never enhanced by rapid eye movements. From the cases where quantitative data is presented it seems that modulations of excitability of 5 to 10% could have been detected. (See the lower graph in their Fig. 7.)

Malcolm, Bruce and Burke (1970) were able to confirm the earlier findings of Bizzi (1966a, b) and others, that the presynaptic component of the orthodromic response in LGN to optic tract stimulation is decreased in the PGO waves of low-voltage-fast-wave sleep in the cat. They showed, however, that during spontaneous eye movements of the same cats when they were awake in darkness neither the pre- nor the post-synaptic components of the orthodromic LGN response were significantly different from those obtained with no eye movements in the preceding 0.5 sec. When eye movements were made in a lighted environment, however, both the pre- and post-synaptic components were reduced, the former only very slightly (2-3%), the latter by about 15%. (The electro-oculogram was used to trigger the stimulus in the eye movement condition.) The cats were in all cases fully alert, as judged by the form of the EEG.

These results were repeated and extended in the experiments of Adey and Noda (Adey and Noda, 1973; Noda and Adey, 1974a, b). They used the preparation of Noda et al. (1971) in which during the experiments the awake cat lay in a hammock with its head restrained by bars passing through tubes permanently fixed to the cat's head with dental acrylic cement. It was sometimes necessary to give amphetamine to maintain alertness, since in this preparation the cat tended to fall asleep.

In shock-evoked-potential experiments (Adey and Noda, 1973) they found that in total darkness neither a presynaptic (t_1) nor a postsynaptic (r_1) LGN response, nor a presynaptic cortical response (c_1) were modified in the 300 msec immediately following a saccadic eye movement. (Components designated after Bishop and McLeod, 1954.) The optic tract shocks were of an intensity which evoked responses with 50% of maximum amplitude. The authors do not specify how they determined whether the cats were fully alert.

In an almost uniformly illuminated environment the postsynaptic LGN response and the presynaptic cortical response were slightly depressed, and in a strongly patterned environment (vertically orientated 2 degree wide dark stripes (5 cd/m^2) separated by 4 degrees wide light stripes (70 cd/m^2), the whole pattern subtending 60 x 45 degrees) the responses were markedly attenuated for about 150 msec following saccade onset. The presynaptic LGN response was however unchanged. Similar attenuation of the postsynaptic response could be produced by rapid passive movement of the retinal image, either at 200 degrees/sec or with a time course derived from the recorded electrooculographic signal produced by saccades. In these single unit experiments (Noda and Adey, 1974; Noda, 1975) the authors found no LGN cells, out of 450 recorded from, which changed activity in association with saccades in complete darkness. The authors do not say what would have constituted a just measurable change in activity.

It is just possible that small effects may have been overlooked by Adey and Noda. For example, careful inspection of Fig. 2 in Noda (1975) suggests that the sustained cell shown there may have been weakly inhibited during saccades in darkness (Fig. 2F). The spontaneous firing rate of the cell is too low (about 10 spikes/sec) for the absence of a small effect to be conclusively excluded. No average response histograms are shown, or indeed referred to.

In 73 units the activity induced by chiasmatic stimulation (set at a level for which there was an 80% probability of the unit firing with the eyes stationary) was found to be modulated with saccades only in a lighted environment. Activity of both sustained and transient units was decreased. The decrease of activity was greater with saccades in a highly patterned environment. The suppression of activity lasted about 200 msec, reaching a maximum effect about 100 msec after the onset of a saccade. The authors showed that there was a class of retinal ganglion cells which gave an after-discharge for about 100 msec following active or passive rapid image movements and suggest that these cells (probably transient cells from the latency of their responses and from their responses to stationary light 'off' and 'on') might mediate the LGN activity depression which followed saccades in light.

Büttner and Fuchs (1973) used light stimulation rather than optic tract stimulation. Their experiments employed rhesus monkeys (Macaca Mulatta) whose visual anatomy is much more similar to that of man's than the cat's, and so the results can with more confidence be related to human psychophysical data.

Each monkey sat with its head restrained at the centre of a large translucent globe which was illuminated by means of reflecting and diffusing surfaces lit by a 10 microsecond flash stimulator. The illumination of the translucent sphere was thus approximately uniform except in the regions at the extreme periphery of the monkey's visual field. The flash stimulator was run at rates from 1 to 25 Hz, to activate LGN neurons whose spontaneous activity was so low that small changes in their excitability could not be reliably observed. The pupils were dilated. Eye movements were monitored by the magnetic search-coil method (Fuchs and Robinson, 1966). In one of the four animals blinks were monitored. In the results for all animals data was excluded from the analysis when the eye movement record suggested that a blink had occurred. The state of alertness of the animal was judged by using the occurrence of slow rolling eye movements as the criterion of drowsiness. At the end of especially fruitful electrode tracks electrolytic marking lesions were placed. These were later identified histologically.

Of 202 units located in the dorsal region of the lateral nucleus, 191 (95%) exhibited no change of activity correlated with saccades. The results for 5 representative units suggest that changes of 10-20% could have been detected. The remaining 11 units exhibited small changes of activity. Of the 55 units isolated in or near the pregeniculate nucleus, however, 39 exhibited strong saccade related changes of activity in complete darkness. (The pregeniculate, orperigeniculate, nucleus is just dorsal to the LGN in the monkey.) These changes were much greater than those observed in the above 11 dorsal LGN neurons. The changes could be either activation of normally inactive units (17 units), or depression of the activity of normally active units (22 units). The change in pregeniculate neurone activity began on average 80 msec after saccade onset (though in some cases it began before the saccade) with a peak effect at a latency of 100 to 200 msec. 26 of the 39 above pregeniculate neurons responded to light flashes alone i.e. received a visual input. The size of eye movement was routinely investigated as a parameter. In most cases no significant variations with eye movement size were observed, but in some of the 11 dorsal LGN units exhibiting modulation of activity with saccades, larger saccades gave increased modulation. The simplest explanation of this phenomenon would be that the larger saccades brought the inhomogeneity of the extreme periphery of the field into the receptive fields of the neurons.

Doty et al. (1974) studied the potential evoked in the optic radiation of alert squirrel monkeys or macaques by optic tract stimulation. The optic tract shocks were triggered at a variable interval after the onset of spontaneous saccades or occurred repetitively at a frequency of 20 or 50 Hz. In darkness or uniform illumination both magno- and parvocellular components of the response were decreased when the shock was delivered between 30 and 100 msec after the onset of a saccade. The maximum decrement observed was 10-20%. In patterned light, however, the magnocellular component decreased as much as 50%. In some cases a smaller and later facilitory effect was present. The authors point out that transitions between wakefulness and momentary sleep produce much greater changes than those associated with saccadic eye movements in darkness or uniform illumination, and express the opinion that the relation of the observed effects to saccadic suppression is 'somewhat questionable'.

None of these experiments provides strong evidence of modulation of LGN excitability concomitant with saccades of the alert intact animal in darkness or uniform illumination.

It should be noted, however, that these results do not conclusively demonstrate that no modulation occurs. The results with optic tract shocks are inconclusive because this sort of stimulation probably excites optic tract fibres in a way that is completely abnormal, both in the temporal relation between firing in different fibres, and in the distribution of fibres activated. What is lacking is a physiological correlate of the psychophysical experiments i.e. an experiment in which the LGN response to just-suprathreshold light flashes (preferably patterned flashes) is examined as a function of time relative to a saccade. (The light flashes in Buttner and Fuchs' experiment were equivalent to a luminance of 0.85 cd/m^2 when repeated at a frequency of 60 Hz, so were considerably above threshold for a substantially dark adapted monkey.) According to Jacobs (1965), working with the lightly anaesthetised squirrel monkey, luminance steps of 0.5 log units cause a change of the order of 50 to 100% in the firing rate of LGN neurons (at adapting luminances of 0.02 to 2 cd/m^2, with a 15 degree diameter unpatterned test field).Baker, Riva Sanseverino, Lamarre and Poggio (1969) obtained similar results with the unanaesthetised paralyzed cat. It should, therefore be possible to establish whether the response of LGN cells to flashes say 0.5 log units above threshold was modified by an amount equivalent to more than say 0.1 log units change of flash intensity.

2.1.1.2 Experiments with encéphale isolé animals

A number of workers have investigated the excitability of the LGN during eye movements in the unanaesthetised encéphale isolé animal. In this preparation the animal is usually reckoned to be in an awake state, as judged by the form of the EEG, the presence of tone in the extraocular eye muscles, and the occurrence of spontaneous eye movements in reaction to visual and auditory stimulation.

Corazza and Lombroso (1971) observed bursts of multiunit activity in the optic radiation and corticofugal projection, but not in the optic tract of encéphale isolé cats in total darkness. These bursts of activity were always found to occur in association with bilateral rapid eye movements. Single units in the LGN were also observed to give bursts of activity shortly after spontaneous rapid eye movements (there is no indication of how many units were recorded from). The authors found that both the bursts of multiunit activity in the optic radiation, and the modulation of LGN unit activity, always followed the onset of rapid eye movement, as indicated by the electromyogram of the extrinsic eye muscles. Corazza, Lombroso and Duffy (1972) found, however, that the latency of the multiunit activity in the optic radiation associated with saccades in darkness (30-60 msec or more) was short enough to precede the afferent barrage resulting from rapid eye movement in light, which had a latency 50-70 sec longer than the above activity. Thus the effect observed 'anticipates' the retinal consequences of rapid eye movement.

The authors showed that proprioceptive outputs from the extraocular muscles, or other extravisual outputs from the eye, could not be the cause of the effects since sudden passive mechanical movement of the eyes did not produce the effects, and also since the effects did not occur in conjunction with 'unilateral rapid eye movements'.

Since Büttner and Fuchs, and Adey and Noda were not able to obtain such results in the alert intact animal, the null hypothesis must be that the encéphale isolé preparation as used by Corazza et al. is not equivalent to the normal alert state. The most obvious possiblity is that the animals were in some semi-alert state where alertness was fluctuating, partly in relation to auditory stimulation (the animal's enclosure was not sound-proofed), partly spontaneously. The bursts of activity would then be due to arousal which was accompanied by a saccade, rather than to the occurrence of the saccade itself. The authors do state, however, that 'generally, the spontaneous eye movement appeared unrelated to acoustic or somesthetic stimuli . . .'.

Jeannerod and Putkonen (1971) and Montero and Robles (1971) also observed modulation of LGN excitability associated with rapid eye movements in the encéphale isolé cat and rat respectively. The eye movements were in both cases induced by abnormal activation of the vestibular system (see below).

Jeannerod and Putkonen occasionally found modulations of LGN unit activity associated with spontaneous saccades (see their Fig. 8), but their results are mostly for the effect on LGN firing of the after-nystagmus produced by electrical stimulation of the vestibular nuclei. This is of course a very unnatural stimulus, and may have other effects than to produce a very consistent and sustained nystagmus (which could last for several minutes).

The authors do not say anything about the state of the animal except that the electrical stimulation was 'alerting', so there is some room for doubt that the animals were in an awake state.

Of 81 units tested in darkness, 42 (51%) exhibited changes of activity time-locked to nystagmic eye movements in darkness. (The 'dark' condition in these experiments was created by placing a black plastic foam mask over the eyes.) Twenty-six units increased their activity, 16 decreased their activity. In some of the neurons whose firing rate increased, the modulation was obvious enough to be seen in the raw data. The latency of the effects was long: the mean latency of the onset of the modulation was 95 msec after the beginning of the fast phase of nystagmus (range 40-200 msec), the mean latency of the maximum effect 195 msec (range 160-310 msec). The delay was longer for the slower fast phases occurring at the end of a prolonged afternystagmus. The latency of these effects is almost certainly too long to interfere at the level of the LGN with visual signals resulting from stimulation of the retina during a saccade.

Montero and Robles immobilised the left eye of the grey rats used in their experiments by cutting the extraocular muscles and gently pressing a small ring, attached to the headholder, into the limbus of the eye. This eye was stimulated. Eye movements were recorded from the freely moving right eye. They do not say how this eye was covered, although it is quite vital to the interpretation of the results that this eye should have been completely un-stimulated during the eye movements. They also did not have any method of directly examining whether there were any residual movements of the left eye. They agree that: 'the fact that saccadic influences were obtained in responses from off-center cells argues strongly against the possibility that the effect observed in these experiments could be due to any residual movement of the stimulated eye . . . since these cells respond during the absence of light on their receptive fields, i.e. in a period when the campimeter is homogeneously darkened.' They do not, however, clearly say that the responses were tested in total darkness.

The eye movements were induced by unilateral labyrinthectomy, which like the method of Jeannerod and Putkonen, is highly artificial and may introduce other effects besides a persistent nystagmus. The animals were given amphetamine (0.5 mg/kg) to prevent drowsiness.

The activity of cells, histologically verified to be in LGN, was studies during stimulation of their receptive fields by moving bars and flashing spots. The responses of 14 'on' and 'off' centre antagonistic surround cells to stationary or moving stimuli was decreased, typically by 20%, after fast phases of nystagmus. The decrement began 30-40 msec after the onset of the fast phase, and lasted until 120-200 msec after the onset of the fast phase. The response of non-direction-sensitive 'on-off' cells was increased after fast phases of nystagmus. These effects were rather larger than in the concentric cells. In 7 directional 'on-off' units it was found that when each cell was stimulated with a grid moving in the preferred direction for the cell, only the units whose preferred direction had a component in the direction of the fast phase of the nystagmus showed a strong modulation (decrease) of activity. If this conclusion could be firmly established it would be the only clear evidence of oculomotor effects on the geniculo-striate visual system related to the direction of the eye movements. Unfortunately, this result is just what one would expect if residual eye movements occurred.

Not all units recorded from exhibited modulation of activity with rapid eye movements, and in at least two cases ('on' centre cells) this effect could not be put down to the nystagmus frequency being 'low and irregular and saccadic eye movements weak'.

It is extremely difficult to reach a definite conclusion regarding these experiments with encéphale isolé animals, since most of them differ in more than one respect from the experiments with awake animals. It does seem, however, that in the absence of clearer evidence, the alertness of the animals in Corazza et al.'s experiments is to be doubted. It is not clear whether the effects reported by Jeannerod and Putkonen and by Montero and Robles are due to the animals not being in a normal alert state, or to the unnatural methods of producing nystagmus, or to some genuine difference between the effects of spontaneous saccades and the fast phases of nystagmus. It may well be that there are modulations of excitability of the LGN associated with the fast phases of normal nystagmus in the alert intact animal, but this remains to be proved.

Kawamura and Marchiafava (1968) showed that 'eye tracking' was associated with modulations in excitability of the LGN of unanaesthetised mid-pontine pretrigeminal cats. It has been claimed that animals prepared in this way can be in an awake state (Batini, Moruzzi, Palestrini, Rossi and Zanchetti, 1959). Whether this is so or not, it is far from clear that the effects observed by Kawamura and Marchiafava could not be due to purely visual interactions at the LGN. It has, for instance, been shown by Hayashi (1972) that similar depolarizations of intrageniculate optic tract fibres can be produced by rapid motion of contours in the visual field of the stationary eye.

2.1.1.3 Experiments with sleeping animals

The only relevance to this subject of the well-established modulation of LGN excitability in deep sleep (Bizzi, 1966a, b; Iwama and Sakakura, 1965) would be if the existence of this effect provided evidence of a direct and specifically oculomotor control of LGN. From the latency of these effects, however, it is clear that they are mediated by polysynaptic pathways (Bizzi and Brooks, 1963), and there is no way in the sleeping animal to tell whether the excitability changes of the LGN are a consequence (a) of the occurrence of rapid eye movements per se, or (b) of some larger pattern of 'activity' of which saccades form only a part.

2.1.1.4 Experiments in which eye movements were induced by stimulation of the reticular formation

In the anaesthetised animal eye movements do not occur spontaneously. Several authors have therefore sought to examine the effects of eye movements on the excitability of the LGN in anaesthetised animals, by using mesencephalic or pontine reticular formation stimulation to induce eye movements. There have also been several studies of the effects of reticular stimulation on LGN excitability in alert or unanaesthetised _encéphale isolé_ animals.

The main difficulty in interpreting the results of these experiments is that the brain stem region which when stimulated produces eye movements is also the location of the 'reticular activating system', which is involved in the control of sleep, wakefulness and level of alertness of the animal. As Bender and Shanzer (1964) point out when discussing the results of extensive stimulation and lesion experiments with alert or cervically transected unanaesthetised monkeys:

> 'In plotting the oculomotor pathway one notes that its location in the brainstem is almost the same as that of the reticular activating system. Certainly the 'core' of this system is situated in the tegmentum of the brain stem, on the two sides of the median plane. This is the same region which on electrical stimulation or lesion causes alterations in eye movements.'

It is therefore difficult to be sure that the effects on LGN excitability of reticular formation stimulation arise from the activation of the eye movement system specifically, and not from some alerting system, of which the occurrence of a saccade is but a part.

In fact the results obtained fit better the concept that the observed modulations of excitability of LGN are due to alerting. In a very extensive study (employing 82 squirrel monkeys and macaques) Doty et al. (1973), Bartlett et al. (1973) and Wildon et al. (1973) showed that in the anaesthetised animal, reticular formation stimulation produces modulations of LGN excitability which are usually biphasic (a short duration inhibition followed by a more sustained facilitation), but can be wholly inhibitory or wholly excitatory, depending on the location of the stimulating electrode. In the awake, alert animal, however, no such effects could be found. The same lack of modulation of LGN excitability by reticular formation stimulation in alert animals has also been observed by Dumont and Dell (1960) and Cohen et al. (1969). A similar lack of modulation of LGN transmission was noted by Singer and Drager (1972) in intracellular recordings in the lightly anaesthetised cat. They say that

> 'When anaesthesia was light the transfer ratio (number of action potentials/number of optic tract EPSPs) was often close to 1 before MRF stimulation. In this case, MRF stimulation caused little or no increase in firing rate.'

If however, an animal is not fully alert, then any arousing stimulus will augment lateral geniculate excitability. Meulders and Godfraind (1969) showed, for example, that somatic stimulation could increase the response to visual stimuli of geniculate units in the awake intact cat.

2.1.1.5 Rapid-eye-movement-related gross potentials recorded in the LGN

A very large number of workers have observed eye movement related field potentials in the LGN since the original reports of such potentials in the sleeping cat (Jouvet and Michel, 1959; Bizzi and Brooks, 1963; Hendley, 1963; Mouret, Jeannerod and Jouvet, 1963). Several authors, following Bender and Shanzer's report in 1964, have shown that similar LGN potentials related to rapid eye movements exist in the alert animal in total darkness.

These rapid eye movement related potentials in the alert animal are generally smaller (Brooks, 1968; Brooks and Gershon, 1971) and may be less widely distributed (Jeannerod and Sakai, 1970) than those of paradoxical sleep. They are not due to any consequence, retinal or proprioceptive, of the eye movement itself, since they persist after bilateral optic nerve section (Brooks and Gershon, 1971; Munson, 1974), or after the extraocular muscles have been cut (Brooks, 1968) or the animal paralysed (Brooks, 1968; Feldman and Cohen, 1968).

According to Feldman and Cohen (1968) 'every rapid movement of the eyes in the dark, whether a saccade or a quick phase of nystagmus, is accompanied by a potential change in the LGN', and other authors have also found that the potentials are not restricted to one class of rapid eye movements.

It is less clear, however, that rapid eye movement related potentials can be recorded at all points within the LGN. Ogawa (1972) mentions that in 2 out of 6 animals LGN potentials related to eye movements could not be detected at the electrode position used. Doty (personal communication, 1974) says that eye movement related potentials are not present at all loci in the LGN. Feldman and Cohen (1968) investigated the distribution of rapid eye movement related potentials in the paralysed encéphale isolé monkey. They found that the potentials were of largest amplitude in the dorsal LGN or in the pregeniculate region (just dorsal to the LGN), but 'eye movement responses in darkness were widely distributed throughout the LGN'. Their electrode positioning technique resulted in very few samples of the rostral portion of the LGN, however. Also, in the ventral portion of the LGN eye movement related responses were sometimes absent, frequently at points where the response to light flash was of maximum amplitude.

Feldman and Cohen consider that the pregeniculate could not be the source of all the eye movement related potentials observed in or near the LGN.

They found that potentials similar to those associated with rapid eye movements could be evoked by blinks or auditory or somesthetic stimuli while the eyes were stationary. When a series of touches or claps was given, however, usually only the first stimulus evoked an

LGN potential. They point out that a similar habituation effect was not seen with repeated rapid eye movements, whether spontaneous or vestibularly induced. It is therefore difficult to argue that the potentials associated with rapid eye movements are entirely due to an arousing mechanism of which a rapid eye movement is a part, since in that case the potentials should habituate when the animal is fully alert. Feldman and Cohen also found that the amplitude and form of LGN eye movement-related potentials did not vary with eye movement direction, duration or velocity.

A crucial question concerning the 'geniculate' slow waves seen in alert animals in darkness is whether they arise in the LGN itself, or whether they in fact originate in adjacent structures i.e. the pregeniculate. Since there is some indication that the distribution of 'geniculate' slow potentials changes between different states of the animal (i.e. awakeness and paradoxical sleep), and since there is some possibility that <u>encéphale isolé</u> animals are not in a normal waking state, then it is necessary to repeat the experiments of Feldman and Cohen with alert intact animals before coming to the conclusion that there is a paradoxical difference between the single unit and slow potential activity of the LGN during rapid eye movements. On the other hand it is of course possible that the single unit findings are not representative, and that further single unit experiments will reveal either that there is modulation of single unit activity under conditions not so far tested (i.e. with say low intensity patterned light flash stimulation) or in a class of single units e.g. very small cells, overlooked due to some sampling bias of the microelectrode experiments.

2.1.1.6 Anatomical pathways for oculomotor modulation of geniculate activity

It does not seem likely from the latency of the various eye movement related potentials observed in the LGN and adjacent structures that they are mediated by a monosynaptic pathway from the oculomotor centres in the brainstem. Jeannerod, however, considers that the effects might be mediated by the reticulo-thalamic connections observed by Scheibel and Scheibel (1958) and Bowsher (1970). (Jeannerod, 1972.) There is some controversy about whether there are in fact such direct connections from the brain stem reticular system to the LGN. Szentagothai (1972), despite numerous careful searches, has been unable to show significant amounts of degeneration in the main laminae of the cat LGN after quite extensive lesions of the reticular formation of the brain stem. He was able to show, however, that there is an abundant projection from the mesencephalic and upper pontine reticular formation to the perigeniculare nucleus of the cat. He also found a projection from the frontal eye fields to the perigeniculate, and confirmed O'Leary's (1940) finding that cells in the perigeniculate typically send a number of recurrent collaterals into both laminae A and A_1 of the LGN. (The main axons join the optic radiation.) Thus oculomotor information from the reticular formation or from the frontal eye fields could be relayed to the LGN via the perigeniculate. The general significance of these findings in the cat is however unclear, since according to Szentagothai in primates there is no known neurone system corresponding to the cat perigeniculate.

2.1.1.7 The pregeniculate nucleus of the monkey and the ventral lateral geniculate nucleus of the cat.

The homologue in the cat of the nucleus in the primate sometimes called the perigeniculate (better, perhaps, called the pregeniculate) is apparently the ventral lateral geniculate nucleus (LGN_v) (Polyak, 1957).

It is possible that some neurones in both structures alter their firing in association with saccadic eye movement in the absence of visual stimulation. This is by no means certain, however. The findings of Büttner and Fuchs (1973) that some neurones in the macaque pregeniculate respond in association with saccades in darkness or in a uniform visual environment have already been mentioned. Putkonen, Magnin and Jeannerod (1973) found units in the LGN_v of the awake cat which had no visual receptive fields and responded selectively to direction of rotation of the animal in total darkness. Whether these units were really responding to the eye movements resulting from this stimulation rather than to the vestibular stimulation itself was however not clear. It should be pointed out that Adey and Noda (1973) mention in passing that they failed to find units in cat LGN_v similar to those reported by Büttner and Fuchs (1973) in the monkey pregeniculate.

According to Buttner and Fuchs little is known of the anatomical connections of the monkey pregeniculate nucleus. None of the pathways they mention seem to be suitable for carrying oculomotor information to the pregeniculate. In the cat, however, Sanderson (1971) has reported fibres coming from the superior colliculus to the LGN_v. These fibres may, however, be concerned with visual rather than oculomotor information.

2.1.2 Excitability of visual cortex during rapid eye movements

2.1.2.1 Single unit experiments

Wurtz (1969a, b) recorded from units in the deeper layers of the parafoveal projection area in the striate cortex of the awake behaving monkey. Of 188 units (some of which could have been LGN fibres) none responded to 20 degree saccades across a large (70 x 90 degrees) uniform field. When stimuli which elicited an excitatory response when delivered to the stationary eye were presented during a saccade, 60 units continued to give an excitatory response, 91 units gave no clear response at all, and 37 units were suppressed. The firing of the last group of units could be suppressed by eye movements across diffuse inhomogeneities of luminance on the screen, and was strongly suppressed by eye movements across a randomly textured field, but was never affected by saccades across a large uniform field.

Wurtz examined 142 neurons in all three of these categories, and found that all of them responded to rapid image movement in an identical manner to their response during rapid eye movement with similar velocity. There is thus no evidence at all for oculomotor modulation of the activity of neurons in this area of the visual cortex of the monkey.

Noda, Freeman and Creutzfeldt (1972) recorded from 357 units in areas 17 and 18 of the cortex of the awake cat. They found 39 neurons which responded during saccades across a patterned field, but did not respond to stationary stimuli, or to stimuli moving at velocities of up to 132 degrees/sec. 29 of these units were excited and 10 inhibited during and after saccades across a patterned field. Of 19 neurons tested in total darkness, 7 (all excited in saccades in light) gave saccade-related responses. These responses had a latency of 100-200 msec after saccade onset. The authors say that auditory effects were excluded by their experimental arrangement. The animals were alert as judged by the form of the EEG. It was sometimes necessary to give amphetamine to maintain alertness.

Valleala (1968) recorded from 32 neurons in the striate cortex of the alert macaque in total darkness, and found that the activity of the cells was often correlated with eye movements induced by caloric irrigation of the ear canals. Some cells fired only during the fast phases of nystagmus, others fired steadily except during the fast phases. The effects were not always obtained (whether the effects existed only in some cells or only at some times in all cells is not clear).

It seems fairly clear that the activity of most units in the striate cortex of the awake animal is not modulated by the oculomotor system during spontaneous rapid eye movements. It is possible that there are differences in the effects associated with spontaneous saccades and nystagmic fast phases, but this is not established by Valleala's preliminary investigation. It is not clear whether the difference between the findings of Wurtz and of Noda et al. is due to a species difference or to a difference in recording site (Noda et al. do not say whether the units they dound which exhibited saccade-locked discharges in darkness were in area 17 or 18). It should perhaps also be pointed out that there has been no investigation of whether the activity of units in the foveal projection of the monkey area 17 is modulated in relation to eye movements. More importantly, there is also no investigation of the activity of units in areas 18 and 19 in relation to eye movements, in either cat or monkey (except for the results of Noda et al., which do not distinguish between units in areas 17 and 18).

2.1.2.2 Gross potential experiments

Several authors have reported rapid eye movement related potentials in the visual cortex of the alert cat in darkness (Brooks, 1968b; Jeannerod and Sakai, 1970; Brooks and Gershon, 1971).

These potentials are not due to proprioceptive signals since similar waves occur after the animal has been paralysed (Jeannerod and Sakai, 1970); neither are they due to any effect of mechanical stress on the retina during the eye movement, since the potentials persist for two days after bilateral optic nerve section (Brooks and Gershon). The onset of the potentials is, according to Jeannerod and Sakai, 30-50 msec after the onset of a rapid eye movement. The potentials are, according to Jeannerod and Sakai, widely distributed in the posterior region of the cortex. Brooks (1968b) reported that rapid eye movement related potentials, beginning about 25-40 msec after the onset of each eye movement, were found throughout the marginal gyrus of the awake cat, and smaller potentials were observed in some parts of the suprasylvian gyrus. These experiments were however performed in 'well-illuminated' surroundings, so that much of the cortical activity observed could be due to the retinal consequences of the eye movements.

Cohen and Feldman (1971) observed potentials during eye movements in light in the groove of the calcarine fissure in monkeys but found that there were no potentials related to eye movement in total darkness.

The significance of these results is uncertain. Possibly the potentials observed in cat visual cortex are due to eye-movement related activity in the extrastriate cortex, but whether this is the case or not can be decided only by more exact gross potential mapping experiments and by studies of the activity of single units in areas 18 and 19 in relation to eye movements. It is also possible that there are significant inter-species variations.

Several authors have investigated whether the cortical flash-evoked potential is modified during saccadic eye movements. Collewijn (1969) reported that a late (about 250 msec latency) component of the flash evoked potential in *encéphale isolé* rabbit cortex was suppressed during fast phases of optokinetic nystagmus. The stimulated eye was restrained by suture to a ring, while the movement of the other eye (the lids of which were sutured together) was monitored. It seems possible that the effect was due to residual eye movements or to proprioceptive signals (the extraocular muscles were intact). The latency of the peak affected is such that it probably reflects activity at the higher levels of processing. Human evoked potential components of this order of latency are known to be markedly affected by psychological factors.

Michael and Stark (1966) found that during eye movements produced by eighth nerve stimulation (but not during those produced by third nerve stimulation) in the mid-pontine pretrigeminal or encéphale isolé cat the form of the flash evoked potential was altered. They were unable to demonstrate such an effect with spontaneous eye movements. Michael and Ichinose (1970) reported suppression of the visual evoked response to a strobe flash during eye movements elicited by continuous electrical stimulation of the vestibular nuclei in the *encéphale isolé* cat. The stimulated eye was restrained by an unspecified method. The effects reported in both these papers could clearly be associated with the vestibular activation rather than with the eye movements so caused. Gorgiladze and Smirnov (1967) have shown that labyrinth polarization by electrical stimulation augments the activity of single cells in the visual cortex of the striate cortex of the paralysed unanaesthetised cat, but this effect is non-specific, and similar effects can be produced by nociceptive stimulation.

All these evoked potential results are of uncertain relevance to the understanding of the functioning of the alert intact animal since they employed various sorts of brainstem section, which may have diminished the level of arousal of the animal.

Jeannerod and Sakai (1971) compared the potentials evoked in the posterior lateral gyri of the awake cat by eye movements and by comparable field motions, and found that the potentials evoked by eye movements and field movements of comparable velocity were very similar. In both cases the wave duration depended on the speed of the movement.

2.2 Possible physiological correlates of MacKay's effect

2.2.1 The periphery effect

2.2.1.1 Physiological data

In 1964 McIlwain reported that the responsiveness to receptive field centre stimulation of cat optic tract axons was increased by moving contours or flashing spots in the peripheral visual field, well outside the conventional receptive field of the cell. Levick, Oyster and Davis (1965) showed that this effect was not a stray light artefact and that it was a commonly occurring phenomenon in the cat's retina. They also showed that it could be observed (as an increase in 'spontaneous' firing of a cell) even without stimulation of the receptive field centre. In 1966 McIlwain showed that the strength of the effect depended on the amount of moving contour visible in the periphery of the visual field.

Cleland, Dubin and Levick (1971) found that the periphery effect, as it came to be called, was obvious and strong with nearly all cat transient retinal ganglion cells, but weak or absent with sustained cells (347 units). Ikeda and Wright (1972) made a detailed study of the periphery effect in 8 transient retinal ganglion cells in the cat. They distinguished an 'unmodulated' component of the effect which had an onset time of 1-2 sec and persists for 1-2 min after stimulation of the periphery had stopped, and a 'modulated' component of the effect, which was time locked to the peripheral stimulus. They claimed that the periphery effect was suppressed by the presence of either black or white spots in the receptive field centre (the example they gave was for an 'on'-centre cell; they did not explicitly claim that they observed the suppression effect in 'off'-centre cells). They claimed that the periphery effect habituated almost completely after about 10 sec of repeated stimulation of the same peripheral area. It seems likely that these results of Ikeda and Wright are unrepresentative since Krüger and Fischer (1973) found (in the same type of preparation) that steady illumination of the receptive field centre enhanced the periphery effect in 'on' centre retinal ganglion cells. In 'off' centre cells they found that a dark spot on the receptive field centre was necessary to augment the periphery effect. The opposite kind of receptive field centre stimulation weakened or abolished the periphery effect. Kruger and Fischerused a rather different stimulus for eliciting the periphery effect than had been used by previous authors: their peripheral stimulus was a sudden displacement of a grating pattern covering an area of the visual field 160 x 120 degrees with the exception of an area 40 x 40 degrees centred on the receptive field of the cell being studied. With this powerful stimulus Fischer, Krüger and Droll (1975) were able to demonstrate a clear periphery effect in many sustained cells.

Several of these authors (McIlwain, 1964; Cleland, Dubin and Levick, 1971; Fischer and Kruger, 1974) have demonstrated that the periphery effect occurs in cells of the lateral geniculate nucleus of the cat. McIlwain found both excitatory and inhibitory effects. Cleland et al. reported that most but not all transient LGN neurones exhibited an excitory periphery effect. Fischer and Kruger (1974) found that in about two thirds of LGN cells either excitatory or inhibitory effects could be produced by placing either an 'adequate' or 'inadequate' stimulus on the receptive fields of the cell. (For an 'on' centre cell, they term a light spot on a dark background an 'adequate' stimulus, and a dark spot on a light background an 'inadequate' stimulus. For an 'off' centre cell, the opposite identification of terms applies.)

Fischer, Krüger and Droll (1975) studied the quantitative aspects of the periphery effect. They found that the strength of the effect was remarkably insensitive to the rate of displacement across the retina of peripheral contours (for speeds down to 10 degrees/sec), although the latency of the effect was longer for slower displacements. The strength of the effect was also rather insensitive to the amplitude of displacement. The strength of the effect was little diminished by reducing the amplitude of the displacement from 5 degrees to $\frac{1}{4}$ degree, and small periphery effects were seen with displacements as small as 6 min of arc.

2.2.1.2 Attempts to find a psychophysical correlate of the periphery effect

Spillman and Gambone (1971) failed to observe a direct perceptual analogue of the periphery effect. They used a stimulus similar to that employed by McIlwain (1966), namely a rotating spoked annulus, with inner diameter more than 30 degrees. The spokes were alternate black (0.2 cd/m^2) and white (70 cd/m^2) bars, each of five degrees width. The test stimulus was an 8 min arc diameter spot appearing at various points in a dark area which filled the central field. At no position of the test stimulus was the threshold for detection of the flash significantly altered by rotation of the annular stimulus either at 40 or 70 degrees/sec.

Sharpe (1972) noticed that oscillating a black card in a distant part of the visual field diminished the rate of fading of entoptically viewed shadows of retinal capillaries, and restored to visibility the shadows of precapillaries and arterioles that had completely faded. This effect could well be due to a periphery effect in the human retina, but its relevance to normal vision is uncertain.

One reason for doubting whether one should expect an enhancement of visual sensitivity as a perceptual correlate of the physiological periphery effect is the much smaller effect of peripheral stimulation on sustained rather than transient retinal ganglion cells. As several authors (e.g. Cleland, Dubin and Levick, 1971 and Ikeda and Wright, 1972) have pointed out, it is quite possible that the detection of small low contrast foveal spots of light is dependent mainly on signals from sustained cells. If this is so, one would not expect peripheral stimulation to alter sensitivity to weak flash stimuli. One might, however, expect peripheral stimulation to alter sensitivity to visual stimuli whose detection is more likely to depend on signals from transient cells (e.g. flickering light). Some experiments along these lines are reported in chapter eight below.

Moreover, it is possible to conceive of ways in which the increase in firing of transient retinal ganglion cells produced by peripheral contour displacement could lead to a loss of visual sensitivity. For example, if transient retinal ganglion cells had an inhibitory influence on sustained cells in the lateral geniculate nucleus, then peripheral contour displacements could impair the sensitivity of sustained cells.[1]

Thus it is possible that MacKay's psychophysical effect and the physiological periphery effect are correlates. More experiments are needed, however, before a firm conclusion can be drawn.

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[1] I am grateful to Professor H. Barlow for this suggestion.

Another reason for questioning whether the physiological periphery effect and MacKay's psychophysical effect are correlated, is that MacKay (1970b) showed that his effect occurs (though perhaps more weakly) under dichoptic viewing conditions. This is not a conclusive argument against a retinal origin for the effect, however, since even a retinal interaction between the periphery and centre of the visual field could raise the noise level in a binocular mechanism receiving inputs from the central visual field of each eye, and so make a flash delivered to the central field of one eye less easily detected when a peripheral stimulus was present in the opposite eye.

2.2.2 Other possible physiological correlates of MacKay's effect

Two other effects have been reported which may relate to the physiological basis of MacKay's effect.

Brooks and Holden (1973) recorded the 'proximal negative response' in the inner plexiform layer of the pigeon retina. They found that the response to a 1 degree diameter light spot was reduced by 30% when the appearance of the spot was accompanied by a rapid displacement (1 degree in 4 msec) of a chequerboard pattern filling a 20 x 30 degree area of the visual field except for an 8 x 8 degree area centred on the receptive field. Slow movements (at 20 degree/sec) had no effect on the proximal negative response.

Jeannerod and Chouvet (1973) studied the interaction between the LGN and optic radiation potentials evoked by a 5 degree diameter flash and a sudden displacement of a grating pattern viewed by unanaesthetised paralysed cats. The grating was of a sufficiently large spatial period that the displacement (3.5 degrees) left the flash on the same stripe of the grating. The luminances of the dark and light stripes of the grating were 1×10^{-4} and 2×10^{-3} cd/m^2 respectively. When the flash occurred about 50 msec after a displacement of velocity 300 degree/sec or more, the flash-evoked potential was strongly depressed. With an interval of 200 msec between the displacement and the flash the flash-evoked potential was normal. The effect could not be clearly seen with displacements of velocity 200 degree/sec or less. It should be pointed out that the maximum velocity of a 3.5 degree cat saccadic eye movement is, according to the data of Stryker and Blakemore (1972) as low as 50 degrees/sec (range 25-75 degrees/sec), so that the faster displacements did not simulate the retinal image displacement associated with a saccade. A detailed criticism of Jeannerod and Chouvet's experiments is presented in appendix five below.

2.3 Summary

The main conclusions of this review are as follows. There is no strong evidence that the excitability of neurones in the lateral geniculate nucleus is altered concomitantly with saccadic eye movements of awake animals in uniform visual environments (i.e. where a saccadic does not cause any displacement of retinal contours). Several workers have, however, reported such changes of excitability of LGN neurones associated with saccadic eye movements of *encéphale isolé* animals. In the absence of a clear demonstration of such effects in awake intact animals the significance of these findings must remain open to doubt.

It seems clear that some neurones in the monkey pregeniculate nucleus do alter their firing in conjunction with saccadic eye movement as such, and it is possible that there are neurones with similar response characteristics in the LGN_v of the cat.

There is clear evidence that neurones in the striate cortex of the monkey alter their firing to the retinal image changes associated with saccadic eye movement in non-uniform surroundings, rather than to the oculomotor activity itself. This may also be so in the cat, since the neurones found in the visual cortex which responded during saccades in darkness may have been in area 18.

Although there are a number of similarities between the physiological periphery effect and MacKay's psychophysical effect, it is by no means certain that the two are correlates.

CHAPTER THREE

Elevation of threshold by small passive image displacements

3.1 Introduction

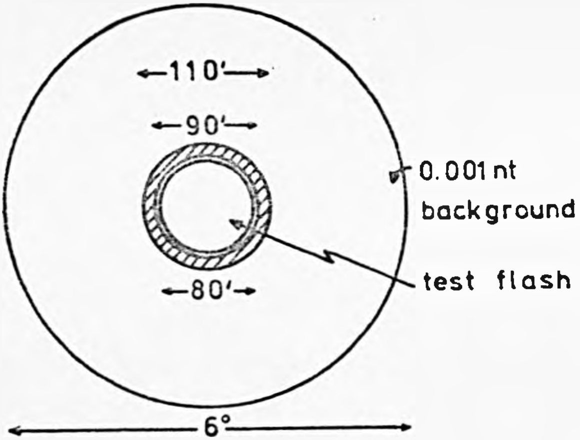
Zuber, Crider and Stark (1964) and Beeler (1967) reported elevation of threshold associated with microsaccadic eye movements in illuminated environments. Krauskopf, Graf and Gaarder (1966) found no elevation of threshold associated with microsaccades in total darkness. The published data on threshold elevation associated with microsaccades were therefore compatible with a 'null hypothesis' that the threshold elevation observed is due simply to the retinal image displacement caused by the eye movement (MacKay, 1970).

The author was, accordingly, rather startled to find that a passive microsaccade-like displacement of Beeler's background was imperceptible, even to a substantially dark-adapted subject fixating at the centre of the background. It seemed unlikely that an imperceptible image displacement would cause an elevation of threshold. (Displacement 6 min arc in 20 msec; background a 6 degree diameter disc of uniform 0.001 nt luminance. Beeler does not specify the adaptation state of his subjects. According to Volkmann et al. (1968) they were light-adapted.)

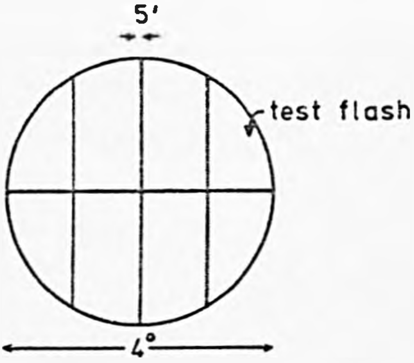
At the time this work was done, there was no method of monitoring microsaccades readily available to the author, so it was not possible to follow up this observation by directly comparing, with the same subjects, the effects on visual thresholds of active image displacement (produced by microsaccadic eye movements) and similar passive image displacements of the same field.

In these experiments the author therefore set out simply to investigate to what extent and under what conditions threshold elevation is produced by passive microsaccade-like image displacements.

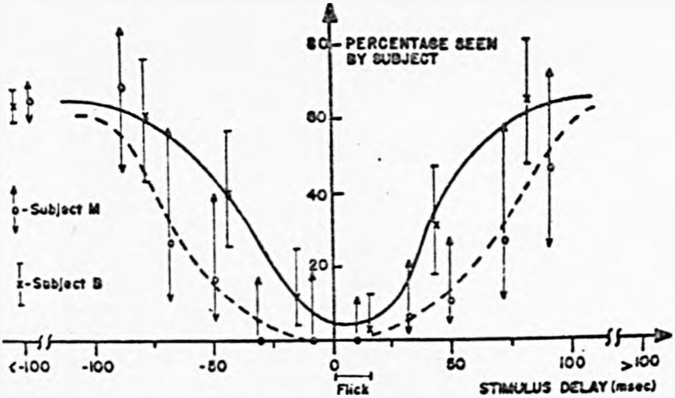
Fig. 3.1 Experiments on the detectability of flashes presented in temporal proximity to microsaccadic eye movements. Beeler's stimulus is described in the text. Zuber et al.'s stimulus was a four degrees diameter flash upon which were superimposed the 5' arc wide black lines shown. The ordinate and abscissa in the sketch of Zuber et al.'s data were the same as those used by Beeler.



a) Beeler's stimulus

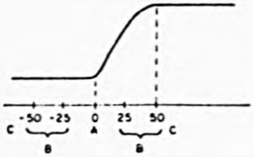


b) Zuber's stimulus



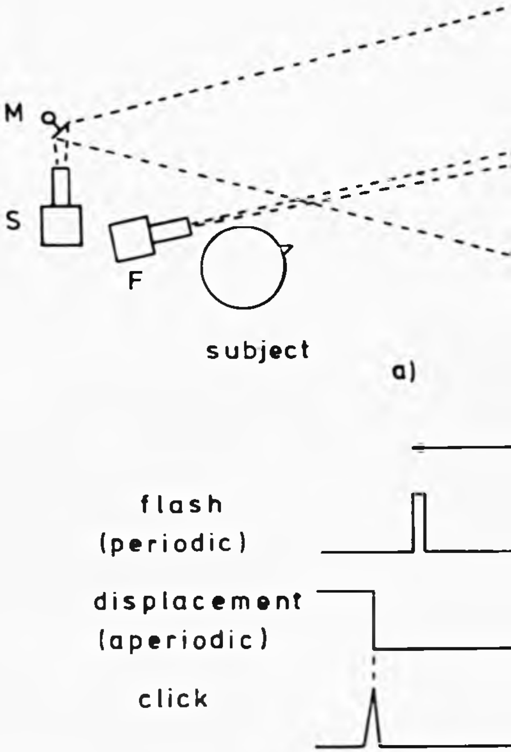
c) Beeler's results

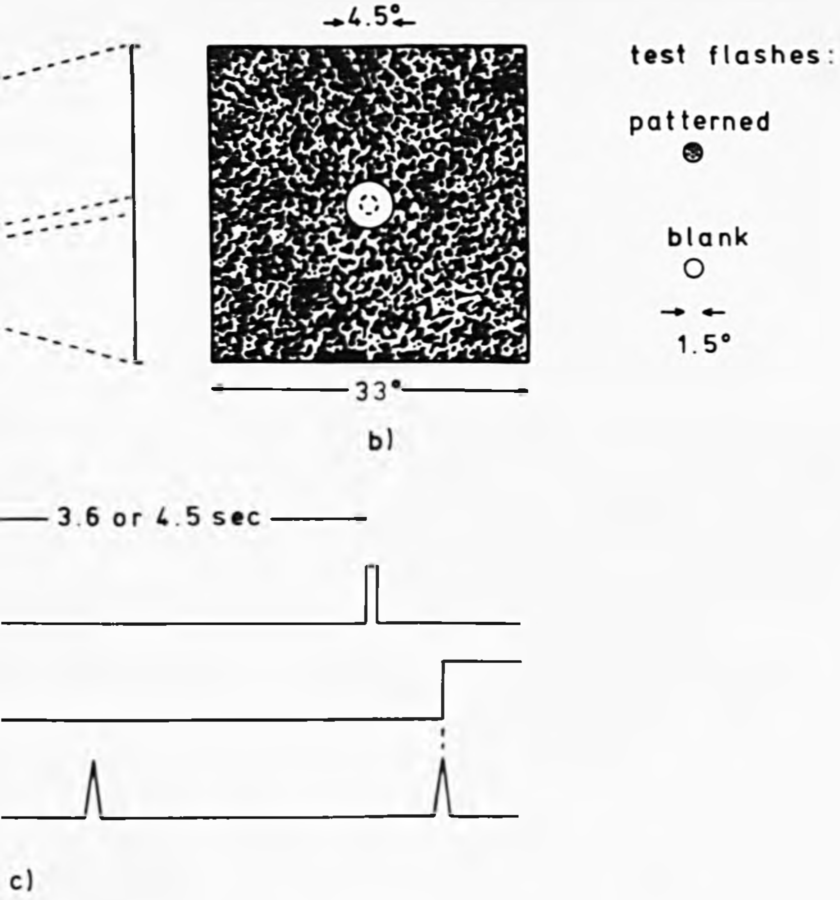
POSITION OF FLASH	SEEN	UNSEEN	TOTAL	% SEEN
(A) -25 < t < 25	0	89	89	0
(B) 25 < t < 50 -50 < t < -25	1	7	8	12.5
(C) 50 < t < -50	61	7	68	90
QUESTIONABLE	8	24	32	25



d) Zuber's results

Fig. 3.2 Apparatus. Projector S provided the static visual noise surround. Rotation of mirror M resulted in a displacement of the surround. Projector F provided the test flash. The lamp from this projector was replaced by a photographic flashgun which produced the flash.


M
S
F
subject
a)
flash
(periodic)
displacement
(aperiodic)
click


4.5°
test flashes:
patterned
blank
1.5°
33°
b)
3.6 or 4.5 sec
c)

3.2 Method

The author's experiments used a test stimulus of the same form as Beeler's i.e. an 80 min arc diameter flash (unpatterned except where otherwise indicated) which appeared at the centre of a background that was of uniform luminance in the vicinity of the test flash. This background could be displaced by 6 min arc in 20 msec (the characteristics of a typical microsaccade, according to Alpern (1969)). The displacement was produced by rotating a mirror in the beam of the projector which produced the background. The frequency response of the mirror system was almost flat to 100 Hz (3 dB reduction in amplitude response), with a slight resonance between 20 and 80 Hz (maximum 2 dB). The test flash did not move with the background. This corresponds to Beeler's stimulus condition, since in his experiments the flash was viewed in stabilised vision, whereas the background was not stabilised. The stimuli were projected on a screen viewed binocularly at a range of 1.5 m. There was a dim red fixation spot in the scotopic experiments, and a black fixation spot in the photopic experiments.

In each experiment the test flash intensity was first adjusted to a just suprathreshold level. The visibility of the test flash was then obtained as a function of the time between the test flash and the displacement onset. (A 'timecourse' experiment.) The temporal relation of the test flash and displacement was randomly varied from trial to trial. For small effects (Beeler found elevation of threshold by 0.4 log units or less) this method is a very efficient way of obtaining information about the timecourse of the effect. The magnitude of the maximum elevation of threshold can be found by increasing the flash intensity until the frequency of seeing is restored to the level obtained when the displacement does not occur or is distant in time. To obtain thresholds (i.e. intensities of flash for which the frequency of seeing is exactly 50%) as a function of the time of the test flash relative to the displacement would take at least four times as long.

In all but the early experiments, the time of onset of the displacement was randomly varied by the experimenter (from 200 msec before to 100 msec after the flash), and the flash occurred repetitively with a fixed period of about 4 sec. By this means the subject was kept in a 'steady state' undisturbed by alerting signals and with no other task than responding 'yes' or 'no' to the stimulus. In the early experiments the experimenter alerted the subject by saying 'ready' slightly before pressing a button which initiated a trial. The displacement occurred at a fixed delay after this, and the flash at a latency varied randomly from trial to trial.

In the early experiments, and also in several of the later experiments with the flash running repetitively, the 'putt' made by the flash stimulator was audible to the subject. In the later experiments this sound was masked by auditory 'noise' in headphones worn by the subject. Except in a few intermediate experiments a warning click was added to the noise, midway between trials, since the intertrial period was so long that the subjects were uncertain when to expect the next trial. The intertrial interval represented the time needed for the flashgun to recharge. This could not be shortened. A click of discriminably different intensity and form was also added coincident with the displacement onset, thus retaining an indication of the approximate time of the flash even when the displacement was zero (i.e. in control trials). If this was not done, the frequency of seeing of the flash when there was no displacement was lower than that for the case when there was a displacement and the flash preceded the displacement. (See, for example, Fig.3.8) This phenomenon was presumably due to the lack of any indication of the temporal whereabouts of the flash in the case when the displacement was zero.

3.3 Results

3.3.1 Experiments with a stimulus of the same form as Beeler's

With a stimulus of the same dimensions as used by Beeler but with the intensity of the background increased one log unit to 0.01 nt, a 6 min arc displacement of the background was just clearly visible to a dark-adapted subject. This stimulus had no detectable effect on the visibility of the central 80 min arc diameter test flash, for flashes delivered at any time within ± 100 msec of the displacement onset. Experiments with the background intensity increased to 10 nt also gave null results for flashes within ± 100 msec of the displacement onset. (See Fig.3.3.) Frequency of seeing changes equivalent to a 0.05 or 0.1 log units change of flash intensity could have been detected.

3.3.2 Experiments with a large high-contrast pattern in the displaced field

At this point in the experiments, the logical step was to test the 'null hypothesis' that there is no elevation of threshold at all associated with passive microsaccade-like image displacements, even with a large high-contrast pattern in the displaced field. A 33 x 33 degree high-contrast static visual noise pattern (see Fig.3.2) with a 4½ degree diameter white area in the centre was therefore used as the displaced field. The luminances of the black and white areas of the pattern were 3 and 30 nt respectively. The mean noise blotch size was about 2 degrees. With this stimulus, a clear elevation of threshold was found for 80 min arc test flashes presented at the approximate centre of the 4½ degree diameter disc. (The flash did not move with the pattern.) For most subjects the frequency of seeing did not begin to drop until 50 msec after the displacement onset. (See Figs.3.4 & 3.5) With two subjects however (RH and CB in Fig.3.4) some runs showed a drop in frequency of seeing beginning before the

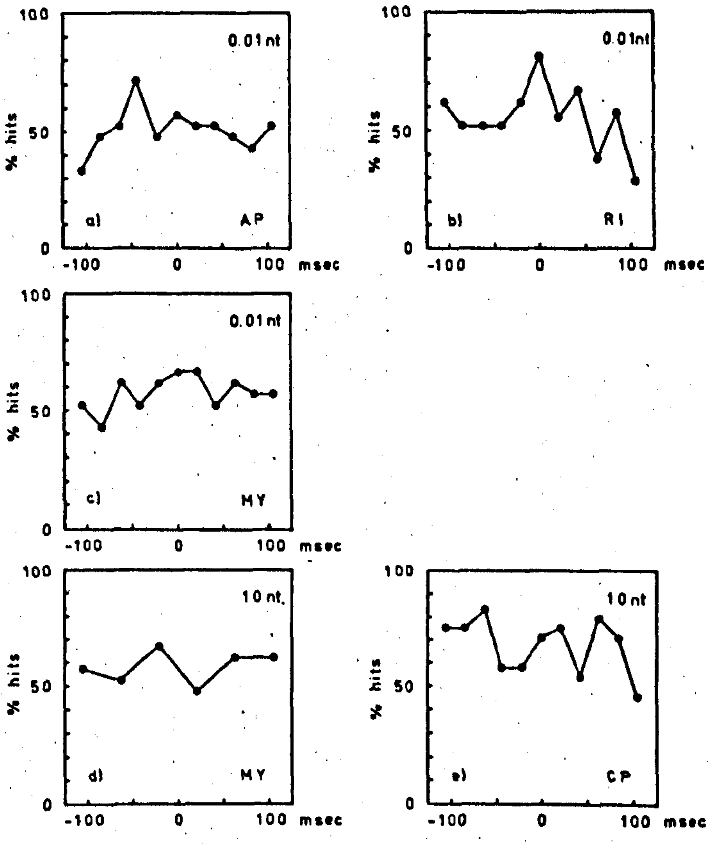


Fig. 3.3 Detectability of flashes presented in temporal proximity to a 6' arc pseudomicrosaccadic displacement of a surround of diameter 6 degrees (as in Beeler's experiments). Each datum point is based on 21 or 24 trials. Figures at top right give surround luminance.
Flash simultaneous with displacement onset when abscissa zero. Flash after displacement onset when abscissa positive.

displacement onset, but this was not consistently obtained with either subject. (See Figs.3.4g & 3.5a,g) The lowest frequency of seeing was always for flashes delivered about 75-100 msec after the displacement onset. This maximum depression of frequency of seeing was equivalent to a decrease in flash intensity of between 0.1 and 0.2 log units, as judged by the increment in flash intensity needed to restore the frequency of seeing to the level for flashes delivered well before the displacement. (See Fig.3.4b,d, f, h and Fig.3.6a,b.) With one subject of the six used (IC) the effect was small or absent. Since this subject's frequency of seeing curve characteristically showed quite large apparently random oscillations, no quantitative conclusions about inter-subject variations in the effect can be drawn.

An attempt to determine the magnitude of the maximum threshold elevation by a different method produced a paradoxical result. In this method the test flash occurred at one of only two epochs, 100 msec before or 100 msec after the displacement onset. The latter was the latency of the maximum depression of frequency of seeing, the former was in the temporal region where the flash visibility is not affected by the displacement. The flash intensity was varied randomly from trial to trial, as was the epoch of the flash, and frequency of seeing was plotted as a function of flash intensity (see Fig.3.5b,d, f, h) separately for the two flash epochs.

The paradoxical result was that there was little or no difference between the thresholds for flashes at the two flash epochs. In no case was the maximum vertical separation of the two functions as great as would be expected from the 'timecourse' experiments carried out with the same subjects. (See Fig.35a, c, e, g.) Experiments b, f and h in Fig. 3.5 were carried out simply by manually rotating a 'filter wheel' attenuator in the flash projector beam. This filter wheel gave

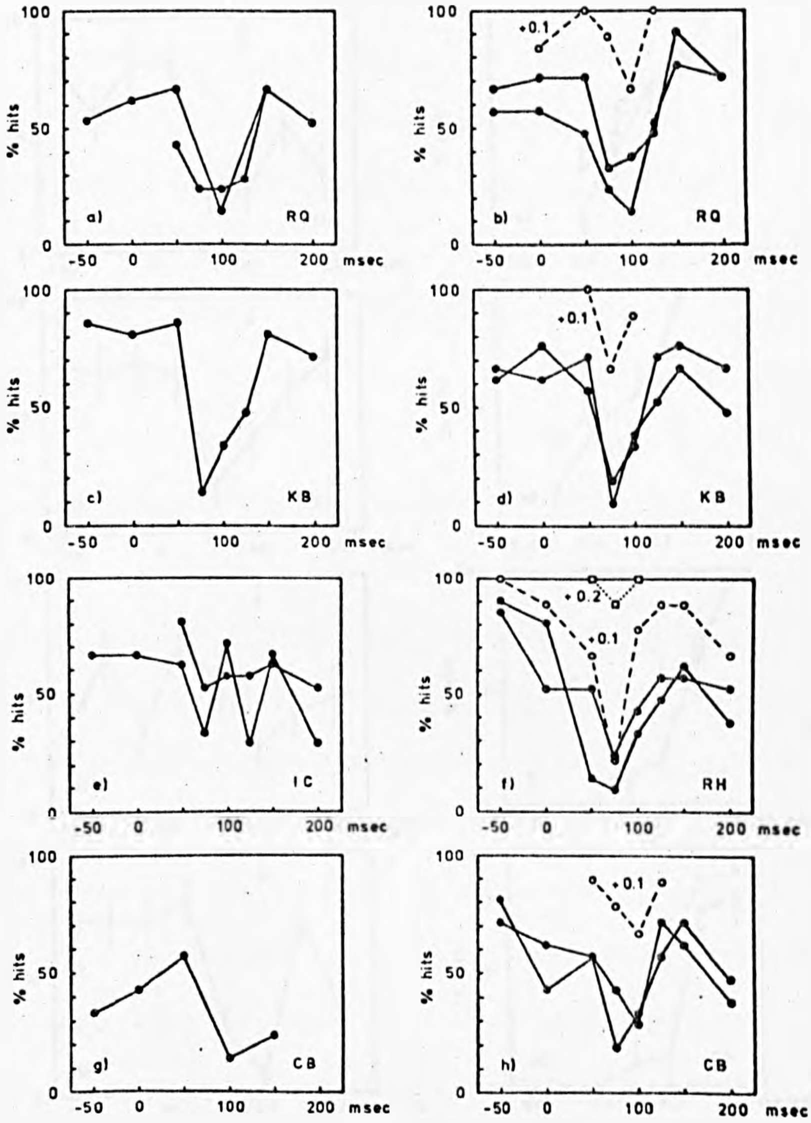


Fig. 3.4 Detectability of a flash as a function of the time of the flash relative to the onset of a 6' arc displacement of a patterned surround, for five subjects. The surround subtended 33x33 degrees and, except for a disc of diameter 4½ degrees, was filled with 'static visual noise' of mean blotch size two degrees. The flash, of diameter 80 min arc, appeared at the centre of the uniformly illuminated 4½ degrees diameter disc. (See Fig 3.2.) Each datum point was based on 21 trials. Flash duration 2 msec.

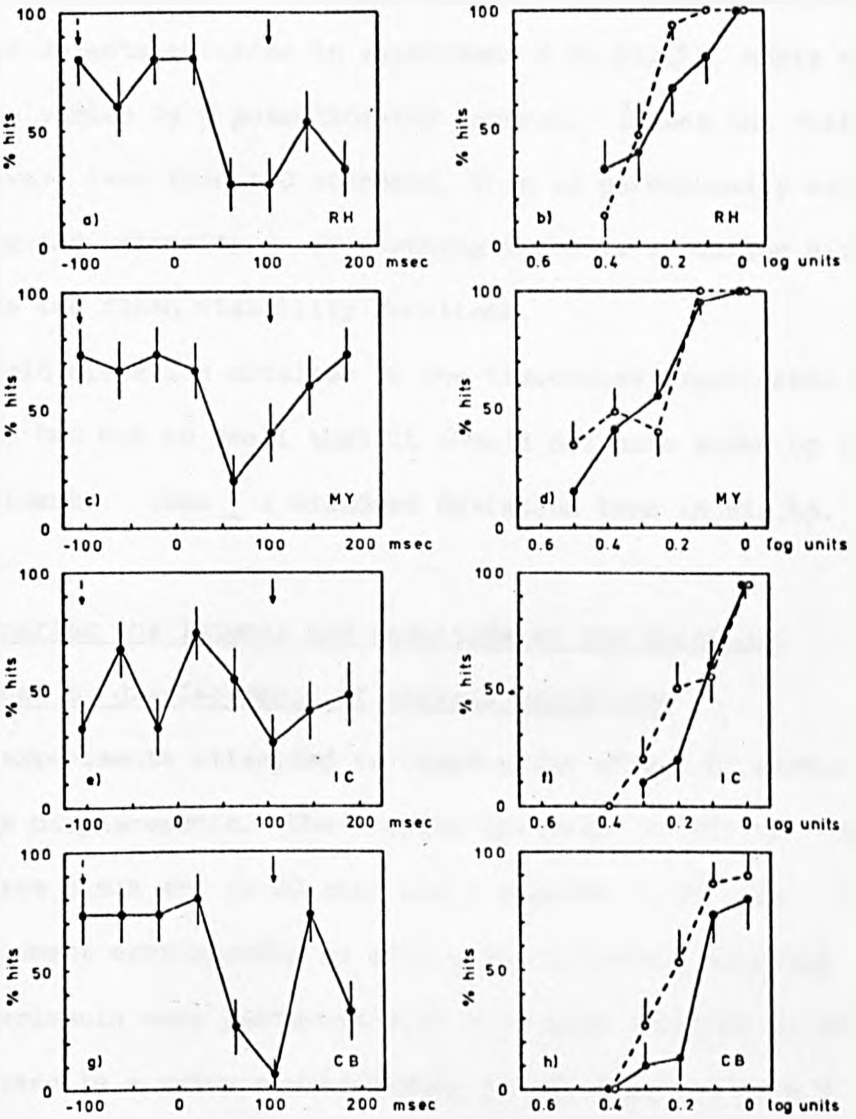


Fig. 3.5 a),c),e) & g): detectability of a flash as a function of time of flash relative to the onset of a 6' arc displacement of the visual noise surround, for four subjects. 2 msec flash. b),d),f) & h): flash detectability for the same subjects as a function of flash energy, for flashes presented 100 msec before (dashed lines) or 100 msec after (solid lines) the onset of the displacement. Flash duration less than 100 microseconds. Arrows in a),c),e) & g) indicate epoch of flashes in b),d),f) & h). Each datum point based on 15 or 20 trials.

audible clicks as it was rotated, but the possibility of the subjects using the number of clicks as a clue to the variation of flash intensity was reduced by sometimes counter-rotating the filter wheel (e.g. increasing the intensity one step by increasing it two and decreasing it one step). Also the randomization was not complete, successive trials often consisting of flashes of the same intensity but alternate epoch. Neither of these defects occurred in experiment d in Fig3.5, where the flash energy was varied by a potentiometer control. (Since the flash duration was always less than 100 microsec, this is perceptually equivalent to varying the intensity.) If anything there is a smaller difference between the two flash visibility functions.

The threshold elevation obtained in the timecourse experiments is certainly small, but not so small that it should not have shown up in the above experiments. (See ± 1 standard deviation bars in Fig3.5.)

3.3.3 Experiments comparing the latency and magnitude of the threshold elevation produced by displacements of various magnitudes

The first experiments attempted to compare the effect of micro- and macro- image displacements. The results are shown in Fig3.6. The displacements were 6 min arc in 20 msec and 3 degrees in 30 msec. The 3 degree displacement corresponded to that used by MacKay, although most of his experiments were performed with a 10 msec duration of displacement. 30 msec is a value corresponding to the duration of a 3 degree saccade. In experiments a and b the flashgun was audible to the subject. In c and d the flashgun was masked by 'noise' in headphones worn by the subject. In experiments e and f a click was added to the noise, coincident with the flash. From c and d compared with a and b it can be seen that the timecourse of the threshold elevation was very different with 6 min arc and 3 degree displacements. In the

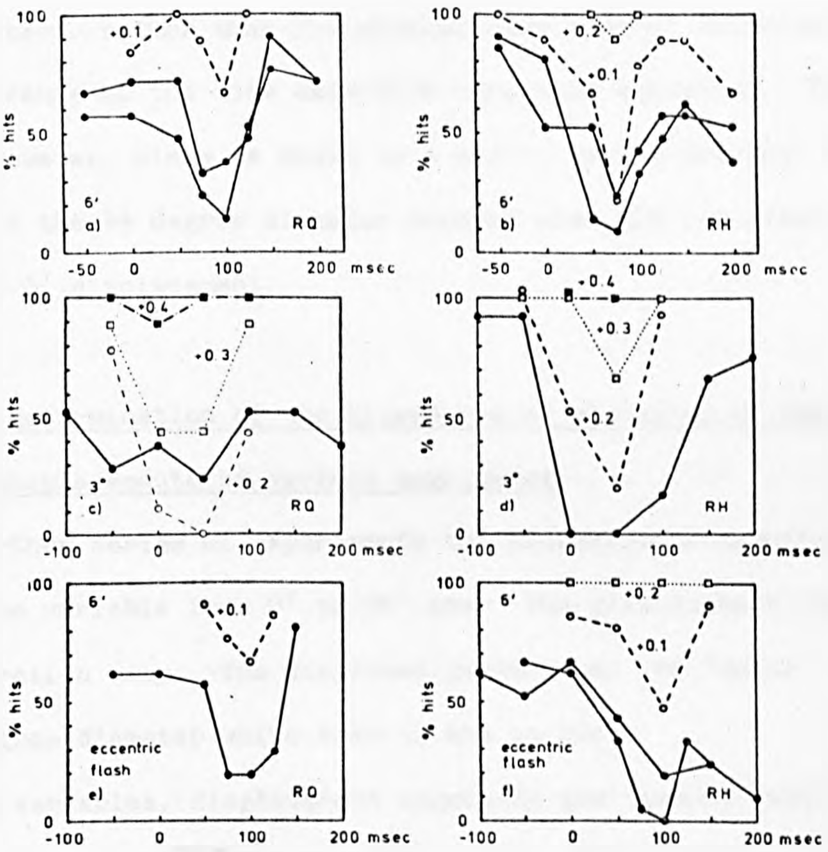


Fig. 3.6 Detectability of a flash as a function of time of the flash relative to the onset of a displacement of the visual noise surround, for two subjects. a) & b): 6' arc displacements; c) & d): 3 degrees displacements; e) & f): 6' arc displacements with the flash eccentrically placed in the surround, so that its border was as close to the inner edge of the visual noise surround as in c) and d). Broken lines indicate runs at higher flash energies (increment shown in log units). 2 msec flashes. Datum points based on between 5 and 21 trials.

latter case the drop in frequency of seeing began much earlier, for flashes somewhat before the displacement. At least in the case of subject RH the effect was larger in magnitude, since the trough of the frequency of seeing curve amounted to an elevation of threshold of 0.35 log units as compared with 0.2 log units for the 6' displacements. Since the 3 degree displacement brought the nearest contours of the displaced pattern to within a few minutes of arc of the test flash boundary, it seemed possible that the closer proximity of the displaced pattern, rather than the greater magnitude of the displacement was the cause of the more extensive threshold elevation. This was not so, however, since as shown in e and f, moving the test flash to the edge of the 4½ degree diameter central area did not alter the effect of the 6' displacement.

3.3.4 Simultaneous determination of the timecourse of elevation of threshold produced by displacements of various magnitudes

In a further series of experiments the displacement magnitude was arranged to be variable from 0' to 96' arc. The displacement form was a 20 msec duration ramp. The displaced pattern was the 'noise' pattern with a 4½ degree diameter white disc in the centre.

The two variables, displacement magnitude and time of displacement onset, were varied haphazardly through a range of combinations by the experimenter. They were usually not both varied between successive trials because the 4.5 sec intertrial period was not usually long enough for the subject's response to be recorded and both of the control settings to be changed. Since the displacement was always symmetrical about the test flash position, when the experimenter changed the displacement magnitude between trials the subject saw the pattern move slowly to the appropriate position for the next displacement magnitude.

The subject did therefore have some idea of the magnitude of the next displacement.

The results of several experiments are shown in Figs. 3.7-3.10. The 0' displacement was obtained by turning the displacement control to zero. In all but the earliest experiments the subject still had an indication of the approximate flash epoch, because there was a click coincident with the displacement onset time which was still present with a zero displacement. In Fig. 3.9 the low visibility of the flash when there was no displacement presumably is due to the lack of such a click. Since the results obtained are similar to those obtained with other subjects in experiments without this defect, they are included.

Fig. 3.10 shows the results of more extensive experiments with one of the subjects. The effects were consistently obtained; the variability is quite small. There is very little difference between the results with unpatterned and patterned test flashes.

The data in Fig. 3.11 are from the same experiments, and show the latency of the fall in frequency of seeing as a function of displacement magnitude. Results from each run with each subject are shown separately. The latency was arbitrarily defined as the time at which frequency of seeing fell to 50%.

It can be seen that the latency versus displacement magnitude curves are approximately logarithmic over this range. The slope of the curves appears to be characteristic of each subject, with a maximum variation between subjects by a factor of about 3 (between CH and PA). The data suggest that the latency of the effect may not increase for displacements smaller than 6' arc.

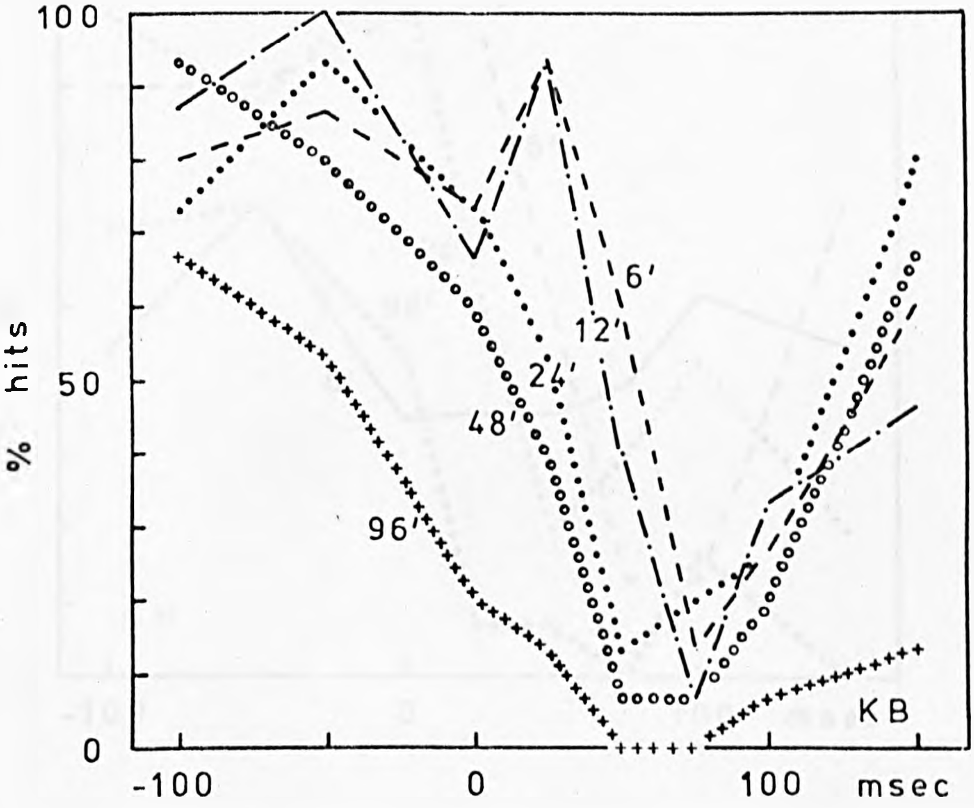


Fig. 3.7 Detectability of a flash as a function of the time of the flash relative to the onset of displacements of the visual noise surround, for displacements of 6' to 96' arc. Subject KB. Data for displacements of different magnitudes were obtained simultaneously in experiments in which both the time of the flash and the extent of the displacement were randomly varied. Flash duration 50 microseconds. 15 trials at each value of displacement magnitude and flash time sampled.

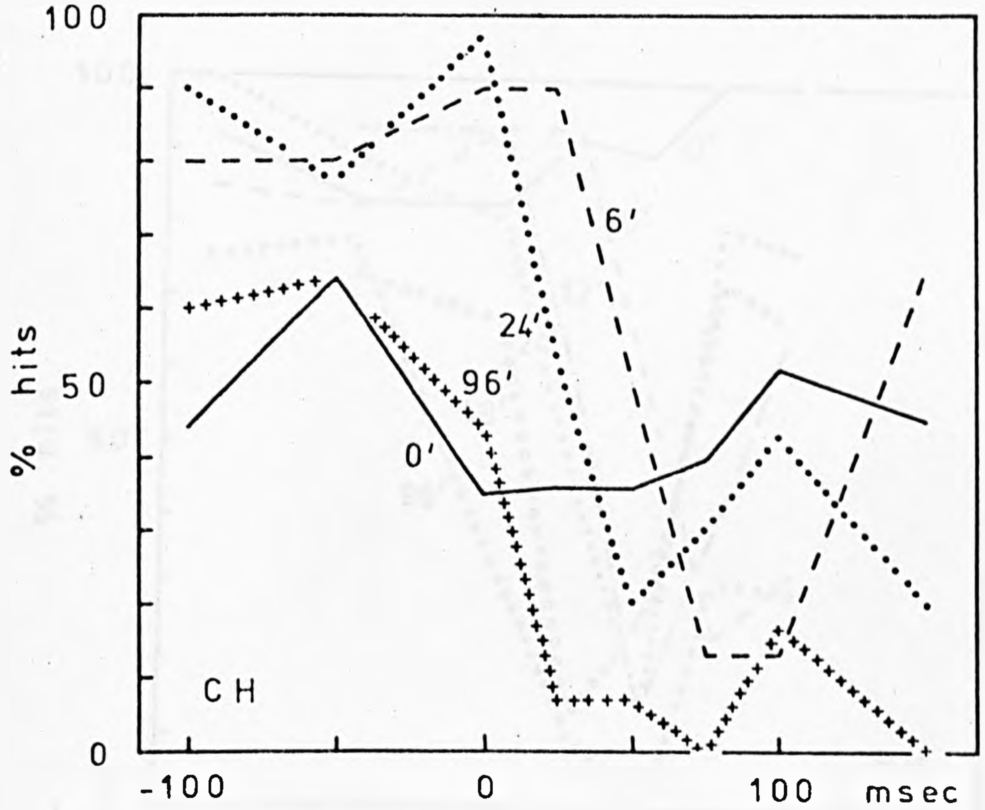


Fig. 3.8 Detectability of a flash as a function of the time of the flash relative to the onset of 0',6',24' and 96' arc displacements of the visual noise surround. Subject CH. Between 11 and 30 trials at each value of displacement magnitude and flash time sampled.

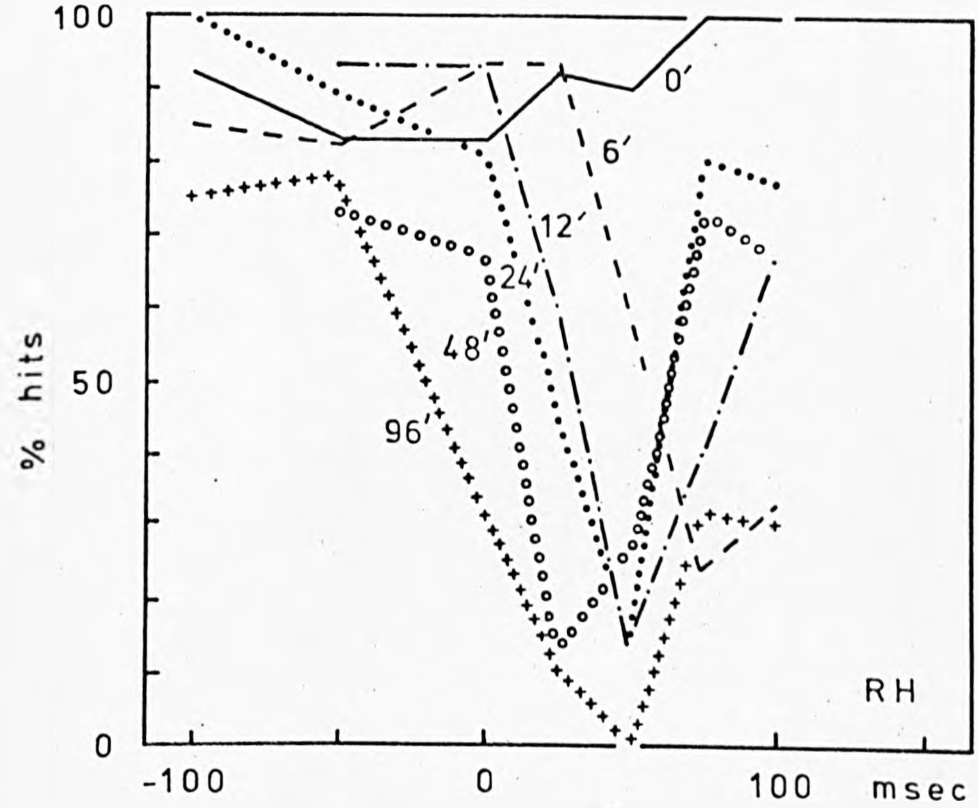


Fig. 3.9 Detectability of a flash as a function of the time of the flash relative to the onset of 0',6',12',24',48' and 96' arc displacements of the visual noise surround. Subject RH. Between 8 and 28 trials at each value of displacement magnitude and flash time sampled.

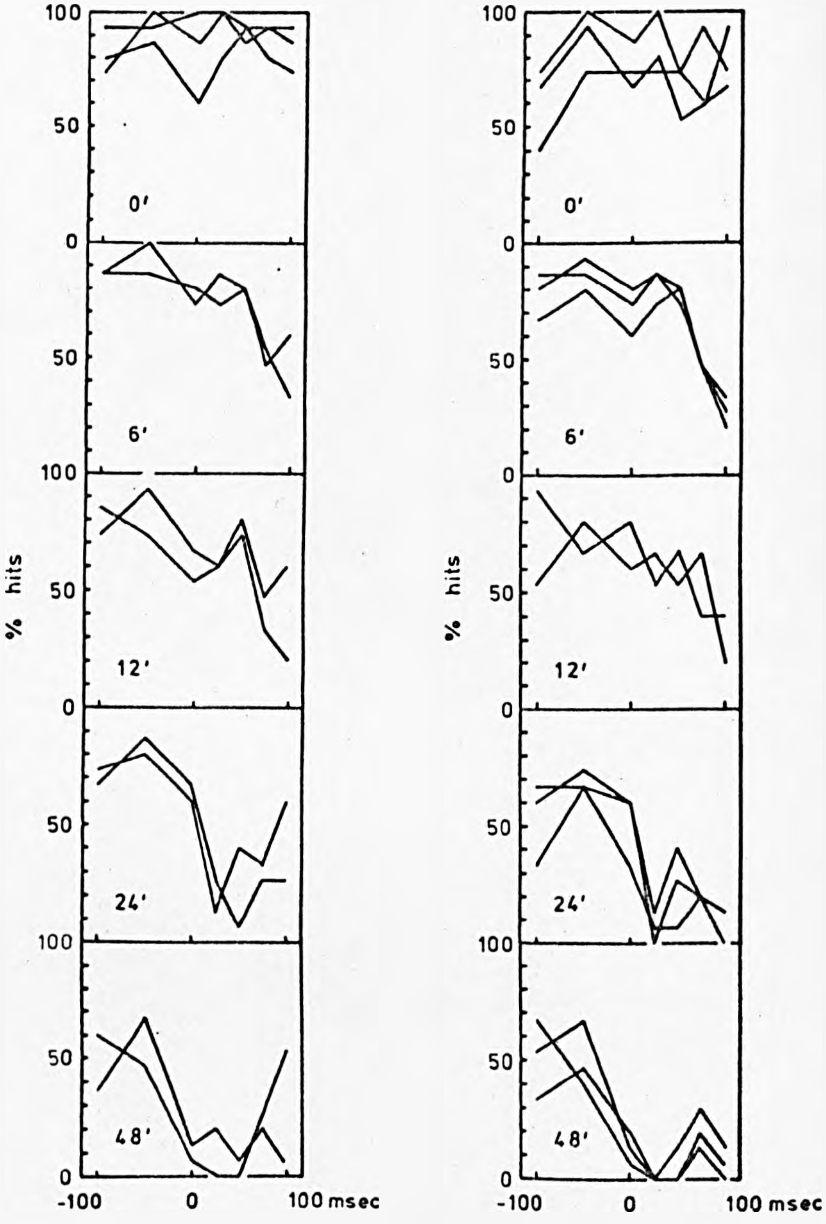


Fig. 3.10a Same data as in Fig. 3.10b, but with the data from each run shown separately, to indicate the small variability of results from run to run.

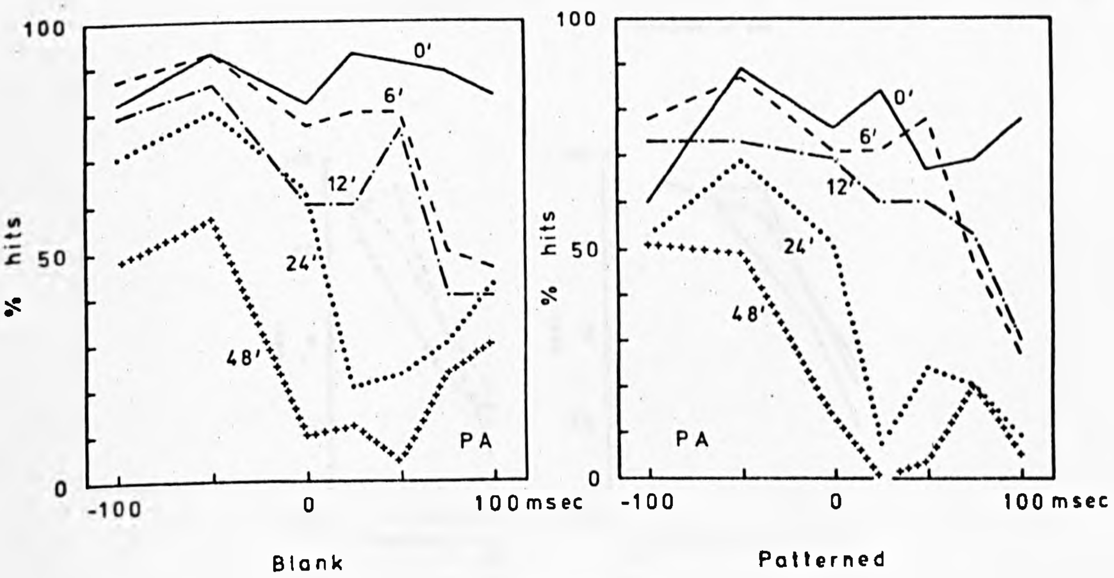


Fig. 3.10b Detectability of blank and patterned flashes as a function of the time of the flashes relative to the onset of displacements of 0',6',12',24' and 48' arc of the visual noise surround. Subject PA. Figures show mean data for two or three runs. Between 28 and 45 trials at each value of displacement magnitude and flash time sampled.

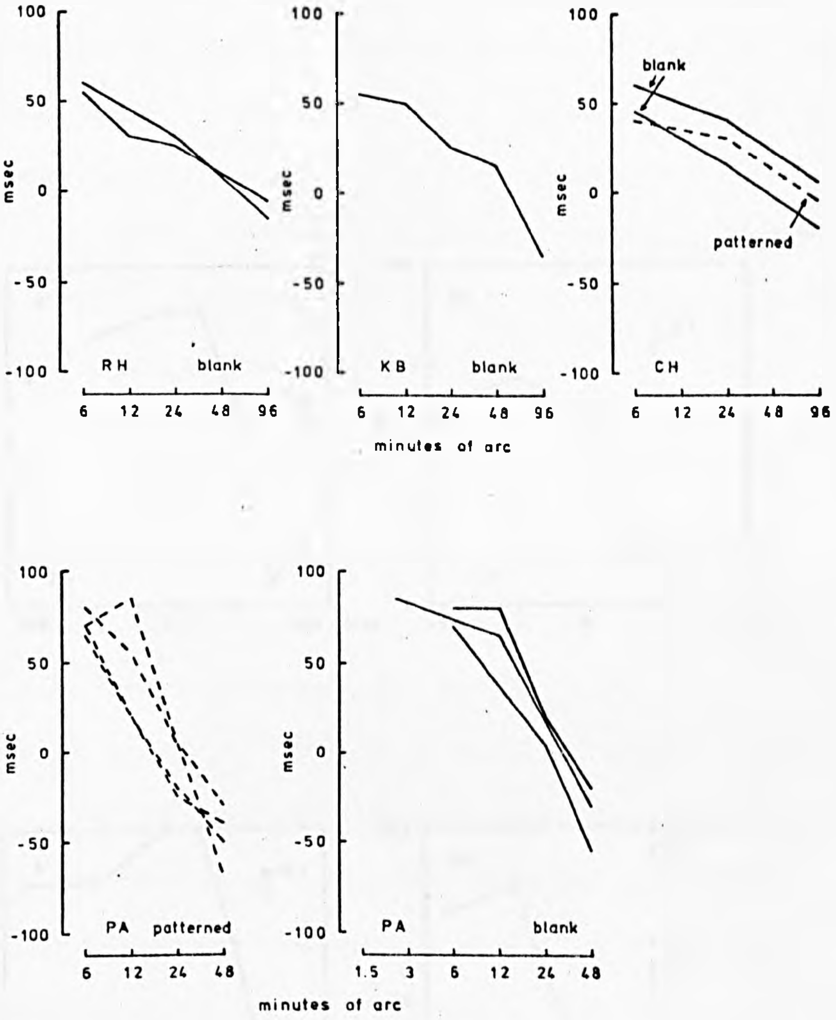


Fig. 3.11 Latency of the drop in detectability of a flash produced by displacement of the visual noise surround, as a function of the displacement magnitude, for four subjects. Latency was defined as the time between the onset of the displacement and the time at which the detectability of the flash fell to 50%. Full lines indicate data for blank flashes, dashed lines data for patterned flashes. Same data as in Figs. 3.7 to 3.10.

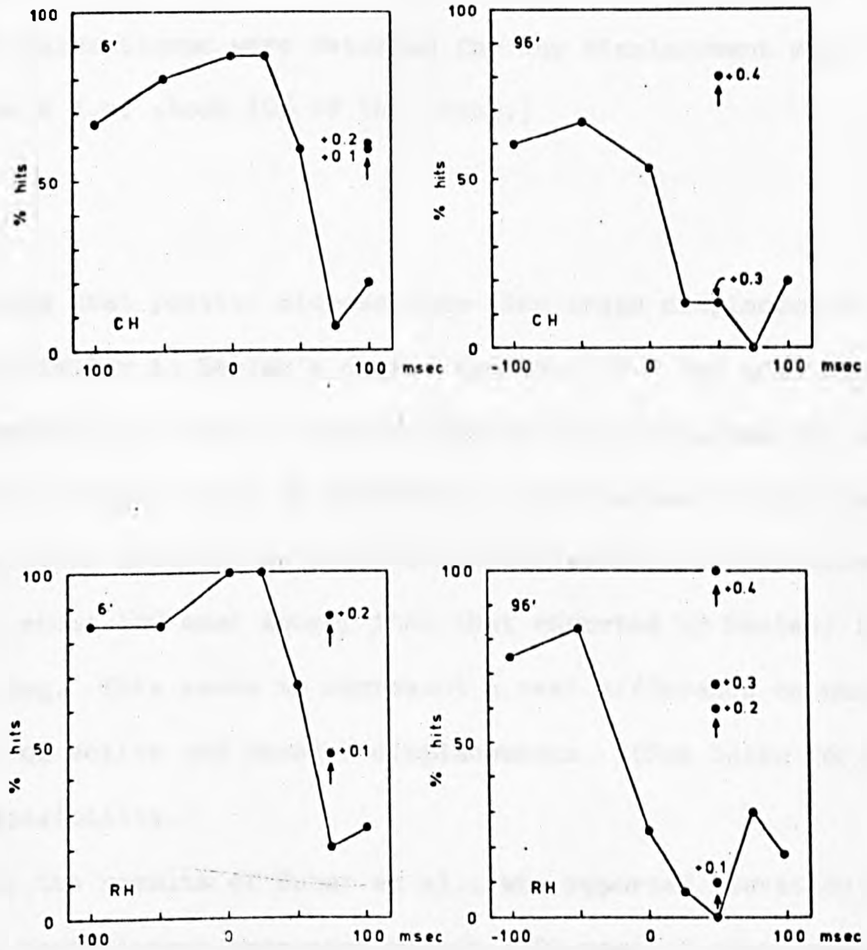


Fig. 3.12 Detectability of a flash as a function of the time of the flash relative to the onset of 6' and 96' arc displacements of the visual noise surround, for two subjects. Data for the two magnitudes of displacement were collected simultaneously in experiments in which the displacement magnitude was varied randomly. Datum points marked by arrows show the detectability of flashes of higher energy interspersed amongst the other flashes (numbers show energy increment in log units). Each datum point based on 15 trials (except for the point marked '+0.4' in the lower righthand figure, which was based on 6 trials).

Fig.3.12 shows a determination of the magnitude of the maximum threshold elevation, for 6' and 96' displacements, and for two subjects. These data were obtained in a normal timecourse experiment by including some higher-energy flashes at the latencies of the maximum depression of frequency of seeing. The maximum threshold elevation is only about 0.2 log units with a 6' arc displacement but is about 0.35 log units with a 96' displacement.

In the later experiments with PA, a check on false alarm rate was made. No false alarms were detected for any displacement magnitude. (50 catch trials i.e. about 10% of the total.)

3.4 Discussion

The finding that passive microsaccade-like image displacements of a stimulus similar to Beeler's do not produce a 0.4 log unit elevation of threshold as found by Beeler with active displacements, and that even with a large amount of contrast in the displaced field the threshold elevation produced by passive microsaccade-like displacements has a latency about 100 msec longer than that reported by Beeler, is very interesting. This seems to represent a real difference between the effects of active and passive displacements. (See below for an alternative possibility.)

Similarly the results of Zuber et al., who reported elevation of threshold for test flashes presented within ± 25 msec of a microsaccade, probably cannot be accounted for by the image displacement caused by the microsaccade, since the latency of the effect does not correspond with the latency of the effect produced by passive image displacements.

There is a possible source of error in Beeler's experiments. If the microsaccades of Beeler's subjects became time-locked to the oscillation of the annulus needed to prevent fading, then the observed decrease in visibility of the test flash could be due to a masking effect of the oscillation of the annulus. At the time of Beeler's experiments, the general opinion was that the visual tracking system cannot respond to target displacements smaller than 0.25-0.5 degrees with a saccade. (Rashbass, 1961.) This is probably not true, however, since Steinman and his co-workers (e.g. Timberlake et al., 1972) have shown that experienced and inexperienced subjects can make microsaccades to track target steps as small as 3.4 min arc. Whether subjects normally do this 'involuntarily' is of course a moot point.

Zuber et al.'s results are not subject to any such possible error. It should be noted, however, that their published data are very slight, and inadequate for any firm conclusion. (See Fig. 3.1d.)

Why the results of the experiments with the test flash restricted to only two epochs do not correspond with the results of the time-course experiments is uncertain. It should be stressed that when the former experiment was in effect combined with the latter (as in the experiments shown in Fig. 3.12) in which the timecourse experiment included flashes of increased energy at the epoch of the maximum depression of threshold, the results obtained were the same as those obtained by simply increasing the flash intensity for a second run in the timecourse experiments (e.g. Fig. 3.4b). This means that the latter estimate of the threshold elevation is not biased by any change of criterion between the repeated timecourse runs with different flash energies, since there is no possiblity of criterion change affecting the combined threshold and timecourse experiments.

The subject's task is of course rather simpler in the two flash epoch experiments, since the flash is either 100 msec before or 100 msec after the displacement. These two cases can easily be differentiated. It is possible that the subjects adopted different response criteria in the two cases. In the results of RH (Fig3.5b) there is a slight suggestion of a non zero false alarm rate (i.e. a lower criterion) in the case where the flash followed the displacement but not in the case where the flash preceeded the displacement. This could however be a statistical fluctuation.

The paradox cannot be resolved without further experiments. It is, however, clear that there is no prima facie case for doubting the genuineness of the threshold elevations observed in the timecourse experiment.

The considerable inter-subject variation in the slope of the latency of threshold elevation versus displacement magnitude curves is very interesting. It would be interesting to see in further experiments whether this variation was associated with an inter-subject variation in the magnitude of the maximum threshold elevation. It is possible that the inter-subject variation in the effect is due to some variation in refraction of the subjects' eyes. Although all subjects had normal (corrected if necessary) central vision, the refractive errors in peripheral vision were unknown. Leibowitz et al. (1972) have recently claimed that large inter-subject variations in peripheral motion thresholds can be accounted for by the normal variation in peripheral refraction.

It is just possible that a salient displacement of a large area of the visual field, as used in these experiments, induces a short latency more or less 'involuntary' microsaccade in the direction of the displacement. Although the saccade latency is usually 200 msec or so with unpredictable target displacements, it has been shown that corrective saccades following inaccurate primary saccades can occur less than

100 msec after the end of the primary saccade. Whether such saccades are activated by a visual error signal, however, is not clear. It would be worthwhile monitoring microsaccade occurrence in future experiments.

It is interesting that in physiological experiments on the periphery effect in *encéphale isolé* cat, Kruger and Fischer (1973) used a similar form of stimulus to the author's. They found that displacements of a large high-contrast peripheral pattern augmented the firing of both 'on' and 'off' cells in the cat's optic tract, even with displacements as small as 6 minutes of arc. (See Fig. 3.13.)

Although there are a number of similarities between the physiological periphery effect and MacKay's psychophysical effect, it is by no means certain that the two are correlates. (See section 2.1.2 of chapter two for a discussion of this matter.)

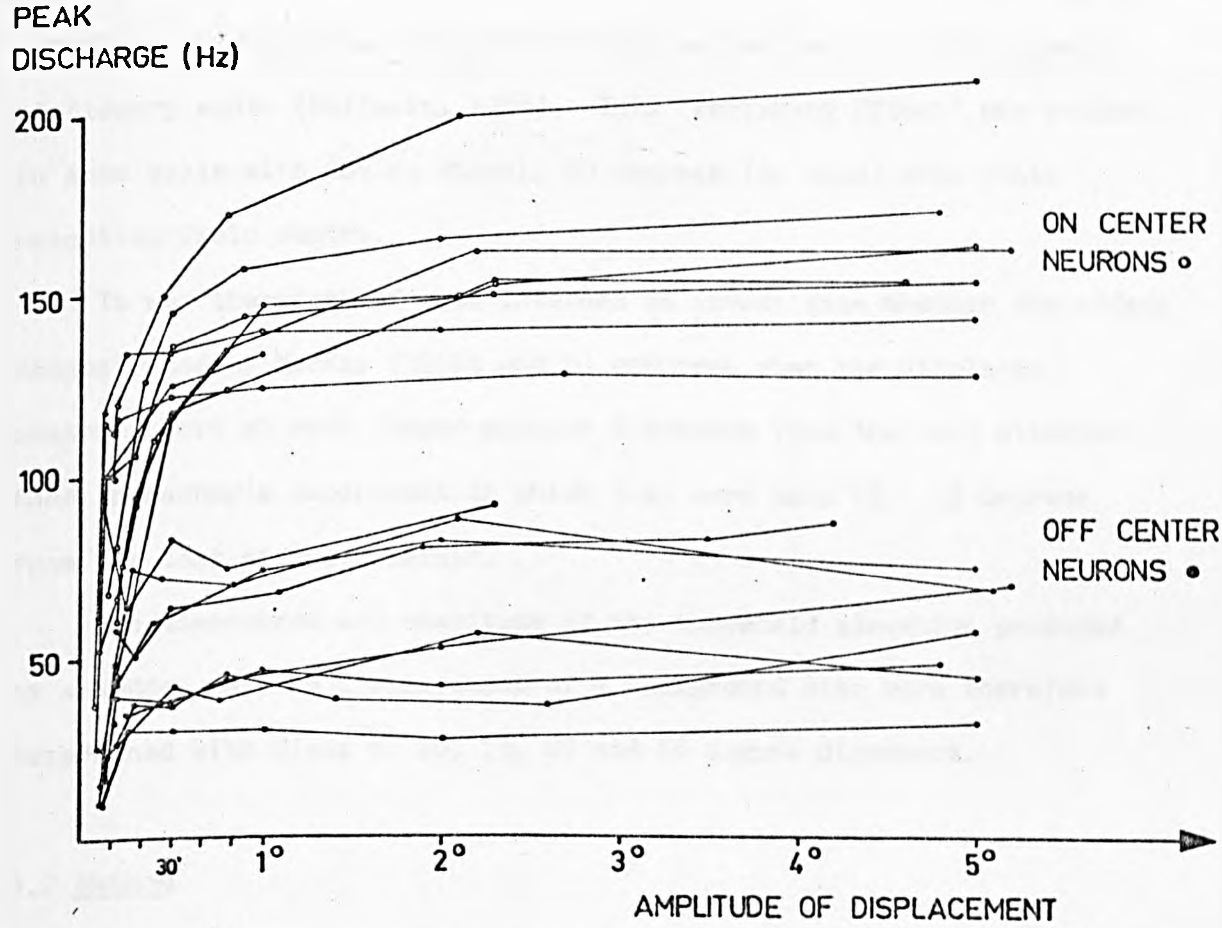


Fig. 3.13 Magnitude of the physiological periphery effect as a function of the amplitude of displacement of a peripheral grating stimulus, for single fibres recorded in the optic tract of the cat. An area 40x40 degrees centred on the receptive field of the unit under study was unstimulated. Thus the stimulus was more peripheral than that used in the author's psychophysical experiments. From Fischer, Krüger and Droll, 1975.

CHAPTER FOUR

A comparison of the elevation of threshold produced by passive displacement of contours at different eccentricities

4.1 Introduction

Retinal ganglion cells respond to movement of contour many degrees outside their classical receptive fields as defined by flashing small stationary spots (McIlwain, 1964). This 'Periphery Effect' was evident in some cells with moving stimuli 40 degrees (or more) from their receptive field centre.

It was therefore of some interest to investigate whether the effect demonstrated by MacKay (1970a and b) occurred when the displaced contours were at much larger angular distances from the test stimulus than in MacKay's experiment in which they were only 2½ - 5½ degrees from the test stimulus margin.

The timecourse and magnitude of the threshold elevation produced by a sudden passive displacement of a background disc were therefore determined with discs of 10, 13, 27 and 86 degree diameters.

4.2 Method

The optical arrangement was similar to that employed by MacKay. A mirror mounted on an EEG pen motor was placed in the optical path of a projector. A white disc (of luminance 32 cd/m^2) was projected onto a translucent screen viewed from the opposite side by the subject. The test stimulus was produced by a stroboscope bulb, mounted in a second projector. In all the experiments the test flash was three degrees in diameter, and appeared at the mean centre of the background disc. The displacement of the disc background was three degrees in magnitude, and was always to the subject's left. (The disc returned to its original position 500 msec afterwards.) The displacement took about 10 msec, which is rather less than for a saccade of similar angular extent (25 msec duration). After this rapid motion the disc continued to move in a very slow drift, for some 500 msec. (This drift was due to creep in the rubber damping mechanism of the pen motor, which could not be rectified and was not thought to be important. The drift was evident to the subject only when special attention was paid to the edge of the disc.)

The rotation of the mirror was initiated by a pulse from one output of a digital timer. The other four output channels of the timer were fed to a random selector which on each trial selected one of the outputs to trigger the stroboscope flash. Thus at any point in an experiment the test flash might occur at one of four different temporal relations to the displacement.

A two epoch forced choice method was used. The subject had to indicated in which of two epochs, both of which contained a displacement of the disc, the test flash occurred. His performance was not fed back to him. Runs were never longer than two hundred trials without a rest.

At the beginning of each experiment the intensity of the test flash was adjusted so that it was just detectable when it occurred well before or after the displacement.

In order to determine the timecourse of the threshold elevation, three runs were necessary, each using test flashes at four different times relative to the displacement (i.e. twelve test flash times in all). In order to avoid systematic errors, the test flash times were assigned in the following way:

Run	Test flash times (relative to displacement)			
1	-45	0	45	90
2	-30	15	60	105
3	-15	30	75	120

To determine the magnitude of the threshold elevation, further runs were made with the test flash 0.1, 0.2, 0.3 . . . log units brighter than above. In these runs the test flash occurred at only two epochs relative to the displacement: either 45 msec before the displacement or 30 (or 45) msec after, the latter being the time at which the test flash was most difficult to detect.

The data for the 13 and 27 degree diameter disc backgrounds were obtained with a viewing distance of 50 cms; the data for the 10 and 86 degree diameter discs with a viewing distance of 20 cms, which was the shortest viewing distance the subject could use without eye strain. One subject (SJJ, the author) was used throughout.

4.3 Results

The results are shown in Figs 4.1 and 4.2.

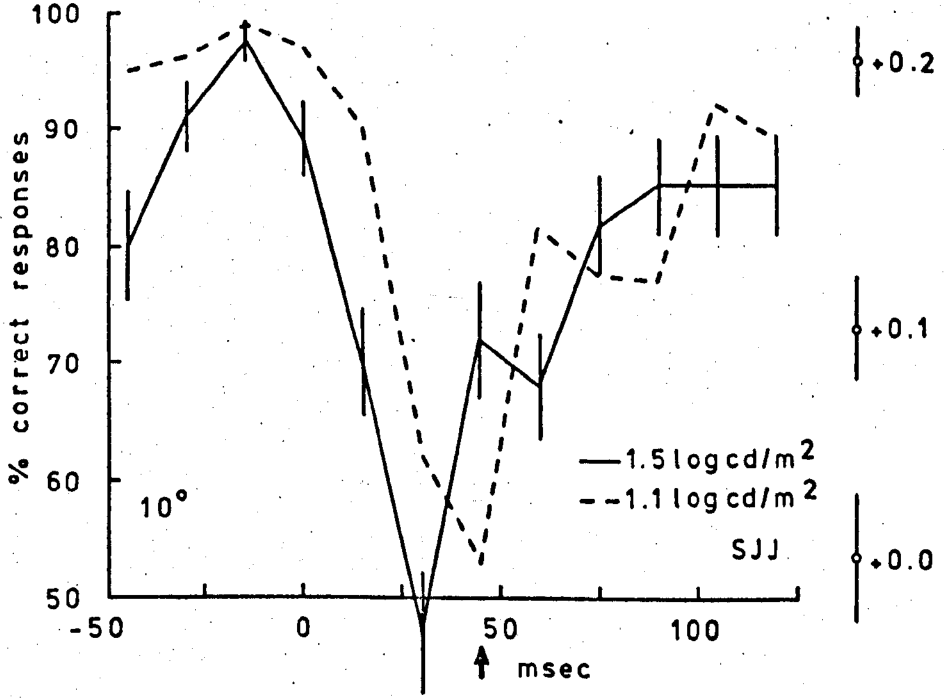
The timecourse of the threshold elevation was similar with 10, 13 27 and 86 degree diameter background discs.

In no case was the elevation of threshold greater than 0.2 log units, when it was measured by the increase in test flash intensity needed to restore the test flash to visibility.

With the 86 degree diameter background disc, the elevation of threshold appeared to be even smaller (0.1 log unit). This decrease in magnitude of the effect might have been due to the lower contrast of the disc edge with the 86 degree diameter disc: although the luminance at the centre of the disc was 1.5 log cd/m^2, the luminance at the edge

Fig. 4.1 Detectability of a flash as a function of the time of the flash relative to the onset of a 3 degrees displacement of a uniform disc background. Upper figure: 10 degrees diameter background. The dashed line shows data with the background luminance reduced by 0.4 log units. Lower figure: 13 degrees diameter background. The points at the right of the upper figure show the detectability of flashes of higher intensity delivered 40 msec after the onset of the displacement (marked by arrow). The intensity increment is indicated in log units. The error bars show standard errors calculated according to the formula for the standard error of a binomial process.

Fig. 4.2 Detectability of a flash as a function of the time of the flash relative to the onset of a 3 degrees displacement of a disc background. Upper figure: 27 degrees diameter background. Lower figure: 86 degrees diameter background. Conventions as in Fig. 4.1.


100
90
80
70
60
50
% correct responses
-50
0
50
100
msec
10°
SJJ
—1.5 log cd/m²
--1.1 log cd/m²
+0.2
+0.1
+0.0

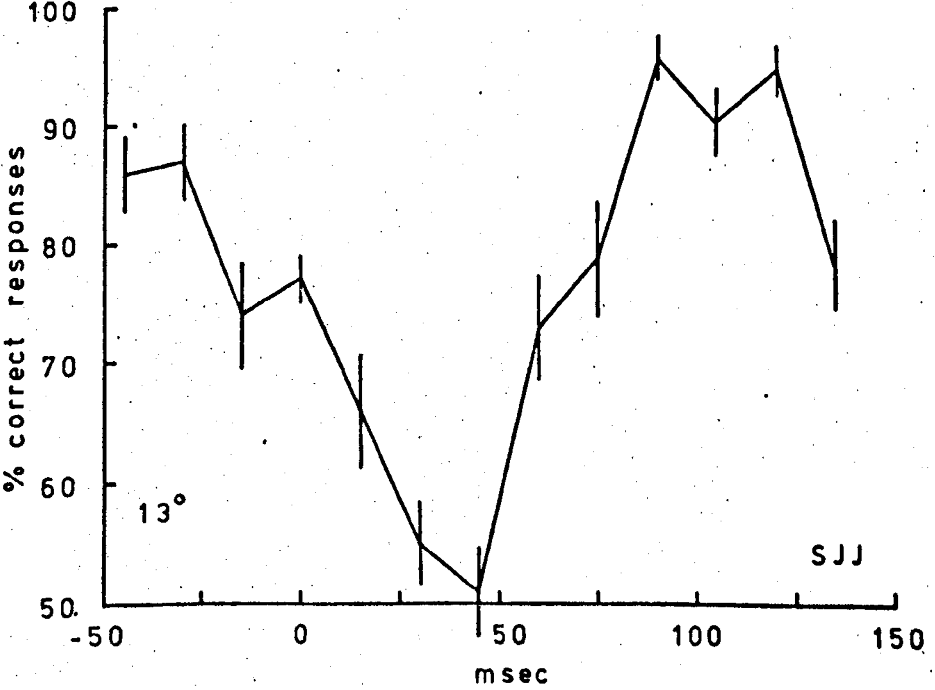

100
90
80
70
60
50
% correct responses
-50
0
50
100
150
msec
13°
SJJ

Fig. 4.1

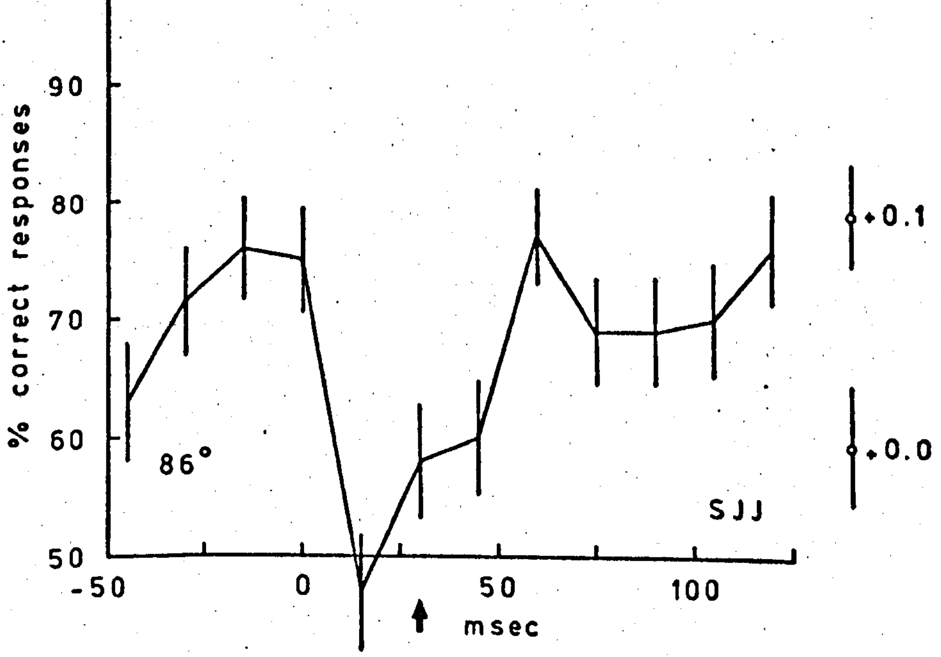
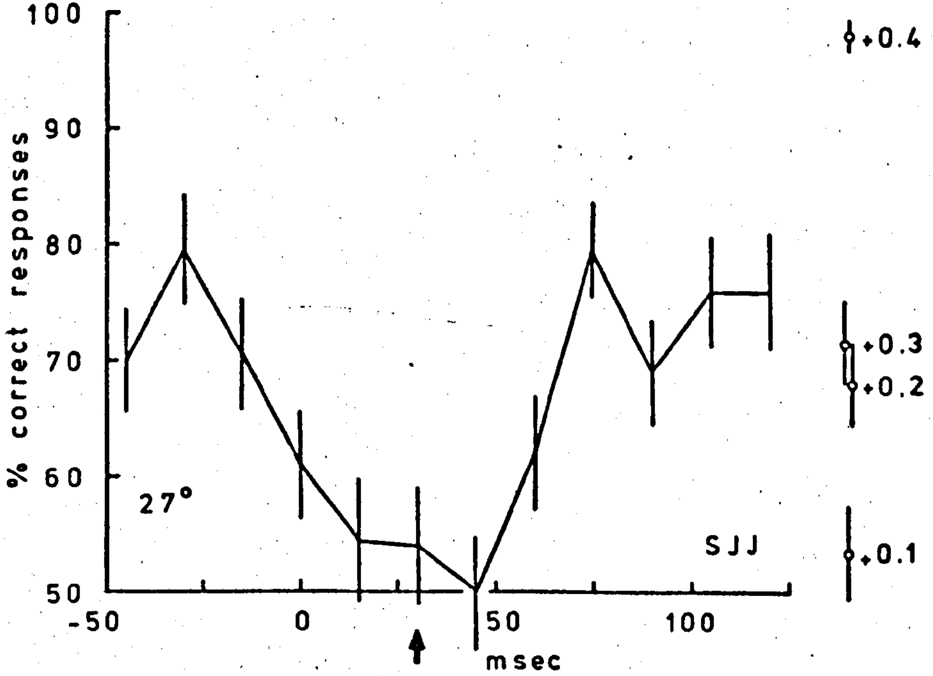


Fig. 4.2


100
90
80
70
60
50
% correct responses
27°
SJJ
-50
0
50
100
msec
+0.4
+0.3
+0.2
+0.1


100

was only 0.8 log cd/m^2. This fall off of luminance with eccentricity is unavoidable with rear-projection, since the screen scatters light preferentially in the direction normal to the plane of the screen. Unfortunately, the overall luminance could not be increased with the apparatus used, so it was not possible to do the control of increasing the disc luminance of the 86 degree disc until the luminance at the edge was 1.5 log cd/m^2. It was, however, possible to show that decreasing the luminance of the 10 degree diameter disc to 1.1 log cd/m^2 had little effect on the magnitude of the elevation of threshold produced. (It is interesting to see that the decrease of luminance of the 10 degree diameter disc increased the latency of the threshold elevation by some 10 - 15 msec, while greater eccentricity of the moving contour had no such effect.) The data from the first and second halves of each run agree well.

4.4 Discussion

Since the threshold elevation persists even with background discs up to 86 degrees in diameter, the effect can fairly be described as a modulation of central visual field sensitivity by peripheral visual field stimulation, rather than an interaction between proximate stimuli. The magnitude of the effect is only slightly dependent on the angular separation of the test flash and the peripheral contour displacement: with the ten degree diameter disc the mean horizontal separation of the edge of the test flash and the displaced contour is 3½ degrees, whereas with the 86 degree diameter disc the mean separation between test flash and displaced contour is 41½ degrees, i.e. twelve times greater, and yet the threshold elevation is only 50% smaller with the larger disc than with the smaller disc.

It is interesting to see that with this subject the magnitude of threshold elevation produced by passive displacement of a ten degree diameter disc is only 0.2 log units. Volkmann (1962) in her classic study of the elevation of threshold associated with saccadic eye movement, found threshold elevations of 0.6, 0.5 and 0.4 for three subjects making 5 degree saccades across a background of unspecified extent (but less than 28 degrees in diameter). MacKay (1970b) reported that the threshold elevation associated with passive displacement of a ten degree diameter disc was 'of the order of 3 dB', but he was concerned to demonstrate the 'anticipatory' character and not to make a precise measurement of the magnitude of the effect.

It is not possible to tell from these experiments whether the larger elevation of threshold found by Volkmann in her experiments was due to the rather larger displacements she used, 5 degrees rather than 3, or to intersubject variation, or to a genuine difference between the effects of active and passive displacement of the peripheral retinal image. Intersubject variation is not a factor which can be lightly dismissed, since it has been shown by Leibowitz et al. (1972) that there are large variations in the accuracy of peripheral refraction between subjects all of whom have normal central refraction. Poor focussing of a peripheral contour on the retina might be expected to produce a decrease in the magnitude of the passive threshold elevation produced by displacement of that contour, and variations in peripheral refraction could thus give rise to variations in the magnitude of threshold elevation associated with displacement of a peripheral contour. (But see chapter five for evidence on this point.)

CHAPTER FIVE

Elevation of threshold associated with active and passive displacements of a nearly uniform retinal image

5.1 Introduction

The experiments reported in chapter four showed that, at least with the one subject used, the elevation of threshold associated with a three degrees passive displacement of a peripheral retinal contour (the edge of a ten degrees diameter disc of luminance 1.5 log cd/m^2) was only about 0.2 log units. Independent studies made about the same time by Johnstone and Riggs (personal communication), using several subjects, found that the threshold elevation associated with six degrees passive displacements was at most 0.25 log units (less in some subjects). These figures are to be contrasted with those obtained, for example, by Volkmann (1962) and Richards (1969) who found that threshold elevations of 0.5 log units were associated with saccadic eye movements of 6 or 5 degrees extent respectively, made under similar conditions to those employed by the above authors.

The difference between 0.5 and 0.2 or 0.25 log units is not of course a large one, and it was known that the extent of threshold elevation associated with saccadic eye movement depended on, for example, the background luminance (Richards, op. cit.). Thus the data of the author and Johnstone and Riggs therefore merely suggested that it would be worthwhile to make a direct comparison between the effects of active and passive displacement of the same retinal image on visual thresholds. This would be the most conclusive method of answering the question of whether or not the retinal image displacement consequent on a saccade can entirely account for the elevation of threshold associated with saccadic eye movement. Another way of resolving the uncertainty would be to examine the effects on visual thresholds of saccadic eye movement in a completely uniform visual environment, where there would be no stimulus to produce MacKay's effect.

A pilot experiment was conducted in total darkness, but this was abandoned because of the difficulty of controlling the retinal locus of the test flash under these conditions. Particularly with a completely dark-adapted subject, control of the retinal locus of the flash is crucial in order to prevent confounding the effects of saccadic eye movement with those of variation in sensitivity across the retina.

5.2 Elevation of threshold associated with saccadic eye movement in a nearly uniform photopic visual environment

5.2.1 Method

5.2.1.1 Apparatus

In order to avoid this problem, and to make possible the study of thresholds during saccadic eye movements in uniform photopic as well as uniform scotopic surroundings, a ping-pong ball 'ganzfeld' was constructed, by cutting a ping-pong ball roughly in half and shaping the edge to fit closely to the eye socket. This apparatus differed from the conventional one (Hochberg et al., 1951) in having cut into it a circular hole subtending just over 20 degrees (later increased to 30 degrees) of visual angle at the pupil. A larger circular piece of the same kind of ping-pong ball, subtending a slightly greater angle than the circular aperture, was placed about two centimetres beyond the aperture in the ping-pong ball. A microscope slide cover-slip was placed between this and the ping-pong ball, to form a partially reflecting mirror in which fixation points and a test flash could be seen. The fixation lights and flash stimulator were in reality to the right of the ping-pong ball assembly, but appeared to be some 30 cm directly in front of the subject's eye when it was in position in the apparatus (see Fig.5.1). Since the whole of the ping-pong ball assembly was within five centimetres of the subject's pupil, the aperture in the ping-pong ball was not evident to the subject and an apparently uniform featureless field could be produced by suitable illumination of the apparatus from the rear and the sides; yet fixation points and a sharply focussed test flash could be introduced onto this background by means of the mirror. The luminance of the background was 15 cd/m^2. Test flashes of two milliseconds duration were produced by fast-phosphor miniature fluorescent tubes. The intensity of the flashes could be varied over a range of one log unit by altering the peak current in the tubes. Both blank and patterned flashes were used. The patterned flash consisted of horizontal white lines 6 minutes of arc wide spaced at regular intervals of 24 minutes of arc. This form of pattern was chosen because it was little degraded by horizontal eye movements.

5.2.1.2 Procedure

With this apparatus two experiments were performed. Firstly the detectability of a large (18 degree diameter) test flash was determined as a function of the time interval between the flash and the onset of a voluntary horizontal saccade between fixation points 9 degrees apart, placed symmetrically with respect to the position of the flash. The large flash was used in order to avoid variations of flash detectability with retinal locus of the flash image: with a large flash on a photopic background it was assumed that the part of the flash falling on the fovea would be most easily detected, and thus the retinal locus of effective stimulation would remain constant.

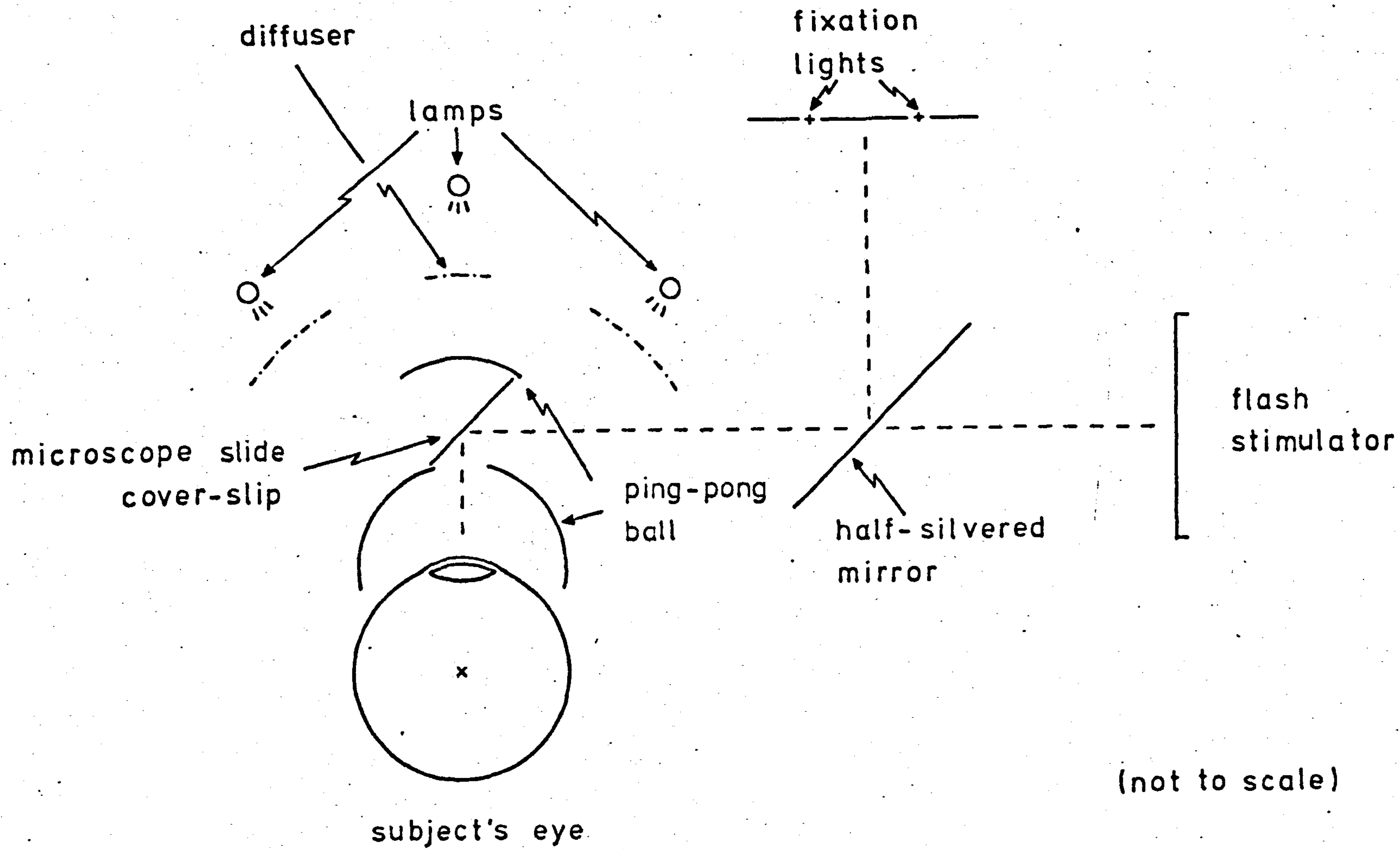


Fig. 5.1 Apparatus for initial experiment examining the threshold for detection of flashes presented in temporal proximity to saccadic eye movements in a nearly uniform photopic visual environment.

The subject waited for a relay click which was the signal to make a saccade. Saccades were detected by means of an EOG monitoring system. (See section 5.4.1.1 below for details.) The test flash was triggered at a randomly varied interval after the relay click. Since there is a minimum delay of the order of 200 msec between an auditory signal to saccade and the onset of the eye movement, flashes could be delivered up to 200 msec before the saccade (and also after the saccade). The time between the flash and the saccade was measured by the method described in section 5.4.1.2. The experiment was controlled by a PDP-8 computer (programmed in the high level language 'FOCAL'), so it was simple to arrange that the mean delay of the flash was automatically adjusted to match the mean saccade latency, and so to sample symmetrically the range of flash-saccade intervals. On 20% of trials the flash was inhibited, so that the subject's false alarm rate could be monitored The subject responded by pressing one of two buttons to indicate whether he did or did not detect the flash. At a randomly varied interval after the response the next trial was initiated by the relay click. The time of occurrence of the relay click was thus unpredictable by the subject.

In order to be able to better quantify the elevation of threshold associated with saccadic eye movement, the method of constant stimuli was employed in a second experiment to compare the threshold for detection of a flash occurring <u>during</u> a saccade with the threshold for detection of a flash delivered some 100 msec <u>before</u> a saccade. In this experiment the flash either occurred some 100 msec after the click which was the subject's signal to saccade, or was triggered by the saccade. These two conditions were randomly interleaved, and the intensity of the flash was also randomly varied from trial to trial.

5.2.2 Results

In the first experiment, a consistent and substantial drop in the detectability of the flash was found, beginning for flashes presented about 75 msec before the onset of the saccade and reaching a maximum effect just before the saccade began. The effect was similar with patterned and blank test flashes, except perhaps that the depression of flash detectability was more prolonged with the patterned flash (see Fig.5.2). Control experiments in which the fluorescent tube stimulator was replaced by a stroboscope which produced flashes of less than 50 microseconds duration gave similar results, suggesting that this small difference in timecourse may be genuine rather than an artefact of blurring of the test flash when it was delivered during the saccade. (Blurring would be expected to have a more pronounced effect on the detectability of the patterned stimulus than the blank stimulus.)

Fig.5.3 shows the results of the second experiment in which the method of constant stimuli was used to compare the thresholds for detection of flashes delivered 100 msec before and during saccades. The patterned test flash was used in this experiment. It can be seen that the elevation of threshold associated with saccade eye movement is about 0.4 log units. It is possible that this figure of 0.4 log units threshold elevation is subject to some error due to slight blurring of the test stimulus. Even though the test stimulus pattern was composed of horizontal lines, a small vertical component of saccade velocity would have produced some blurring. For example, the maximum angular velocity of a 9 degrees saccade is about 300 degrees/sec. Thus if the flash were delivered when the eye was moving most rapidly, a 5% vertical component in saccade velocity (15 degrees/sec) would be sufficient to move the stimulus through nearly 2 minutes of

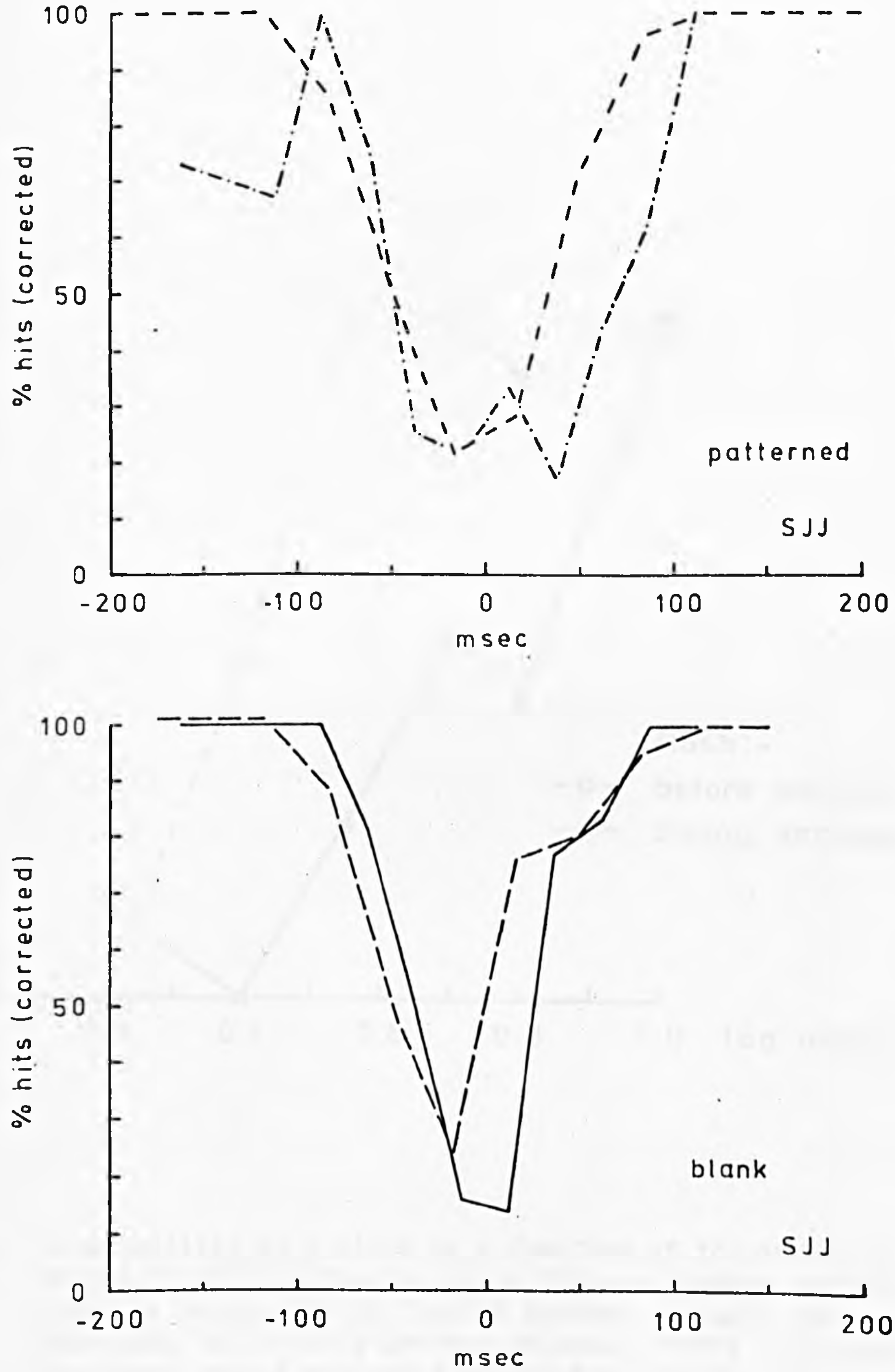


Fig. 5.2 Detectability of a flash as a function of the time of the flash relative to the onset of a 9 degrees saccadic eye movement in a nearly uniform photopic visual environment. 20 degrees diameter flash, either patterned with fine horizontal lines, or unpatterned (blank). See text for details.

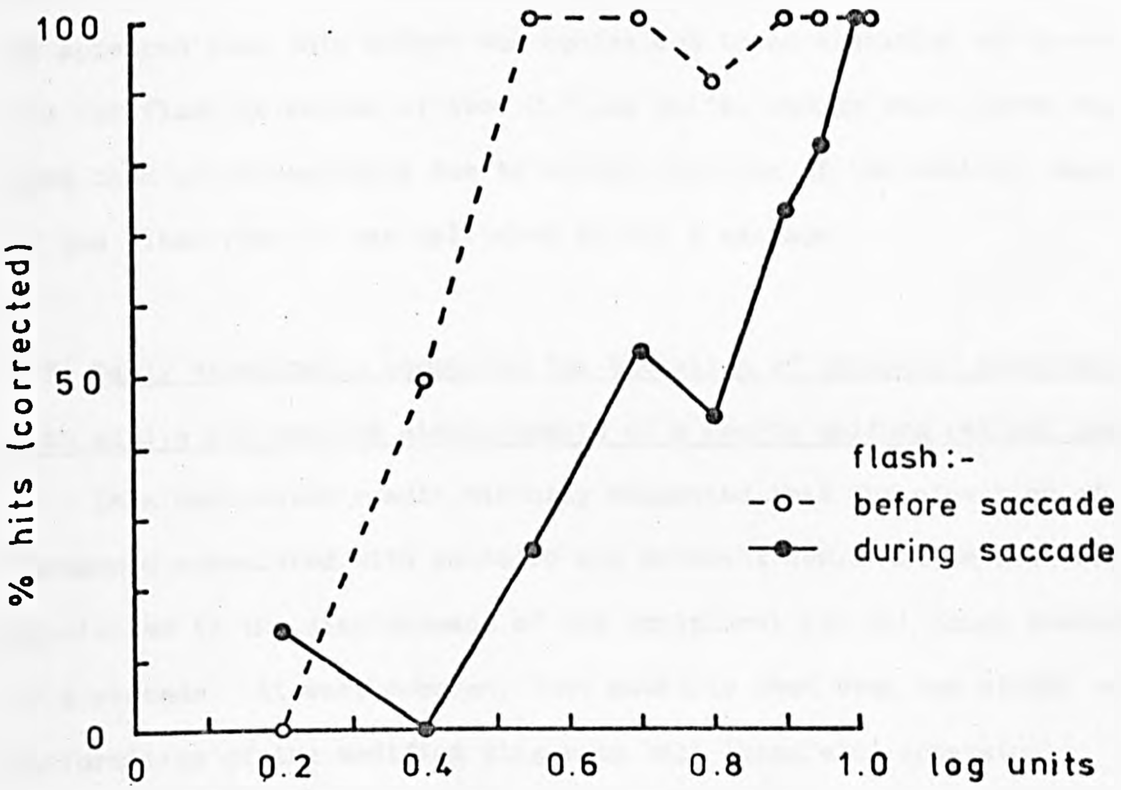


Fig. 5.3 Detectability of a flash as a function of the intensity of the flash, for flashes about 100 msec before (dashed line) or during (solid line) 9 degrees saccadic eye movements in a nearly uniform photopic visual environment. The elevation of threshold associated with the saccade is about 0.4 log units.

arc vertically during the 2 msec flash presentation. This would compare with the stimulus line width of 6 minutes of arc. Even so, the blurring would only be expected to contribute about 0.13 log units of threshold elevation.

5.2.3 Summary

Considerable depression of the detectability of a test flash was associated with saccades in a nearly uniform photopic environment. It appeared that this effect was equivalent to an elevation of threshold for flash detection of some 0.4 log units, though this figure may have been an overestimate due to slight blurring of the retinal image of the flash when it was delivered during a saccade.

5.3 Early experiments comparing the elevation of threshold associated with active and passive displacements of a nearly uniform retinal image

This unexpected result strongly suggested that the elevation of threshold associated with saccadic eye movement could not be entirely attributed to the displacement of the peripheral retinal image produced by a saccade. It was, however, just possible that even the slight non-uniformities of the modified ping-pong ball 'ganzfeld' apparatus, notably the fall-off of luminance in the far periphery, especially in the extreme nasal field, and also more centrally the slight and unavoidable annular shadow, cast by the piece of ping-pong ball beyond the mirror, were never-the-less sufficient to produce a substantial threshold elevation effect of the kind reported by MacKay (1970a, b).

In order to resolve this matter experimentally, the ping-pong ball apparatus was altered so that it could be rotated in a pseudo-saccadic fashion about the centre of rotation of the subject's eye. The details of these alterations to the apparatus, and of the methods employed in the experiments, are described in Appendix One.

The data obtained in these experiments are also relegated to that appendix since the design of the apparatus was imperfect in two respects. Firstly, since the test flash and fixation points were, as above, seen in a partially reflecting mirror fixed to the ping-pong ball assembly, when the apparatus was rotated through a given angle the retinal image of the fixation points and the retinal locus of the test flash moved through twice that angle, whereas the retinal image of the ping-pong ball assembly itself moved only through the given angle. In contrast, when the eye was rotated through a given angle, the retinal image of the fixation points, the retinal locus of the flash and the image of the ping-pong ball assembly all moved through that given angle. Thus it was not possible to equate, in the active and passive displacement conditions, both the extent of displacement of the images of the fixation points and test flash, and the extent of displacement of the image of the background. Secondly, the maximum angular velocity with which this early apparatus could be rotated fell short by a factor of two from that of a saccade of comparable extent. The principal finding of these early experiments was that active displacement of the retinal image was accompanied by a greater elevation of threshold than that associated with passive displacement of the retinal image. This difference could not be attributed to the first imperfection of the apparatus mentioned above, since not only was there a significant difference between the effects of active and passive displacements which rotated the images of the fixation points and test flash through equal angles (i.e. between the effects of 9 degrees saccades and 4½ degrees 'ganzfeld' rotations), but there was also a significant difference between the effects of active and passive displacements of the background through equal angles (4½ degrees). It was not, however, feasible to rule out the possibility that the difference in effect of active and passive image displacements was due to the greater angular velocity of the active displacements. The apparatus was therefore completely re-designed and rebuilt, and a new series of experiments performed, as described below.

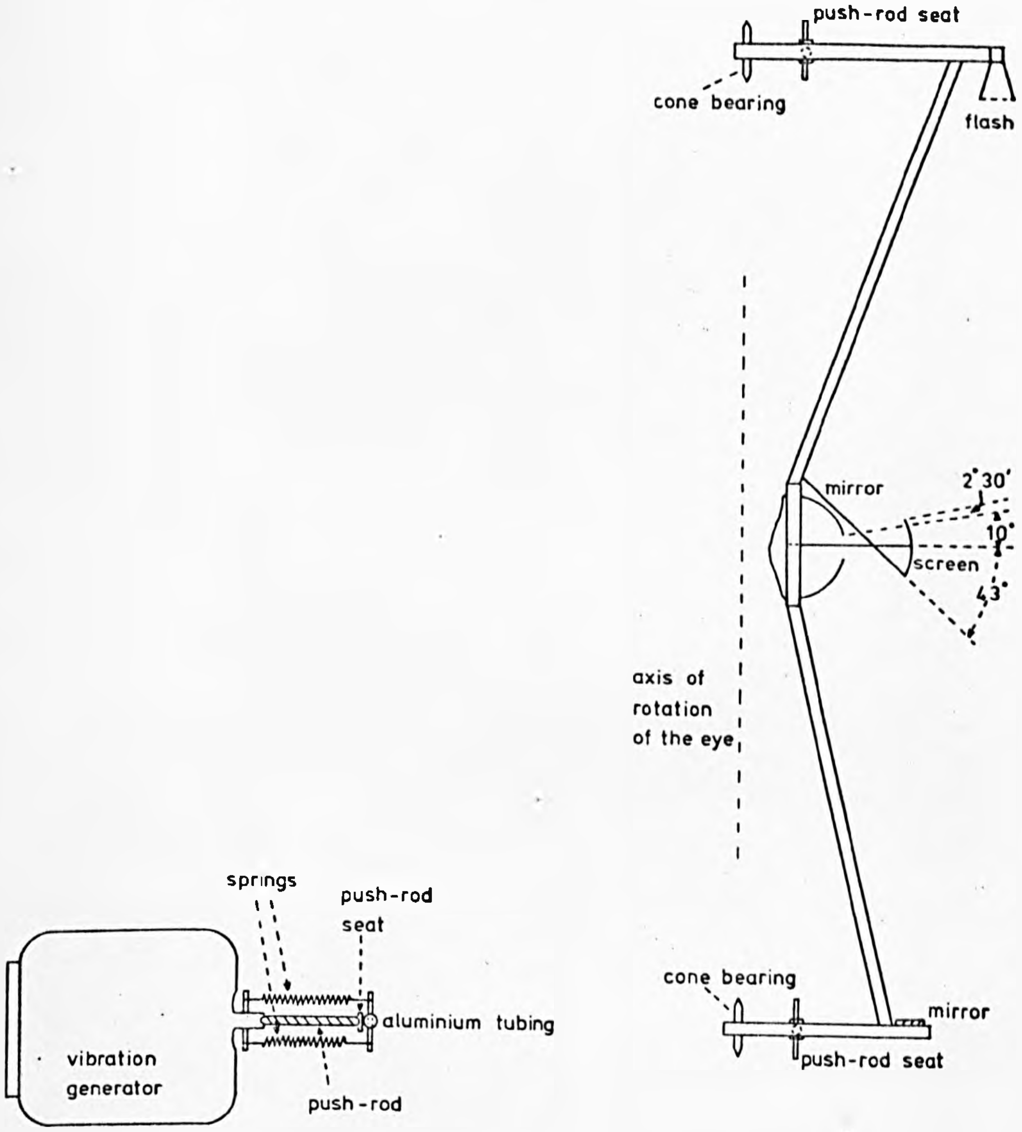
5.4 Final experiments comparing the elevation of threshold associated with active and passive displacement of a nearly uniform retinal image

5.4.1 Methods

5.4.1.1 Mechanics, optics and eye-movement monitoring

Fig.5.4 is a scale drawing of the rotating part of the apparatus; Figs.55a and b are photographs of the apparatus. The half ping-pong ball was mounted in a perspex ring to the top and bottom of which were glued (with 'araldite') oblique struts of thin-walled aluminium tubing. These struts were in turn glued to horizontal aluminium tubes in the end of which short brass rods with conical ends were mounted to form the cone part of cone and cup bearings. This assembly was rotated by two Ling Altec 3 ohm 'vibration generators' which were coupled to the rotating assembly by means of push-rods held in place by twin tensioned springs. The vibration generators were connecected in series to a conventional power amplifier fed with a trapezoidal waveform of transition time 20 msec. The trapezoidal input was smoothed with an RC integrator of time constant 10 msec in order to reduce a slight overshoot and oscillation to insignificant levels (5-10%), and to make the rotation timecourse more truely saccade-like.

The timecourse of rotation was monitored before, during and after the series of experiments by mounting an oscilloscope above the apparatus and observing the sweep of the beam via the mirrors of the apparatus. The timecourse of rotation was closely similar to that of a saccade of



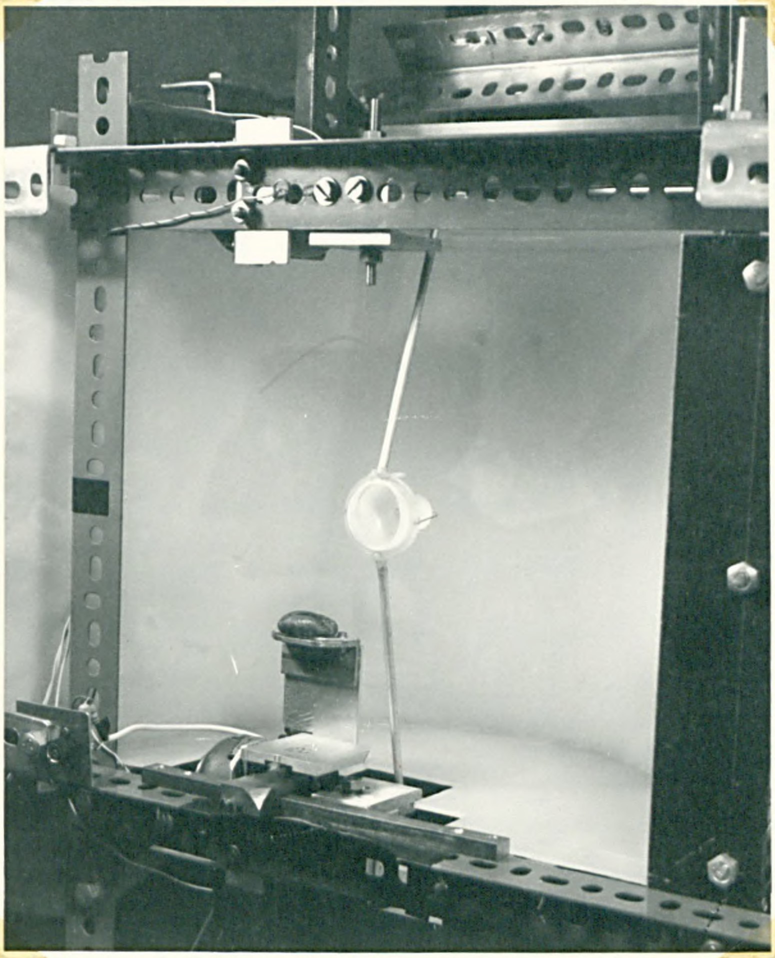
a) Front view of drive assembly

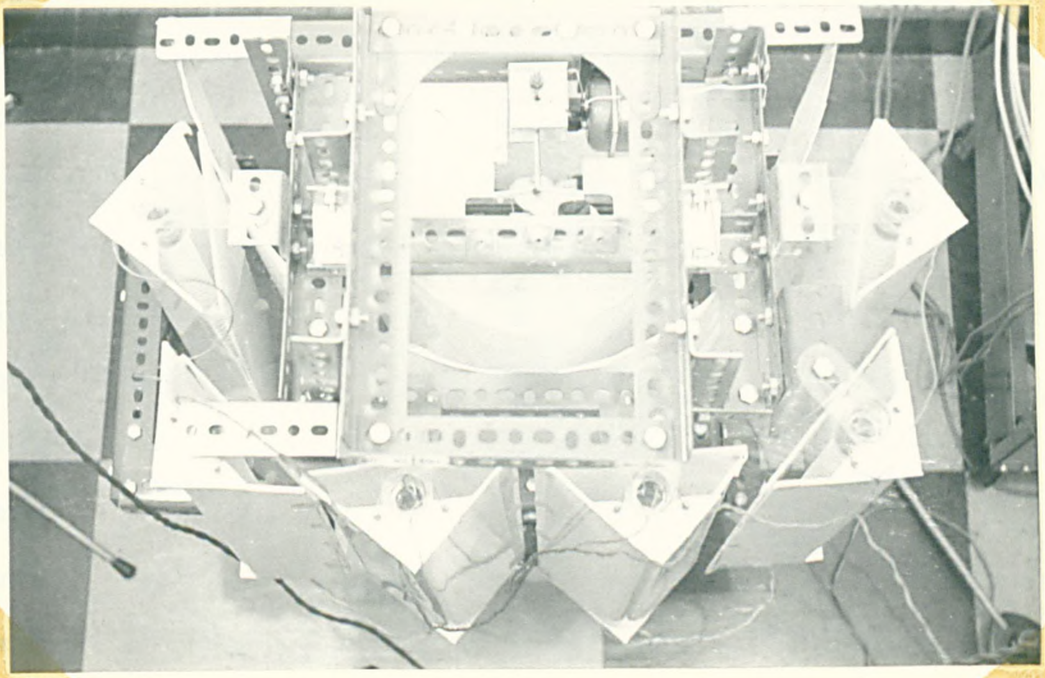
b) Side view of 'ganzfeld' mounting

Fig. 5.4 Scale drawings of the ping-pong ball ganzfeld mounting and of the mechanical assembly for rotating the ping-pong ball.

Fig. 5.5a View of the apparatus from the front. The ping-pong ball mounting, the vibration generators and the bite bar mounting can be seen. At the extreme top of the photograph the sleeves in which the fibre optics were mounted can just be seen. The fibres have been removed for the photograph. In the centre of the photograph, behind the ping-pong ball, the inner perspex diffusing screen is visible.

Fig. 5.5b View of the apparatus from above and behind, to show the arrangement of the fluorescent tubes providing the source of illumination, and the diffusing screens. The fibre optics have been removed for the photograph.





the same amplitude (six degrees), having a duration of 30 msec and approximately the same form. No significant delay was present between the onset of the electrical input signal and the onset of the rotation. Observation of the undamped oscillation of the apparatus suggested that the natural resonant frequency was about 100 Hz.

The aperture in the ping-pong ball subtended 20 degrees at the subject's eye. The 'screen' was made of the same ping-pong ball, and was mounted on fine horizontal wire supports. Between the ping-pong ball assembly and vertically-mounted 15 w fluorescent tubes providing the background illumination were three diffusing screens. Each fluorescent tube was connected via a 1.5 K resistor to the anode of a valve, the other end of the fluorescent tube being connected to a 250 v D.C. power supply. The luminance of the tubes could thus be individually adjusted by altering the grid-bias on the valves. By this means the luminance of the background field could be balanced up so that it was uniformly 160 cd/m^2 ± 0.025 log units within ± 70 degrees horizontally of the axis of the apparatus. At the start of the series of experiments each subject made a 'bite' into dental impression compound mounted on a plate rigidly fixed to a chin rest itself mounted on a calibrated X-Y framework. By this means the subject's eye position could be reliably reproduced in different runs. Before the series of experiments were started the position of the bite was carefully adjusted so that, according to the subject, his eye was centrally placed in the apparatus, both fixation points being visible in all conditions, and equidistant from the slight annular shadow of the 'screen'. The fixation points were made as dim as was compatible with theirremaining visible throughout an experimental session.

Fundamental to the design of these experiments was the principle that the test flash (of one degree subtense at the subject's eye) and the fixation points (which were separated by 6 degrees of arc)) rotated with the ping-pong ball assembly, so that their retinal images moved across the retina as they would during a saccade. This was achieved by means of fibre optics (Crofon 1610 plastic light conduit from Fibre Optic Suppliers). This sixty-four fibre bundle was dissected at each end. Seven fibres were used for each fixation point, and some forty or so for the test flash. The fibre bundles were loose and unsupported for some 15 cm between their ends fixed to the rotating assembly and sleeve supports on the frame of the apparatus, so that no significant load was applied to the rotating assembly by the fibre bundles. At the other end of the fibre bundles the fixation light sources were provided by two small filament lamps, and the test flash by a Sunpak Auto 22 flashgun. Neutral density filters could be inserted between the flashgun and the end of the fibres carrying the light from the flashgun. The subject's eye movements were monitored by EOG electrodes placed on the skin near the temporal corner of each eye. The difference between the potentials of the two electrodes was amplified by a conventional preamplifier whose output was displayed on a storage oscilloscope and fed to a rectifier followed by a Schmitt trigger set to trigger on saccadic eye movement signals. The storage oscilloscope was used firstly to check that the subjects did not make reflex saccades when the apparatus rotated, and secondly to check that subjects made clean single saccades between the fixation points, and did not break the movement into two or more smaller saccades. The first error was insignificant after the subjects' first 'dry run' in the apparatus; the second error was less easy for the subjects to avoid. All subjects were given training in not making double saccades or other irregular eye movements between the fixation points. After training EM and ST performed well, making only a few percent saccades in which there was a second saccade of more than $\frac{1}{4}$ the main saccade, and in most cases making clean saccades with no detectable second saccade. SJJ (the author), however found it difficult to avoid making double saccades. In his case, the saccade trigger-level was raised so that only 'good' saccades (ones of at least two-thirds of full amplitude) were detected.

Subjects were carefully instructed not to blink as they made saccades or in the temporal vicinity of saccades, and the EOG signal was monitored by the experimenter for evidence of blinking - which was rarely seen.

5.4.1.2 Stimulus control and data analysis

Two computer programmes, TAID and TPID were used to investigate respectively the timecourse of threshold elevation during active image displacement and the timecourse of threshold elevation during passive image displacement.

During TAID experiments, the sequence of events was that the subject waited for a 'click' to indicate to him that he should make a saccade to the opposite fixation point. A loud click indicated a rightward saccade, a quieter click a leftward saccade. At a randomly varied interval after the click the test flash was triggered (or randomly on 10% of trials *not* triggered, so that a check could be kept on false-positive responding). The length of the time interval between the flash and the saccade was reckoned by the computer counting the 'ticks' of a clock while a bistable was set, the bistable being set either by the flash or saccade trigger signals (whichever came first) and reset by the complementary signal. The sense of the time interval was then reckoned by reading the state of a second bistable set only by the saccade and reset only by the flash signal. The subject's response was read and assigned to the appropriate bin on the basis of the flash-saccade interval and the direction of the saccade.

After every twenty trials the mean flash delay was adjusted to keep the centre of the flash delay range approximately equal to the mean saccade latency.

During TPID experiments the sequence of events was similar, except that the click was now an indication to the subject to keep looking straight ahead when the ping-pong ball apparatus rotated in a pseudosaccadic fashion 200 msec later, bringing the opposite fixation point into his fovea.

As in TAID , the flash occurred at a randomly varied interval after the click (except on 'catch' trials). In TPID experiments, however, there was no need to measure the interval between the flash and the displacement, since the latency of the displacement was constant, and the subject's response was simply assigned to the appropriate bin on the basis of the flash delay and the sense of rotation.

In both TPID and TAID runs the mean intertrial interval (between onset of each trial) was 3 sec. The intertrial interval length was randomly varied by ± 0.3 sec to make the time of the click indicating the start of the next trial not exactly predictable by the subject. At the end of each run (120 responses or 6 minutes), the computer typed out for each sense of displacement the hit rate as a function of flash-displacement interval, the standard deviation of the hit rate, and the false alarm rate. The absolute numbers from which these statistics were calculated were also output, both on the teletype and onto magnetic tape to facilitate aggregration of data from different runs.

5.4.1.3 Procedure and miscellaneous details

After a number of preliminary experiments, the following design was settled on. The timecourse of detectability of the test flash as a function of time relative to the displacement was determined for both active and passive displacements with flashes at two intensity levels differing by 0.2 log units. Four experimental sessions were run with each of the three subjects (EM, ST and the author, SJJ). In each of these sessions eight runs were made alternately with active and passive displacements. The first pair of runs were made at one level of flash intensity, the second pair at either 0.2 log units higher or lower intensity, the third pair at the original intensity, and the fourth pair at the same intensity as the second pair. In the four different sessions the order of use of higher and lower intensities and of active and passive displacements was balanced, all possible different orders (within the scheme above) being used. A session lasted about 70 minutes in all, since some time was needed between runs to type out the results of the last run, reset the computer and alter the apparatus settings. In addition to the main experiments, various control experiments were performed as described below.

In all the experiments the subjects wore headphones into which 'white' noise was injected to mask the sound of the flashgun. The subjects wore a special eye patch over the eye not viewing the stimulus. This eye patch was extremely light-tight after careful adjustment at the start of each run, and did not touch the eyelashes as many eye patches do (which interferes with eye movement). The subjects also wore a white 'blinker' at the temporal edge of the eye viewing the stimulus, so that it was not possible to glimpse the edge of the apparatus in the extreme temporal margin of the visual field when the ping-pong ball was rotated in the nasal direction.

5.4.2 Results

5.4.2.1 Subjective appearance of the ping-pong ball apparatus

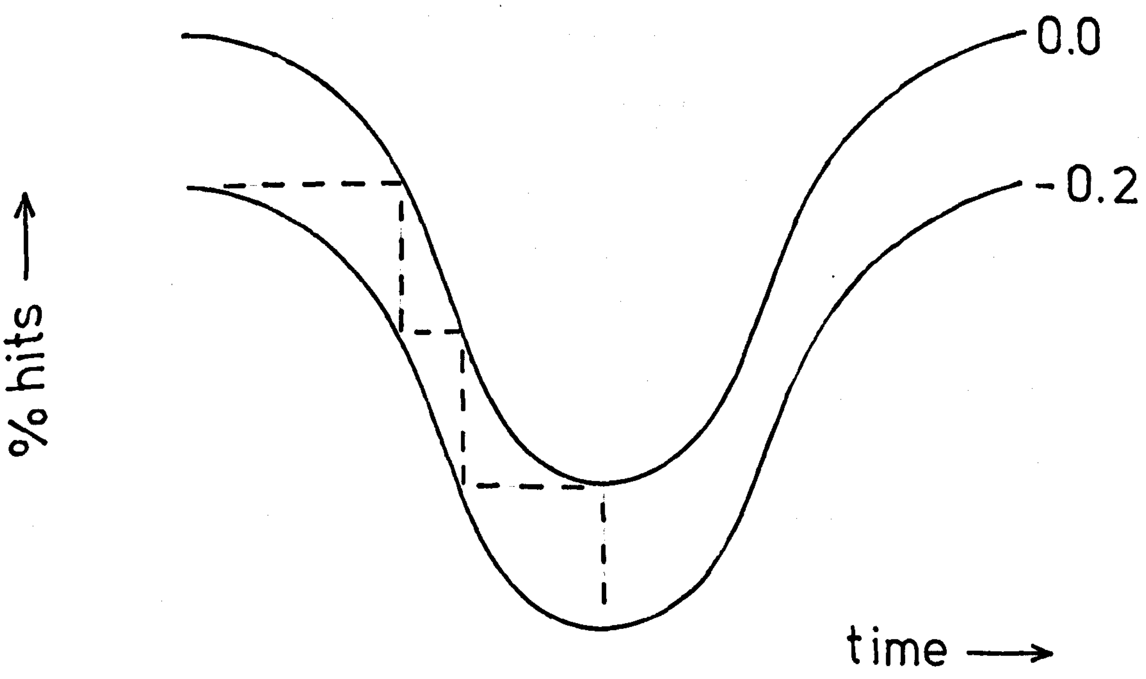
As a subject, the author invariably noted the onset of one of the classical 'ganzfeld' phenomena some time after the beginning of each run: the field of view as apparently darkened in whole or in part. Also, the fixation points were frequently subject to autokinetic movement, especially towards the end of each session.

If the apparatus remained stationary and the subject fixated one of the fixation points, no feature was evident in the field of view. When the apparatus was rotated or the eye moved, however, three features were evident in the field of view. The first was a slight darkening of the field corresponding with the inner edge of the ping-pong ball. This was presumably due to partial shadowing of this part of the ping-pong ball by the 'screen'. The second and third features were dark crescents in the extreme nasal and temporal periphery of the visual field corresponding to the outer edge of the ping-pong ball. The nasal feature was the more salient. The visual sensation associated with saccadic eye movement was similar to that associated with a pseudo-saccadic rotation of the ping-pong ball assembly.

5.4.2.2 Comparison of the effects of active and passive image displacement on flash detection with subjects ST and SJJ

Figs.5.6 & 5.7show the results of the main series of experiments for two of the subjects, ST and SJJ. Each figure shows the aggregate data from four sessions. In no case was the false alarm rate greater than five percent, so the ordinate is simply the hit rate (percentage of positive responses on trials in which a flash was present). Directions of displacement indicate the sense of the retinal image displacement i.e. rightward active displacements correspond to rightward saccades and rightward passive image displacements correspond to leftward rotations of the ping-pong ball assembly. As can be seen, subjects ST and SJJ gave similar results which will now be described. A third subject, EM, gave different results which for various reasons are believed to be anomalous. The data for EM will be dealt with later.

For both ST and SJJ active image displacement always produced a greater depression of ability to detect the test flash than did passive image displacement. The differences between the effects under the two conditions were, however, never large. By constructing 'staircases' between the timecourse curves for the two intensities of flash differing by 0.2 log units the threshold elevations were estimated in terms of the decrease of flash intensity which would have produced a similar drop in flash detection rate. The peak threshold elevation (in log units) is given by the total number of steps needed in the staircase, multiplied by 0.2 log units (the step size). For example, in the hypothetical case given below the peak threshold elevation is 0.6 log units.



The numbers in the bottom left corner of each part of the figures are these estimates of peak threshold elevation, hereafter referred to simply as 'threshold elevation'. Overall, for the two subjects the mean threshold elevation so estimated amounted to 0.3 log units for passive image displacements and 0.5 log units for active image displacements.

The timecourse of the depression of flash detectability was similar for active image displacements with both subjects; the drop in flash detectability began for flashes presented some 40 msec before saccade onset, reached a maximum for flashes presented during the saccade, and ended for flashes presented some 75 msec after saccade onset. For SJJ the effect of passive image displacement had a similar timecourse to that of the effect of active image displacement, while for ST the effect of passive displacement seemed to have a latency perhaps 20 msec longer (see Fig.5.6 & 5.7).

The reliability of the data points is indicated on all figures by bars extending one standard error above and/or below each datum point. Standard errors were calculated from the formula for the standard error, s, of a binomial process:

$$s = \sqrt{\frac{p(1 - p)}{n}}$$

where p is the hit rate and n the total number of trials.

Fig.5.8 indicates the reliability of the data in another way. The data from SJJ were split into two parts (those from the first two sessions, and the second two sessions), and these data were plotted separately in Fig.5.8. As can be seen, most of the corresponding datum points are in good agreement.

5.4.2.3 Comparison of the effect of leftward and rightward image displacement with subjects ST and SJJ

In both subjects rightward active image displacement seemed to be associated with a rather greater threshold elevation. This effect is very slight for ST in the data shown in Fig.5.6 but is clearly evidenced with the same subject in the data shown in Fig5.9 for a control run with ST. Reference to Fig.5.8 showing the split data for SJJ, shows that this effect is consistent from one session to another. (Different sessions were run on different days or at times of the same day separated by several hours.) Both these subjects used their right eye to view the apparatus, so rightward saccades were in both cases saccades in a temporal direction. Whether the effect is associated with temporal or rightward saccades cannot be distinguished from these experiments.

In the case of passive image displacements there is no such inter-subject consistent difference in the effects of rightward and leftward displacements.

5.4.2.4 Effect of the presence of the fixation points

A control experiment was performed with ST to investigate the contribution to the threshold elevation of the sweep across the retina of the fixation points. Fig.5.9 shows the results of this experiment. The fixation points were automatically switched 'off' when the click occurred at the start of each trial and were switched 'on' again about one second after the active or passive image displacement had taken place. Runs in which the fixation lights were switched 'off' were interspersed with runs in which, as before, the fixation lights remained 'on' during the displacement. It can be seen that there was no great difference between the threshold elevation whether the fixation lights were or were not present. There was if anything a slightly greater threshold elevation when the fixation points were not present, but

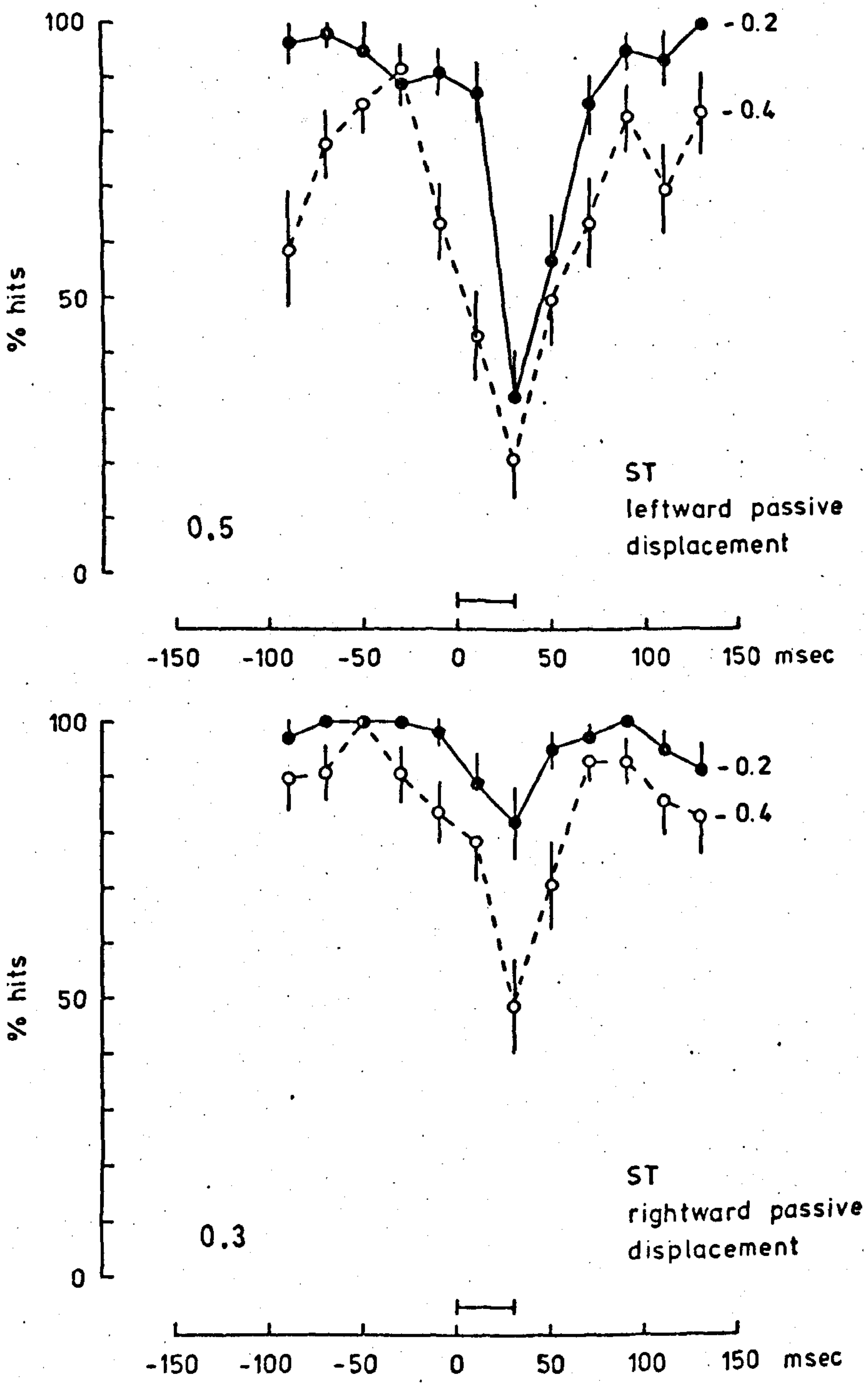


Fig. 5.6a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject ST. Error bars show standard errors calculated from binomial process formula (see text).

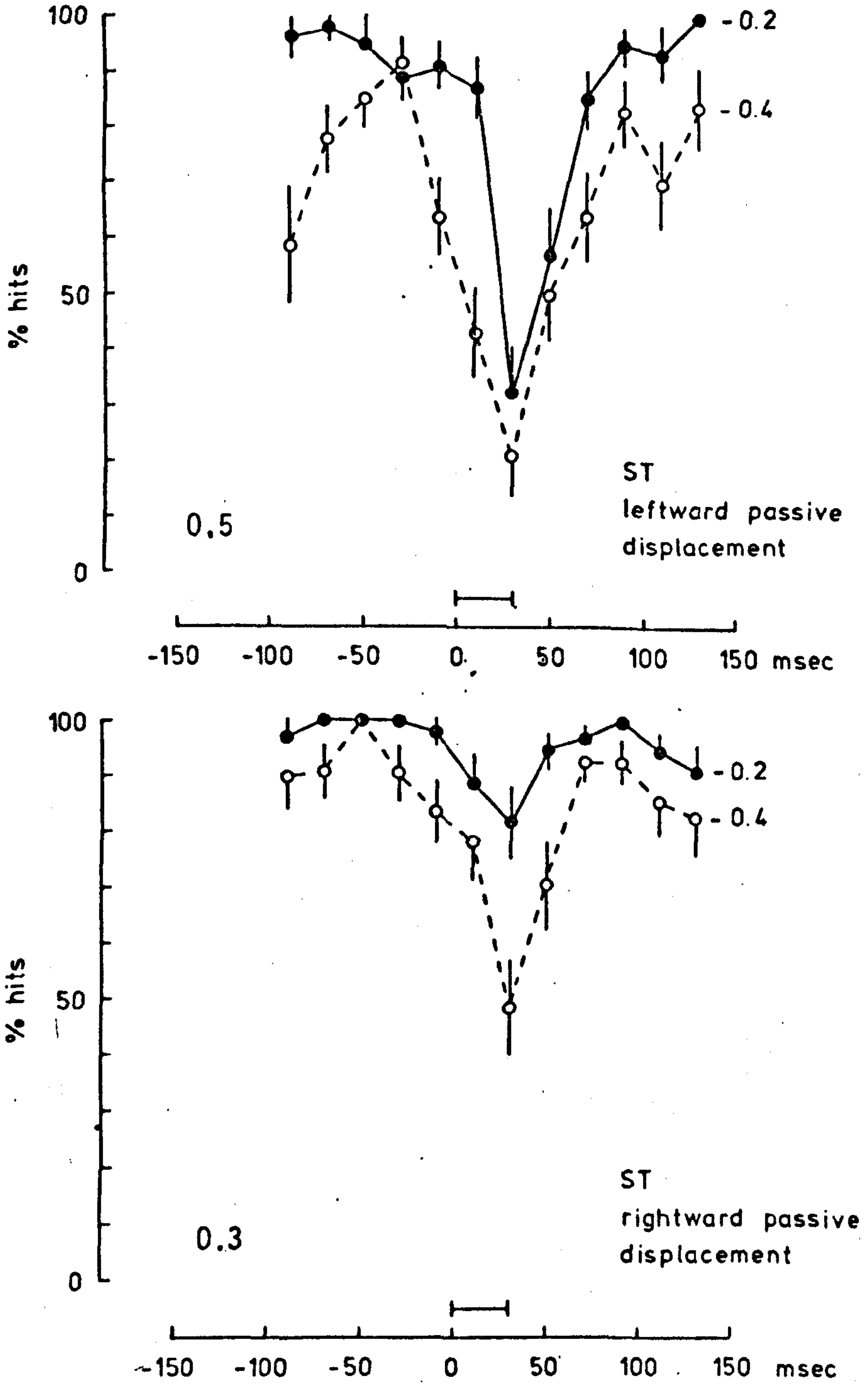


Fig. 5.6a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject ST. Error bars show standard errors calculated from binomial process formula (see text).

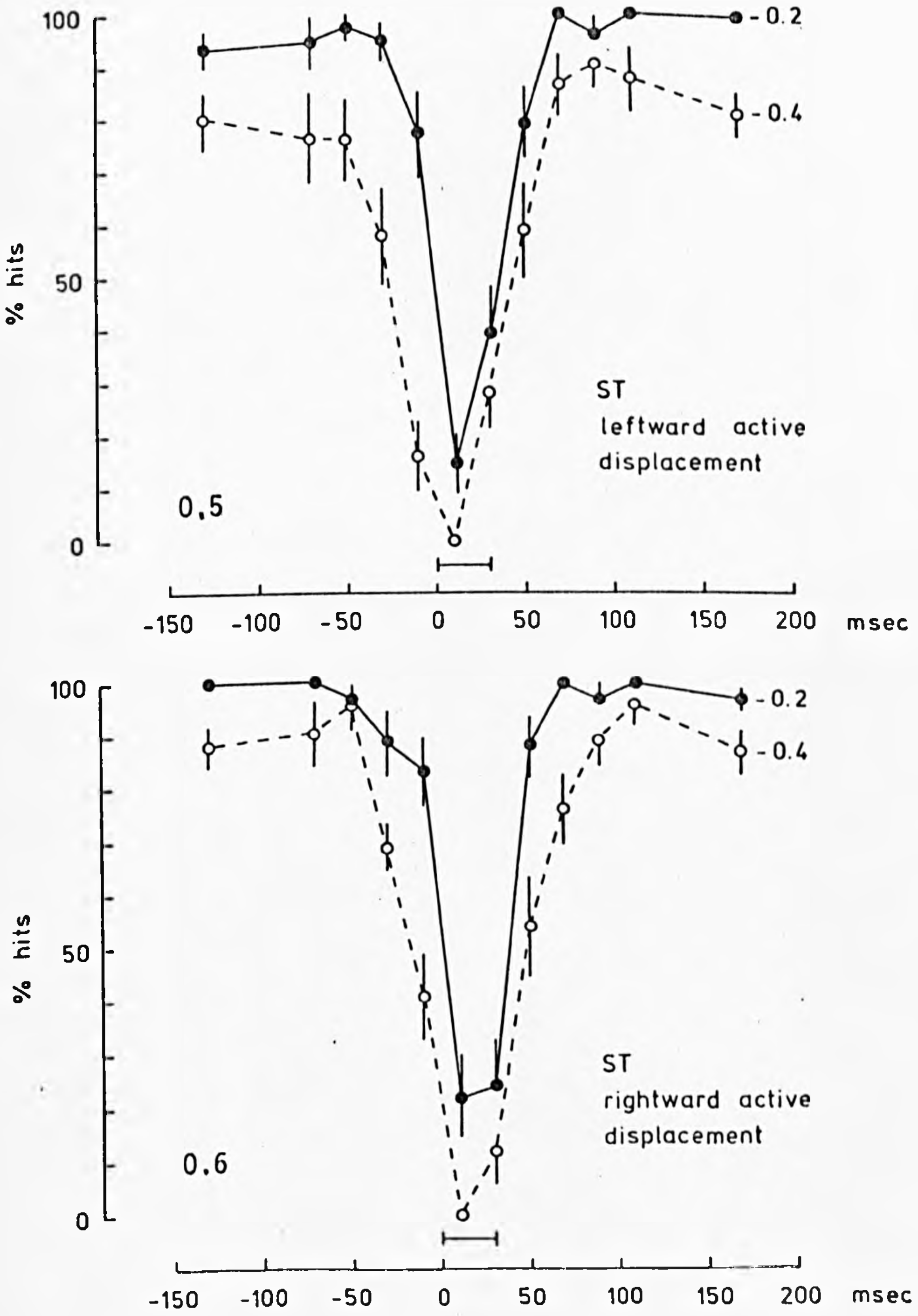


Fig. 5.6b Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees active image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject ST.

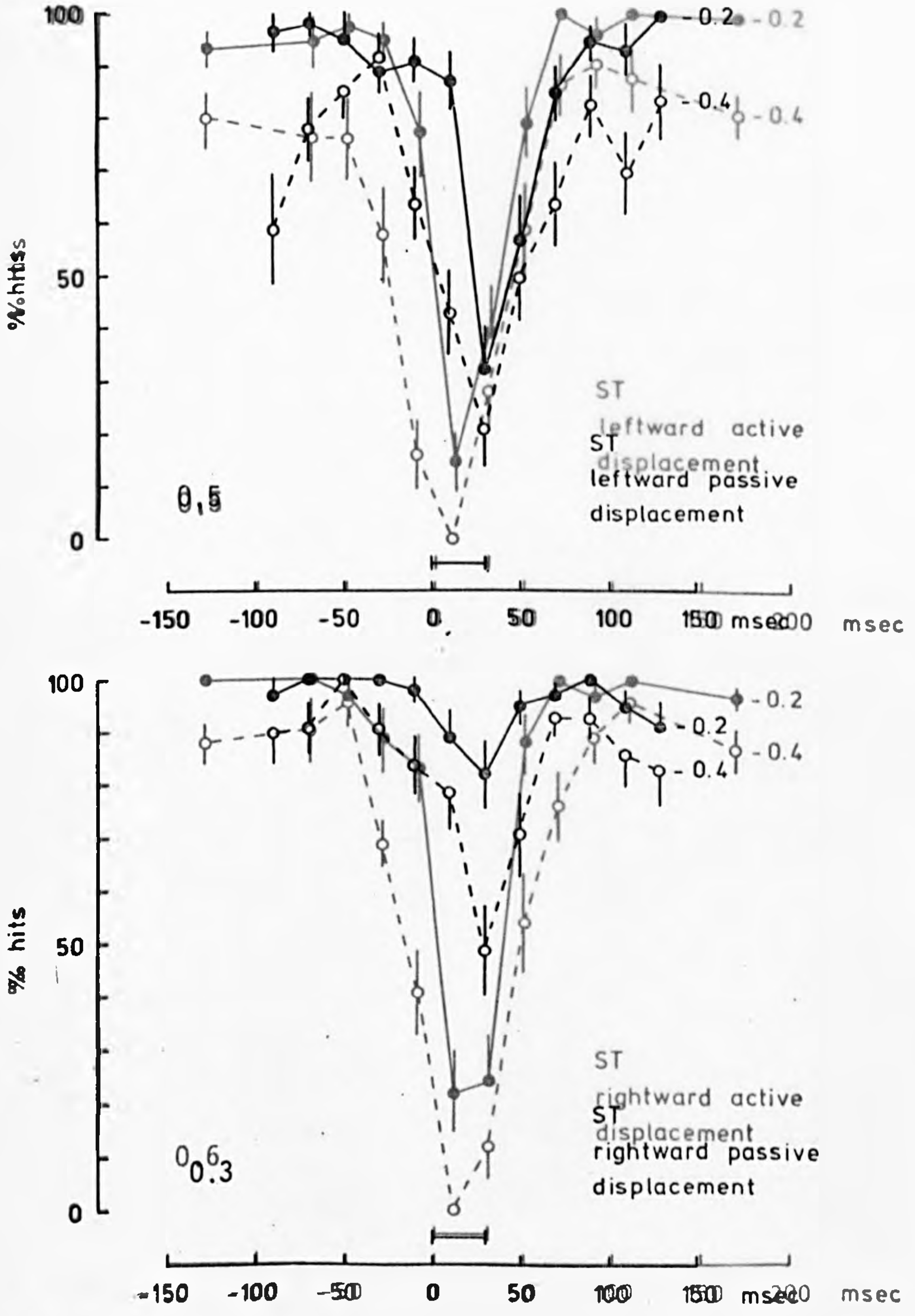


Fig. 5.6a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject ST. Error bars show standard errors calculated from binomial process formula (see text).

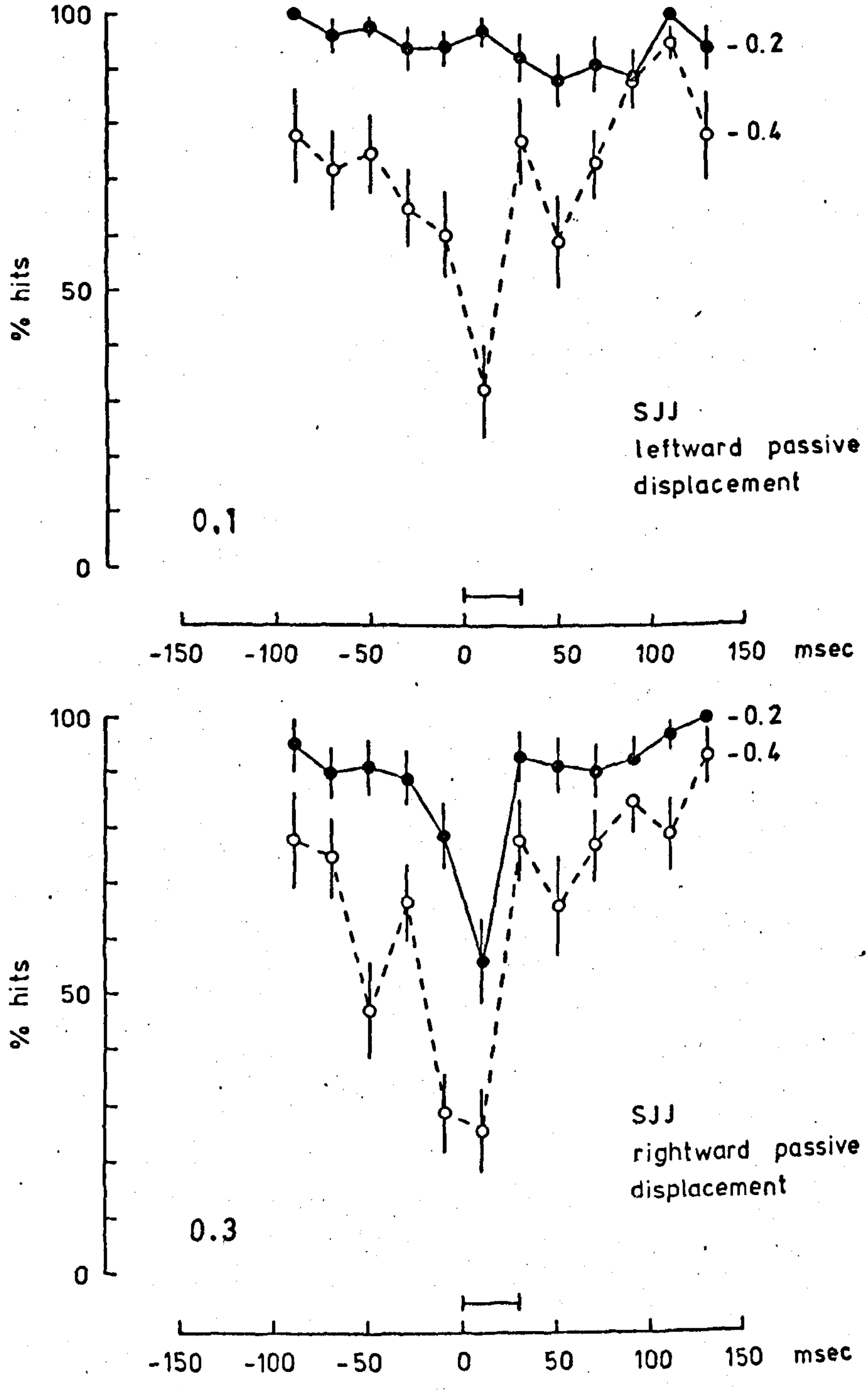


Fig. 5.7a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject SJJ.

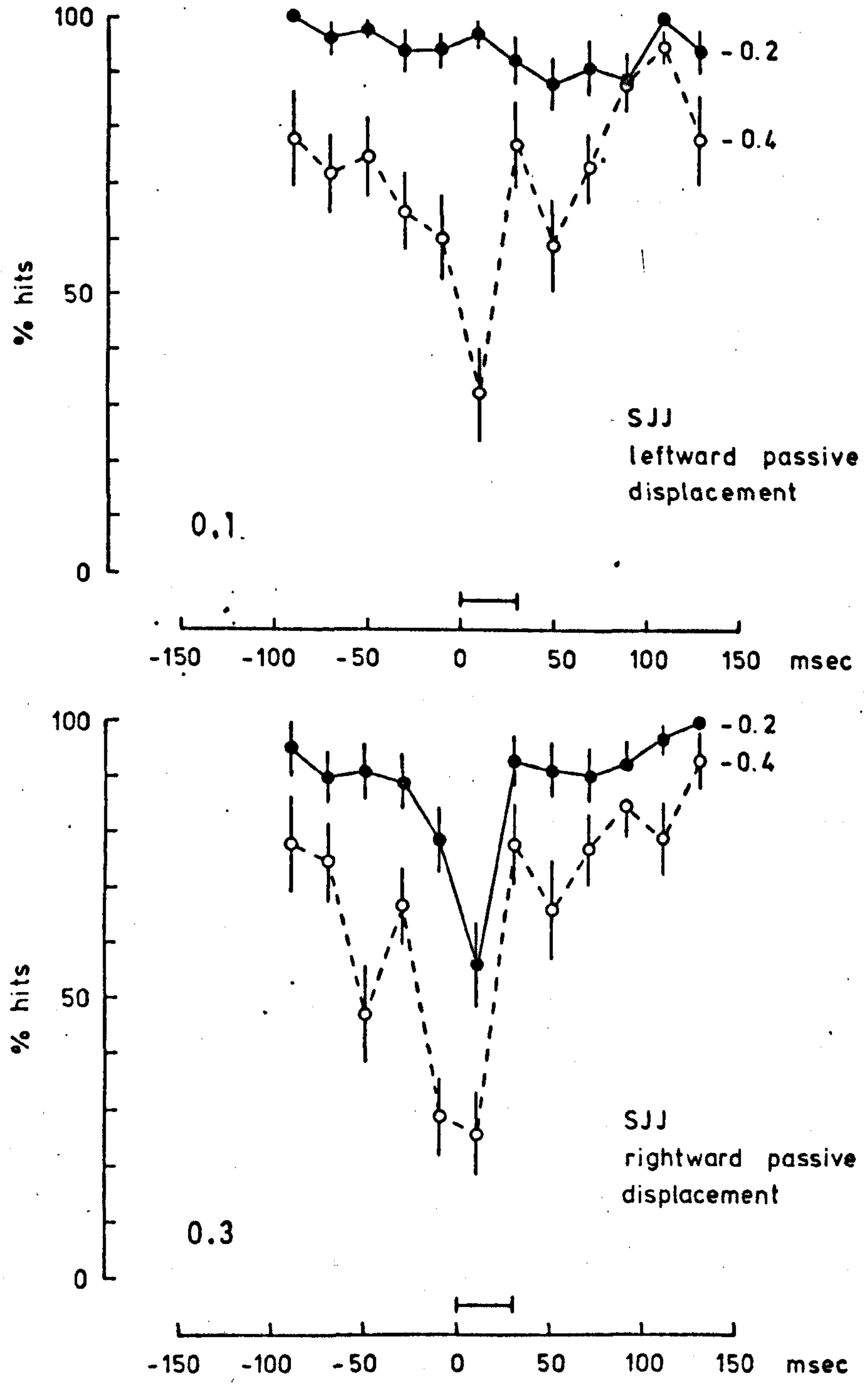


Fig. 5.7a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject SJJ.

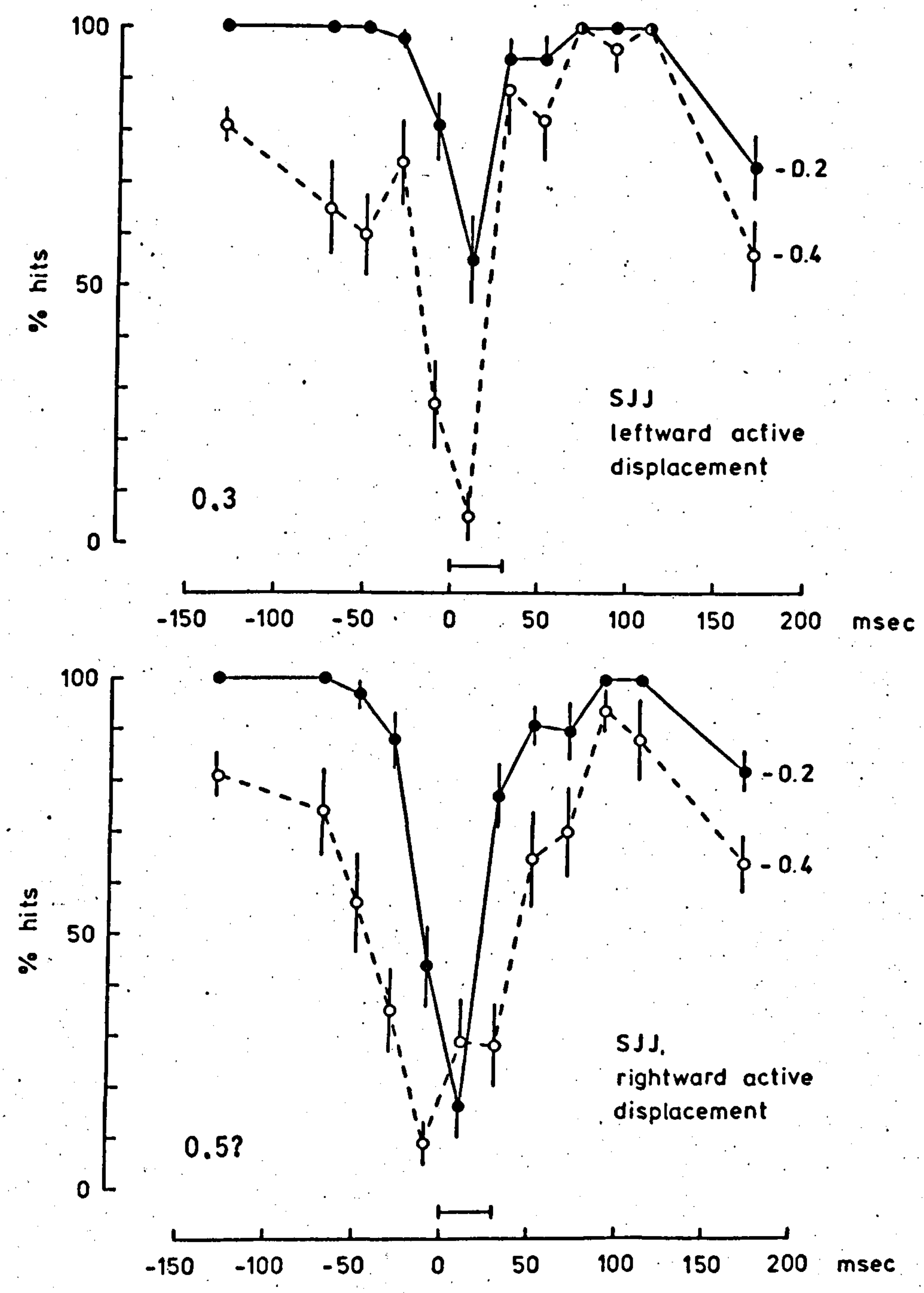


Fig. 5.7b .Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees active image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject SJJ.

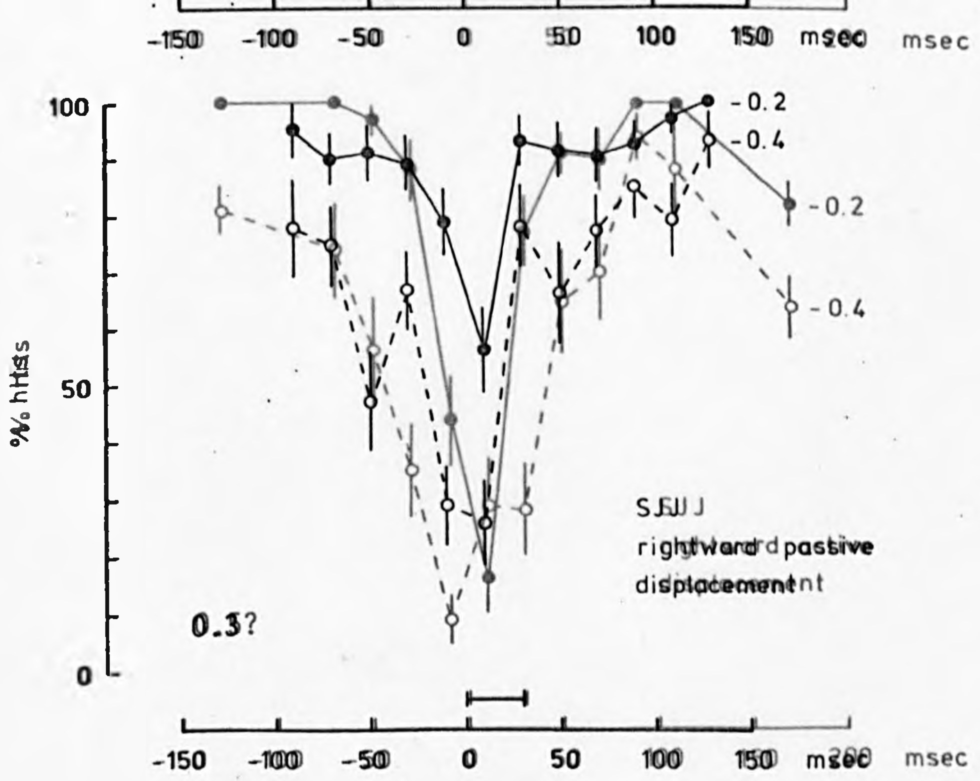
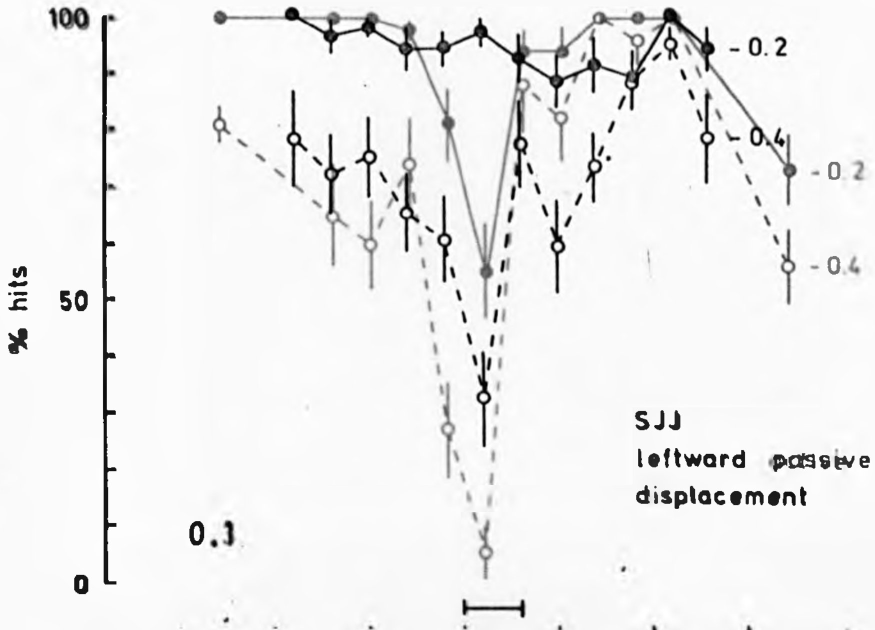


Fig. 5.7b Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degree passive image displacements (shown by horizontal bars) for two flash intensities differing by 0.2 log units. Subject SJJ.


100
50
0
% hits
0.1
- 0.2
- 0.4
- 0.2
- 0.4
SJJ
leftward passive
displacement

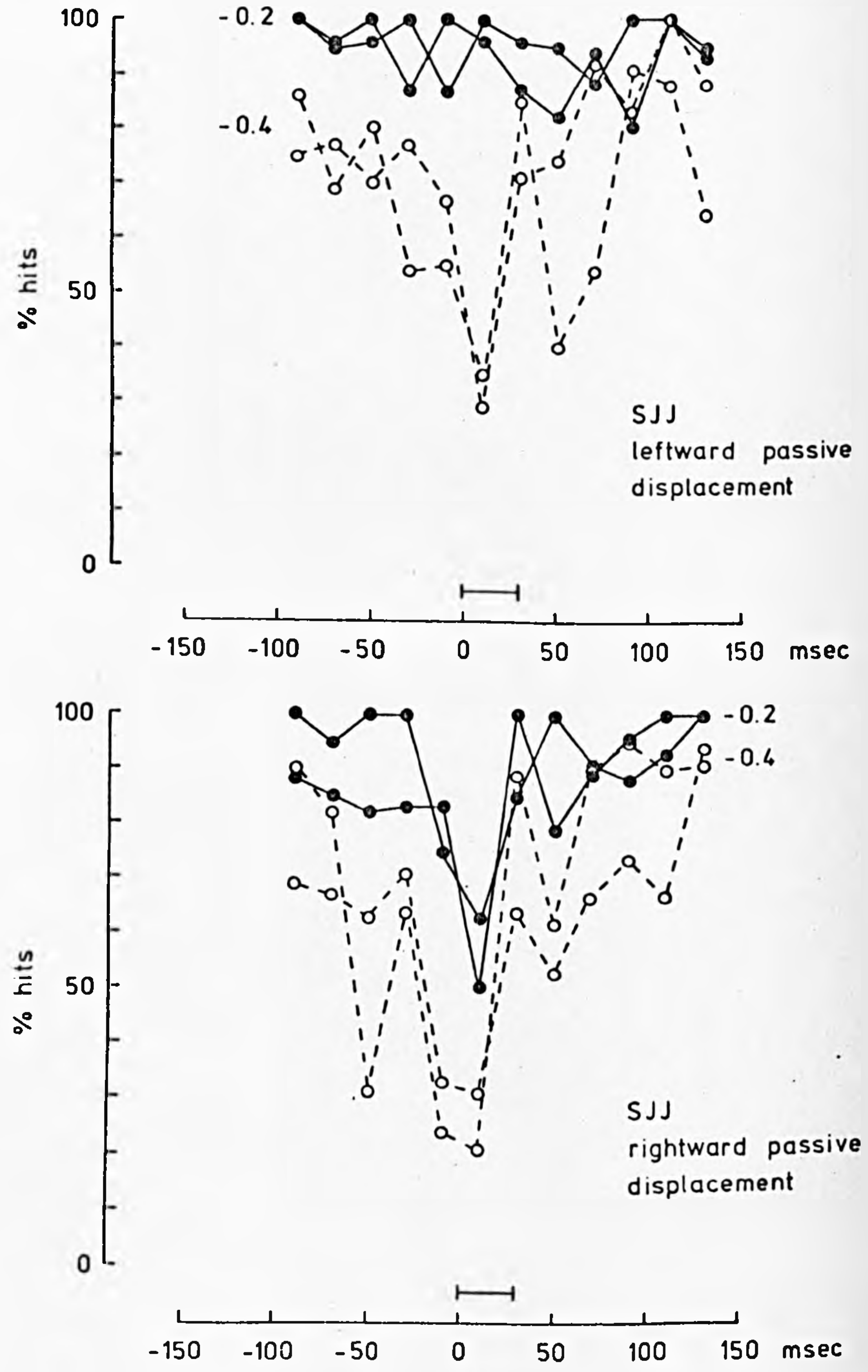


Fig. 5.8a Same data as in Fig. 5.7a, but with the data from the first and second halves of the experiment plotted separately. (See text.)

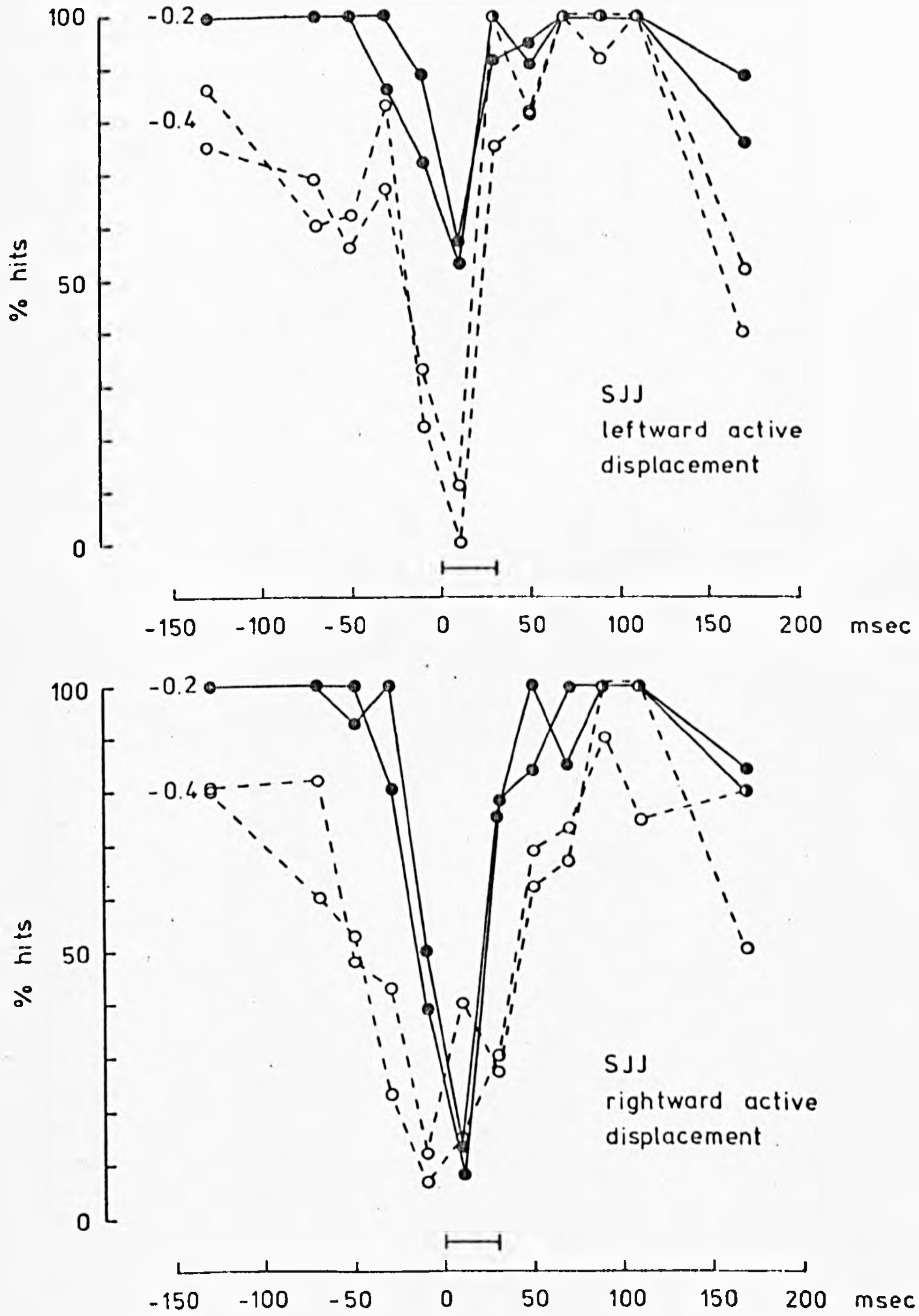
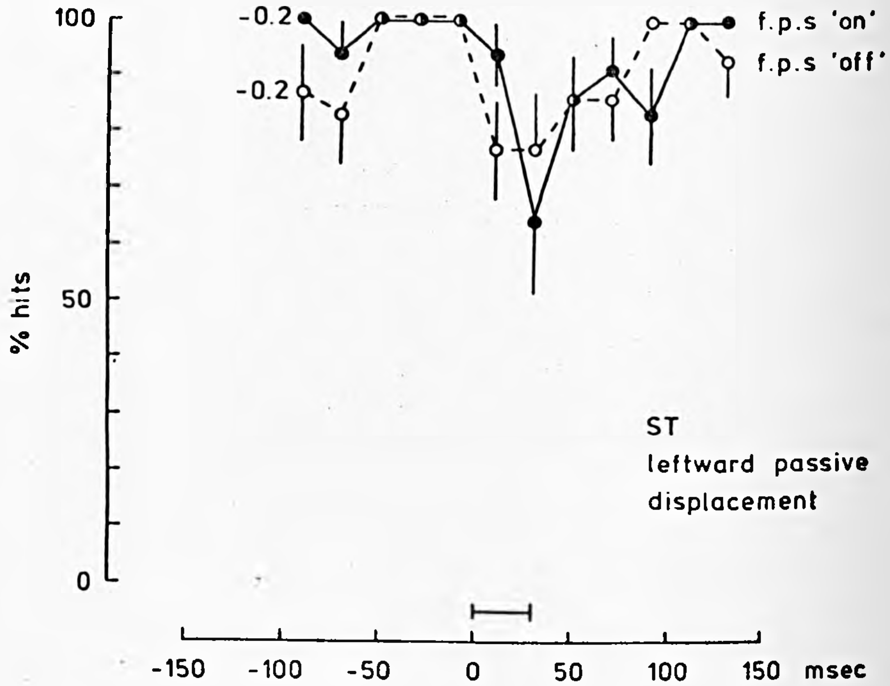


Fig 5.8b Same data as in Fig. 5.7b, but with the data from the first and second halves of the experiment plotted separately. (See text.)



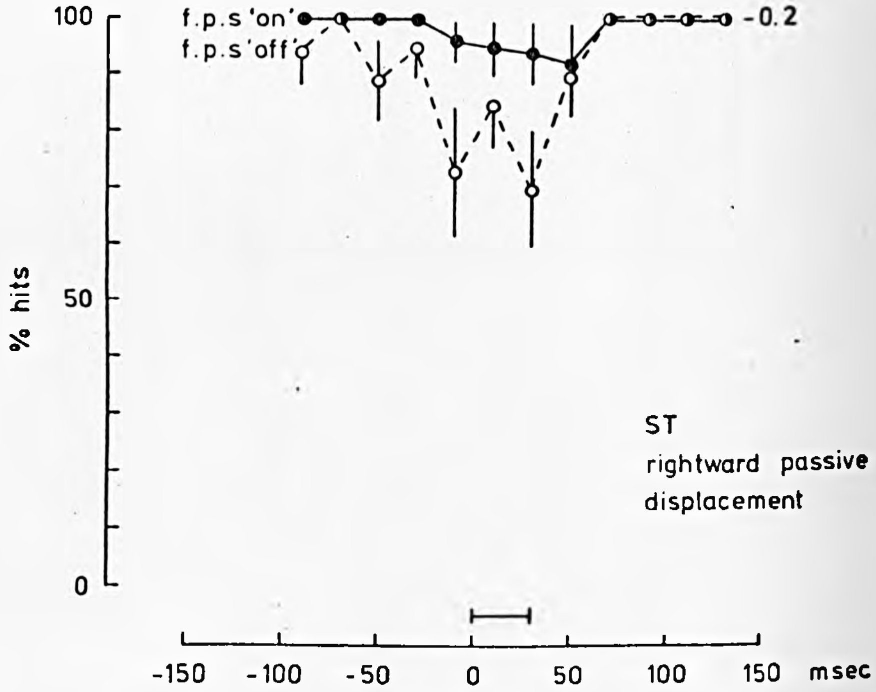


Fig. 5.9a Control experiment. The solid line shows the timecourse of flash detectability with the fixation points 'on' continuously. The dashed line shows the timecourse of flash detectability when the fixation points were switched 'off' during the passive image displacement. Subject ST.

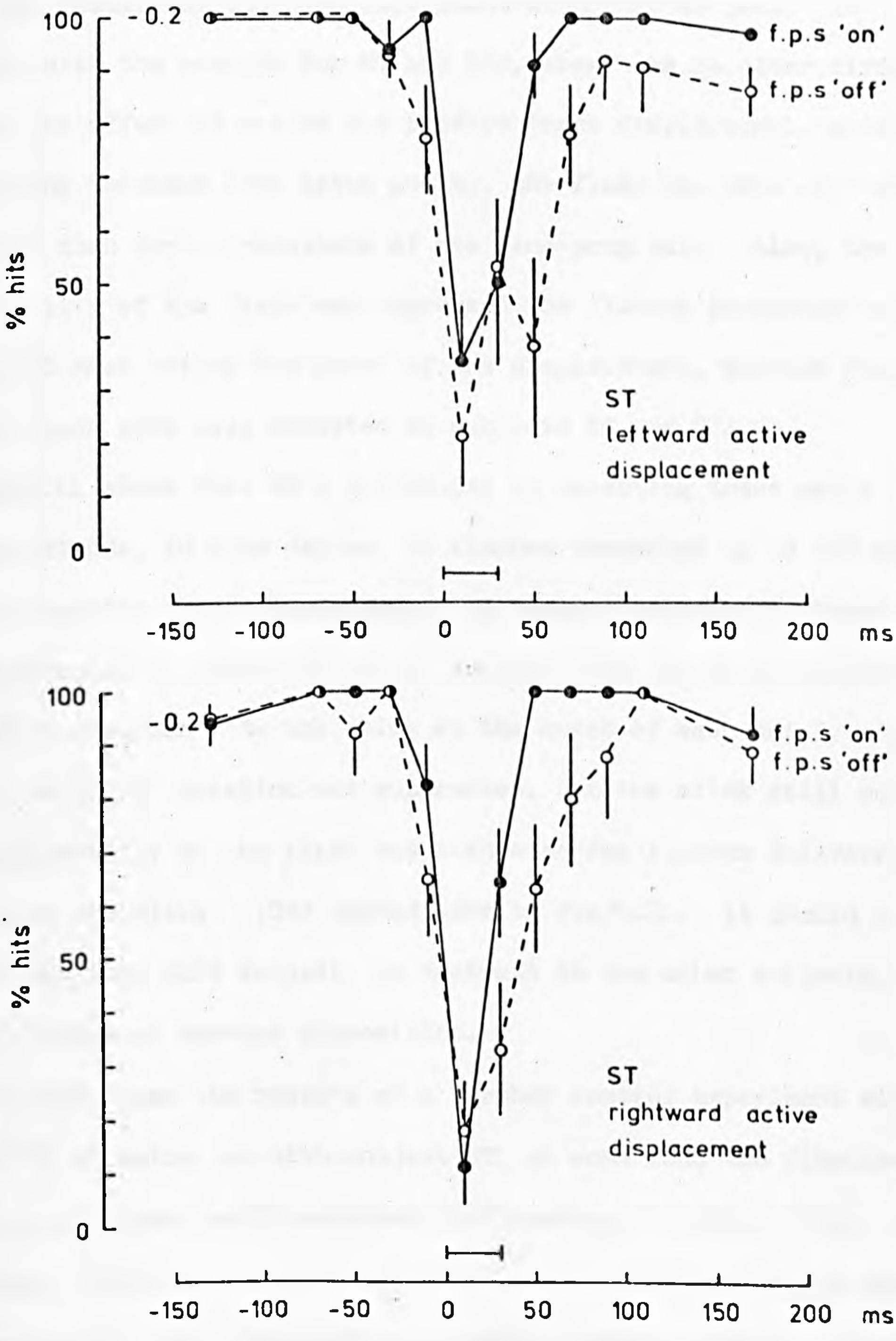


Fig. 5.9b Control experiment. Conventions as in Fig. 5.9a. Both in Fig. 5.9a and b there is little difference between the detectability of the flash whether the fixation points remain 'on' or not during the image displacements.

this could well be attributed to the greater difficulty of the subject's task in this case.

5.4.2.5 Anomalous data for subject EM

The anomalous data for subject EM will now be described. Fig.5.10 shows the results of the main experiment with this subject. In contrast with the results for ST and SJJ, there was no clear difference between the effect of active and passive image displacement, except that during saccades (one datum point), the flash was more difficult to detect than during rotations of the ping-pong ball. Also, the detectability of the flash was depressed for flashes presented between 50 and 100 msec before the onset of the displacement, whereas flashes in this epoch were well detected by subjects ST and SJJ.

Fig.5.11 shows that EM's difficulty in detecting these early flashes extends, to some degree, to flashes presented up to 150 msec before a passive image displacement. A control experiment showed that this difficulty in detecting early flashes could not be attributed to a 'startle reaction' to the click at the onset of each trial, since if the 'ganzfeld' rotation was suppressed, but the click still occurred, the detectability of the flash was high even for flashes delivered just after the click. (See dashed line in Fig.5.11.) It should be pointed out that this subject, in contrast to the other subjects, was of a somewhat nervous disposition.

Fig.5.12 shows the results of a further control experiment with subject EM in which, as with subject ST, on some runs the fixation points were automatically switched 'off' during rotation of the 'ganzfeld' apparatus. Contrary to the finding with subject ST, switching the fixation points 'off' produced a substantial improvement in the ability of the subject to detect flashes presented about the same time as passive displacements of the retinal image. It seems that EM's

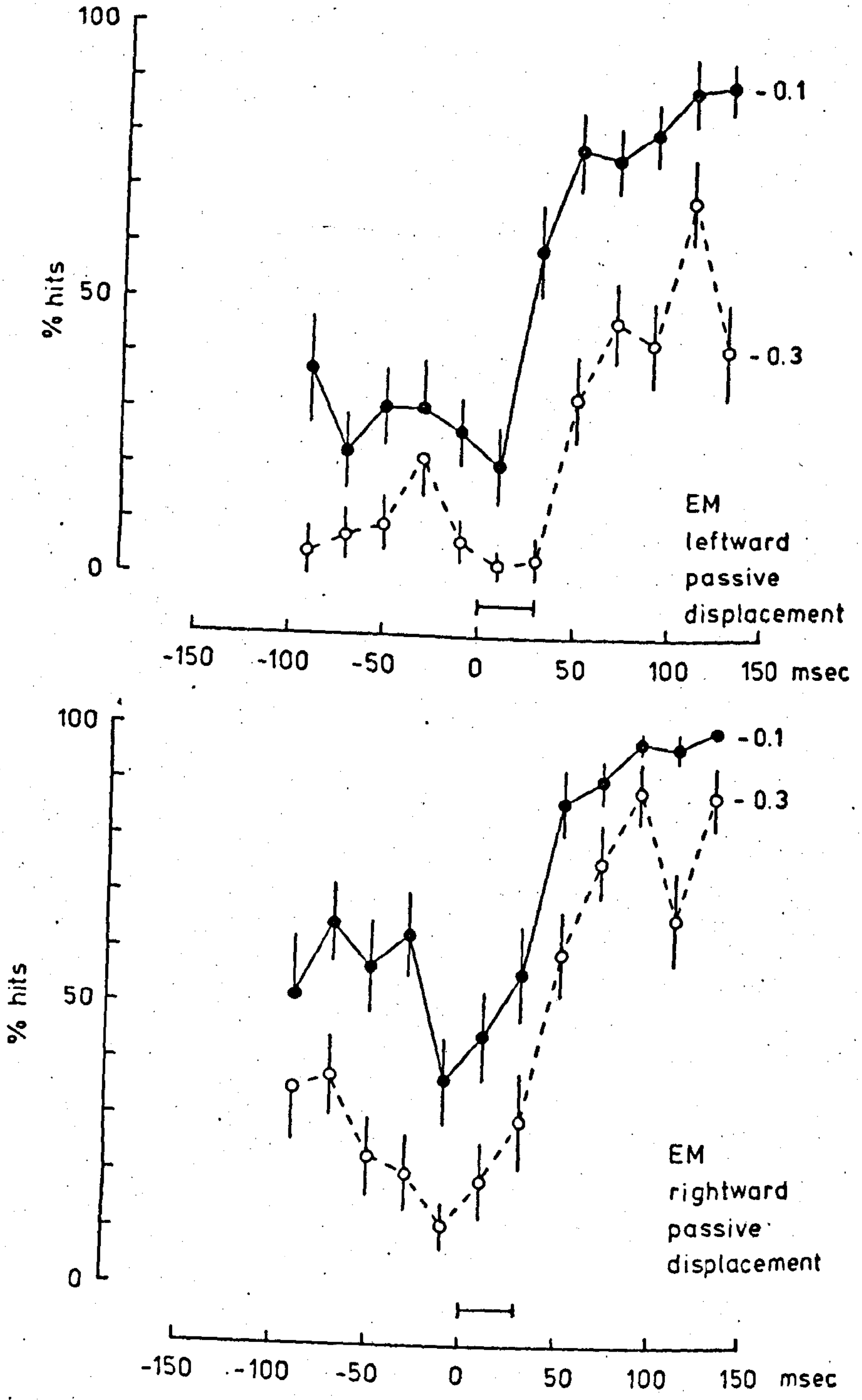


Fig. 5.10a Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees passive image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject EM. (See text.)

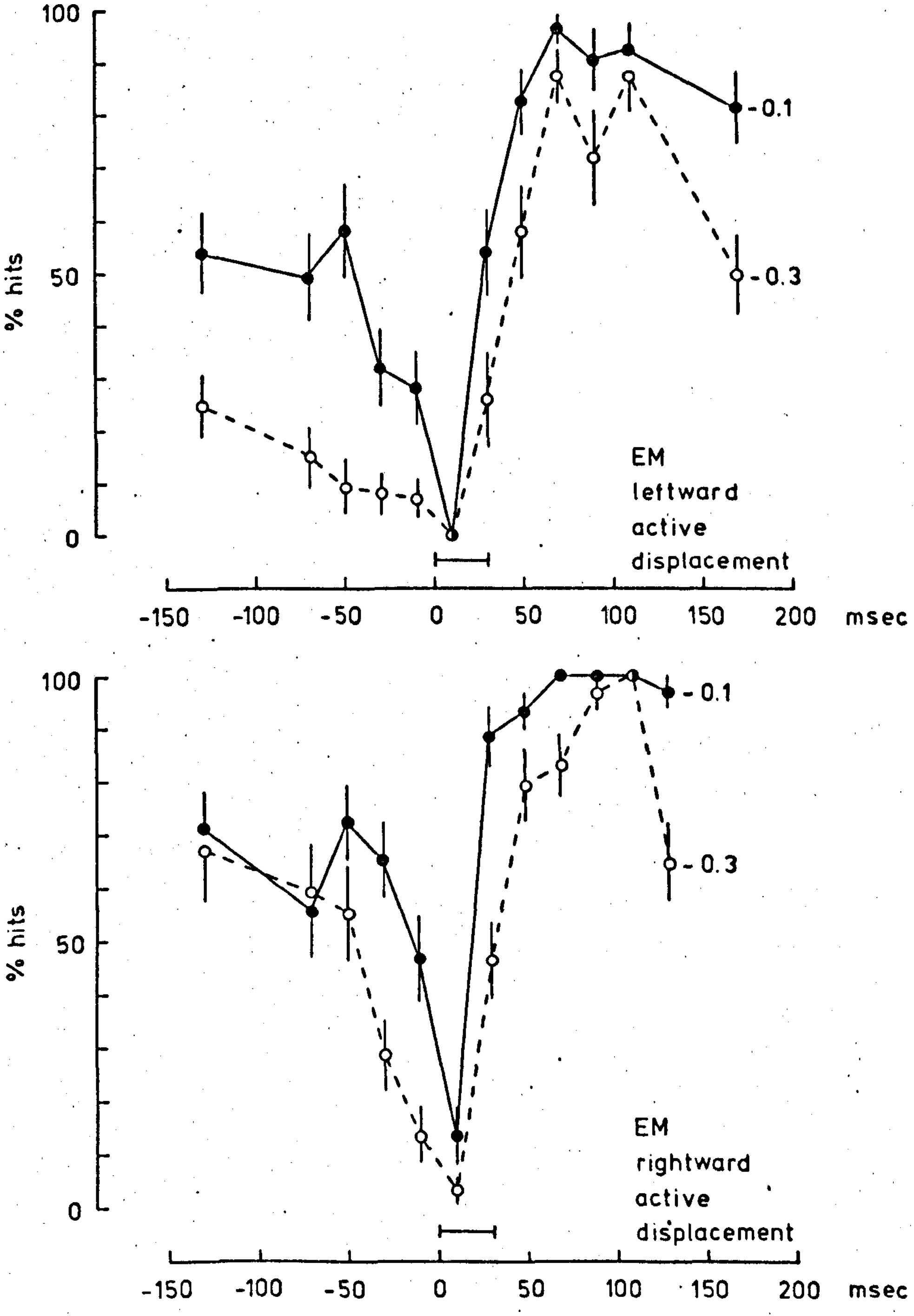


Fig. 5.10b Detectability of a one degree diameter flash as a function of the time of the flash relative to the onset of six degrees active image displacements (shown by horizontal bars), for two flash intensities differing by 0.2 log units. Subject EM. (See text.)

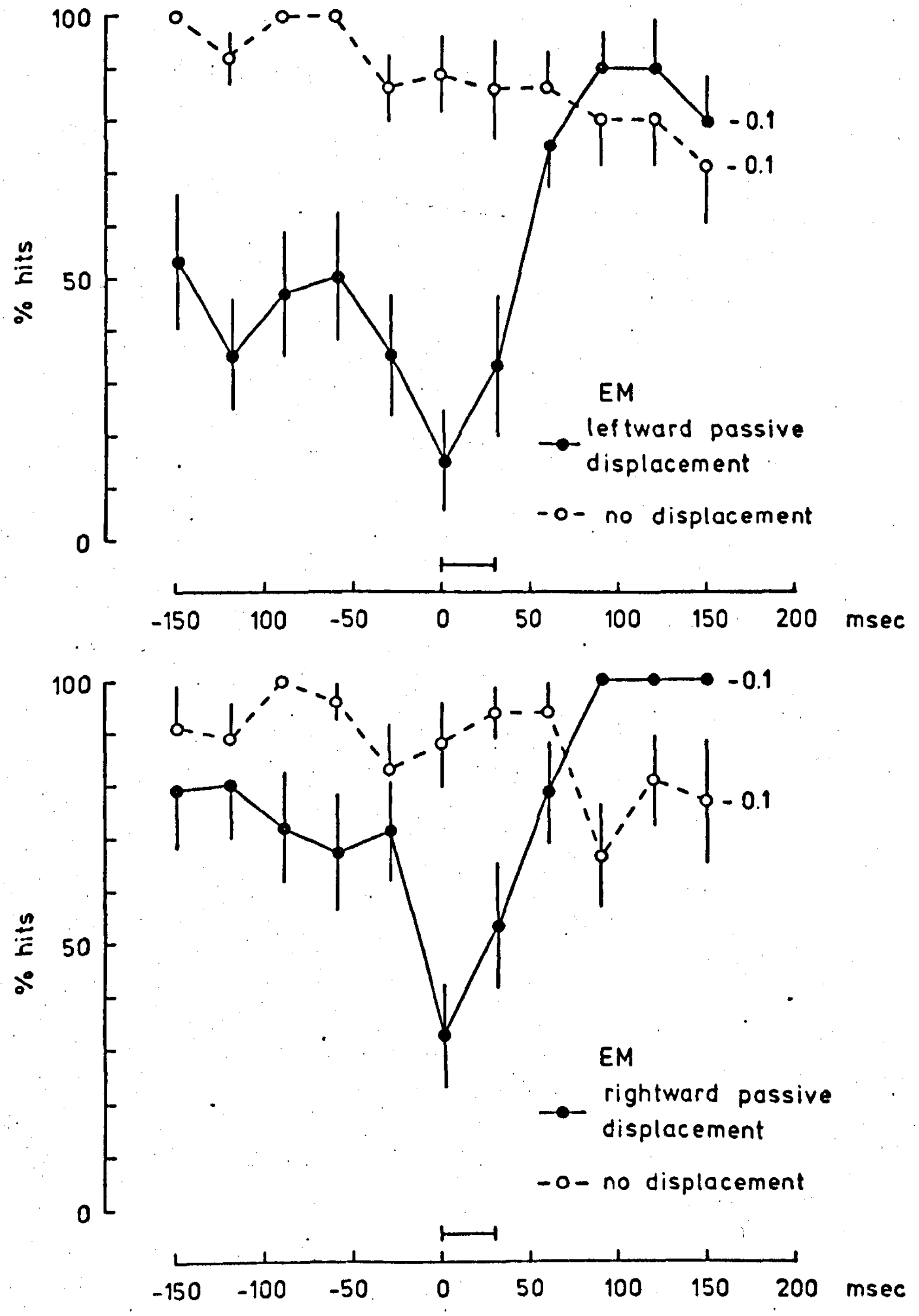


Fig. 5.11 Control experiment with subject EM, showing that in the absence of passive image displacement the 'click' at the onset of each trial does not impair the detectability of the flash (see dashed line). Note also that the detectability of the flash is impaired for flashes delivered as early as 150 msec before the displacement.

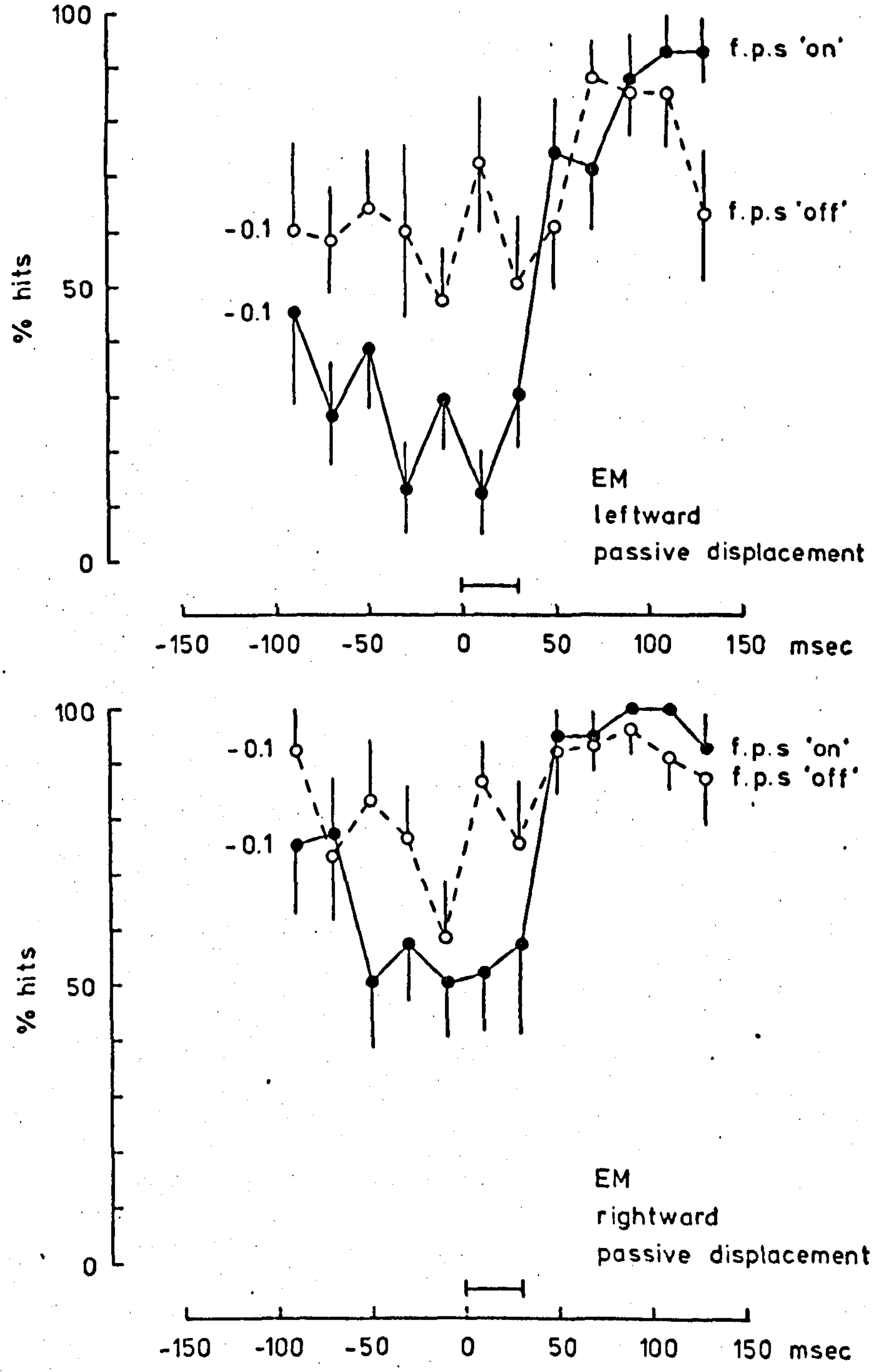


Fig. 5,12 Control experiment with subject EM, showing that the depression of flash detectability associated with passive displacements of the retinal image is significantly smaller with the fixation lights switched 'off' during the displacement (dashed line) than with the fixation points continuously illuminated (solid line).

ability to detect the test flash was much more easily disturbed than ST's by the sweep of the fixation points across the retina.

5.4.3 Discussion

The main finding of these experiments is that the threshold elevation associated with saccadic eye movement in a ping-pong ball 'ganzfeld' is about 0.2 log units greater than the threshold elevation associated with a pseudo-saccadic rotation of the ping-pong ball assembly about the centre of rotation of the eye.

It is hard to believe that this difference can be attributed to the displacement of the small area of the retinal image (corresponding to the extremities of the field of view beyond the edge of the ping-pong ball) which occurs during a saccade but not during a rotation of the ping-pong ball. Nor does it seem at all likely to the author that slight differences between the form of a saccade and that of the pseudo-saccadic displacement can account for the discrepancy, since the durations and the mean velocities of the two kinds of displacement were closely matched.

It seems likely that this small discrepancy must be due either to some mechanical disturbance of vision associated with saccadic movement of the eye (Richards, 1969), or to some centrally mediated alteration of visual sensitivity associated with the occurrence of a saccade (Holt, 1903; and others).

The data of one subject, EM, were anomalous. The control experiments described above showed, however, that this subject's ability to detect the test flash, unlike that of the other subject tested, was greatly disturbed by the sweep of the image of the fixation points across the retina. It seems likely that this feature of the subject's performance was related not to a difference in sensory processing but to higher order effects associated with the subject's nervous disposition. Also, since the degree of threshold elevation associated with passive image displacement is so sensitive to a factor found not to be important with the other subject tested, it is not necessary to look for any further reason to account for the lack of a significant difference between the effects of active and passive displacement of the retinal image, since it is likely that the disturbance of the subject's performance by the presence of the fixation points would have masked any underlying difference between the effects of active and passive image displacement on visual thresholds.

CHAPTER SIX

Elevation of threshold by tachistoscopically presented parafoveal stimuli

6.1 Introduction

When these experiments were initiated, two separate questions were in mind. One was whether peripheral motion, real or perceived, was necessary to produce elevation of threshold for perception of a central flash. The kind of experiment suggested by this question was to examine whether flashing stimuli of positive or negative contrast in the periphery, or reversing the contrast of a pattern in the periphery, raised the threshold for perception of a central test flash. The other question in mind was the more particular one of what features of MacKay's jumping disc stimulus were necessary to produce the elevation of threshold observed, and what were merely incidental.

Different types of experiments are outlined below which are appropriate to the efficient investigation of these two questions.

The elevation of threshold produced by the rapid passive displacement of a disc shaped surround in MacKay's experiment is not likely to be due to the transit of the edge of the disc over the peripheral retina. There is no physiological evidence that retinal ganglion cells respond to stimuli moving at velocities as high as those in MacKay's experiment (300 degrees/sec). It is when making such an assertion of course necessary to make it clear that one is talking of a sensitivity to continuous motion at 300 degrees/sec, rather than to the offset and onset of motion of 300 degrees/sec velocity, which is quite a different matter. If the actual transit of the contour at the edge of the disc is not likely to be the source of the elevation of threshold, then the experiment to try is whether a 'phi displacement' stimulus, consisting of the disappearance of the disc from one position and its reappearance ten msec or so later in its final position is as effective a means of raising the threshold for a central test flash as the real displacement.

Should such a stimulus produce equal elevation of threshold then one could ask several further questions. First is whether the succession of offset of the stimulus from one position and onset later in another position is necessary, or whether instantaneous offset from one position and onset in the new position will equally effectively raise the threshold. The second question, leading on from the first if instantaneous displacement is an effective stimulus, is whether either offset of pattern alone, or onset of pattern alone will give rise to a similar elevation of threshold. When talking of offset and onset of pattern here one is talking of darkening and illumination of the crescent-shaped areas which are the only areas in which a change in illumination occurs in the experiment with the displaced disc (see Fig. 6.1).

On the other hand, if one is interested in the general question of whether peripheral stimuli other than displacement of contour will produce elevation of central threshold, then rather different experiments are appropriate. One would want to use peripheral stimuli covering a large area, and would also want to avoid stimuli which gave an impression of displacement, even if no real displacement occurred.

The conflation of these two separate questions led to the choice of some curious stimuli in the first experiments, carried out in June and July 1972.

6.2 Method

Five different peripheral stimuli were used in these experiments. The first stimulus was the reversal of contrast of a chequerboard pattern (with check size 15 min arc) in a crescent shaped area of radii 4 degrees and width $1\frac{1}{2}$ degrees. The reason for using such a stimulus was to see if elevation of threshold could be produced without any overall change of luminance, and with only local contrast alterations. The pattern could well have been annular, on the principle that symmetry should be preserved unless there is a reason for breaking it. The reason the crescent stimulus was used was that the author had the mistaken impression that it was possible to simultaneously investigate the above general question and the origin of MacKay's effect. (See Fig. 6.2.)

The second stimulus was the darkening (for 500 msec) of the same crescent area. This experiment is almost the same as one of those of the series envisaged to investigate MacKay's effect. The reason for using a white surround rather than a black one was to avoid the impression of motion that would otherwise have occurred at the edge of the disc on which the crescent-shaped area lay. (See Fig. 6.2.)

The third stimulus was a change from having a dark crescent on the left to having a dark crescent on the right (see Fig.6.2). This is similar to the instantaneous displacement stimulus depicted in Fig.6.1a Again, the reason for filling in the surround was to minimise the impression of displacement when the switch took place.

The fourth stimulus was the darkening of the peripheral crescent for only 25 msec before illuminating it again. This experiment was conceived to investigate the general question of whether a peripheral flash might raise the threshold for perception of a central test flash, and once again there was no reason why a symmetrical stimulus should not have been used.

The reason for avoiding stimuli in which there was an overall increase in luminance was to circumvent the possibility of elevation of threshold by light scatter. In retrospect, this seems to have been an unnecessary precaution since the test flash was always presented on a

Fig. 6.1 Explanation of the use of crescent-shaped parafoveal stimuli in these experiments.

a) shows an instantaneous rightward phi-displacement of a background disc. This can be regarded as the simultaneous darkening of a crescent-shaped area at the left of the disc and illumination of a complementary crescent-shaped area at the right of the disc.

b) shows that the subjective impression associated with real displacement of a disc background is similar to that associated with instantaneous phi-displacement.

c) and d) show the separated components of the phi-displacement stimulus, namely the darkening of a crescent-shaped area at the left of the disc (c)) and the illumination of a crescent-shaped area at the right of the disc (d)).

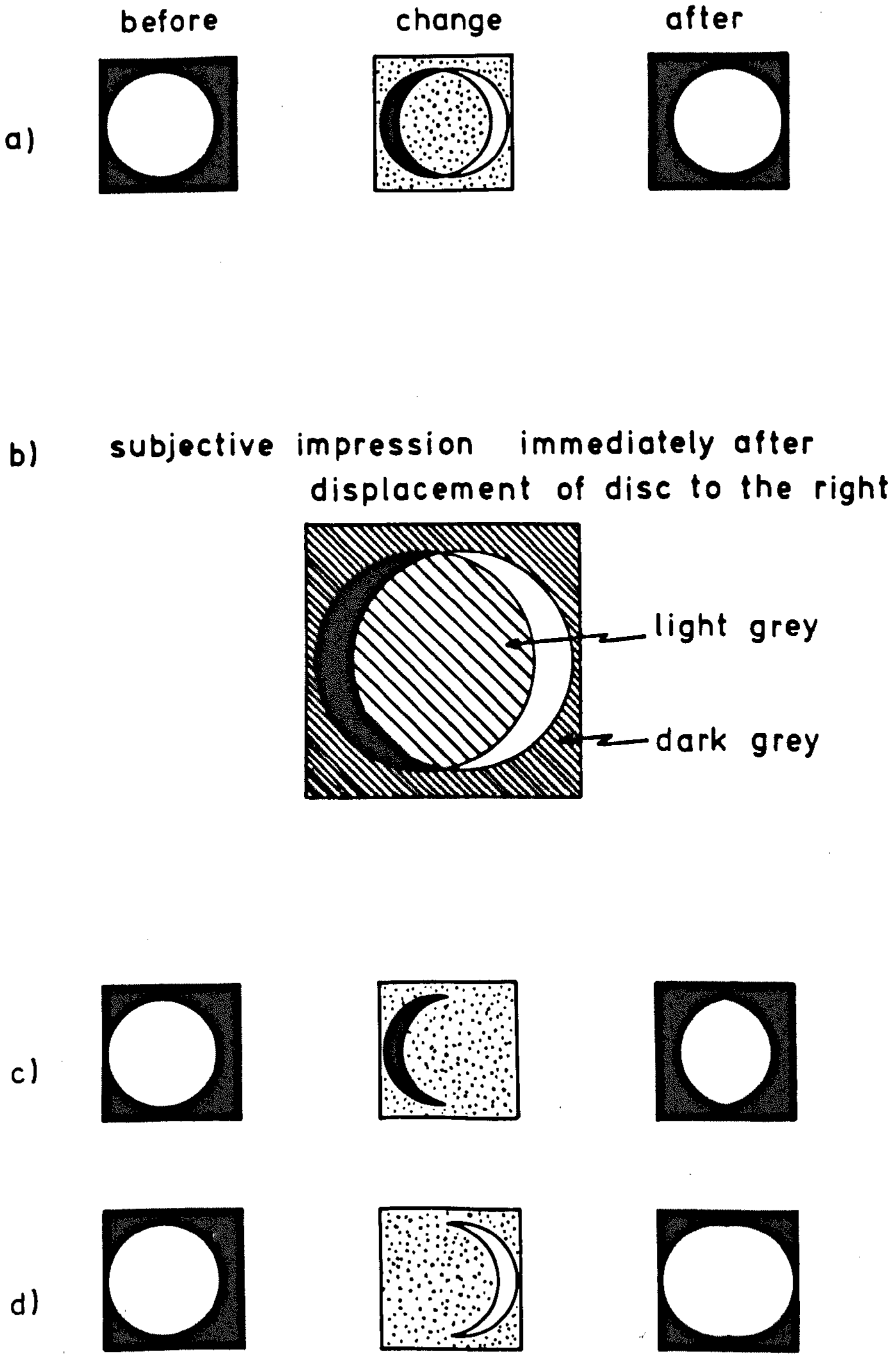

before
change
after
a)
b)
subjective impression immediately after displacement of disc to the right
light grey
dark grey
c)
d)

Fig. 6.2 The stimuli which could be produced with the four-field tachistoscope. The phi-displacement stimulus was not used in these experiments.

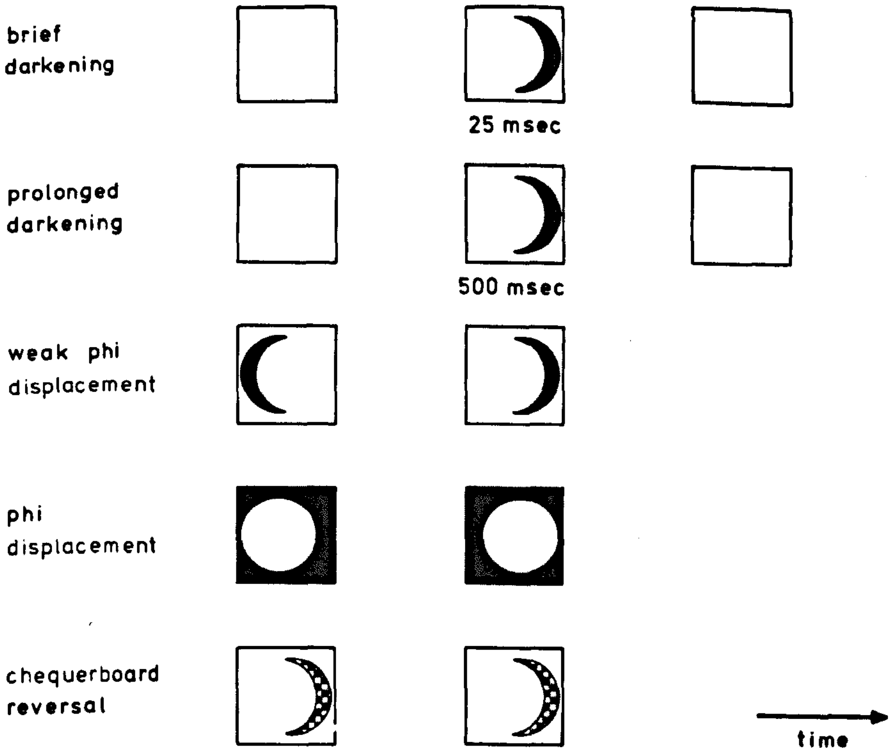
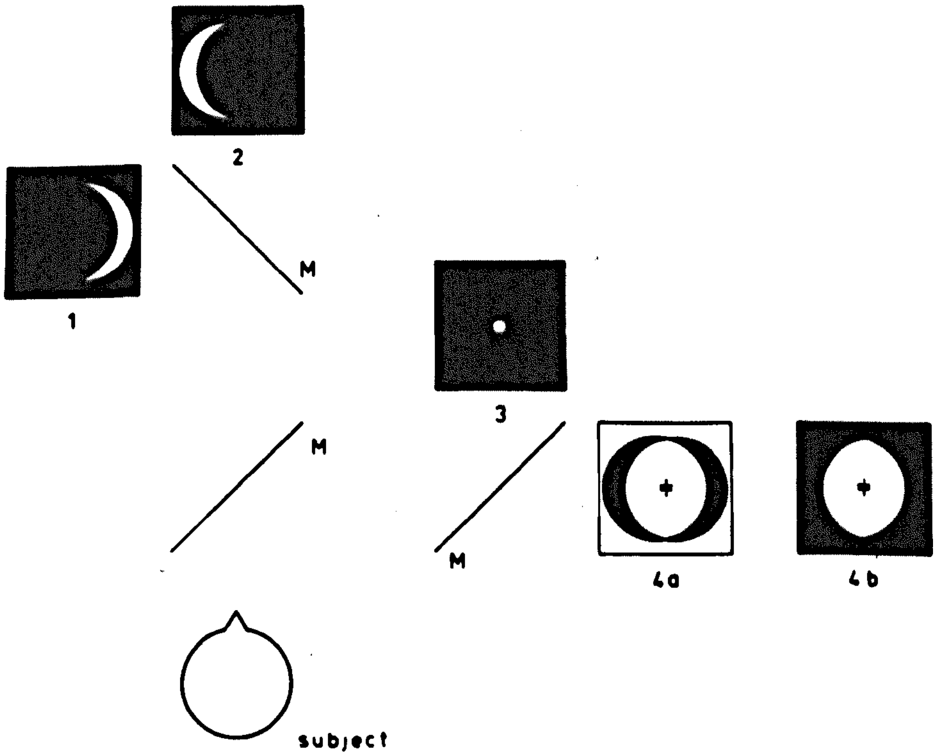

brief darkening
25 msec
prolonged darkening
500 msec
weak phi displacement
phi displacement
chequerboard reversal
time

Fig. 6.3 The four-field tachistoscope used to produce the stimuli. Fields 1 to 4 are optically superimposed by means of half-silvered mirrors (M). Field 4a only (not 4b) was used in these experiments. Field 4a, the central part of the background and the fixation target, was continuously illuminated. The peripheral stimuli were produced by switching fields 1 and 2 'on' and 'off' as appropriate. The test flash was produced by field 3. See text for further details.


2
1
M
3
M
M
4a
4b
subject

photopic background (of luminance approximately 200 cd/m^2) compared with which the light scattered from peripheral stimuli of this same luminance would have been negligible.

The various stimuli were produced by a tachistoscope described by Jeffreys and Axford (1972a). In brief, each of the four fields of the tachistoscope was capable of being illuminated by a panel of three small fluorescent tubes (Mazda, 6W). These tubes had a blue phosphor which gave rise and fall times of less than 1 msec. The tubes were driven by bistable circuits, and were either fully on or off at all times. The four fields necessary to produce most of the above stimuli are shown in Fig.6.3. The almond-shaped area at the centre of which the test flash appeared was always illuminated, so that there was no possibility that the switch of the test flash background caused spurious changes in test flash visibility.

The duration of the test flash was less than 10 msec. At the beginning of each run the duration of the test flash was adjusted so that the flash was just suprathreshold. The test flash occurred at one of three times: 100 msec before, 40 msec after and 150 msec after the peripheral stimulus. The reason for using the +40 msec epoch was that this was the period at which the elevation of threshold produced by passive displacement of a disc was a maximum. (See Chapter Four.) The time at which the test flash occurred was randomly varied from trial to trial, by using a large (500 entry) random number table.

The experiment was performed by a two epoch forced choice method. On each trial two successive peripheral stimuli were presented. The test flash occurred in one or other, but not both, of these two epochs (chosen at random). The subject had to decide whether he thought that the test flash occurred in the first or the second epoch.

The reason for using such a method was that since the subject was presented on each trial with a positive and a negative stimulus, he was invited to make a comparative rather than an absolute judgement. Intersubject and intrasubject variations of criterion were thus likely to be diminished. It is often said that the two epoch forced choice method gives results which are criterion free. It is true that if the assumptions of signal detection theory are valid, then variations in false alarm rate will not bias the results of two epoch forced choice experiments. The basis of this inference can, however, be undermined in two ways. Firstly, the subject may not actually make the judgement comparatively, and secondly, the subject may be operating in a mode to which it is doubtful whether signal detection theory can be applied, namely where he may be making no false alarms at all.

The experiments were controlled and analysed by a PDP-8 computer, programmed in FOCAL.

6.3 Results

The results of these preliminary experiments were rather interesting. The only stimulus to produce a clear elevation of threshold consistent across subjects was the transient darkening of the crescent. The other stimuli produced either negligible effects on the visibility of the test flash (prolonged darkening of crescent, all three subjects; chequerboard contrast reversal, subjects SW and JJ); a small increase in visibility of the test flash (chequerboard contrast reversal and weak phi-displacement, subject SJJ); or variable effects (weak phi-displacement, subject SW). (See Figs. 6.4 & 6.5. The comparison between detectability of the flash when at 100 msec before and 40 msec after

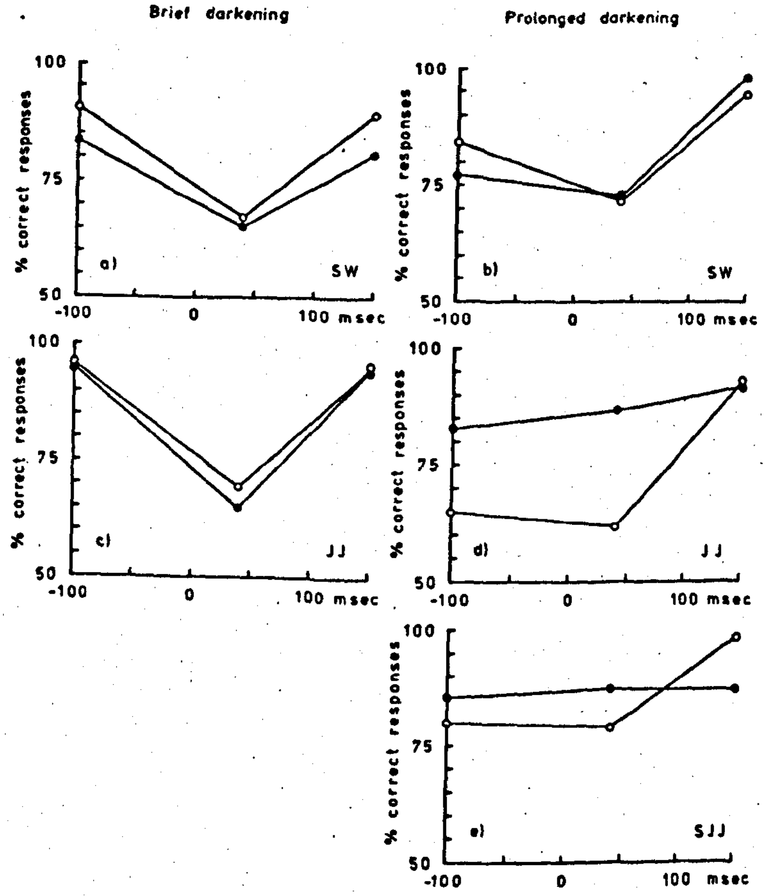


Fig. 6.4 Detectability of foveal flashes delivered 100 msec before, and 40 msec and 150 msec after the appearance of parafoveal tachistoscopically presented stimuli, for three subjects. The type of parafoveal stimulus is indicated at the top of the columns. The 'brief darkening' stimulus produces consistent depression of the flash detectability. Each datum point based on approximately 50 trials.

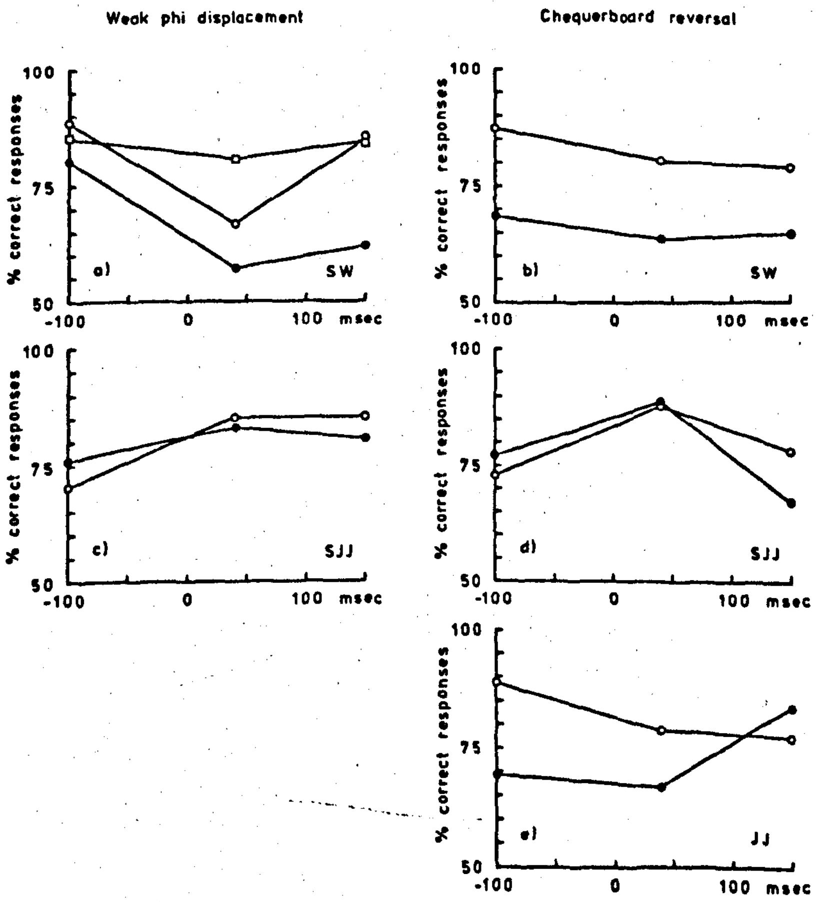


Fig. 6.5 Detectability of foveal flashes delivered 100 msec before, and 40 msec and 150 msec after the appearance of parafoveal tachistoscopically presented stimuli, for three subjects. The type of parafoveal stimulus is indicated at the top of the columns. Neither of these types of parafoveal stimulus produced consistent alteration of the flash detectability. Each datum point is based on approximately 50 trials.

the peripheral stimulus is the one of most interest.)

One way of reconciling almost all these data would be to assume that some <u>succession</u> of stimulation of the periphery is necessary to produce the elevation of threshold for perception of the central test flash. If this were the case, one would expect only the transient darkening stimulus to produce elevation of threshold, as is the case. More data would of course be needed to make this idea more than a formal solution of the puzzle presented by the above results.

These experiments do, however, show that peripheral stimuli in which there is no displacement of contour, real or apparent, can raise the threshold for perception of a central flash. The effect demonstrated is weaker than that reported by MacKay, who found that sudden displacement of a peripheral contour diminished the visibility of his test flash from 100% to 0%. The effect reported here produced at most only a reduction of detectability from 95% to 65% in a two epoch forced choice experiment (equivalent to a drop from 90% to 30% visibility in a yes-no response experiment like MacKay's). It should be noted, however, that the magnitude of MacKay's effect certainly varies with the subject or method used, as shown in Chapter Four.

6.4 Further experiments

In April 1974, further experiments were carried out to examine the timecourse of the elevation of threshold produced by stationary peripheral stimuli, and to measure the size of the effect in terms of the additional test flash energy needed to make the test flash visible in the presence of the peripheral stimulus. Two different kinds of peripheral stimuli were used, one a change from one static visual noise pattern to another of equal mean luminance and contrast, the other a transient appearance of a static visual noise pattern in a blank field of the same mean luminance. The stimuli were parafoveal rather than peripheral. Their outer border was a square of side 10 degrees arc, and their inner border a circle of diameter 4½ degrees arc. The test flash was of diameter 80 min arc. The last two parameters were chosen to match those used in the experiments on the elevation of threshold produced by small passive image displacements. (See Chapter Three.) The mean luminance of the stimuli was of the order of 35 cd/m^2, and their contrast was 90%.

The results of these experiments are shown in Figs. 6.6 & 6.7.

The experiments were carried out in two ways. In the first method, the timecourse of the threshold elevation was obtained by presenting a sequence of stimuli with the test flash in a randomly varied temporal relation to the parafoveal stimulus. Such runs were repeated for several different test flash durations. Since the duration of the test flash was always less than 20 msec, the effect of varying the duration of the flash was perceptually equivalent to varying the intensity of the flash (Bloch's law). In the first method, the time of occurrence of the test flash was fixed, and the duration of the flash varied to obtain a psychometric function. This was done for the test flash 100 msec before, and at the same time as the parafoveal stimulus, and also without a parafoveal stimulus. In both types of experiment, the parafoveal stimulus was accompanied by a brief tone burst, which was present also in the control trials where no parafoveal stimulus occurred.

The 'pulse' stimulus caused a larger elevation of threshold than the 'change' stimulus. The magnitude of the effects varied from subject to subject: MY and RH gave larger effects, about 0.3 log units for the pulse stimulus and 0.15 for the change stimulus. Subject RQ gave smaller effects, which were negligible with the change stimulus.

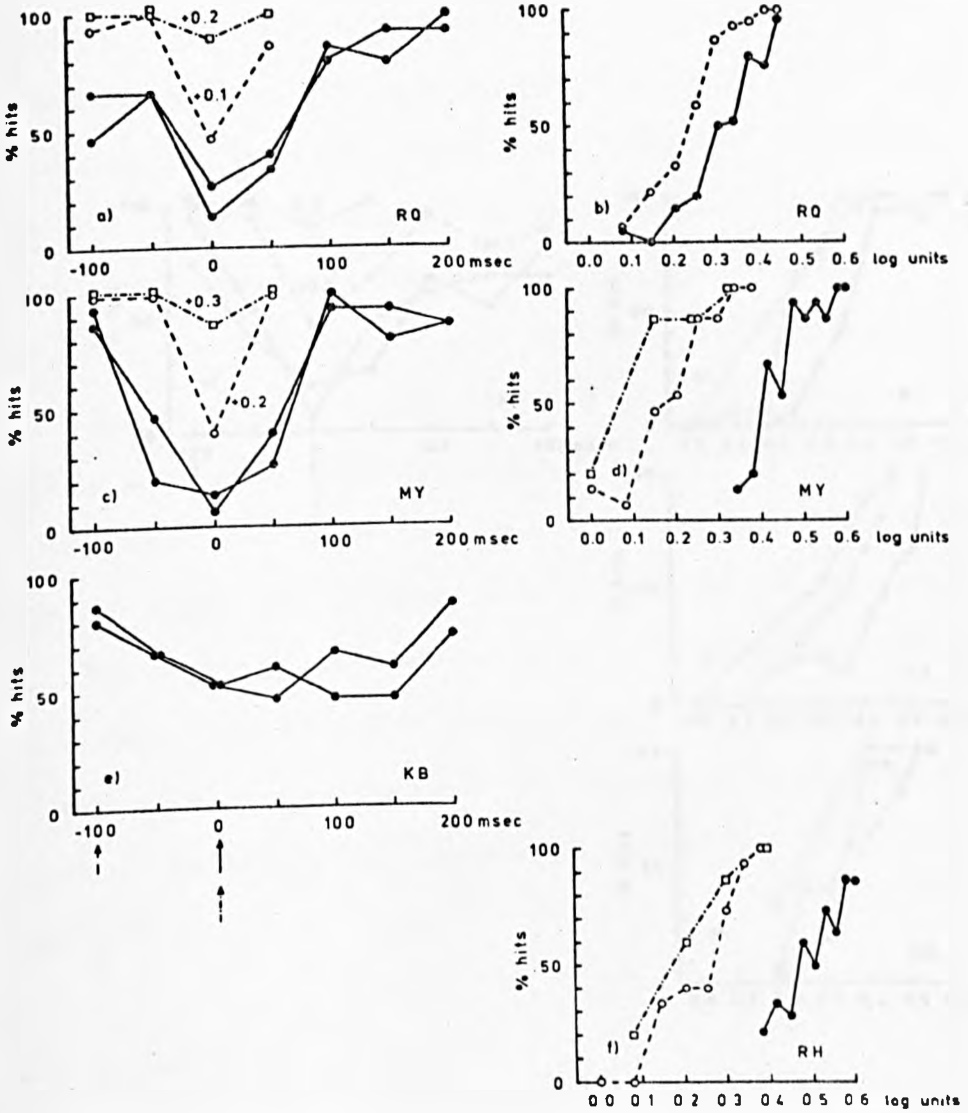


Fig. 6.6 Impairment of detectability of a flash associated with the appearance of parafoveal contours for 25 msec ('pulse' stimulus), for four subjects. Lefthand column: detectability of the flash as a function of the time of the flash relative to the onset of the parafoveal stimulus. Solid lines show repeated runs with the same flash energy, and broken lines show repeated runs with flashes of higher energy (energy increment shown in log units). Righthand column: detectability of the flash as a function of the energy of the flash, for flashes 100 msec before (dashed lines) or simultaneous with the appearance of the parafoveal stimulus (solid lines). The dash-dot lines show the detectability of flashes in the absence of a parafoveal stimulus. The arrows in the figures in the lefthand column show the epoch of occurrence of the flashes used in the experiments shown in the righthand column. Datum points show the results of 10, 15 or more trials.

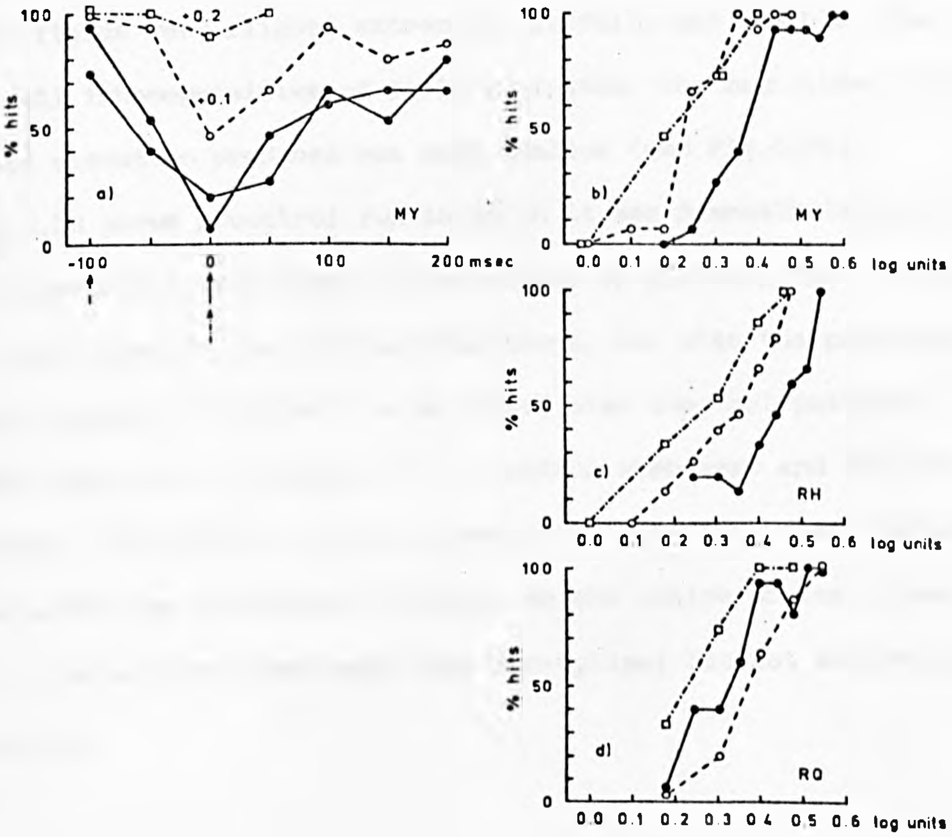


Fig. 6.7 Impairment of detectability of a flash associated with the substitution of one parafoveal pattern with another of equal mean luminance ('change' stimulus), for three subjects. Conventions as in Fig. 6.6. Each datum point based on 15 trials.

Fig.6.8a, b and c show that even with a blank pattern in the pulsed field, a considerable elevation of the threshold still occurred. This effect was probably due to inhomogeneities in the illumination of the tachistoscope fields, and other small defects of the images, since when the fields were aligned extremely carefully and trouble taken to avoid small inhomogeneities of field luminance, the magnitude of the threshold elevation produced was much smaller (see Fig.6.8b).

Fig.6.8d shows a control run in which it was demonstrated that there were no electrical artifacts in the system, by plotting the visibility of the test flash in the various conditions, but with the parafoveal stimulus masked out by black cards placed over the test patterns.

The elevation of threshold is a maximum when test and mask are coincident. The effect is still present with the test flash presented 40 msec after the parafoveal stimulus, so the choice of test flash epoch in the earlier experiments was non-optimal but not entirely inappropriate.

6.5 Conclusion

In conclusion, it seems clear that parafoveal stimuli not involving displacement of contour do produce elevation of threshold for perception of a centrally fixated test flash. Furthermore, some threshold elevation can be produced by parafoveal stimuli of low contrast and without sharp contours.

On the more specific question of the origin of the elevation of threshold in MacKay's experiment, no definite conclusion is possible from these data.

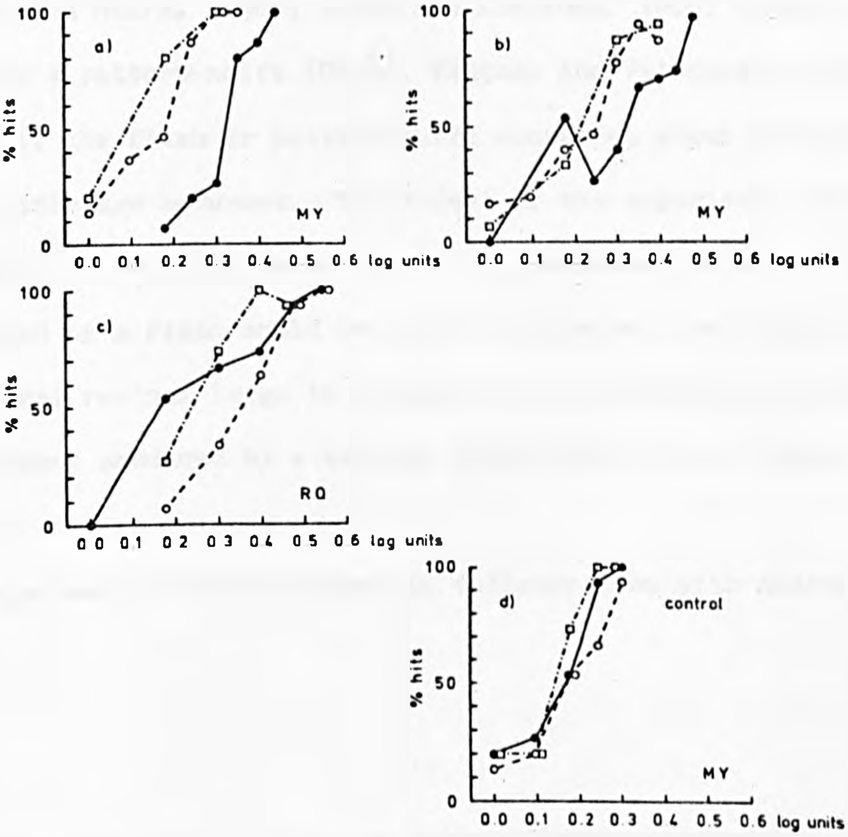


Fig. 6.8 Impairment of detectability of a flash associated with the transitory subsitution (for 25 msec only) of one unpatterned parafoveal field for another of nominally equal luminance (a),b) and c)). The impairment of detectability was presumably caused by small inequalities of the two fields. In b) the fields were aligned and matched more precisely than in a), and the impairment of flash detectability is correspondingly reduced. The anomalous results in c) were probably due to fatigue of the subject.

d) shows the results of a control experiment in which the parafoveal stimulus was occluded. Each datum point based on 15 trials.

CHAPTER SEVEN

Human scalp potentials evoked by flashes presented in temporal proximity to rapid displacements of a peripheral contour

7.1 Introduction

It has been reported that the scalp potential evoked by a brief flash (Michael and Stark, 1967; Duffy and Lombroso, 1968; Chase and Kalil, 1972) or a pattern-shift (Gross, Vaughan and Valenstein, 1967) is attenuated if the flash or pattern-shift occurs at about the same time as a saccadic eye movement. The object of the experiments described below was to investigate whether a similar attenuation of the potential evoked by a flash could be produced by a passive displacement of the peripheral retinal image in a manner which mimicked the retinal image displacement produced by a saccade in any non-uniform visual environment.

These experiments were performed in collaboration with Andras Pellionisz.

7.2 Method

The stimuli used were of similar form to those employed by MacKay (1970) but were of approximately twice the angular size. The flash, which was six degrees in diameter, was generated by a stroboscope lamp mounted in a projector. The flash appeared at the mean centre of a background disc eighteen degrees in diameter, of luminance 0 to 1 log cd/m^2. The background could be displaced by three degrees with a time constant of 7 msec, by means of a small mirror mounted on a pen motor in the background projector path. The background returned to its original position 300 msec after the displacement. The stimuli were rear-projected onto a screen viewed binocularly from a distance of 60 cm.

Each run in the experiments consisted of three types of stimuli quasi-randomly interspersed. These three types of stimuli were a flash alone, a displacement of the background alone, and a flash and a displacement of the background together. A run consisted of one hundred presentations of each kind of stimulus - making three hundred trials in all. The quasi-random sequence of stimuli was generated by a thirty position multiselector switch. The stimuli were presented aperiodically, usually with a mean interstimulus period of 550 ± 50 msec, in order to avoid contamination of the responses by after-discharges time-locked to the previous stimulus.

A standard electroencephalograph was used to amplify the EEG signals (Beckmann Type TC). The passband of the amplifiers was set at 3 to 50 Hz. Recordings were made in a soundproof and electrically screened enclosure in order to eliminate the possibility of acoustical and electrical artefacts.

The subject's left earlobe was grounded and monopolar recordings made with the right earlobe as a reference.

EEG activity was usually recorded not just from one electrode but from a number of electrodes placed in some regular array on the occipital region of the scalp. The use of multi-electrode recordings is a precaution strongly recommended by MacKay and Jeffreys (1973) in order to rule out the possibility that the potentials recorded are unrepresentative of cortical activity due to localised cancellation of potentials from two different cortical sources.

The EEG data from the electrode array were recorded on a multichannel FM taperecorder with a bandwidth of 0 to 300 Hz, together with two marker pulses indicating the time of occurrence of the flash and displacement respectively. The EEG from one electrode was averaged on-line using a Mnemotron CAT 400 B whose inputs were gated so that the four channels accumulated respectively:

1. VEP to flash alone
2. VEP to both flash and displacement together
3. Channel 2. - channel 4.
4. VEP to displacement alone.

Data from the other electrodes were analysed off-line using the same system. Analysis time was 250 msec starting with the time at which the displacement was initiated (if there was a displacement).

7.3. Results

Preliminary investigations were made of the effect of the presence of the background, and the location of the fixation point, on the flash evoked potentials. The distribution of these potentials across the occipital region of the scalp was also examined.

At a point on the mid-line about 5 cm above the inion the averaged evoked potential (AEP) to the flash (on a dark background) was the familiar 'W' shape. When the flash was seen against a photopic background the potential evoked was dominated by a single peak of approximately 150 msec latency. The AEP to the flash was somewhat dependent on the fixation point, but varying the fixation point (centre of flash, or margin at 3, 6, 9 or 12 o'clock) did not produce a qualitative change in the waveform of the AEP. The form of the AEP to a flash on a photopic background was similar at the four electrode sites used (5 and 9 cm above the inion on the midline, and 4 cm to either side of the former point). The potential was largest at the site 5 cm above the inion.

The effect of varying the relative intensity of the flash (achieved by altering the intensity of the background) is shown in Fig.7.1. As the relative intensity of the flash was increased, the latency of the

AEP to the flash decreased and its magnitude increased. The intermediate relative flash intensity was used in subsequent experiments. It should be noted that at this level the flash was of the order of 1 log unit above threshold. It would have been better to have used a lower flash intensity, to correspond more closely with the threshold flashes used in psychophysical experiments, but the experiments would then have had to be longer to achieve a satisfactory signal-to-noise level.

The results of the main experiment are shown in Figs.7.1-3. When the flash and displacement were approximately coincident in time, the potential evoked by the flash and displacement together (the 'joint stimuli') was not significantly different from the potential evoked by the displacement alone, except with the highest relative intensity of flash (i.e. with the lowest background intensity) (Fig.7.1). In the latter case, the AEP to the joint stimuli and the displacement alone were different, butthe difference between the potentials was not similar to the potential evoked by a flash of 0.5 log units lower relative intensity (compare potential in last column and row of Fig.7.1 to the potential in the first column and row). Thus although there was a non-additive interaction between the potentials evoked by the flash and displacement, it is not clear that this interaction was of the same kind as that occurring in the threshold psychophysical experiments, where the effect of the displacement was similar to that of a reduction in the intensity of the flash by 0.5 log units or so.

Fig.7.2 shows the effect of varying the time of the flash relative to the displacement. When the flash was at the same time as the displacement or 25 msec later than the displacement, the potentials evoked by the joint stimuli and the displacement alone were not significantly different (see column 4). On the other hand, when the flash was 25 msec before or 50 msec after the displacement, the AEP to the joint stimuli was significantly different from the AEP to the displacement stimulus alone. Once again, however, the difference between these potentials was not similar to the potential evoked by a flash of lower relative intensity, either differing in latency or form to that produced by the flash alone.

In Fig.7.3(third column) the departure from additivity of potentials can clearly be seen. The dotted waveforms show the AEPs to the joint stimuli. Only when the flash is 50 msec after the displacement is the sum of the flash evoked potential and the displacement evoked potential similar to the potential evoked by the joint stimuli. The most interesting feature of Fig 7.3 is that the difference between the sum of the potentials evoked by the joint stimuli is principally one of magnitude of the response. (This is not the case when comparing the potential evoked by the single stimuli to the potential evoked by the joint stimuli: in several cases (indicated by a box round the waveforms) there is a clear difference in latency of the responses.) Thus one can describe the difference between the summed potentials and the potentials evoked by the joint stimuli as only one of scaling.

Fig. 7.4 shows the result of two control experiments. In these experiments the flash intensity was about 0.5 log units greater than in the above experiments. The figures above the waveforms show the mean period, in msec, between stimuli of the same kind. It can be seen that the potentials evoked are similar whether the stimuli are presented in a sequence of diverse or uniform types of stimuli (e.g. the flash AEP is not significantly altered by interspersing flash stimuli with displacement stimuli), but increasing the mean interstimulus period increases the size of the AEPs to both flash and displacement stimuli. Thus the interstimulus period used above was too

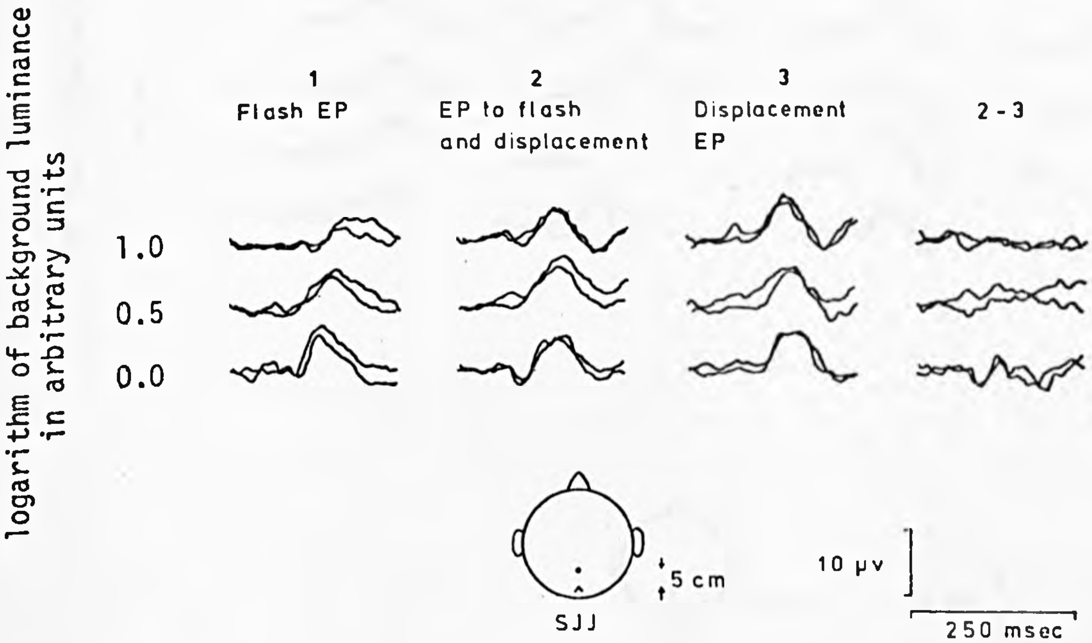


Fig. 7.1 Average potentials evoked by a flash (column 1), a displacement of the background (column 3) and by both stimuli presented simultaneously (column 2), for three different background luminances. The fourth column shows the waveform obtained by subtracting the displacement response from the response evoked by both stimuli presented together. The flash response increases in amplitude and decreases in latency as the luminance of the background is reduced. The waveforms in column 4 are not similar to the waveforms in column 1, which shows that there is a non-linear interaction between the flash and displacement responses. The reproducibility of the waveforms is indicated by showing in every case data from two runs under identical conditions. The stimuli were presented synchronously with the start of averaging.

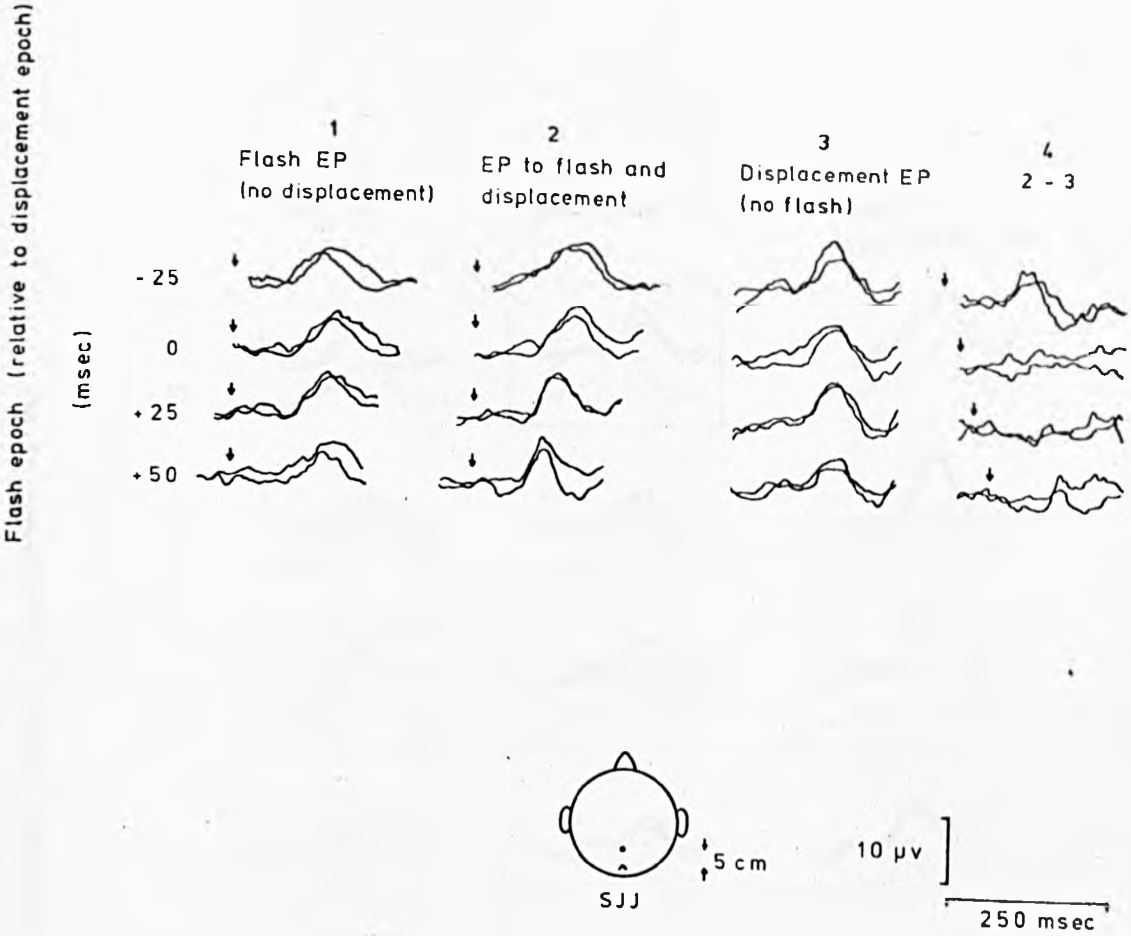


Fig. 7.2 Average potentials evoked by a flash (column 1), a displacement of the background (column 3) and by both stimuli presented together (column 2), as a function of the time of the flash relative to the onset of the displacement. Vertical arrows indicate the time at which the flash occurred. The displacement was always synchronous with the start of averaging. Note that the waveforms shown in column 4 (obtained as in Fig. 7.1 by subtracting the displacement response from the response to both stimuli presented together) are not similar either to the flash responses shown in column 1 or to the response to a flash of 0.5 log units lower relative intensity (see column 1 of Fig. 7.1).

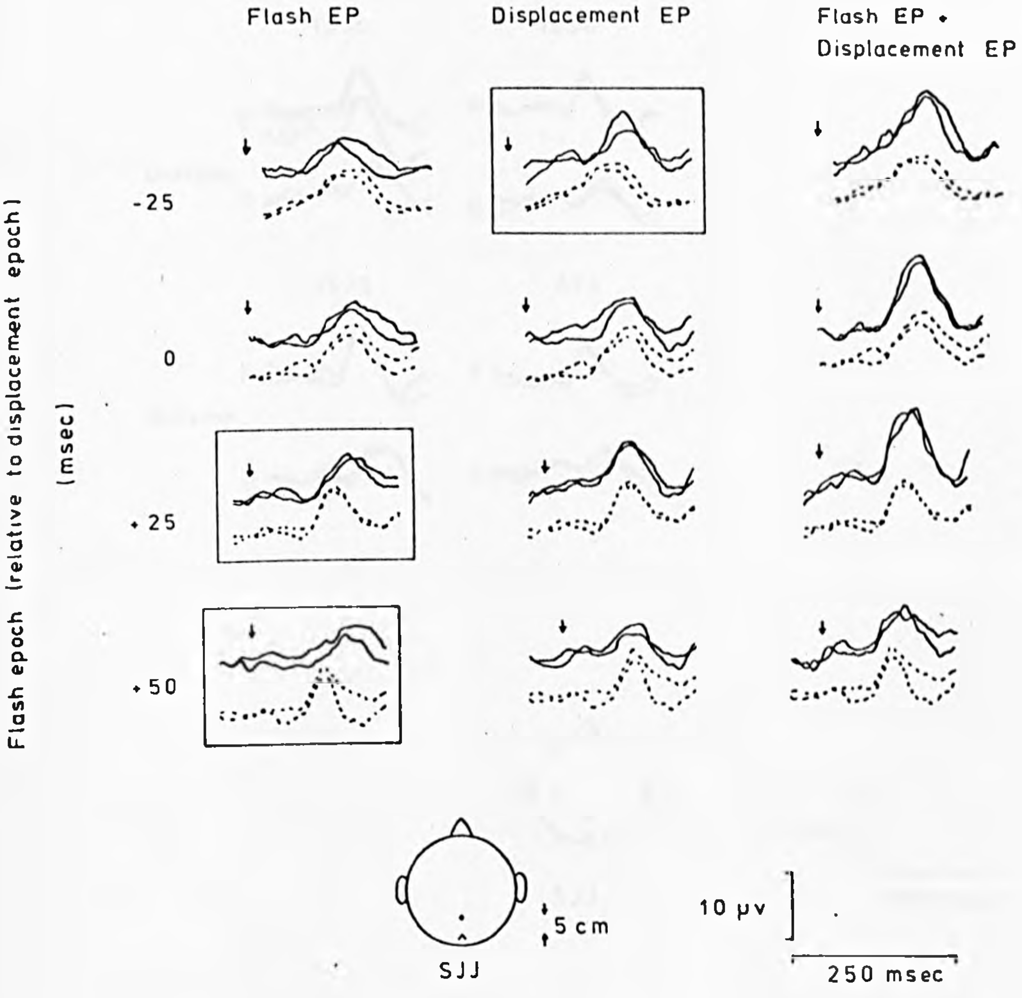


Fig. 7.3 Comparison of the waveform of the potential evoked by both flash and displacement presented together (dashed lines), with the waveforms of the flash potential (column 1), the displacement potential (column 2), and the sum of the flash potential and the displacement potential (column 3). The boxes indicate cases in which there is a clear difference in the form of the waveforms compared. Differences of amplitude alone are not so indicated. Note that the waveforms compared in column 3 are similar in form and differ substantially only in their amplitudes. Same data as in Fig. 7.2.

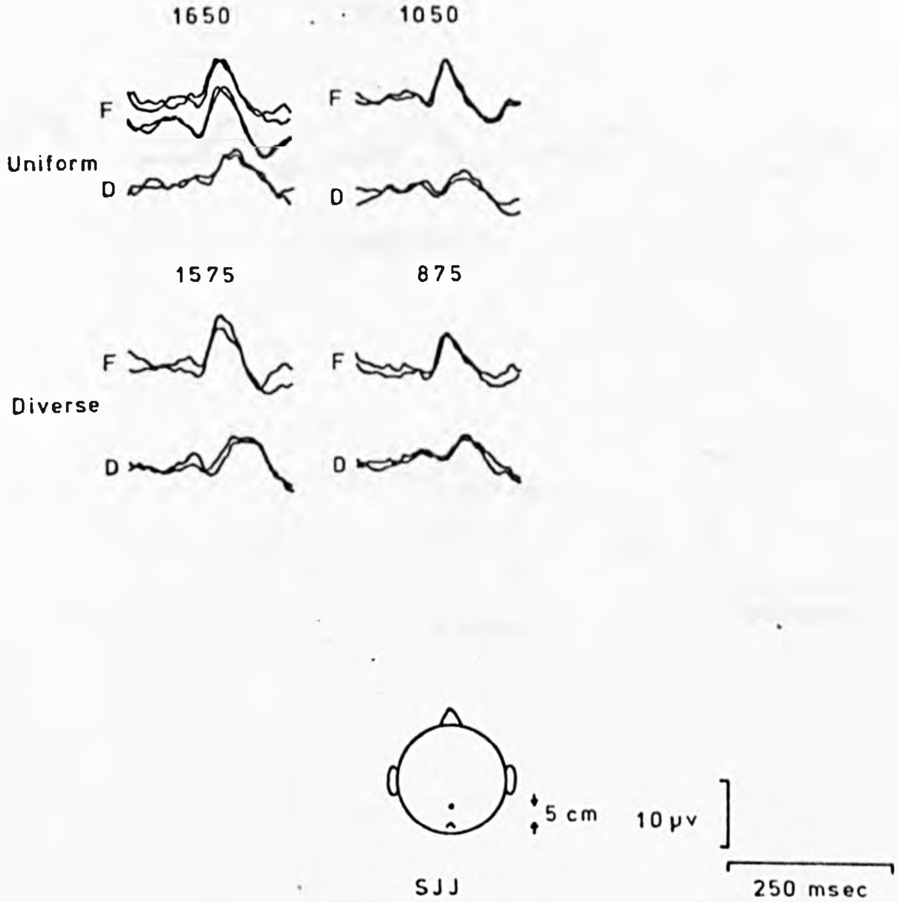


Fig. 7.4 Control experiments examining the effects of a) varying the mean interval between stimuli of the same kind, and b) presenting different kinds of stimuli in a run, compared with presenting only one kind of stimulus in each run. The potentials evoked with the shorter inter-stimulus intervals are somewhat attenuated compared with those obtained with longer inter-stimulus intervals. (The 875 msec interval was used in the main experiments.) There is little difference between the potentials evoked in runs with diverse and uniform kinds of stimuli. F: flash potential; D: displacement potential.

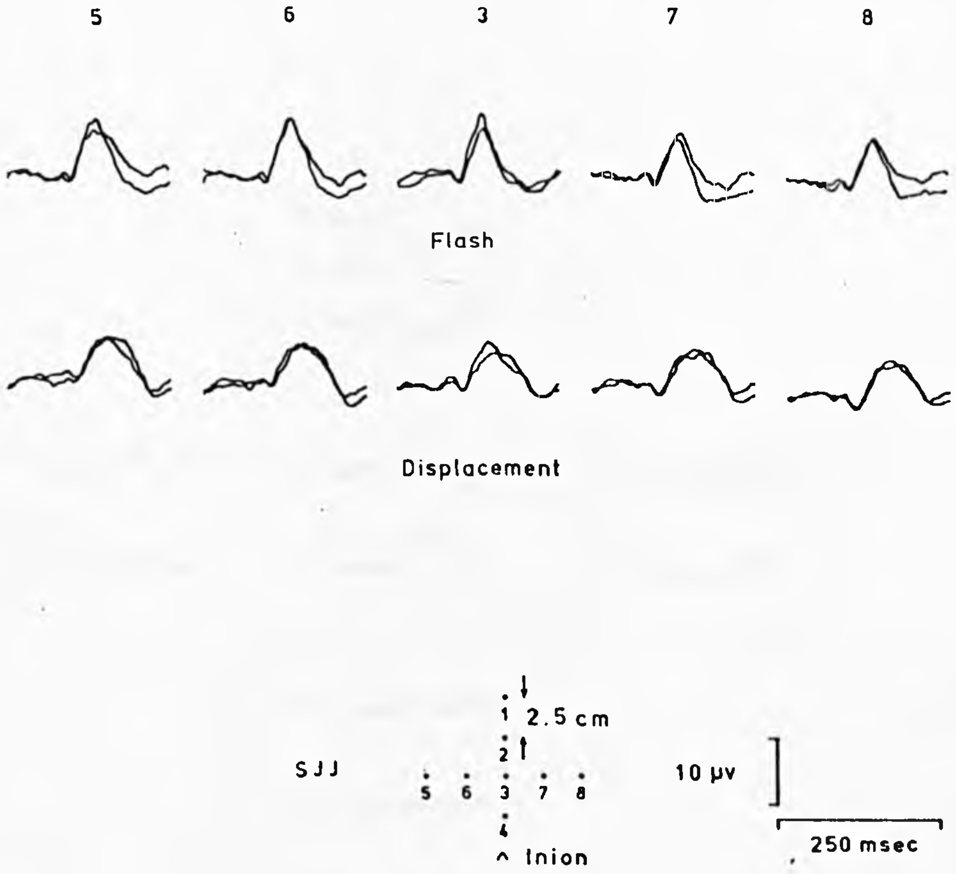


Fig. 7.5 Distribution of potentials across the scalp, for five electrodes placed in a line orthogonal to the midline and five centimetres above the inion. There is little variation of potential waveform across the scalp. Data obtained with a background luminance 0.5 log units lower than in the main experiments.

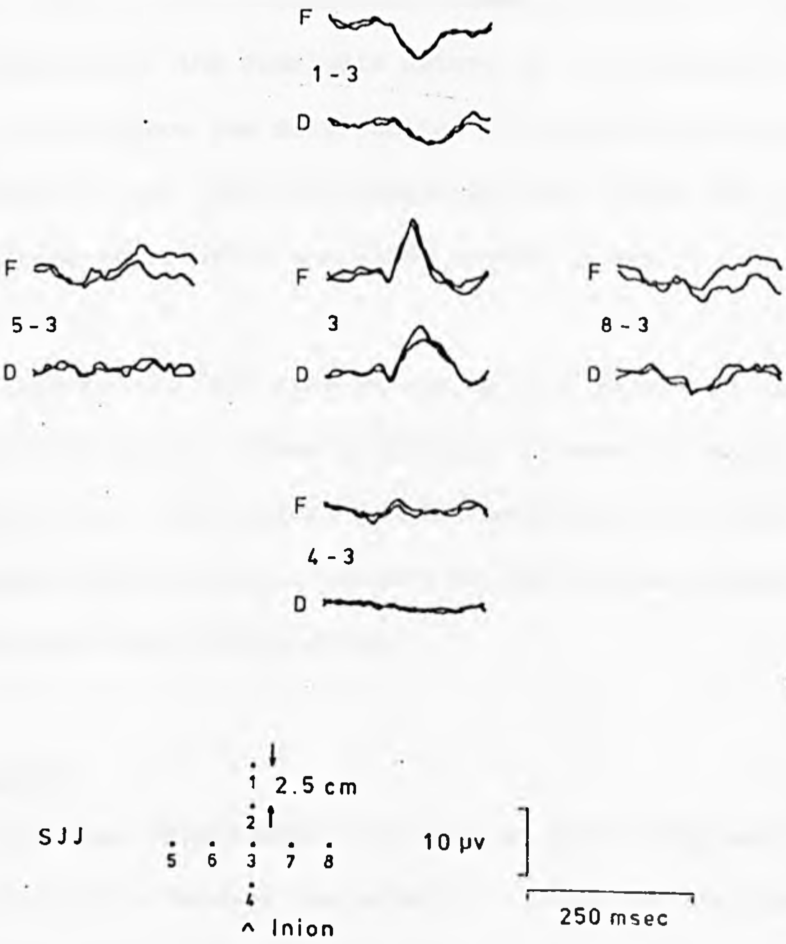


Fig. 7.6 Distribution of potentials across the scalp. The central waveforms show the flash (F) and displacement (D) responses at an electrode five centimetres above the inion on the midline. The other waveforms show the difference between the responses obtained at the indicated electrode sites and the central responses. Apart from an attenuation of both responses at the most anterior electrode site ('1') there is little variation of the waveform of the responses with position on the scalp.

short. Since the period used is normally long enough to avoid attenuation of response, this effect was at first somewhat puzzling, until it was realised that the background disc returning to its original position 300 msec after the displacement would occur only 250 msec before the next flash or displacement, and that this could well interfere with the response to the next stimulus. The responses are not distorted in form by this interaction between successive trials, presumably because of the aperiodic nature of the stimulation.

Figs. 7.5 & 7.6 show the distribution of the potentials over the scalp. It can be seen that the potentials vary little with recording site. (In these experiments the flash intensity was at the higher level used above.)

Pilot experiments were carried out using a patterned flash, in the attempt to obtain larger evoked potentials of short latency, but even with a bright flash seen against a dark background (achieved by making the displaced stimulus annular instead of disc shaped) large short latency responses were not obtained.

7.4 Discussion

Although these experiments demonstrated that there was a non-additive interaction between the potential evoked by the flash and that evoked by the peripheral contour displacement, it is not clear that this occurred because the flash potential was attenuated when the flash was accompanied by a peripheral contour displacement. In particular, the potential evoked by the two stimuli presented together was not similar to that which would have been expected had the effect of the displacement been simply to reduce the effective intensity of the flash. This could be observed in the fact that the waveform obtained by subtracting the displacement potential from that evoked by the conjointly presented stimuli was not similar in latency and form to that of a flash of lower intensity. Furthermore, the flash and displacement did not generate distinctively different potentials. Therefore the fact that the potential evoked by both the stimuli presented together was less than the sum of the potentials evoked by the two stimuli separately could alternatively have reflected an attenuation of the displacement evoked potential in the presence of the flash, or an attenuation of both potentials when the stimuli were presented together.

Whilst there is no particular reason to suggest that the occurrence of the flash should have attenuated the response to the displacement, there is a possible reason for suggesting that both potentials may have been equally attenuated. This is that the potentials generated by both stimuli may have reflected the activity of a single non-specific mechanism, rather than the activity of two specific mechanisms signalling the presence of the flash and displacement respectively. Saturation of the single non-specific system would then account for effect observed. In favour of this interpretation of the effect is the fact that the form, though not the amplitude, of the potential evoked by the conjointly presented stimuli was very similar to the sum of the potentials generated by the two stimuli separately. Against this interpretation, however, is the observation that the size of the potential evoked by the flash was related to the relative intensity of the flash. Thus at least the flash potential bore some relation to the sensory characteristics of the stimulus, and was not completely non-specific.

Whatever the status of these alternative explanations of the non-additive interaction of the two potentials, it is clear that there is no compelling reason to interpret the effect as one of attenuation of the flash response in the presence of the displacement. In other words, the fact that the difference between the potential evoked by the conjoint stimuli and that evoked by the displacement alone was small compared with the potential evoked by the flash alone should not necessarily be taken as evidence that the presence of the displacement attenuated the response to the flash.

This is exactly what was assumed in two of the reports of experiments investigating the size of the flash-evoked potential when the flash was associated with a saccadic eye movement. Gross, Vaughan and Valenstein (1967) and Chase and Kalil (1972) assumed that it was valid to subtract the potential evoked by a saccade alone from that evoked by a flash in association with a saccade, in order to examine whether the flash evoked potential was attenuated by the occurrence of the saccade. Without specific justification, which seemed to be lacking, this procedure is of very doubtful validity.

There are a number of variations of the author's experiment which should be performed in the hope of obtaining more conclusive data. In particular, smaller and patterned flashes restricted to the fovea should be used. The eccentricity of the displaced contour should also be reduced to make it exactly comparable with that used in MacKay's psychophysical experiments. Furthermore, it might be worthwhile using stimuli restricted to one half of the visual field, since a number of authors have shown that the waveforms of pattern-evoked potentials generated by the same stimulus presented in different half-fields can be quite different in form and even have different polarities (e.g. Jeffreys, 1970; Michael and Halliday, 1970; Jeffreys and Axford, 1972a, b). Thus whole-field stimulation may give misleading results.

CHAPTER EIGHT

Decreased parafoveal flicker sensitivity induced by motion of peripheral contours: a possible correlate of the McIlwain Periphery Effect

8.1 Introduction

These experiments arose from a suggestion made by Ikeda and Wright (1972). They reported that the periphery effect only occurred in transient retinal ganglion cells. Fischer, Krüger and Droll (1975) have since reported periphery effects in sustained cells, so the difference in sensitivity to peripheral stimulation of transient and sustained cells may well be relative rather than absolute. Ikeda and Wright pointed out that the lack of modulation of luminance increment thresholds by peripheral stimulation, reported by Spillman and Gambone (1971), could be explained if it were assumed that discrimination of luminance increments was mediated by sustained cells. They suggested that detection of flicker and movement might, however, be mediated by transient cells, and that peripheral stimulation might alter sensitivity to flicker and movement in the centre of the visual field but have no effect on luminance thresholds.

The author's experiments were a preliminary examination of whether peripheral stimulation does in fact alter sensitivity to flicker in the centre of the visual field.

A parafoveal flickering test stimulus was used in preference to a foveal stimulus since at the time it seemed that transient cells might be rare in and near the area centralis of the cat (which corresponds in some respects to the primate fovea).

8.2 Methods and Results

Subjects adjusted the frequency or the amplitude of flicker of a

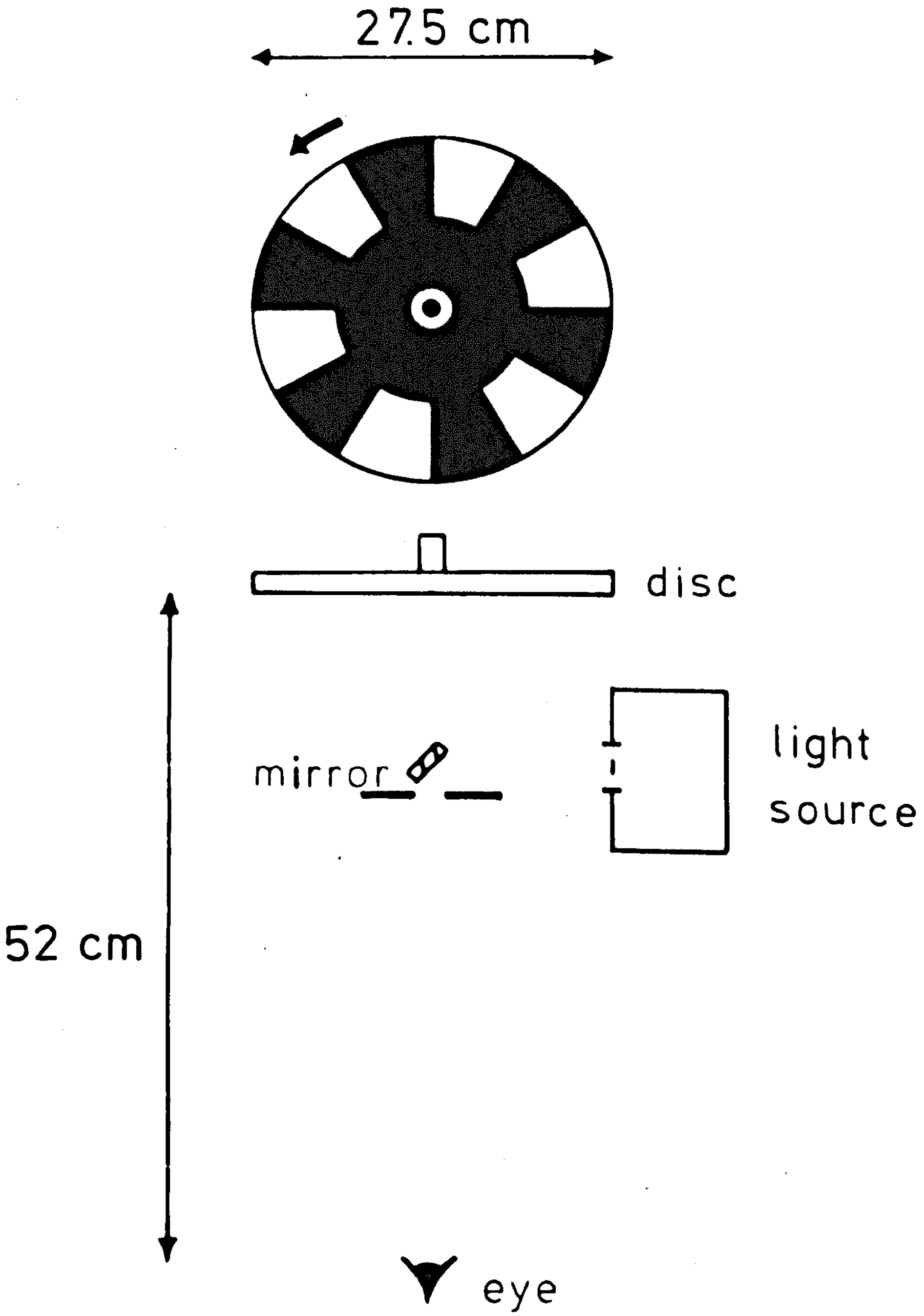


Fig. 8.1 Apparatus

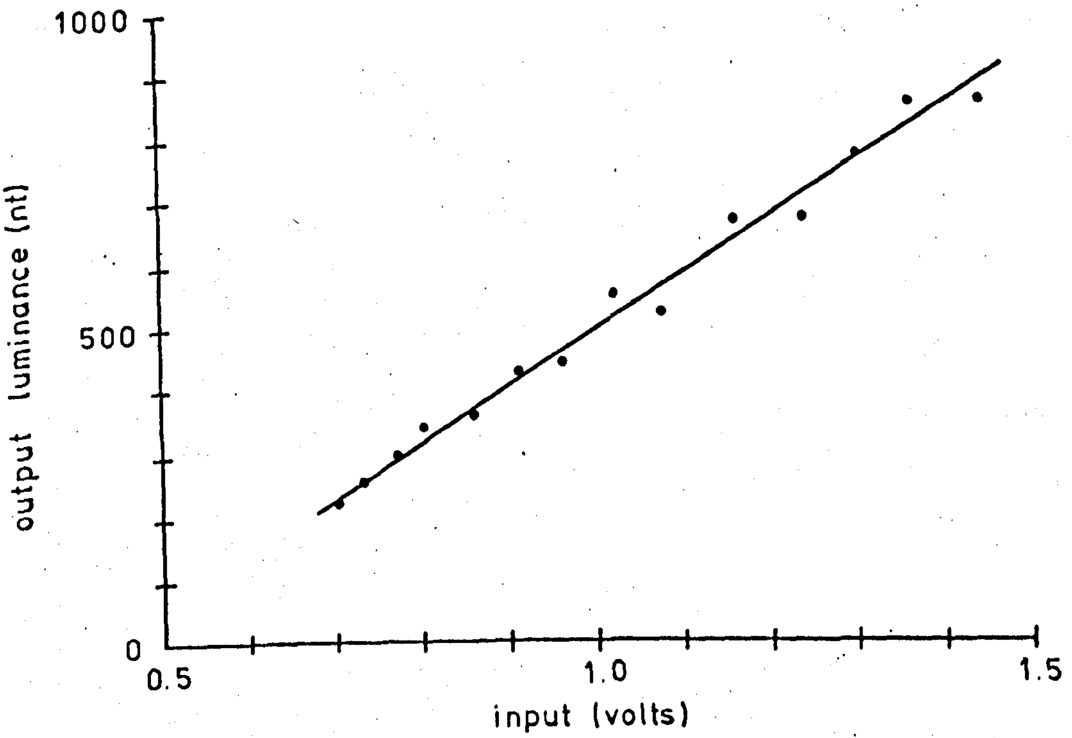


Fig. 8.2 Calibration curve for sinusoidal light intensity modulator.

parafoveal test stimulus until the flicker could just not be seen. Adjustments were made while an annular peripheral pattern (of form and dimensions similar to that used by McIlwain (1966)) was rotating, and while it was stationary, and the flicker thresholds for the two conditions were compared. Subjects viewed the stimulus monocularly.

The stimulus configuration is shown in Fig. 8.1.Unless otherwise indicated, the test stimulus was an annulus of inner diameter 1.5 degrees and outer diameter 4 degrees, and the peripheral pattern was an annulus of alternate black and white spokes, each 3 degrees wide. The inner boundary of the spokes was 6 degrees from the edge of the test stimulus.

In the first series of experiments the flickering light source was a stroboscope. In initial experiments with subject SJJ, it was found that the effect of peripheral stimulation on flicker fusion frequency was small - causing a decrease of at most 5% in flicker fusion frequency. The range of the settings in each block of ten settings was ± 5%, so the effect was near the noise level of the method. Varying the speed of rotation of the annulus from 9.5 to 120 degrees/sec had little effect on the flicker fusion frequency. In these initial experiments the test stimulus was a 4 degree diameter disc. The subject fixated the left hand or right hand edge of the disc.

Using a second subject (SRH) a clear decrease of about 5% in flicker fusion frequency was obtained with a 30 degrees/sec speed of rotation of the peripheral pattern. (This speed was selected to match that used in McIlwain's physiological experiments on the periphery effect, and was used in all subsequent experiments.) When the peripheral stimulation ceased, however, the flicker fusion frequency did not return to its original level, even when the motion after-effect had almost disappeared (Fig.8.3). In this and subsequent experiments the test stimulus was annular, and the subjects wore headphones in which 'noise' was played to mask the sound of the stroboscope, which might otherwise have been used as a cue to flash frequency. The luminances of the black and white spokes of the peripheral pattern were 1.5 and 2.5 log cd/m^2 respectively.

A similar effect was obtained in a second run of the same subject (Fig.8.4). These data were obtained in a session in which the two subjects made blocks of 10 settings alternately (taking 3-4 minutes for each block). SRH is much more consistent than SJJ. In the data for SJJ there are significant differences between the means for different blocks of settings made under the same conditions, so the statistically significant difference between flicker fusion frequencies for moving and stationary peripheral patterns should be treated with caution.

Because of the steepness (about 20 dB/octave) of the slope of the relation between threshold modulation depth and frequency in the high frequency region, an effect such as the one above, which induced a 5% change in flicker fusion frequency, might be expected to produce a much greater (about 25%) change in threshold modulation depth in an experiment in which the experimental variable was the modulation depth of a sinusoidally modulated stimulus. A sinusoidal-light-intensity-modulator was therefore built to replace the stroboscope. This was simply a panel of small (6 Watt) fluorescent tubes, driven by a transistor amplifier. The relationship between the input voltage and the output luminance was linear (Fig. 8.2).

The data from four pilot runs are shown in Figs.8.5(3 degree wide spokes in the periphery) and Fig.8.6(30 degree wide spokes).

The data for RFJ show no consistent relation between thresholds for the stationary and moving peripheral pattern conditions, and

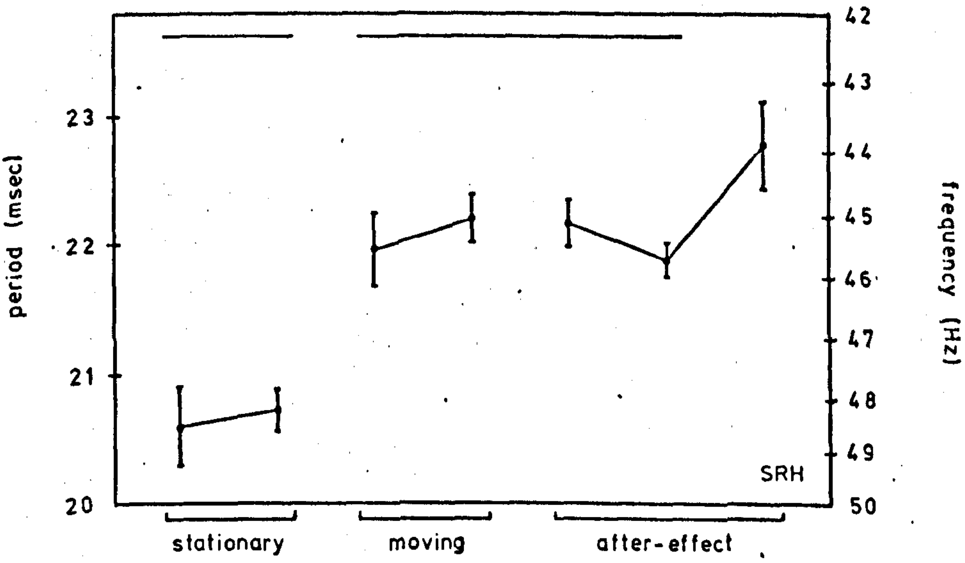


Fig. 8.3 Flicker fusion frequency (ordinate) with a stationary peripheral pattern, with a moving peripheral pattern, and immediately after cessation of movement of the peripheral pattern. The vertical bars show the standard errors of the means of blocks of ten settings. The horizontal bars at the top of the figure indicate that the differences between the means below the bars are not significant at the 5% level. The difference between the overall means for the 'stationary' and 'moving' conditions is significant (at the 1% level).

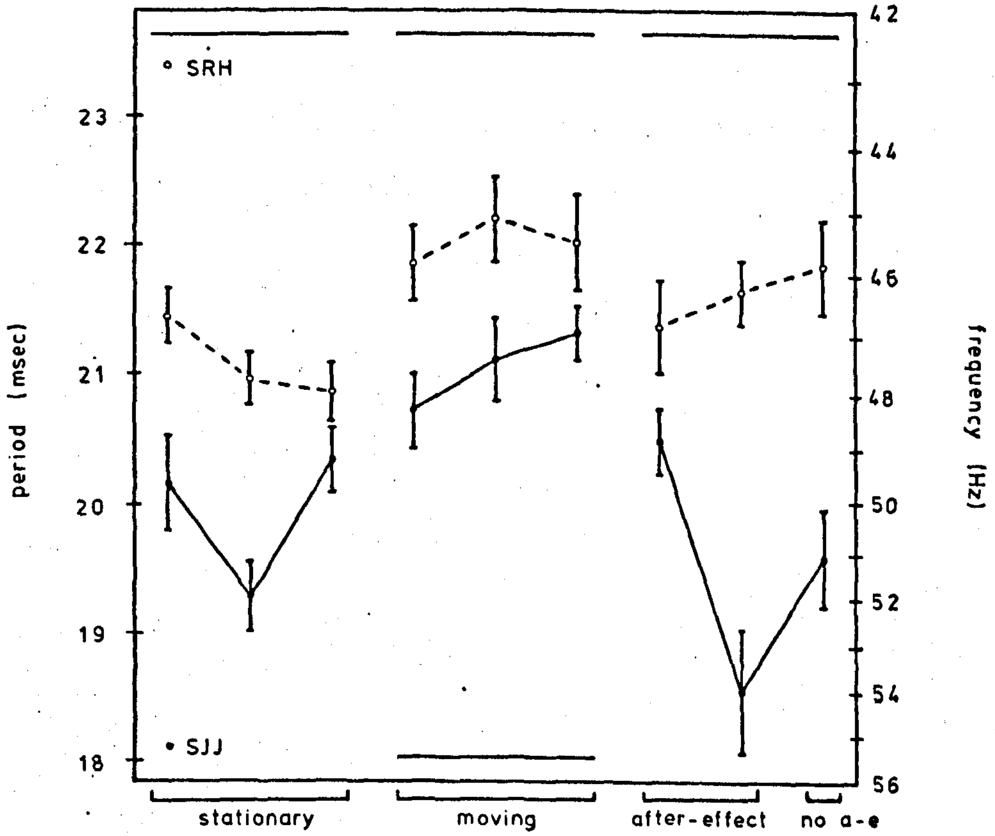


Fig. 8.4 Flicker fusion frequency (ordinate) with a stationary peripheral pattern, with a moving peripheral pattern, and after cessation of movement of the peripheral pattern, for two subjects. The horizontal bars at the top of the figure apply to the data for SRH. For SRH the difference between the overall means for the 'stationary' and 'moving' conditions is significant (at the 1% level), but the difference between the overall means for the 'moving' condition and for the final three blocks is not significant (at the 5% level). See the text for comments on the data for SJJ.

furthermore the shape of the threshold versus frequency of flicker function is anomalous.

For SRH the thresholds with moving peripheral pattern are about 5% greater with 3 degree wide spokes in the periphery(Fig.8.5) and 10 - 20% greater with 30 degree wide spokes in the periphery (Fig.8.6). These data were obtained by successively determining the threshold versus frequency functions for the three conditions: peripheral pattern stationary, peripheral pattern moving (at 30 degrees/sec), and peripheral pattern stationary (with after-effect visible). Within each condition the thresholds were determined in order from higher to lower frequencies. Open symbols show repeat determinations of the threshold for 45 Hz flicker made after the determination of the threshold for 30 Hz flicker, and thus show the small degree of drift or adaptation of threshold with time.

For VM (Fig 8.6)the thresholds were determined in pairs for stationary and moving peripheral pattern, at each frequency. The problem with this method is that the after-effect of the last moving stimulus increases the threshold for the stationary condition at the next frequency sampled. This effect may go some way to explaining the large drift in threshold evident. The difference in threshold between stationary and moving peripheral pattern conditions is 5 - 20%.

The data suggest that the peripheral stimulus with the wider spokes has a larger effect on the modulation depth thresholds. It should be noted that under the same conditions as the flicker fusion frequency experiments (3 degrees wide peripheral spokes), contrary to expectation, there is <u>not</u> a 25% increase in threshold modulation depth.

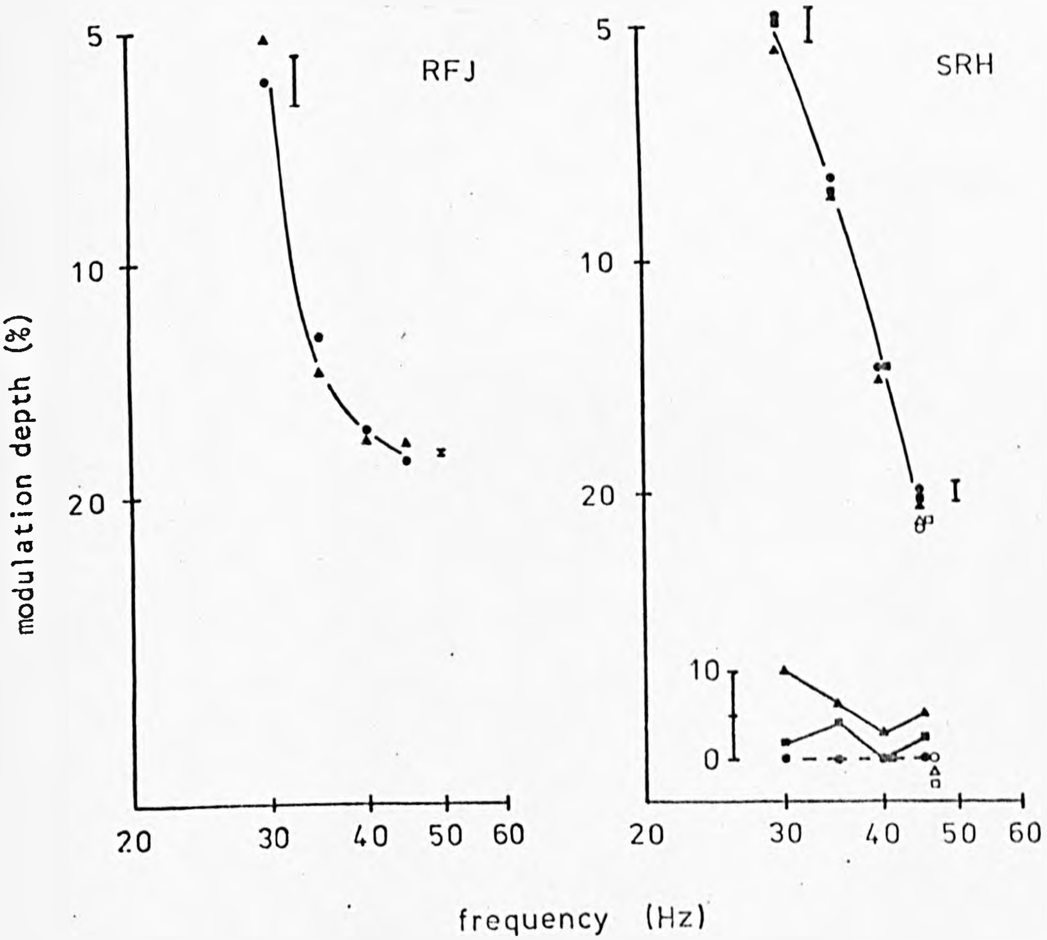


Fig. 8.5 Threshold modulation depth as a function of frequency, with and without movement of 3 degrees wide spokes in the periphery. Circles show data for stationary peripheral pattern, triangles data for moving peripheral pattern, and squares data for stationary peripheral pattern with after-effect of movement visible. The inset shows the percentage increase in threshold modulation depth relative to the initial settings with the peripheral pattern stationary. The vertical bars indicate twice the typical standard error of the mean of the 6 or 7 settings on which each datum point is based.

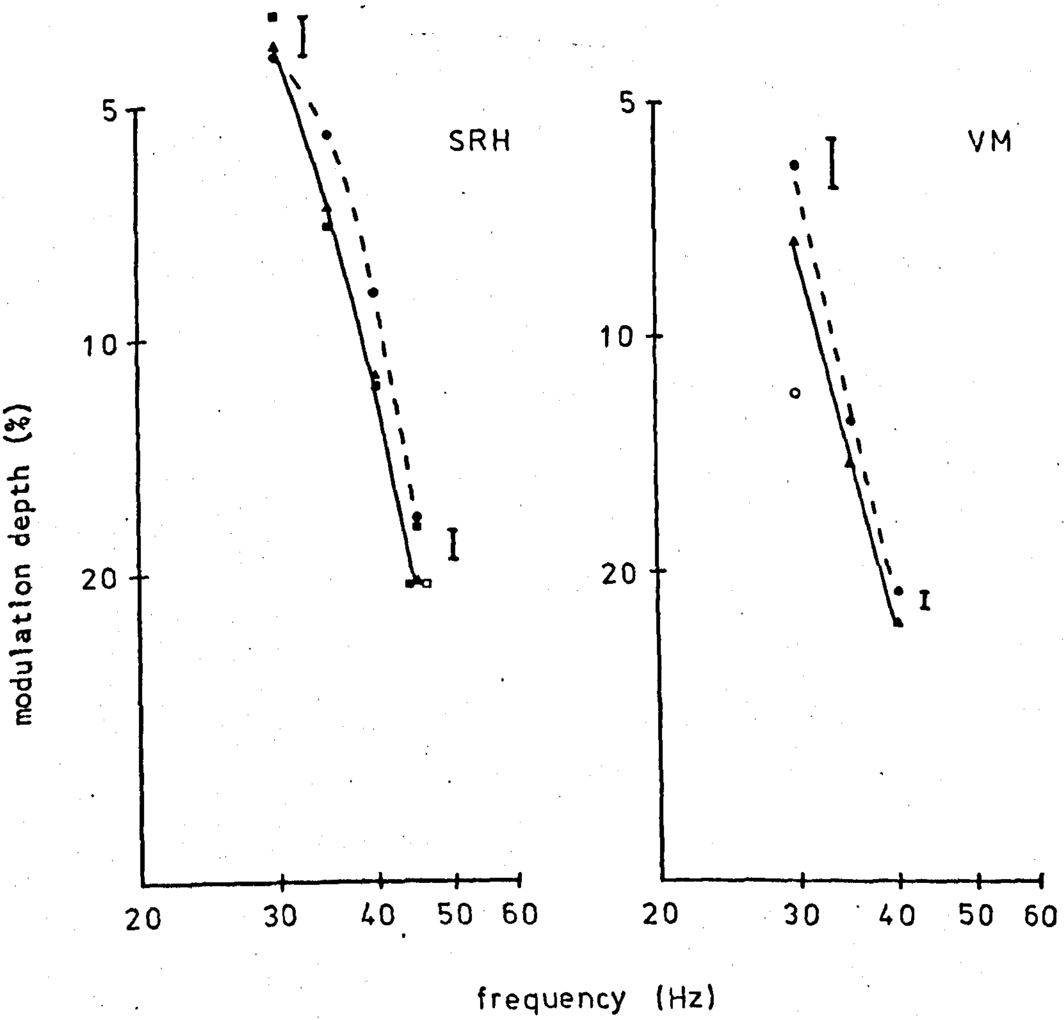


Fig. 8.6 Threshold modulation depth as a function of frequency, with and without movement of 30 degree wide spokes in the periphery. Circles and dashed lines show data for stationary peripheral pattern, triangles data for moving pattern, and squares data for stationary peripheral pattern with after-effect of movement visible.

8.3 Discussion

Although it seems clear that sensitivity to flicker is diminished by movement of contours in the periphery of the visual field, the author's data are not sufficiently extensive to permit of firm conclusions about the size of the effect.

It is quite possible that the stimuli used were not optimal. Since the author's experiments were conducted, Kruger and Fischer (1973) have shown that rapid displacements are extremely potent as generators of the periphery effect in cat retinal ganglion cells. Rapid displacements of large patterned peripheral stimuli produce periphery effects even in sustained cells (Fischer, Krüger and Droll, 1975). Using such a peripheral stimulus it may well be possible to produce larger effects on psychophysical flicker sensitivity.

The second possible non-optimal aspect of the author's experiments is the retinal location of the test stimulus. The effect should be studied with foveal, as well as parafoveal test stimuli, since it has now been shown that the smaller proportion of transient cells relative to sustained cells recorded near the area centralis of the cat's retina (e.g. Cleland and Levick, 1974) is probably an artefact of electrode sampling bias. The reason for asserting this is that Cleland, Levick and Wässle (1975) have been able to produce strong evidence that the main type of transient cell, the brisk transient type, is to be identified with the 'alpha' type of ganglion cell seen in cresyl violet preparations of the retina, and the same workers have been able to show (Wässle, Levick and Cleland, 1975) that the alpha type of cells constitute a constant 2 - 4% of retinal ganglion cells at every retinal eccentricity, even in the area centralis.

CHAPTER NINE

Summary and concluding discussion

9.1 Minor results

9.1.1 Elevation of threshold by tachistoscopically presented parafoveal stimuli

The experiments described in chapter six showed that the threshold for detection of a foveal test flash was raised by the occurrence of non-contiguous parafoveal stimuli at about the same time as the flash, even when these stimuli involved no change in the mean luminancé of the parafoveal region in which they appeared. This threshold elevation could be of similar magnitude to that produced by displacement of peripheral contours. Thus displacement of contour as such is not necessary to produce alterations of visual sensitivity similar to those which MacKay (1970a) showed could be produced by displacement of peripheral contours.

9.1.2 Human scalp potentials evoked by flashes presented in temporal proximity to rapid displacements of a peripheral contour

The scalp evoked potential experiments described in chapter seven revealed that there was a non-linear interaction between the potentials evoked by a flash in central view and by the displacement of a peripheral contour. It was argued that it was unlikely that this non-linear interaction reflected an attenuation of the flash response brought about by the occurrence of the displacement. Therefore the effect observed was probably not an evoked potential correlate of the psychophysical threshold elevation which occurs under similar conditions. It was noted that the same critical arguments could be used to call into question the validity of some of the experiments which claimed to show that the potential evoked by a flash was attenuated when the flash was presented at about the same time as a saccadic eye movement.

9.1.3 Decreased parafoveal flicker sensitivity induced by motion of peripheral contours

Chapter eight described experiments in which it was shown that parafoveal flicker sensitivity was decreased by movement of contours in the periphery of the visual field. This effect may be related to the physiological periphery effect.

9.2 Major results

9.2.1 Elevation of threshold by small passive image displacements

It was shown that displacements as small as 6 minutes of arc of a large, high-contrast peripheral and parafoveal static visual noise pattern produced an elevation of threshold for foveal flashes presented just after the displacement. The variation of this effect with the amplitude of the displacement was studied.

This effect cannot account for the elevation of threshold reported by Beeler (1967) to occur for flashes presented within ± 75 msec of the onset of microsaccadic eye movements, since a passive 6 minute arc displacement of a retinal image similar to that present in Beeler's experiments did not produce any significant alteration in the detectability of flashes presented within ± 100 msec of the onset of the displacement. (6 minute of arc is the size of a typical microsaccade.)

The latency of the above mentioned elevation of threshold produced by small passive displacements of a peripheral retinal image is in any case quite different from that of the threshold elevation reported by Beeler

It is possible, however, that Beeler's experiments were subject to an artefact (see chapter two for details) so before one can conclude that active and passive micro-displacements of the retinal image are not accompanied by similar alterations in detectability of test flashes it is necessary to perform further experiments.

The best way of conducting further experiments would be to compare with the same subjects the elevation of threshold associated with active and passive micro-displacements of the same retinal image. Such experiments would be facilitated by the use of the device for monitoring eye movements recently described by Findlay (1974). This enables the detection of microsaccades without the use of contact lenses and optical levers.

9.2.2 Comparison of the elevation of threshold produced by passive displacement of contours at different eccentricities

The experiments reported in chapter four showed that elevation of threshold for the detection of foveal flashes was produced by displacement of contours lying at greater eccentricities than that used by MacKay (1970a, b). Even displacement of a contour 40 degrees eccentric to the fovea still produced clear elevation of threshold, albeit rather smaller than that associated with displacement of less eccentric contours. The mechanism underlying MacKay's effect was thus shown to be effective with extraordinarily large separations between the interacting stimuli. In this respect MacKay's effect is similar to the physiological 'periphery effect'.

9.2.3 Elevation of threshold associated with active and passive displacements of a nearly uniform retinal image

The experiments reported in chapter five and appendix one constituted attempts to establish whether the threshold elevation associated with voluntary saccadic eye movement could or could not be entirely accounted for by the displacement of peripheral retinal contours which frequently accompanies saccades. To minimise the component of threshold elevation associated with retinal image displacement (and so make any contribution to the threshold elevation from other sources more apparent), the experiments were conducted in a modified ping-pong ball ganzfeld. The result of the experiments was that rather less than half of the total threshold elevation associated with saccadic eye movement under these conditions could not be attributed to the displacement of the peripheral retinal image which accompanied the saccade. Saccadic eye movement was on average associated with about 0.5 log units elevation of threshold for the detection of a test flash one degree in diameter, whereas pseudo-saccadic rotation of the 'ganzfeld' about the centre of the eye was accompanied by a mean threshold elevation of about 0.3 log units.

It would seem likely that some of the difference of 0.2 log units between the threshold elevation associated with active and passive displacements of the retinal image must be attributed either to mechanical disturbance of visual processing brought about by saccadic movement of the eye (Richards, 1968 and 1969), or to centrally mediated alteration of visual sensitivity associated with the occurrence of a saccade (Holt, 1903; and others). The only other possible explanation of the discrepancy would seem to be that the displacement of the small area of the retinal image in the extreme periphery which occurs during saccadic eye movement but not during 'ganzfeld' rotation contributes 0.2 log units additional threshold elevation. This does not seem likely since it was shown in chapter four that threshold elevation of only 0.1 log units was associated with displacement (through 3 degrees) of a sharp, high-contrast contour lying at an eccentricity of more than 40°. Up to that eccentricity, displacement of contours of increasing eccentricity was associated with progressively less elevation of threshold for the detection of a central test flash. Thus it seems to the author unlikely that the displacement, albeit through 6 degrees, of a small, poorly-focussed low-contrast retinal image lying at eccentricities of more than 80 degrees should produce 0.2 log units threshold elevation. Never-the-less the possibility cannot be excluded that part of the additional 0.2 log units threshold elevation found to occur in association with saccadic eye movement was produced by this means.

9.3 Recent literature concerned with the threshold elevation associated with saccadic eye movements

9.3.1 Summary of reports

Since the author's experiments were begun, a number of reports have appeared of experiments concerned with the origin of the threshold elevation associated with saccadic eye movement.

Mitrani et al. (1973) studied the effect of contrast in the field of view on the extent of threshold elevation associated with saccades. They showed that if a blotch pattern was presented only during 9 degrees saccades the threshold for detection of flashes delivered during a saccade was little different from that in the absence of a saccade. If the blotch pattern was present continuously or was switched off 7 msec after the beginning of the saccade and switched on again immediately after the saccade, large changes of threshold were associated with the saccadic eye movement. They showed that greater degrees of threshold elevation were produced by patterns of higher contrast. This experiment showed that only the offset of contours from one position on the retina and their onset in a new position was necessary to produce the threshold elevation associated with saccadic eye movement, and that the actual sweep of contour across the retina during the saccade was unimportant.

In a second paper (Mitrani et al., 1975) it was shown that the extent of threshold elevation associated with saccadic eye movement in a patterned visual environment depended not only on the amount of pattern present but also on the angular separation between the test flash and the pattern, larger separations being associated with smaller threshold elevation.

Brooks and Fuchs (1975) repeated many of the experiments of Mitrani and his colleagues and obtained the same results, notably that little if any threshold elevation was associated with saccadic eye movements in dim illumination, and that not only the luminance but also the structure of the background influenced the degree of threshold elevation associated with saccades. Like Latour (of whose experiments they appear to have been unaware) they showed that the form of the test flash is important. Brooks and Fuchs found that diffuse flashes were perceived with more difficulty than punctate flashes (of one degree diameter) during saccades over a contour-free background. On the other hand, contours in the background raised saccadic thresholds for small stimuli much more than for diffuse test flashes. They arranged that the background could be pseudosaccadically displaced in some of the experiments, and found that the amount and time course of threshold elevation produced by pseudosaccadic displacement of the background compared well with that associated with saccadic eye movement.

Riggs, Merton and Morton (1974) studied the threshold for detection of electrical phosphenes delivered just after saccadic eye movements of 10 degrees extent made in total darkness. They made subsidiary experiments to relate the current used to produce the phosphenes to the brightness of the light perceived. Expressed in terms of the estimated real light equivalent, they found in three subjects that threshold elevations of 0.47, 0.36 and 0.44 log units were associated with saccadic eye movement in total darkness.

9.3.2 Discussion

The large degree of threshold reported by Riggs et al. (1974) to be associated with saccadic eye movement in total darkness stands in great contrast to the minimal threshold elevation found by Richards (1969), Mitrani et al. (1971) and Brooks and Fuchs (1975) in dim illumination, and strongly suggests that there must be some error involved in the use of electrical phosphenes rather than real light to study the threshold elevation associated with saccadic eye movement. One experiment which might clarify the issue is to examine whether phosphene thresholds are altered by passive pseudosaccadic rotations of the eye in total darkness. It is just possible that the alteration of phosphene threshold observed by Riggs et al. was a consequence of the mechanical disturbance to the eye produced by the saccade.

Riggs et al. (1974) criticised Richards (1969) and MacKay (1970a) for using $\frac{1}{4}$ degree diameter black fixation targets, suggesting that the displacement of these fixation points across the retina may have produced some of the threshold elevation observed by these workers.

In the case of MacKay's experiments, this criticism is mistaken since the fixation point was not displaced with the background. This criticism of Riggs et al. is in any case completely beside the main point arising from their own experiments which is to explain why workers such as Richards (1969) found so little threshold elevation at low background illumination levels.

It seems that with the exception of the results reported by Riggs et al. (1974), there is now a fair consensus in the literature that the threshold elevation associated with saccadic eye movement is small (relative to the classical '0.5 log units') when the effect of the retinal image displacement which normally accompanies saccadic eye movement is excluded.

In particular, the author's experiments show that the mean difference between the threshold elevation associated with active displacement (produced by saccadic eye movement) and that associated with passive displacement of the same retinal image (brought about by pseudosaccadic rotation of the visual environment about the axis of rotation of the eye) is 0.2 log units, and it is possible that part of this difference is due to the displacement of a small additional area of the extreme periphery by saccadic eye movements. Any centrally mediated attenuation of visual sensitivity associated with saccadic eye movements must therefore be very slight.

APPENDIX ONE

Early experiments comparing the threshold elevation associated with active and passive displacements of a nearly uniform retinal image

A1.1 Introduction

These experiments originated in the finding, reported in chapter five, that in a roughly uniform visual environment created by the ping-pong ball method (somewhat modified, as described op. cit.), saccadic eye movements were accompanied by an elevation of threshold of similar magnitude to that associated with saccades in patterned surroundings.

This unexpected result strongly suggested that the elevation of threshold associated with saccadic eye movement could not be entirely attributed to the displacement of the peripheral retinal image produced by a saccade. It was just possible, however, that even the slight non-uniformities of the modified ping-pong ball 'ganzfeld' apparatus, notably the fall-off of luminance in the far periphery, especially in the lower nasal field, and also more centrally the slight and unavoidable annular shadow of the 'screen', were never-the-less sufficient to produce a substantial threshold-elevation effect of the kind reported by MacKay (1970a, b).

In order to resolve this matter experimentally, the ping-pong ball apparatus was altered so that it could be rotated in a pseudo-saccadic fashion about the axis of rotation of the subject's eye.

A1.2 Method

A1.2.1 Apparatus

The moment of inertia of the apparatus was greatly reduced by replacing all metal and perspex parts with balsa wood. The ping-pong ball assembly was mounted on pivots directly above and below the centre of rotation of the subject's right eye. A vibration generator (Ling Altec; 3 ohms) rotated the assembly at a velocity of the same order of magnitude as that of a saccadic eye movement of similar angular extent, but with peak velocity half and duration twice those of a saccade of the same extent. Since the apparatus was rotated about the centre of rotation of the subject's eye, the retinal image displacement was similar on every part of the retina to that associated with saccades, except in the far periphery corresponding to the edge of the ping-pong ball (see Fig. A1.1).

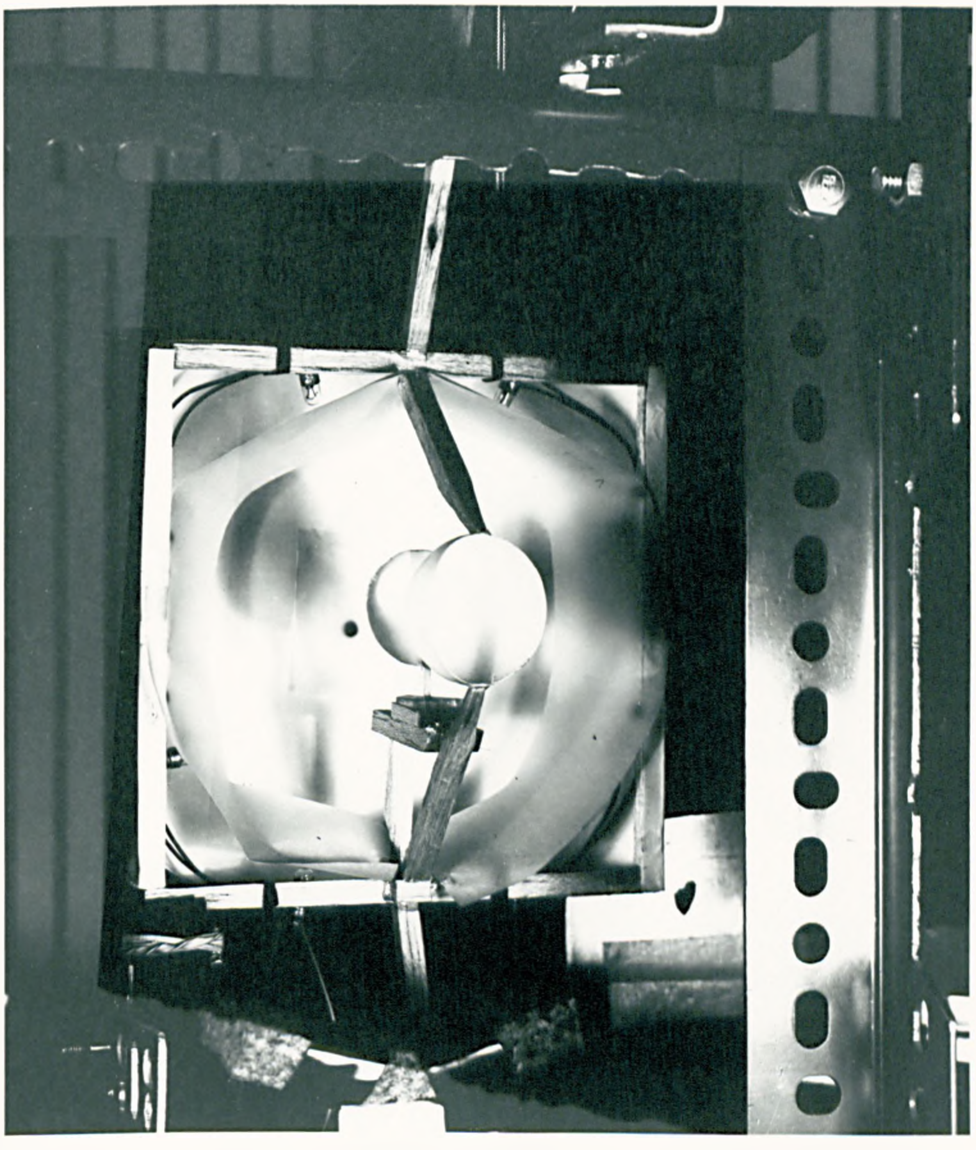
The field luminance was 17 cd/m^2, and the size of the test flash was 18 degrees in diameter (as before). The flash was produced by a modified 'computer electronic' flashgun described in appendix two. Its duration was less than 120 microseconds.

In other respects the apparatus was unchanged from that used in the first experiments reported in chapter five.

Because the test flash and fixation lights were seen in a mirror, when the apparatus was rotated through 'x' degrees, the images of the flash and fixation points rotated through '2x' degrees. This important point was unfortunately overlooked during the main series of experiments reported below, in which passive and active displacements which rotated the fixation points (and test flash) through equal angles were employed i.e. $4\frac{1}{2}$ degrees passive displacements and 9 degrees active displacements. Control experiments were performed using $4\frac{1}{2}$ degrees active displacements to investigate whether this deficiency of the experimental design could undermine the main results.

Fig. A1.1 Apparatus for the early 'ganzfeld' experiments. The ping-pong ball was mounted in a balsa wood frame, which also supported a paper background and nine miniature incandescent lamps which illuminated the ping-pong ball. Translucent paper diffusers were placed infront of these lamps. The chin rest can just be seen at the bottom of the photograph. See the text for further details.

The author gives his apologies for the poor quality of the photograph, which was made under adverse circumstances. Unfortunately, it was absolutely impossible to obtain another photograph.



A1.2.2 *Procedure*

Experiment 1: Thresholds

In the first or 'threshold' experiment, a variation of the method of constant stimuli was used. Each run of one hundred trials was divided into blocks of twenty trials during any one of which the flash energy was randomly selected from a set of six values covering a range of 0.5 log units in 0.1 log unit steps. At the end of each block the centre-point of the flash energy level range was adjusted so as to narrow any discrepancy between the centre-point of the stimulus range and the subject's estimated threshold (stimulus level at which the stimulus was detected on 50% of trials). The algorithm for performing this function was:-

> $E(n + 1) = E(n) - \text{Integer part of } ((50 - \bar{H})/12))$
> Where $E(n)$ specified the centre-point of of the energy range employed in the previous 20 trials, and $E(n + 1)$ the new centre-point. $\bar{H}$ was the mean hit rate for the whole run as far as it had proceeded. In words, the centre-point of the energy range was increased by one unit (0.1 log units energy) for each 12% deficiency of the overall hit rate below 50%.

Separate runs were necessary for obtaining the thresholds for detection of flashes delivered during rightward and leftward active displacements of the retinal image (the flash was triggered by the saccade signal from the electro-oculogram), but thresholds for flashes delivered during rightward and leftward passive image displacements were determined in the same run. Separate runs were also made to determine the threshold for flashes delivered some 200 msec before both active and passive image displacements.

Thresholds, with their standard errors, were estimated by probit analysis (Finney, 1964), performed by means of a computer programme written by D. P. Andrews.

Experiment 2: Timecourses

In the second or 'timecourse' experiment the energy of the flashes was held constant and only their time of occurrence (relative to the image displacement) varied. The flash could occur at one of twelve intervals after the trial onset in the passive displacement condition (25 or 30 msec separation between adjacent flash delays). In the active displacement condition the flash occurred at one of five intervals (differing by 50 msec) after the trial onset, and the natural variation in saccade latency provided additional variation of the interval between the test flash and the saccade. The interval between the two events was measured as described in chapter five, and the subject's response assigned to the appropriate bin. There were twelve bins, each with width 25 or 30 msec except for the extreme bins, which were of 100 msec width. The mean delay of the flash in the active displacement condition was automatically adjusted to reduce any discrepancy between this parameter and the mean saccade latency.

Timecourses of flash detectability associated with rightward and leftward active image displacements were determined in one run, since the hardware had been modified to make this possible. As before, the effects of rightward and leftward passive image displacement were also determined in one run.

A1.3 Results

Experiment 1: Thresholds

The data for the two subjects most extensively studied (CH and RSM) are shown in Figs. A1.2,A1.3.The third subject gave data similar to those of CH. Both CH and RSM gave similar elevations of threshold with leftward and rightward active image displacements. The mean elevations of threshold for CH were: 0.24 (leftward displacement) and 0.17 (rightward displacement) log units; for RSM: 0.36 (leftward displacement) and 0.38 (rightward displacement). Both subjects gave significantly less elevation of threshold with passive image displacements than with active image displacements.. Mean threshold elevations for leftward and rightward passive image displacements were for CH 0.09 and 0.03 log units respectively. RSM's mean thresholds were hardly altered by the passive displacements: leftward image displacements produced no significant threshold change, and rightward image displacements produced a tiny (0.02 log units) decrease of threshold. Standard errors of the individual threshold determinations were typically 0.02 log units (maximum 0.03 log units).

Experiments were also conducted with one subject (CH) in which the background luminance was reduced to a scotopic level. As at the photopic levels, the elevations of threshold associated with active image displacements were significantly greater than those associated with passive image displacements.

Comparison of the results of experiments in which runs were made in different orders did not reveal any clear effect of run order.

The source of the considerable difference in results of different runs (amounting in the case of RSM and passive displacement to a reversal of the sense of the effect of the image displacement) is unknown.

Experiment 2: Timecourses

Three subjects were used (CH, RSM and the author). The author's data were similar to those of RSM.Figs. A1.4 &A1.5show data for CH and RSM. In both cases a greater depression of detectability of the

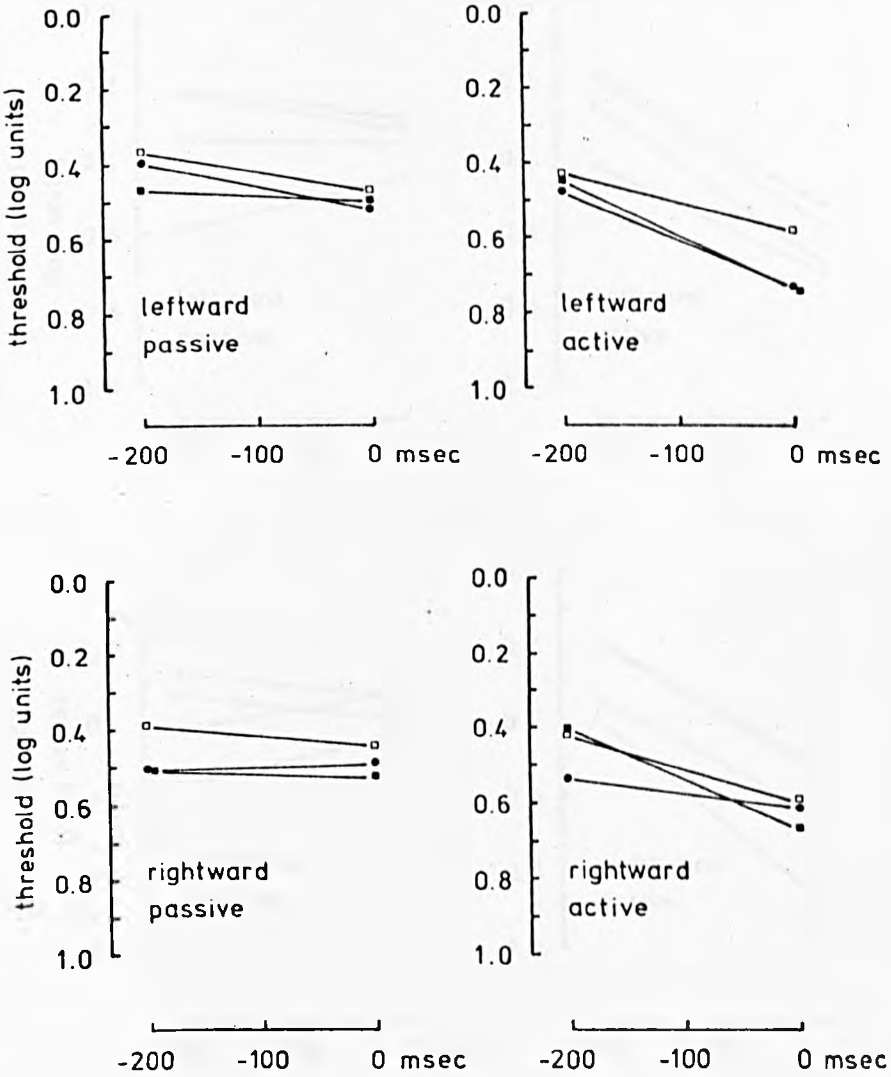


Fig. A1.2 Thresholds for the detection of flashes presented 200 msec before or during active and passive image displacements. Subject CH. Thresholds (energy of flash at which the probability of detection of the flash was 0.50) were estimated by probit analysis from the results of experiments using the method of constant stimuli. The standard errors of the threshold estimates were typically about 0.02 log units.

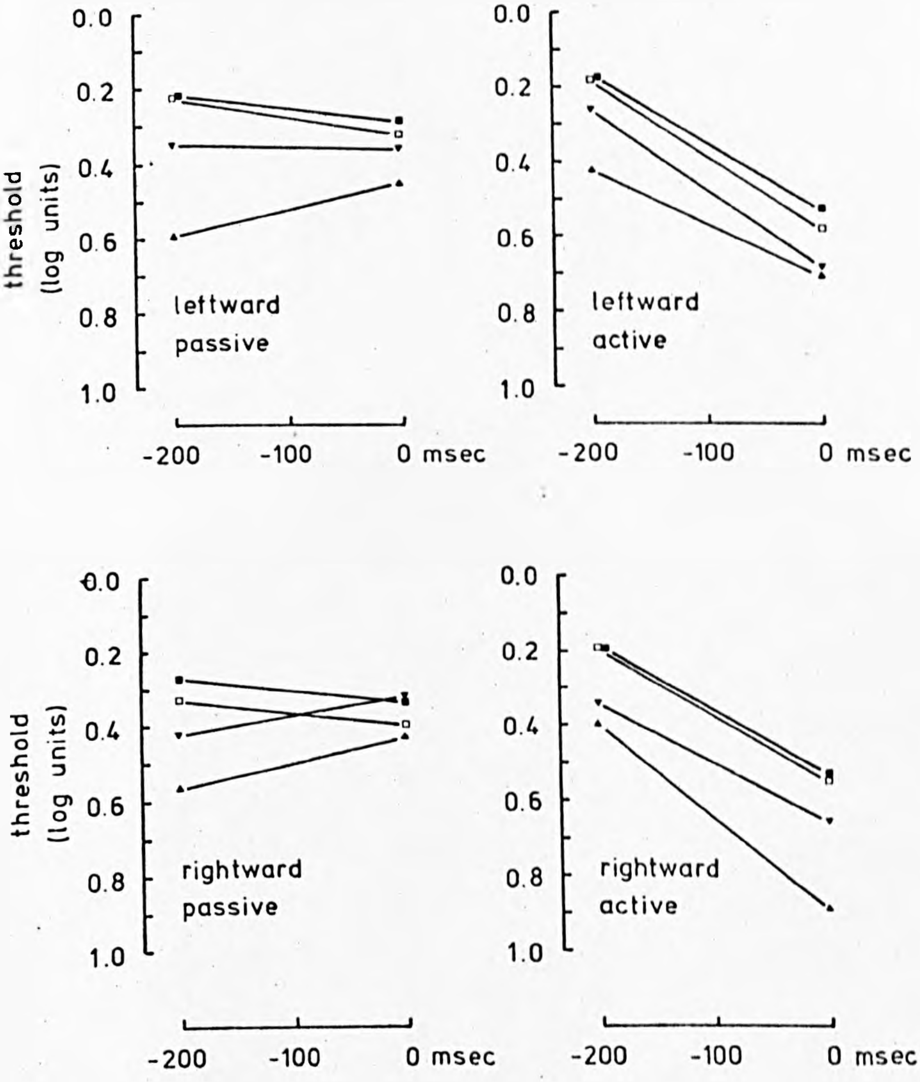


Fig. A1.3 Thresholds for the detection of flashes presented 200 msec before or during active and passive image displacements. Subject RSM. Thresholds (energy of flash at which the probability of detection of the flash was 0.50) were estimated by probit analysis from the results of experiments using the method of constant stimuli. The standard errors of the threshold estimates were typically about 0.02 log units.

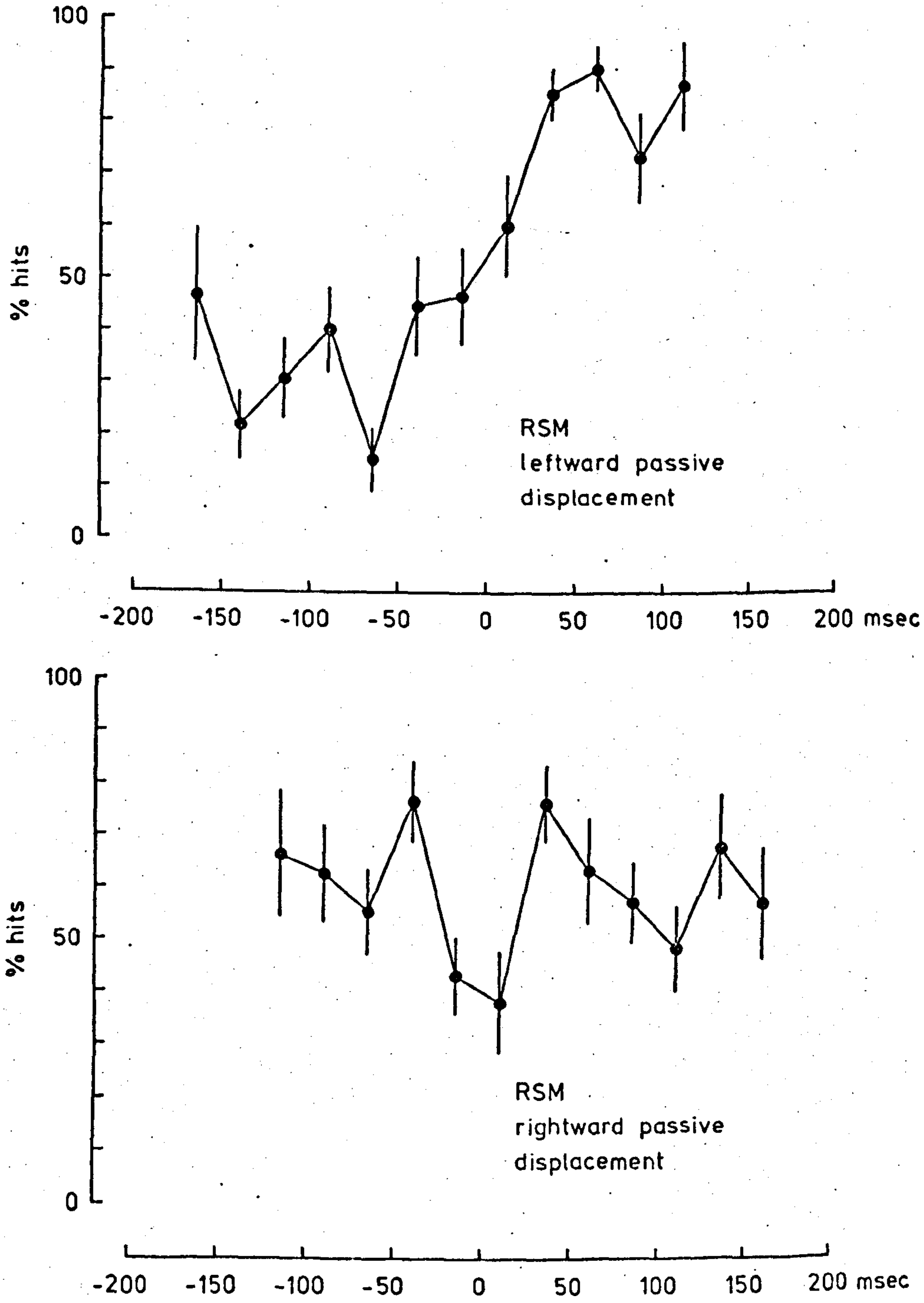


Fig. A1.4a Detectability of a flash as a function of the time of the flash relative to the onset of a passive displacement of the retinal image. Error bars show the standard errors calculated from the formula for the standard error of a binomial process.

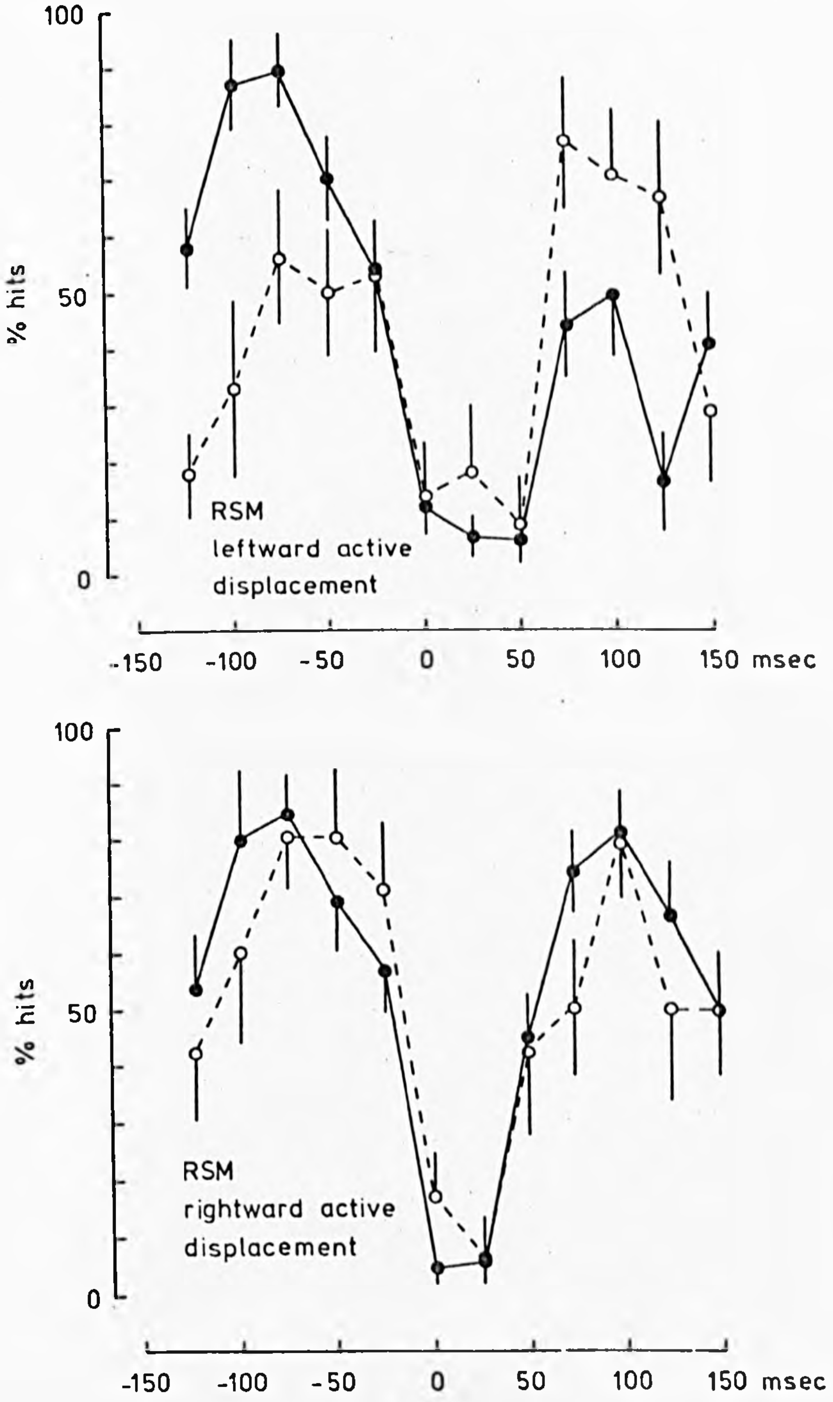


Fig. A1.4b Detectability of a flash as a function of the time of the flash relative to the onset of an active displacement of the retinal image. Solid lines: 9 degrees active image displacements; dashed lines: 4½ degrees active image displacements. Note that even with the 4½ degrees active displacements, the depression of flash detectability associated with active image displacements is greater than that associated with the passive image displacements.

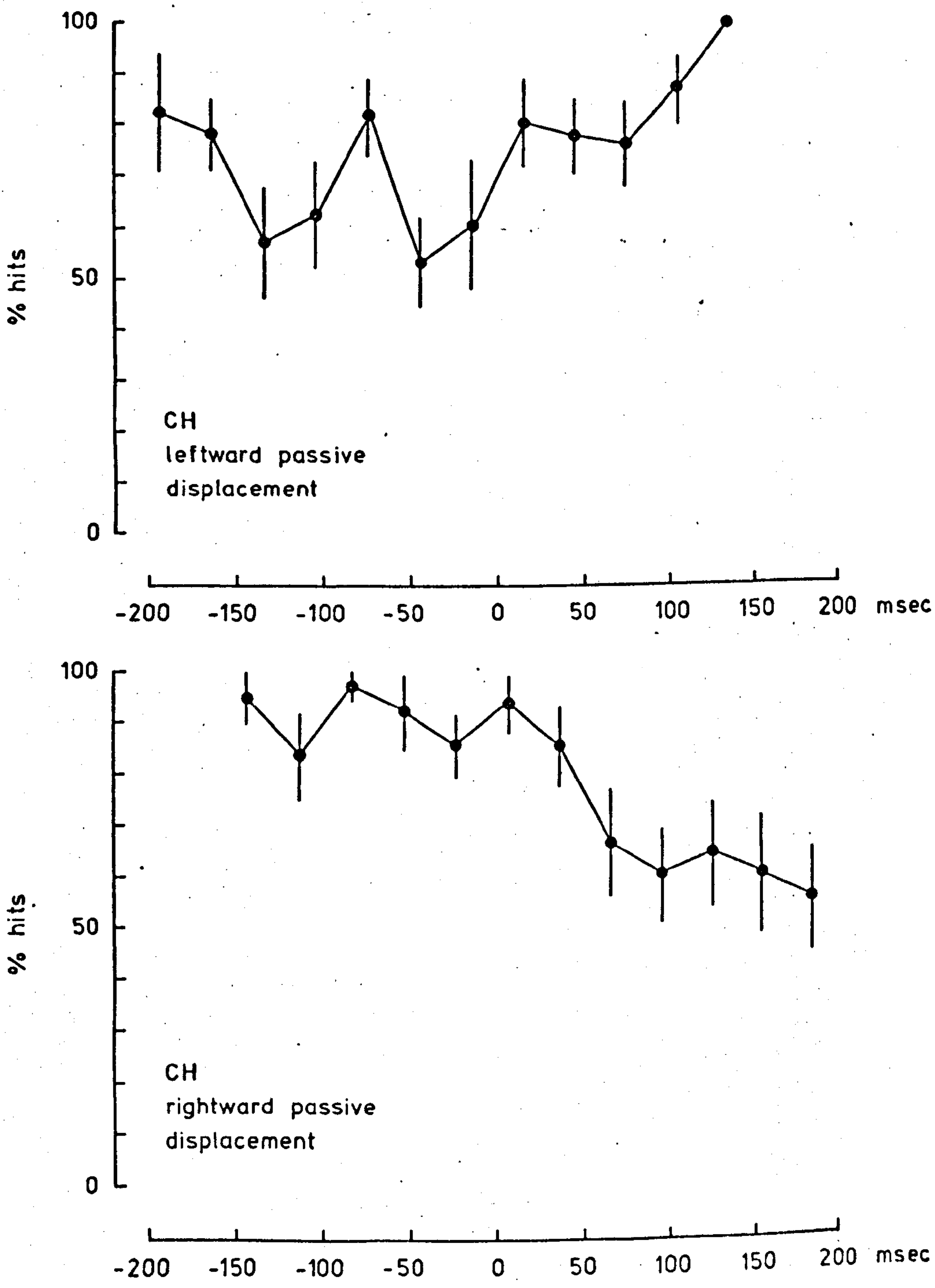


Fig. A1.5a Detectability of a flash as a function of the time of the flash relative to the onset of a passive image displacement. Subject CH. Scotopic luminance level.

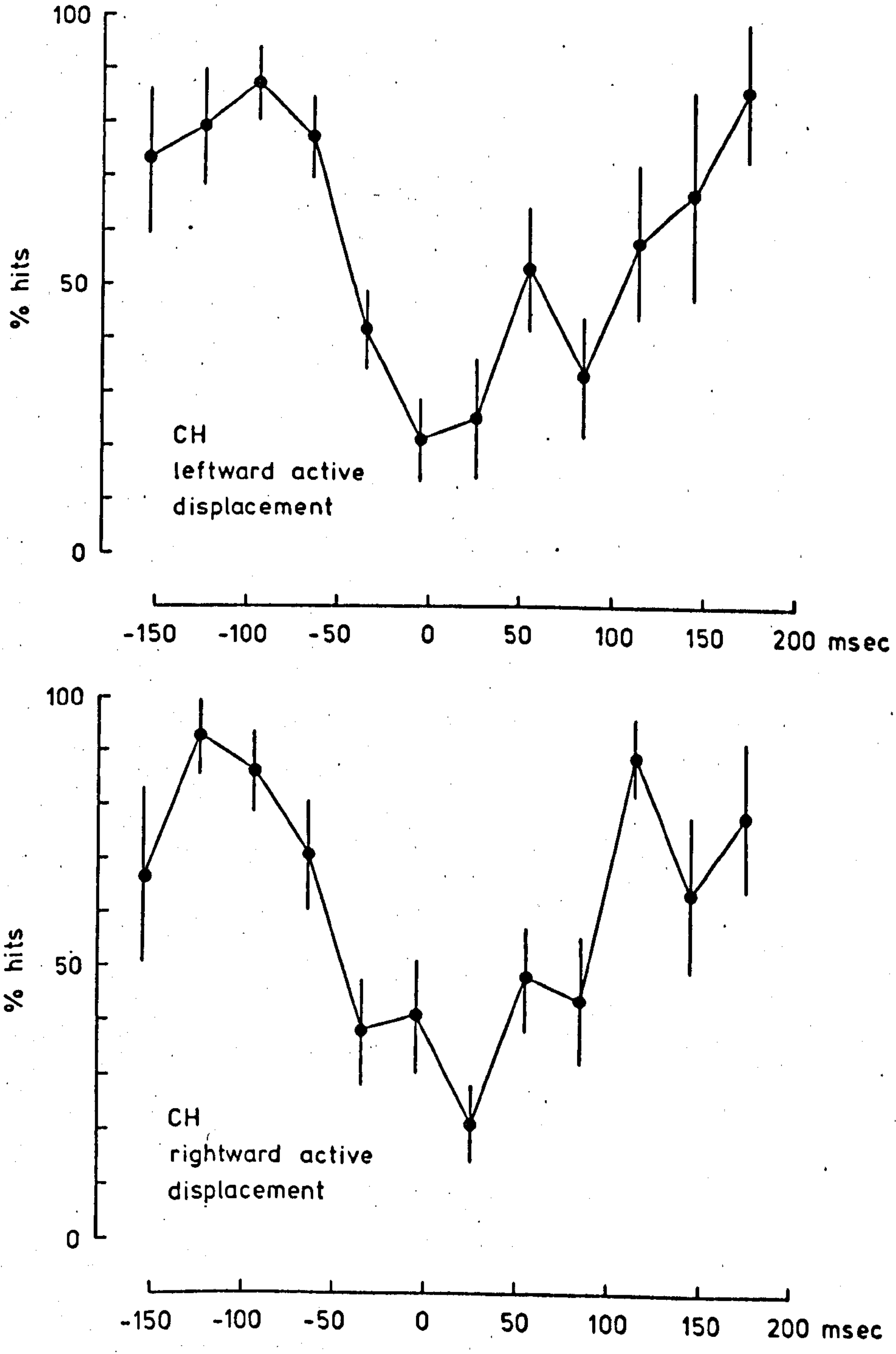


Fig. A1.5b Detectability of a flash as a function of the time of the flash relative to the onset of an active image displacement. Subject CH. Scotopic luminance level.

test flash was produced by active image displacement than by passive image displacement. With RSM, the experiment was conducted at a photopic luminance level; with CH at a scotopic level. The dotted line in Fig A1.4 shows that reducing the extent of the active displacement to $4\frac{1}{2}$ degrees (the same as that of the passive displacement) did not result in an effect similar to that of the passive displacement. Thus the difference between the effects of active and passive image displacement, in the main series of experiments, cannot be attributed to the different size of the displacements. The same control with subject CH gave similar results.

The greater detectability of the flash after compared with before leftward passive image displacements for subject RSM is difficult to account for with certainty. The same effect was shown by SJJ, but not by CH, at least not to anything like the same extent. Possibly the effect was the compounded result of non-optimal placement of the subject's eye in the apparatus, and a slight variation of the intensity of the flash with the angular position of the 'ganzfeld'. The latter effect would have arisen because at different angular positions of the apparatus (or eye) the light from the test flash impinged on the partially reflecting mirror at slightly different angles. It was not clear, however, when calculations of the size of this effect and its sign were made that this effect alone could account for the anomaly in the data.

A1.4 Conclusions

These experiments showed that in this ping-pong ball apparatus saccadic eye movement was associated with a larger elevation of threshold than that produced by pseudo-saccadic rotations of the apparatus about the centre of rotation of the eye. The design of these experiments was subject to the weakness that in most of the experiments the effect of $4\frac{1}{2}$ degrees passive image displacements were compared with the effect of 9 degrees active image displacements. Controls with $4\frac{1}{2}$ degrees active image displacements showed, however, that $4\frac{1}{2}$ degrees and 9 degrees saccades produced similar effects on the detectability of a test flash, and thus the difference between the effects of active and passive image displacements in the main series of experiments cannot be attributed to the different size of the active and passive displacements in those experiments.

There was, however, another difference between the active and passive image displacements, namely their speed. The mechanics of the apparatus were such that the passive image displacements were too slow by a factor of two. Thus there was room for doubt as to whether the low speed of the passive image displacement was not the cause of the small threshold elevation associated with passive displacement.

The apparatus was accordingly completely re-designed and rebuilt, firstly to avoid the image of the flash rotating through double the angle of the 'ganzfeld' rotation, and secondly to make the angular velocities of active and passive image displacements match exactly. The rebuilt apparatus and the experiments performed with it are described in chapter five.

APPENDIX TWO

Electronic flashguns

A device was required which would produce unblurred flashed stimuli on the saccadically moving retina. Since the resolution of the human visual system is of the order of one minute of arc, and the peak velocity (v) of, for example, a ten degree saccade is about 450 degrees/sec, the duration of the flash (d) should be no more than 40 microsec to completely avoid blurring, since:

$d = r/v$ when blurring is equal to resolution

i.e. $d = \frac{1/60}{450} = 40 \times 10^{-6}$ sec.

It was necessary to be able to vary the energy of the flash over a range of one log unit, preferably by means of a voltage-control which could be computer-driven.

This device was to be capable of producing flashes at a rate of 0.5 to 1.0 Hz without decrease of flash energy.

A2.1 Computer electronic flashguns

D. P. Andrews suggested that a 'computer electronic flashgun' might meet these requirements. This is a device used to produce accurately exposed flash-illuminated photographs. A photo-sensor monitors the intensity of the light reflected back into the camera from the object to be photographed. The output of this photo-sensor is integrated, and when a preset level of light energy has been received the flash tube is extinguished automatically. 'Computer' flashguns thus produce flashes of variable energy by varying the duration of their flash.

Various methods can be used to modify such flashguns to make the energy of the flash controllable by an applied voltage. The most successful method used by the author was to mount a wedge-density filter in front of the photo-sensor, on the pointer of a galvanometer, so that the current of the galvanometer coil controlled the proportion of the reflected light which was received by the photo-sensor and thus the light energy emitted before the flash tube was extinguished.

This and other methods are described below in order of their development.

All but the most expensive computer flashguns work in the following manner. When the flash tube is triggered, the light reflected back onto a phototransistor produces charge at a rate proportional to the intensity of the light received. This charges a capacitor. When the voltage on this capacitor reaches a given level, via a chain of intermediaries (unijunction transistor, silicon-controlled rectifier and autotransformer), a trigger voltage is applied to an internal 'quench' tube, of much lower impedance than the flash tube and connected in parallel with it. When the quench tube is triggered, it empties the main capacitor of the flashgun almost instantaneously, and the flash tube is extinguished.

The most expensive flashguns (such as the Rollei E36 RE) extinguish the flash tube by disconnecting it from the main capacitor. This makes possible higher flash repetition rates since there is no wastage of energy in a quench tube. Such flashguns were, however, outside the author's budget.

A2.2 Mark 1 flashgun

Fig. A2.1 shows the circuit of the first flashgun used by the author (a Reliant Variant 416C, supplied by Photopia Ltd.). The only feature of the circuit which is likely to puzzle the reader is the source of the power supply to the computer section of the circuit. There is no permanent power supply to this section of the circuit, only a transient supply which is created by triggering the flash tube, and which disappears after a few milliseconds. When the flash tube is triggered, the voltage at point D falls, pulling down the voltage at C. R_{14} and C_{14} smooth this voltage step, and the zener diode Z_{12} clamps the excursion on E at -10 volts.

Several modifications were made to the manufacturer's circuit. The manufacturer's manual trigger was replaced by a voltage-controlled trigger. The main capacitor was reduced from 400 microfarads to 100 microfarads, and zener clamping at 268 volts introduced on the main capacitor. The latter changes allowed a complete recharge of the main capacitor in 2.5 seconds rather than the 10 seconds required with the original circuit. It was not useful to decrease further the main capacitor since this would have restricted the range of flash energy variation. The reason is that with a smaller main capacitor the flash is so short that even with a modified quench-timing-circuit, the quench cannot be made to occur sufficiently quickly to permit a full range of flash energy variation. (Would-be constructors should note, by the way, that electronic flashguns require non-standard electrolytic capacitors which release all their energy rapidly, rather than in two stages as do ordinary electrolytics.)

R_{14} was reduced from 4.7K to 1.8K, to decrease the time required for the power supply to the computer section to become established, and thus make possible briefer flashes than the standard circuit will produce.

Two methods of controlling the flash energy were used with the Mark 1 flashgun. Initially the phototransistor was replaced with a p-channel FET (2N 3820), used as a voltage-controlled resistance. Although this method was initially promising, it was never very reliable, and was abandoned.

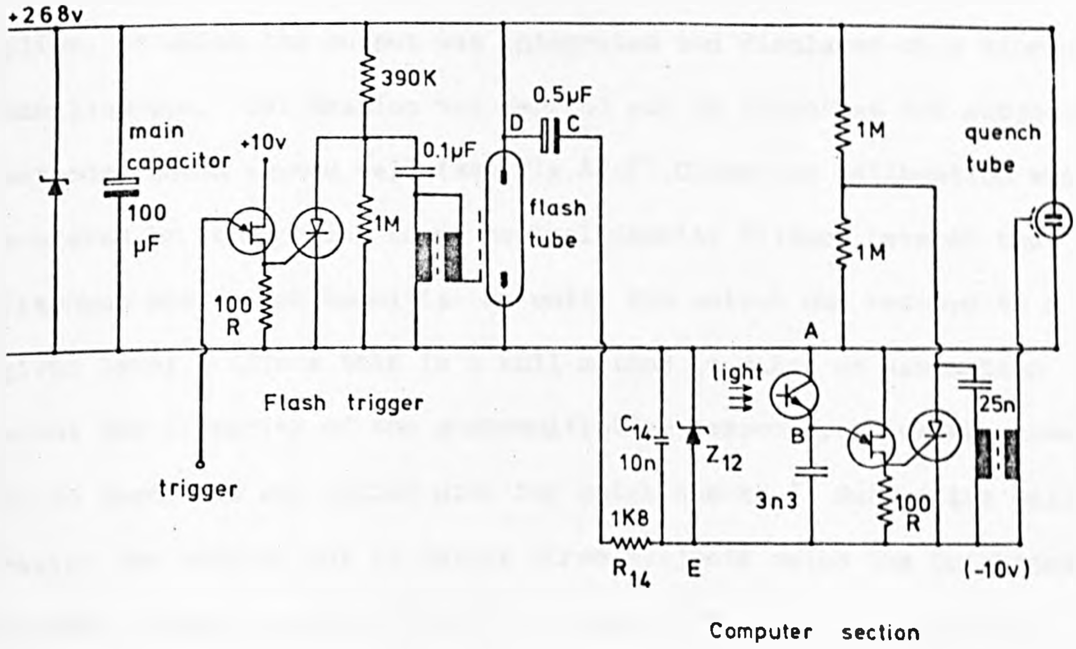


Fig. A2.1 Circuit of the Mark 1 flashgun. See text for explanation of operation.

The second method was to replace the phototransistor by an array of resistors, any one of which could be selected by means of a voltage-controlled gate. This method worked well, and was used until the flashgun wore out.

Several experiments were performed using a hand-operated control which was simply a potentiometer connected in place of the phototransistor.

The performance of the flashgun was monitored with a photomultiplier, of which the output was integrated and displayed on a storage oscilloscope. Calibration was carried out by objective and subjective methods, which agreed well (see Fig.A2.2).Objective calibration was achieved by interposing known neutral density filters between the flashgun and the photomultiplier until the output was reduced to a given level. (Since this is a null method it makes no assumption about the linearity of the photomultiplier response, which was however quite good, and was relied upon for quick checks.) Subjective calibration was carried out by having three subjects match the brightness of the flashgun pulse to that of a flash of fixed intensity, by manipulating a filter wheel placed in front of the flashgun.

The duration of the longest flash used was 60 microseconds (90% of energy was emitted in this time).

In the course of time the Mark 1 flashgun became unreliable, and this continued to be so even when the flash and quench tubes were replaced. Eventually the flashgun had to be discarded. It should be pointed out that the flashgun was far from new when acquired, and so this behaviour is not representative of the performance to be expected from a new flashgun of this type.

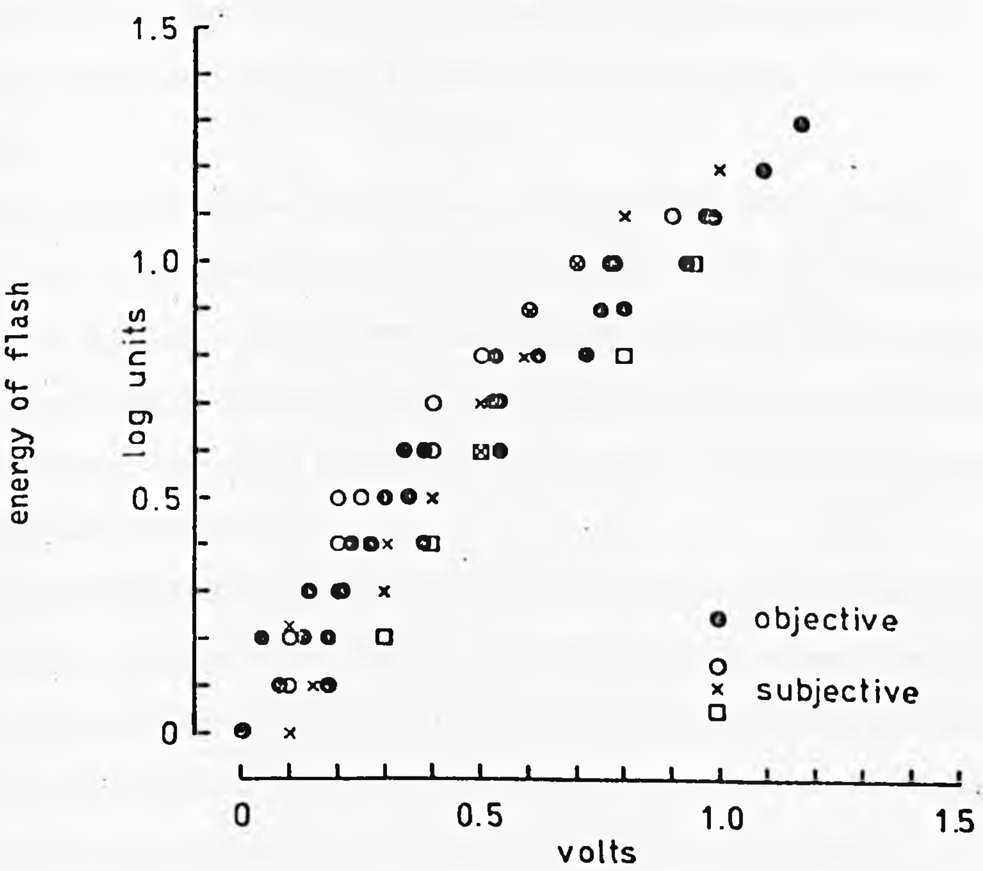


Fig. A2.2 Calibration of Mark 1 flashgun voltage-control of flash energy. (See text.)

A2.3 Mark 2 flashgun

This was a Sunpak Auto 22 model flashgun. No alterations to the circuitry were made except to connect the same voltage-operated trigger used above, and to replace the built-in H.T. power supply by an external 250 volt stabilised power supply. (At first the flashgun was run off a 6 volt accumulator connected in place of the standard dry cells. The transformer in the inverter circuit which generated the H.T. voltage was, however, incapable of coping with the heat dissipation involved in running continuously for several hours at a time, and broke down.)Fig. A2.3 shows the modified circuit of the flashgun.

The flash energy was controlled by the neutral density wedge method mentioned above (see Fig. A2.3).Care must be taken to ensure an adequate light-tight seal between the flashgun and the filter wedge housing, and the galvanometer must have adequate damping to settle in the inter-trial period (3 seconds in this case). Otherwise the method is simple and trouble-free.

The galvanometer coil was driven (via a resistor) from one of the analogue outputs of the PDP-8. The relationship between the current in the galvanometer coil and the flash energy was nearly logarithmic. (See Fig. A2.3.)Fig. A2.4 shows that the flashes produced by the flashgun were of consistent energy (variation less than 0.1 log units).

The duration of the longest flash used was 120 microseconds (for 90% of the flash energy to be emitted). Whilst this performance was someway from achieving the target of 40 microseconds maximum flash duration, it was considerably better than could be achieved using fast-phosphor fluorescent tubes, and even in 120 microseconds the degree of blurring of most forms of stimuli presented to the saccadically-moving retina was negligible.

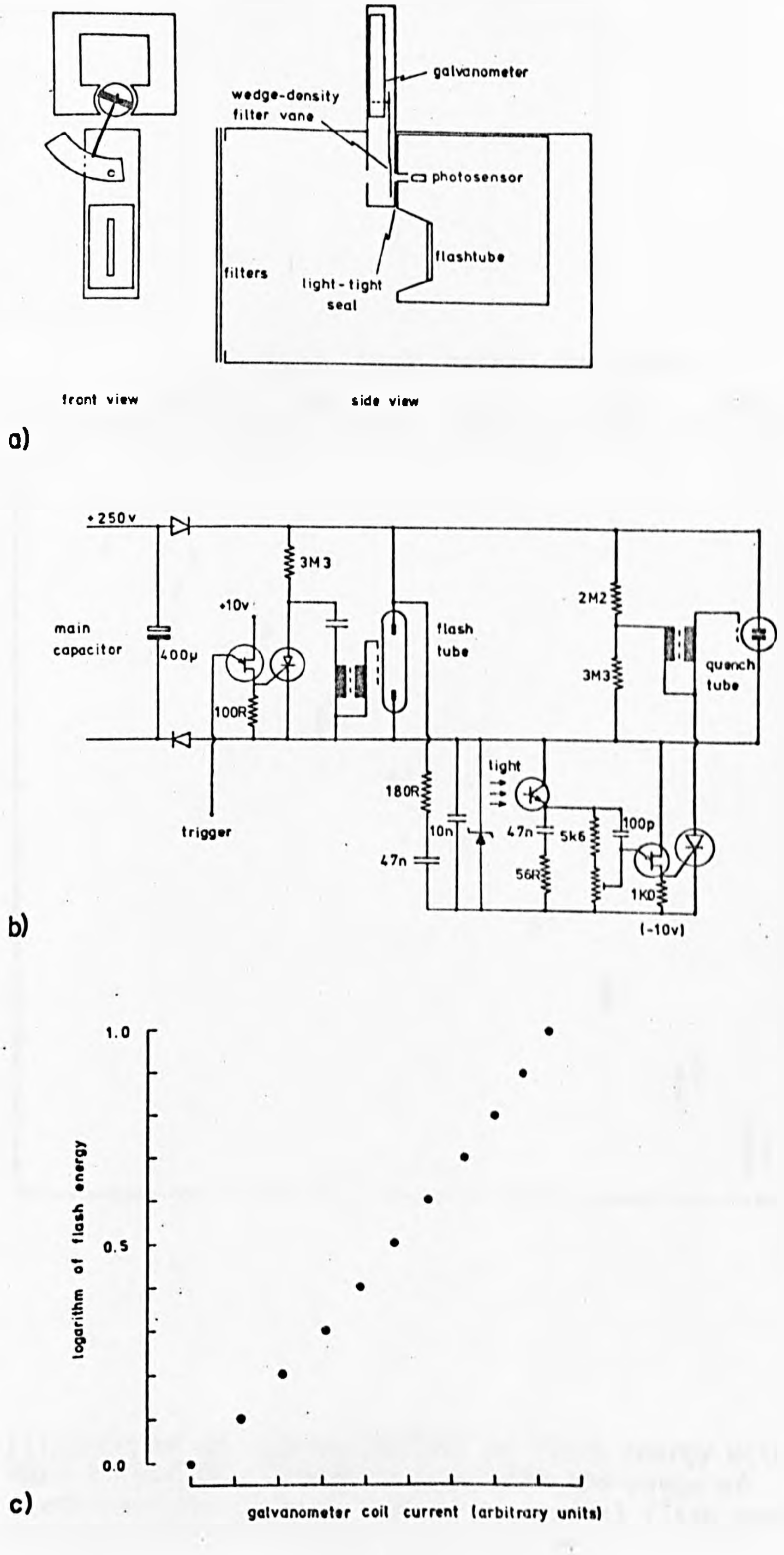


Fig. A2.3 a) Mark 2 flashgun.
b) Circuit of Mark 2 flashgun.
c) Calibration curve for flash energy control of Mark 2 flashgun.

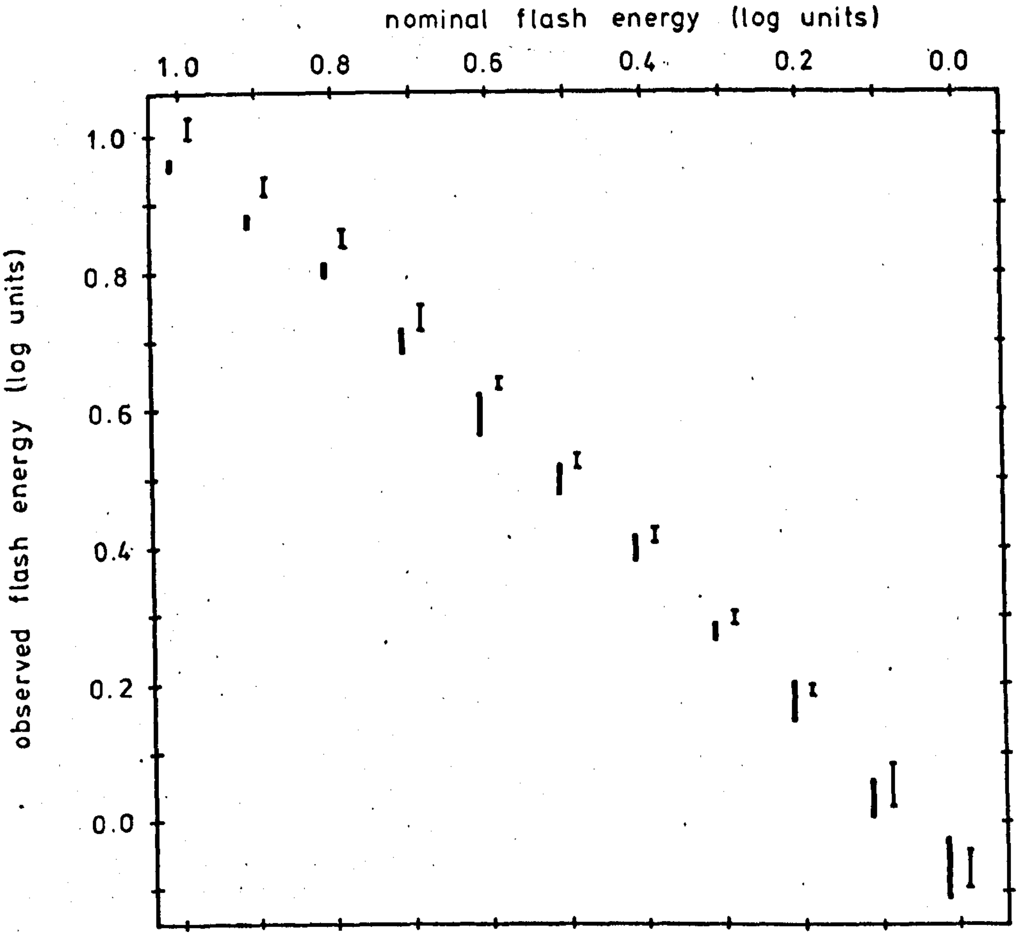


Fig. A2.4 Illustration of reproducibility of flash energy with the Mark 2 flashgun. Vertical bars show the range of flash energies at each setting of nominal flash energy, for two different calibration sessions.

The main advantage of the wedge-density filter method of control of flash energy over the other methods described above is that it preserves the optical feedback loop between flash tube and quench tube, and so eliminates variability of the flashgun output due to fluctuations of the flash-tube output.

The other great advantage of flashguns over, for example, fast phosphor fluorescent tubes, is the enormously greater energy available from flashguns.

APPENDIX THREE

Recent literature concerning possible physiological substrates for alteration of visual sensitivity associated with saccadic eye movements

A3.1 Summary of reports

Singer and Bedworth (1974) studied transmission through the lateral geniculate nucleus during and after spontaneous saccades and saccades induced by mesencepahlic reticular formation stimulation, in the *encéphale isolé* cat. They showed that in both cases saccades were followed 50-100 msec after their onset by field potentials in the LGN and visual cortex, and that the cortical evoked response to optic tract stimulation was enhanced when the optic tract shocks were given in the above interval after a saccade. Corresponding facilitatory effects on some neurones in the LGN were also observed. The experiments were performed with the eyes of the cats occluded by opaque contact lenses.

Magnin, Jeannerod and Putkonen (1974) reported in full the experiments briefly reported in Putkonen et al. (1973). They found changes in the firing rate of neurones in both the dorsal and ventral divisions of the lateral geniculate nucleus of the awake cat which were related to the fast phases of vestibular nystagmus in darkness. The most frequently encountered kind of fast-phase-related modulation of activity was an increase in firing about 250 msec after the onset of the fast phase, which was closely related to fast phases in one direction only.

Duffy and Burchfiel (1975) studied the activity of neurones in the lateral geniculate nucleus and the visual cortex of the *encéphale isolé* monkey in total darkness. In contrast to the previous results reported by Duffy's group (Corazza and Lombroso, 1971; Corazza, Lombroso and Duffy, 1972) they found that the activity of lateral geniculate neurones was not altered in association with saccadic eye movement. It is disturbing to find that the authors of the paper under discussion do not even feel that it was necessary to refer to the discrepancy between their earlier results and the present ones, let alone account for the discrepancy. Duffy and Burchfiel went on to report the interesting finding that 25 out of 33 cells studied in the striate cortex displayed a period of inhibition related to spontaneous saccades. This saccadic eye movement related inhibition was, they say, direction specific: for each cell there was one quadrant of eye movement direction for which inhibition was most prominent. The authors point out that individual eye movements, even within the same quadrant, were not associated with a consistent degree of inhibition, and averaging was necessary to clearly demonstrate the effect. Eye movements occurring in association with blinks or immediately after alerting stimuli were excluded from analysis.

Bartlett, Doty, Lee and Sakakura (1976) found a small decrease (up to 20%) in the amplitude of the optic radiation potential evoked by optic tract stimulation in the awake monkey in darkness. This effect was consistently greater in the magnocellular component of the response than in the parvocellular component. The 'suppression' was often followed by a 5-10% facilitation about 100 msec after the detection of the saccade.

A3.2 Discussion

As Singer and Bedworth point out, the facilitatory rather than inhibitory sense of the effect they reported implies that the effect cannot be the cause of 'saccadic suppression'.

The long latency of the effects reported by Magnin et al. suggests that these effects have little to do with modification of sensitivity to stimuli presented during saccadic eye movements. Also, the effects were demonstrated with the fast phases of nystagmus induced by rotating the animal. It is far from clear that one would expect the same effect with spontaneous saccades made in the absence of a vestibular stimulus.

Interesting though the results of Duffy and Burchfiel are, more evidence is needed before one can be sure that the effect reported is genuine, particular since Wurtz (1969) in extensive investigations of the responsiveness of striate cortex neurones in awake monkeys to eye movements and displacements of the retinal image did not find such effects.

Wurtz's negative results also call into question the meaning of the small decreases in geniculo-striate pathway excitability reported by Doty's group to occur in association with saccadic eye movement. Bartlett et al. explicitly point out that alterations in attentive state produce changes of excitability 'as large and often larger than any seen in relation to saccadic eye movements'.

Thus the conclusions of the review given in chapter two remain substantially valid.

APPENDIX FOUR

Attempt to determine several thresholds simultaneously by the PEST method

A 4.1 Introduction

The problem was to determine the thresholds for perception of a test flash under three conditions: with a peripheral masking stimulus 100 msec after, 40 msec before and 150 msec before the test flash (see chapter six). In order to avoid the possibility of drift in the subject's criterion biassing the results, the thresholds were determined simultaneously in an experiment in which all three stimulus conditions were randomly interspersed.

PEST (Parameter Estimation by Sequential Testing) is the name given by its inventors, Taylor and Creelman (1967), to an adaptive method for determining thresholds. In PEST experiments, the stimulus level is held constant until the detectability of the stimulus is found to be significantly greater or smaller than 75% (in a two-epoch forced choice experiment), or 50% (in a 'yes-no' paradigm). The stimulus level is then altered in the direction which would be expected to produce a detection level closer to 75% (or 50%). The size of the step in the stimulus level is given by an algorithm which is, according to Taylor and Creelman, a highly efficient means of converging on the threshold. A threshold is reckoned to be determined when the step size called for falls below an arbitrarily chosen level: the smaller this is the more precise the threshold determination, but the longer the experiment takes.

The algorithm recommended by Taylor and Creelman is:-

1. On every reversal of step direction, halve the step size.

2. The second step in a given direction, if called for, is the same size as the first.
3. The fourth and subsequent steps in a given direction are each double their predecessor (except that, since large steps may be disturbing to a human observer, an upper limit is set on step size).
4. Whether a third successive step in a given direction is the same as or double the second depends on the sequence of steps leading to the most recent reversal. If the step immediately preceding that reversal resulted from a doubling, then the third step is not doubled, while if the step leading to the most recent reversal was not the result of doubling, then the third step is double the second.

The fourth rule is necessary to prevent oscillatory instability.

The calculation of when the detectability of a stimulus is significantly different from 75% is extremely simple, and is due to Wald (1947). A running count is made of the number of trials, N, and the number of correct responses, C, at the current level of the stimulus. After each trial, C is compared with the expected number of correct responses $E = 0.75 \times N$. Only when C deviates from E by a preselected small integer, W (the Wald parameter), is the detectability of the stimulus judged to be significantly different from 75%. In the experiments repeated here $W = 2$.

A4.2 Method

The apparatus used was the same as in the experiments described in chapter six, except that the duration of the flash was varied by means of a voltage-controlled monostable connected to one of the PDP-8 Digital-to-Analogue Converter outputs. Over the range of durations used, the energy of the flash was proportional to its duration, and since the duration of the test flash was never greater than 20 msec. the detectability of the flash was, according to Bloch's law, dependent only on its energy (or duration).

A programme was written in FOCAL, a high-level computer 'language', to direct the PDP-8 computer to present the three kinds of stimuli in a randomly interspersed series, and to vary the test flash energy (independently for three conditions) in the manner prescribed by the PEST algorithm. Fig. A4.1is a block diagram of the 'PEST' computer program.

A4.3 Results

The results of two runs, one with each subject, are shown in Figs. A4.2 & A4.3. The main feature of interest, and the reason for reporting the results of these experiments at all, is the drift and 'hysteresis' evident in the subjects'performance. By 'hysteresis' is meant the phenomenon that the subjects give more correct responses when a given stimulus level is attained by increasing the stimulus energy than when the same level is reached by decreasing the stimulus energy. (See Figs. A4.2b & A4.3c). The subjects' performance also sometimes shows evidence of drift (see Fig. A4.3a).

A4.4 Discussion

It seems likely that the reason for both the hysteresis and the drift of performance sometimes evident in these 'PEST' experiments is the long series of stimuli of equal or nearly equal energy which not infrequently occurred in the runs. During such a long series it is only to be expected that the subject's response criterion would shift somewhat.

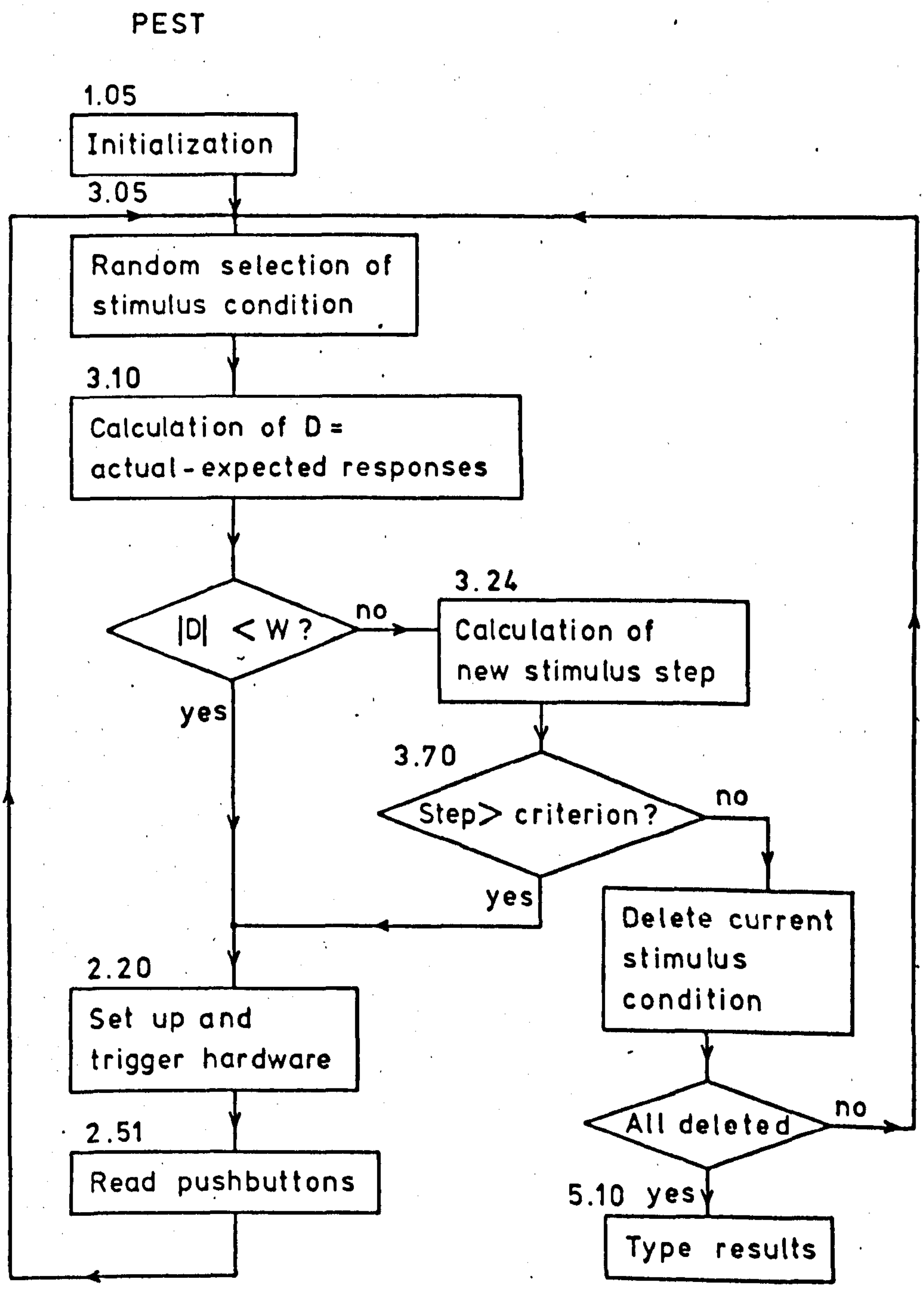


Fig. A4.1 Flowchart of the computer program used to control the PEST experiments.

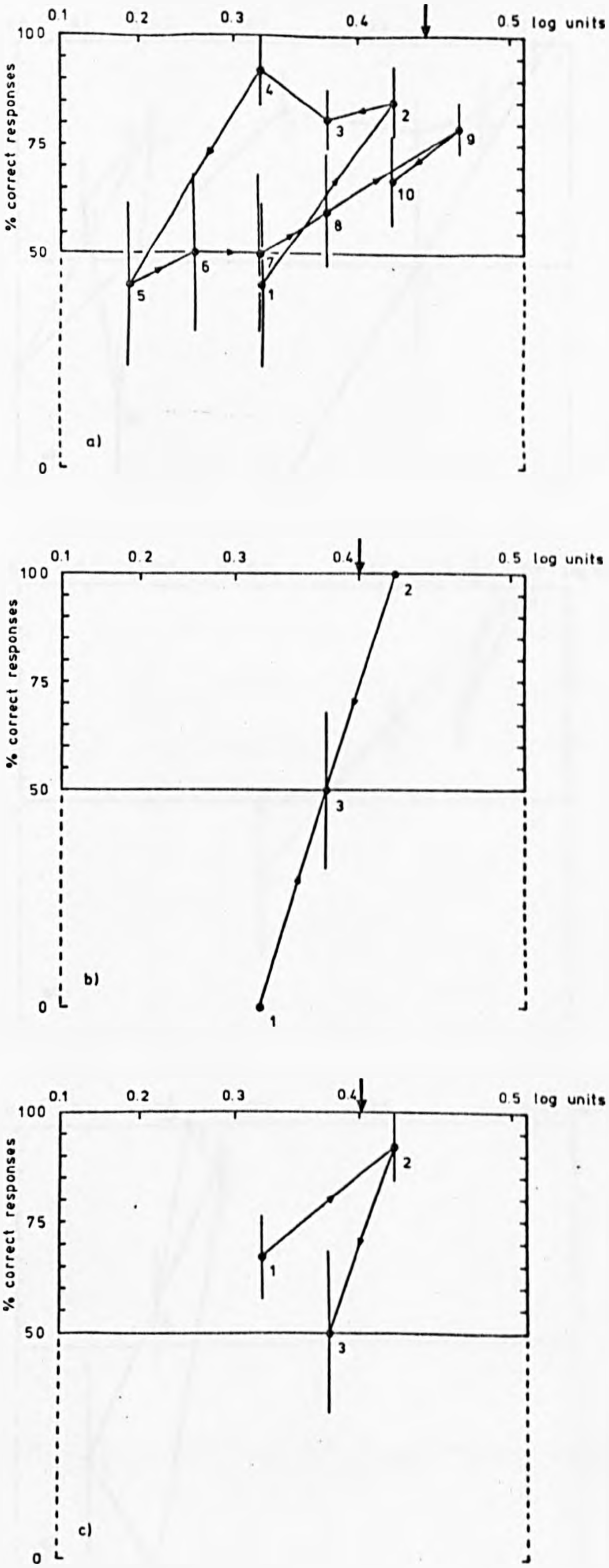


Fig. A4.2 Results of a PEST run with subject SJJ. The arrows indicate the thresholds as estimated by PEST. See text.

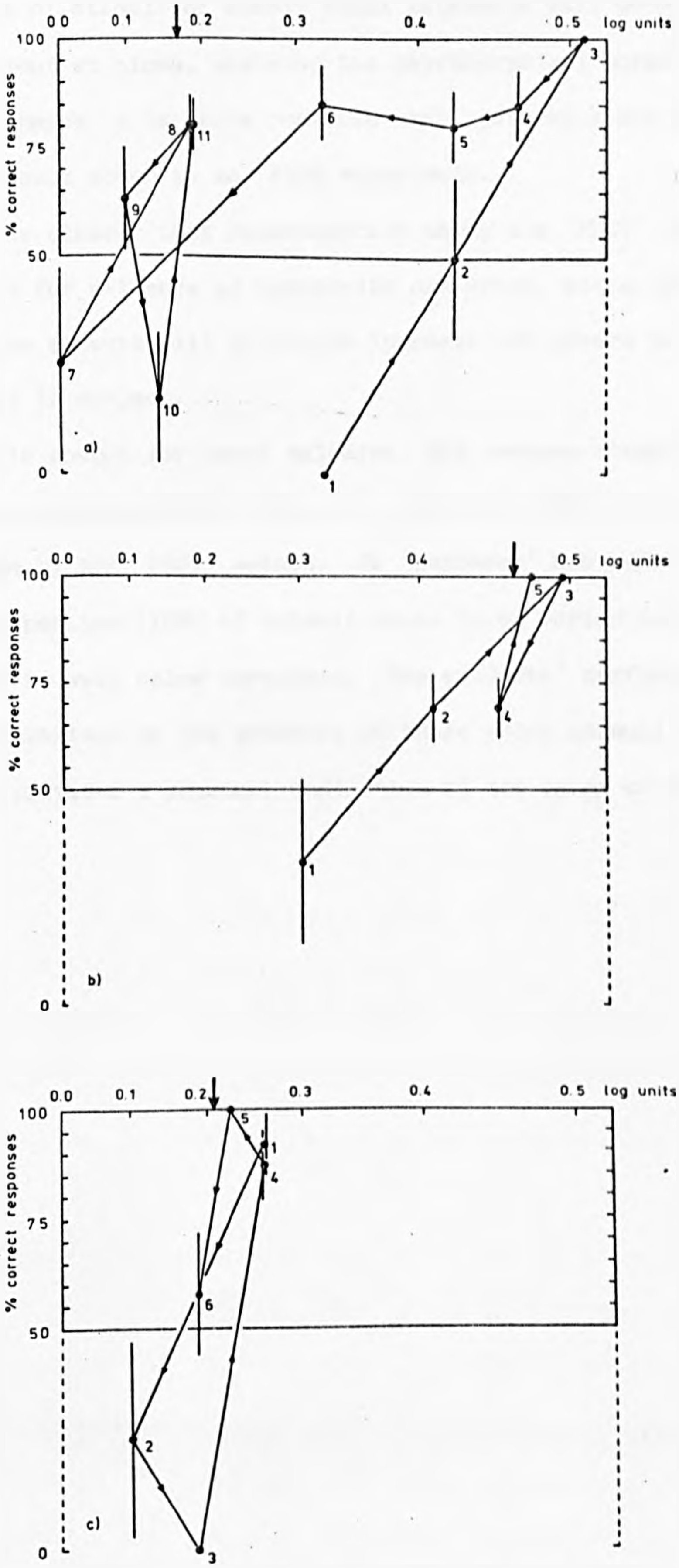


Fig. A4.3 Results of a PEST run with subject JJ. The arrows indicate the thresholds as estimated by PEST. See text.

Long series of stimuli of nearly equal intensity will occur in any PEST experiment at times, whatever the psychophysical threshold being studied. Hence it is quite possible that hysteresis and drift in performance could occur in any PEST experiment.

The moral is clearly that experimenters using the 'PEST' method should watch out for evidence of hysteresis and drift, since the presence of these effects will of course increase the errors to which the final result is subject.

If a cure is sought for these maladies, the readers attention is directed to the technique found useful by G.F. Pick (1973) in auditory experiments made by the PEST method. He 'peppered' his PEST run with a small proportion (10%) of stimuli whose level varied randomly from well above to well below threshold. The subjects' performance seemed to be stabilised by the presence of these extra stimuli which on the average provided a constant indication of the range of stimulus variation.

APPENDIX FIVE

Critical analysis of the data presented by Jeannerod and Chouvet

Jeannerod and Chouvet (1973) recorded the gross potentials evoked in the lateral geniculate nucleus, optic tract and visual cortex of paralysed cats by low intensity flashes either immediately preceded or followed by sudden shifts of a pattern adjacent to but not contiguous with the flash. They found that the potentials evoked by a 5 degree diameter flash were diminished when the flash occurred some 50 msec or so after the sudden pattern displacement. Their claim was that this result 'confirms the importance of a purely visual factor in saccadic suppression'. There are, however, several features of Jeannerod and Chouvet's data which make it difficult for the critical reader to admit the validity of this claim.

The main difficulty with their argument is that, as they are careful to mention in their abstract, the potential induced by the displacement was reduced when the flash occurred 50 msec before the displacement. Since they did not claim, and there was no question of their claiming, that this diminution of the _displacement_ potential was related to a decreased visibility or salience of the displacement, it is not at all clear that the diminution of the flash potential when the displacement preceded the flash can be regarded as confirming the psychophysical evidence that saccadic suppression is due to visual rather than oculomotor factors.

Another criticism of the argument in this paper is that the effects reported were not observed when the speed of the displacement was less than 200 or 300 degrees per second. (The amplitude of the displacement was $3\frac{1}{2}$ degrees.) The maximum velocity of cat saccades of this amplitude is, however, only of the order of 50 degrees per second (Stryker and Blakemore, 1972). Questioned on this point Jeannerod altered his statement in the paper and provided data (personal communication) showing a small interaction between flash and displacement at displacement velocities of 50 degrees per second. (The flash potential was reduced by up to 30%.)

Another limitation of the data was that there were no control recordings showing the effects on the flash potential of a 0.5 log unit decrease of flash intensity. (The intensity of the flash is not stated, but would appear to have been about 1 log unit above human threshold at the background level used.) Also there was no investigation of the effect on the interaction of altering the angular separation between the flash and the displaced pattern, nor was the magnitude of this separation given.

A further oddity of the paper was that although cortical evoked potentials were clearly recorded, there was no report of the interaction between flash and displacement potentials at the cortical level, which one would expect if anything to be more closely related to perceptual phenomena than lateral geniculate or optic tract potentials.

Further analysis of Jeannerod and Chouvet's data

In order to be able to examine further the main feature of Jeannerod and Chouvet's data, i.e. the form of the interaction between the flash and the displacement potential, the data given in their Fig. 6 were digitalised using an IBM 'D-Mac'. This device outputs on papertape numbers representing successive X- and Y-coordinates of crossed-hairs, the operator determining by pressing a button the points at which the position of the crossed-hairs is sensed.

In order to obtain an accurate representation of the graphs with the minimum number of samples, the sampling density was approximately matched to the curvature of the part of the graph being digitalised, regions of high curvature requiring many samples, and regions of low curvature few. This procedure provided sample data with no common set of X-coordinates. In order to obtain data with common X-coordinates, which could be arithmetically combined with one another, the sample data were linearly interpolated, using a Focal program ('Inter') written for the purpose. A second program ('Oplot') then took the interpolated data, and performed a point-by-point linear combination of the Y-coordinates of the data sets, and plotted the result on an x-y plotter. By using this program twice, one could assess the adequacy with which any particular combination of flash and displacement potentials could simulate the potential evoked by the two stimuli together. If $J(t)$ was the potential evoked by both the flash and the displacement together, and $F(t)$ and $D(t-t_o)$ were the potentials evoked by the flash and the displacement respectively, then the first pass of Oplot produced

$$J(t) - B.D(t-t_o),$$

and the second pass produced

$$J(t) - B.D(t-t_o) - A.F(t),$$

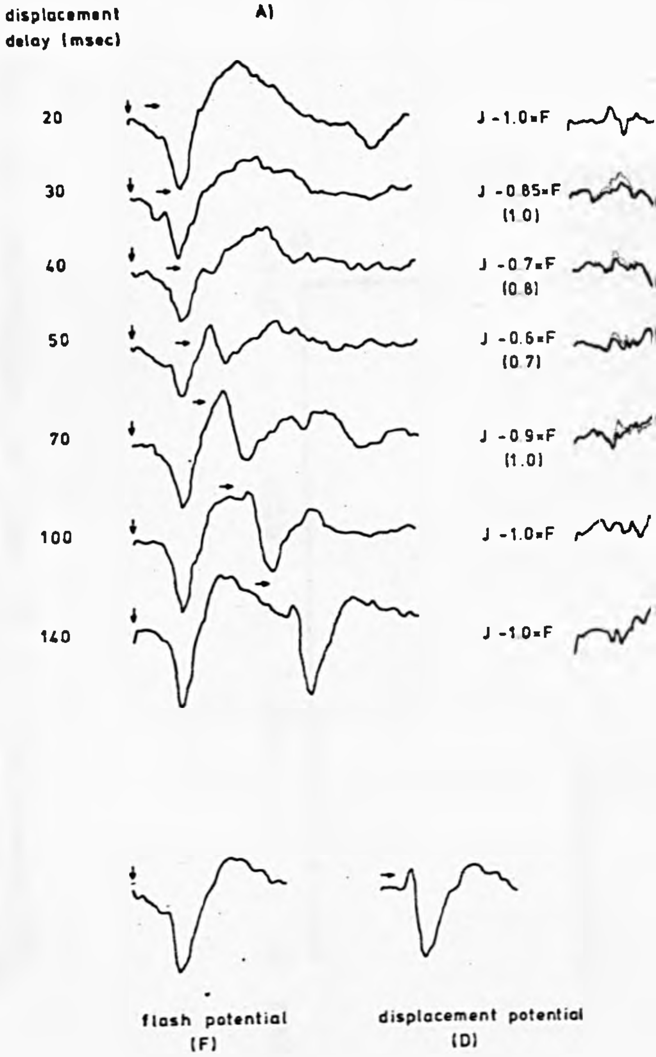
where A and B were coefficients chosen by the operator and t_o represented the time interval between the flash and the displacement. By making several runs with various values of A and B, the optimal values of A and B for the combination of flash and displacement potentials to match the potential evoked by the joint stimuli could be determined. In Fig. A5.1 the lefthand column shows Jeannerod and Chouvet's original Fig. 6. The centre column shows the results of the first pass of Oplot, using the optimum values of B. The dotted curves show the results obtained with values of B (given in brackets) slightly different from optimal. The righthand column shows the results of the second pass of Oplot.

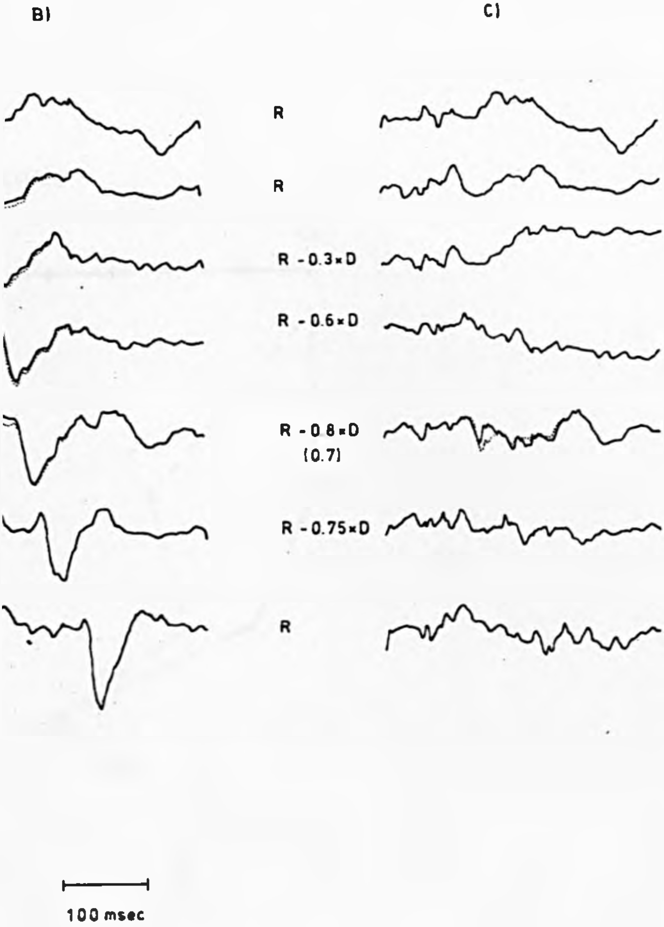
Fig. A5.1 A) Jeannerod and Chouvet's Fig. 6. The potential evoked by both a flash and a displacement, as a function of the time between the flash and the displacement. Downward arrows show the flash epoch, horizontal arrows show the displacement epoch.

B) The residual waveform obtained after subtracting the indicated multiple of the flash waveform from the waveform shown in column A), as a function of time between the flash and the displacement.

C) Residual waveform obtained after further subtracting the indicated multiple of the displacement waveform (offset by the appropriate amount) from the residual waveform (R) in column B), as a function of time between the flash and the displacement.

The dotted waveforms show some sample slightly off-optimum results. The solid lines always show the results obtained using the optimum parameters as multipliers.


displacement delay (msec)
A)
20
30
40
50
70
100
140
J -1.0×F
J -0.85×F
(1.0)
J -0.7×F
(0.8)
J -0.6×F
(0.7)
J -0.9×F
(1.0)
J -1.0×F
J -1.0×F
flash potential
(F)
displacement potential
(D)


B)
C)
R
R
R - 0.3×D
R - 0.6×D
R - 0.8×D
(0.7)
R - 0.75×D
R
100 msec

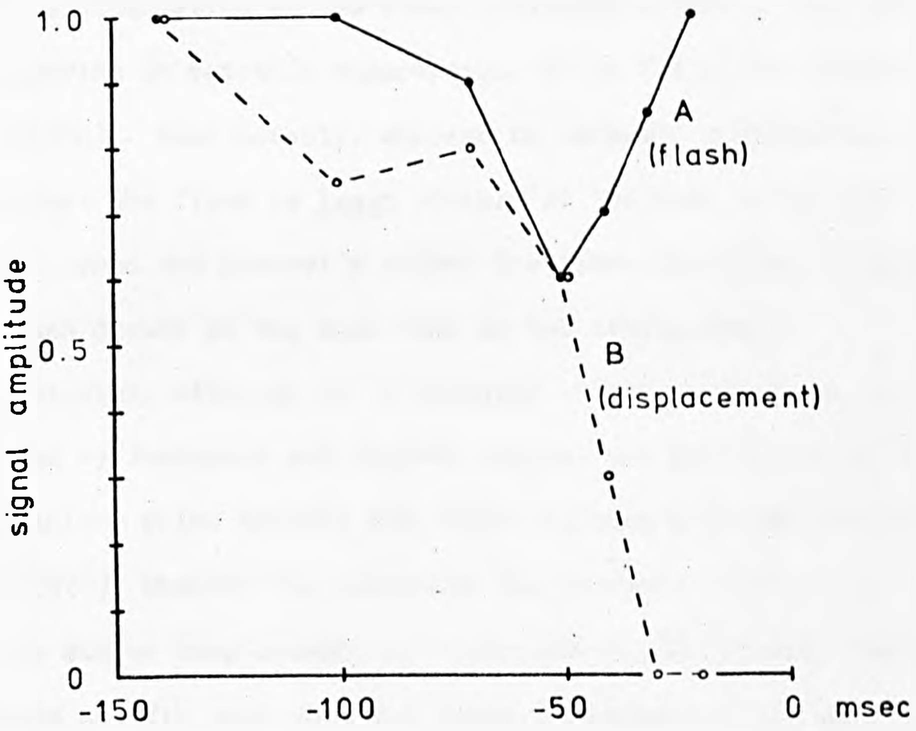


Fig. A5.2 Multipliers of flash (A) and displacement (B) signals in the linear combination of flash and displacement signals which was estimated to best match the waveform of the potential evoked by both the stimuli presented together, as a function of the time of the flash relative to the displacement onset. See text.

Fig.A5.2 shows the values of A and B as a function of t_o, the time interval between the flash and the displacement.

It should be noted that it is not possible to trade A and B, since even at the smallest t_o used (20 msec), the contributions of the flash and displacement potentials to the joint response are clearly distinguishable in latency.

It can be seen from FigA5.2 that when the flash precedes the displacement, the attenuation of the displacement potential is much greater than the attenuation of the flash potential. Furthermore, the time-course of the attenuation of the flash potential is not at all similar to that occurring in saccadic suppression, or in the effect reported by MacKay (1970). Most notably, whereas in saccadic suppression and MacKay's effect the flash is <u>least</u> visible at the time of the displacement, in Jeannerod and Chouvet's effect the flash potential is <u>unaffected</u> when the flash occurs at the same time as the displacement.

In conclusion, although it is possible that some features of the data reported by Jeannerod and Chouvet reflect the activities of the neural mechanisms which mediate the effect demonstrated psychophysically by MacKay (1970), whereby the threshold for perception of a flash is altered by a sudden displacement of a non-contiguous pattern, the data as a whole do not fit well with the known parameters of the psychophysical effect, and particularly in view of the large alterations of the displacement potential observed, could well be due to some non-specific mechanism. Their case is not proven.

APPENDIX SIX

Temporal interaction between human voluntary saccades and rapid phases of optokinetic nystagmus

The experiments on this subject which were briefly reported in the article reprinted below were made in an interlude between the experiments described in the main body of this thesis. Time was not available for the more extensive series of experiments suggested in the last paragraph of the paper.

After submitting the manuscript of the above paper to the publisher, the author discovered a brief publication by Cohen and Takemori (1973). They showed that a cerebellar mechanism is involved in the suppression of vestibular and optokinetic afternystagmus by visual signals. In normal monkeys, the slow phase velocity of caloric nystagmus is decreased by 50% in illuminated surroundings, and optokinetic afternystagmus is abolished. After bilateral lesions of the flocculus of the cerebellum, however, there is little or no suppression of caloric and optokinetic afternystagmus in illuminated surroundings.

It seems not unreasonable to suggest that the floccular mechanism discovered by Cohen and Takemore may be responsible for the short latency inhibition of optokinetic nystagmus postulated by the author to explain the results of his experiments. (See the accompanying reprint.)

APPENDIX SEVEN

A device for demonstrating the involuntary nature of a saccadic eye movement

It is often asserted (Alpern, 1969; Robinson, 1968; Becker and Fuchs, 1969) that the timecourse of a saccadic eye movement of a given amplitude is not open to voluntary control. This is consistent with the function of a saccadic eye movement which is presumably to bring the image of a possibly significant object onto the fovea as quickly as possible, for detailed examination. There does not appear, however, to have been any experimental test of whether in fact it is impossible to modify the timecourse of a saccade voluntarily. It is well known, however, that saccades are slower when subjects are drowsy (e.g. Robinson, 1968).

The apparatus represented in FigA7.1 was designed to examine directly whether saccade timecourses can or cannot be modified voluntarily. The eye position signal used was in fact the electro-oculogram, but in principle any means of continuously monitoring eye position could be used. The eye position signal was differentiated and rectified. A pulse height reader registered the peak saccade velocity. This circuit held a voltage representing this parameter for several hundred milliseconds with negligible decay. When the saccade velocity fell below some arbitrarily determined level, a gate connecting the output of the pulse height reader to the frequency modulation input of a voltage controlled oscillator was opened, and then closed again after some 150 msec or so. This oscillator fed a loudspeaker. The subject thus heard a brief alteration of the pitch of a tone each time he made a saccade. The bias control of the pulse height detector could be set so that no pitch change was induced by a normal saccade between two given points. The change of pitch associated with subsequent saccades between the same points was thus a measure of the alteration of saccade velocity achieved.

The timecourses of the saccades were also monitored on a storage oscilloscope.

Preliminary experiments with the author as subject showed that it is at least very difficult to alter saccade velocity voluntarily. No clear changes of saccade velocity were produced except on one occastion when the subject became drowsy, which produced a clear decrease of saccade velocity by about 15%. Attempts to make slow saccades always resulted in a double saccade (i.e. two saccades separated by a small interval). The subject was unaware of the discontinuity in such eye movements. (This lack of salience of a brief discontinuity in gaze shift was known to Dodge (1900).)

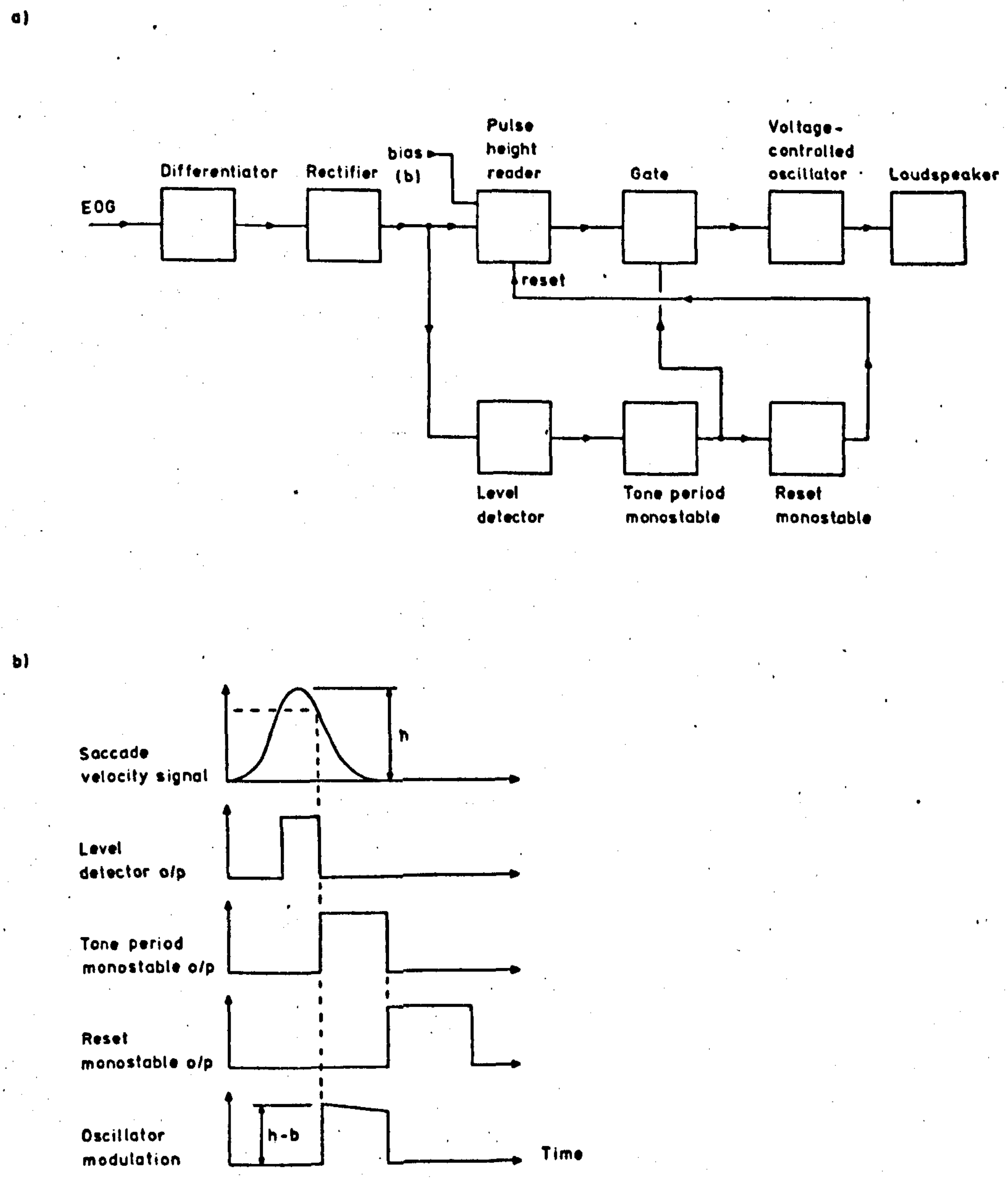


Fig. A7.1 a) Block diagram of the apparatus. The circuits were constructed using discrete components and 741 linear operational amplifiers.
b) Mode of operation of apparatus.

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