

AN INVESTIGATION
OF
SMALL EYE MOVEMENTS AND CONTOUR INTERACTION
IN
VISUAL PERCEPTION

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BY
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ABSTRACT

A series of experiments was conducted to examine situational variation in small saccadic eye movements and their relationship to contour effects in visual perception. Both the amplitude distribution and the timing of saccade onsets were found to vary from one situation to another. Interaction between contours was demonstrated over separations of just a few minutes of arc. Where perception of a target contour was relatively unlikely there was a marked shift in the distribution of saccade amplitudes. The notion of a single neural mechanism initiating all saccades and the role of small saccadic eye movements in sustained perception were considered. In addition, similarities between contour interaction and the functional organization of visual cell receptive fields were discussed.

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CHAPTER ONE

INTRODUCTION

The purpose of this thesis is to investigate the nature and function of small saccadic eye movements. The approach is essentially empirical. As considerable time was required for either the collection or the analysis of data in each study and, as there were several questions of interest to the author, a rather broad approach was chosen over an in-depth analysis of any single area. Consequently several issues are addressed and the results suggest lines of research which may be pursued to further our understanding of the mechanism and function of small saccadic eye movements.

The work reported here is addressed to the general question of the relationship among small eye movements, spatial interaction between visual contours and the perception of fine detail in a visual target. The motivation for seeking a relationship among these variables derives from at least two, essentially discrete, bodies of literature concerning the role of small 'involuntary' eye movements in visual perception and the perceptual effects of spatial interactions between visual contours.

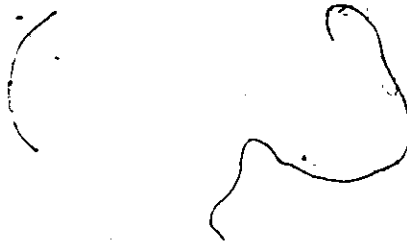
Small eye movements play a role in the sustained perception of a visual target. With abolition of the motion of the visual image relative to the retina, part or all of the image tends to alternately disappear and reappear. Fragments may be imperceptible for a substantial portion of the time that the target is available for viewing indicating that relative motion between the visual image and

the retina is essential for sustained perception of the image. Indeed, when an inexperienced observer first views a 'stabilized' retinal image, the eye tends to move about in an exaggerated fashion as though attempting to restore perception of the visual image.

A contour is essentially the interface between two areas of differing luminance and, for present purposes, may be taken as an edge. Studies of visual masking and of letter recognition provide evidence that the spatial and temporal relationships between contours affect perception of an individual contour. Given some range of separations (either spatial or temporal) between two contours, the likelihood of perceiving an individual contour may be reduced.

As both small involuntary eye movements and the spatial separation between contours affect perception of a target contour, several questions arise from a review of these literature. Typically, microsaccades have been recorded when an observer has been fixating a small stationary target. This constrained situation may elicit a different pattern of eye movements than would a less structured situation. The latter should provide a general idea of the possible variation in the amplitude and frequency of these small movements. Manipulation of the likelihood of perceiving a target in a free-viewing situation (as opposed to stabilized viewing) should elicit a concomitant change in the pattern of small eye movements. If contour interaction were demonstrated at spatial separations comparable to the amplitudes of microsaccadic eye movements, contriving to reduce the perceptibility of a target contour with the addition of a nearby contour should provoke a predictable change in the pattern of small eye movements.

In addition to these questions consideration is given to whether a single generating mechanism is associated with saccades of varying amplitude. As well, the general shape of the contour interaction function is explored and the possibility of summative effects is discussed.



CHAPTER TWO

SMALL EYE MOVEMENTS AND VISUAL PERCEPTION

How the sense of vision provides information about the environment has been a question of interest to psychologists and physiologists for many years. A wide variety of techniques have been employed in the study of vision each one concentrating on a particular feature of the visual process and each one characterizing it in a particular way. One such feature which has been of considerable interest is the movement of the eyes.

Movements of the eyes are executed by a system of twelve extraocular muscles. The oculomotor system is most sophisticated and may be considered to serve several roles in the visual process. In addition to a possible role in the process of information extraction (Festinger, 1971; Noton & Stark, 1971) the oculomotor system can be said to serve at least three broad functions in the visual process (Turkel, 1974). The first of these is maintenance of the physical alignment between the receptor surfaces of the two retinas which is necessary for binocular vision. The second general function is to move the receptor surfaces of the eyes so that new information can be brought onto the specialized central region of the retina, where acuity is best, and kept there. Thirdly eye movements serve to provide a change in the stimulus array which is necessary to prevent the array from fading (Pritchard, Heron & Hebb, 1960).

Several issues arising from the eye movement literature are of particular interest in the study of contour effects. The possible role

of eye movements in visual acuity (the capacity for the spatial resolution of contours) generated considerable research for several years. One major question raised during the research was the role of eye movements in ensuring that a contour remained visible. Upon this notion followed the suggestion that very small eye movements served to keep the image of a target within an optimal retinal region by correcting very small position errors. This raised the question of the smallest position error which could be corrected, a question which was broken down into several parts regarding the smallest target step (displacement) which could be detected, the smallest target step which could be tracked (corrected) and whether or not small eye movements were produced by the same mechanism as were larger voluntary eye movements. The relationship between eye movements and the spatial resolution of contours is still a question of interest but for quite different reasons than was originally the case.

A brief review of some of the work on small eye movements will trace the evolution of our understanding of the relationship between eye movements and vision. The development of thought in the field will be followed through work on visual acuity, target visibility and accuracy in maintaining eye position. This will be followed by a discussion of more recent findings which suggest that small saccadic eye movements and larger 'voluntary' saccades are initiated by the same neural mechanism and serve similar functions. The review will conclude with a discussion of the concept of an oculomotor 'dead zone', a narrow relatively insensitive area next to a contour where a small target step is less likely to be detected or tracked.

Fixation Eye Movements

When a human is asked to fixate a small stationary target such as a spot or the point of intersection of the arms of a cross (Ratliff and Riggs, 1950; Ditchburn and Ginsborg, 1953) he rotates his eye causing the image of the fixation target to fall within an area of the retina about 20 minutes of arc in diameter where detail vision is best and relatively uniform (Le Grand, 1967). When the subject is required to maintain fixation on the target his eyes are constantly in motion in a pattern of slow and fast "miniature" eye movements. These extremely small eye movements have been considered "involuntary", "spontaneous" or "reflexive" because their occurrence seems to be a random event not under the conscious control of the "fixator". Measurement of these minute changes in the eye's position (by the reflection of light from a mirror mounted on a contact lens on the eye) requires that the subject's head be held steady, usually by having him bite down on a dental impression solidly attached to a rigid bar. The typical fixation pattern consists of three forms of eye movements: saccades, drifts and high frequency tremor (Ratliff and Riggs, 1950; Barlow, 1952; Ditchburn and Ginsborg, 1953).

Fixation saccades or microsaccades are small, very rapid changes in eye position. They may occur one to three times each second and range in amplitude from about two minutes of arc to a maximum of 40 to 50 minutes, however they rarely exceed 20 minutes in amplitude. Their average size is about 5 or 6 minutes of arc (Riggs and Ratliff, 1951; Steinman et al., 1967) though at least one investigator has reported a typical amplitude of 11 minutes (Fender, 1956). Saccade

duration depending on amplitude is typically 10 to 25 milliseconds (Riggs and Ratliff, 1951; Ditchburn and Foley-Fisher, 1967). The peak velocity of fixation saccades is linearly related to amplitude (Zuber et al., 1965). Ditchburn and Ginsborg (1953) found that the horizontal and vertical components of saccades occur simultaneously in the two eyes and that in general their magnitude and direction are similar. Other investigators have reported that microsaccades are more or less binocularly synchronized (Krauskopf et al., 1960; Yarbus, 1967; Fender and Julesz, 1967; St. Cyr and Fender, 1969).

In the intervals between saccades the eyes drift slowly back and forth. Drifts may range in amplitude from 0.8 to 6.0 minutes of arc (Riggs and Ratliff, 1951; Fender, 1956; Ditchburn and Foley-Fisher, 1967) and may last at least 100 milliseconds (Riggs and Ratliff, 1951). Although the line of sight moves irregularly the retinal image of the fixation point nevertheless remains inside the central fovea (Ditchburn, 1956). As drift velocity is about 6 minutes of arc per second and as the cone diameter in the central fovea is about 0.6 minutes of arc, the retinal image of the fixation point may cover approximately 10 cone diameters a second during the drift (Yarbus, 1967).

Superimposed on the drifts of the eye is a high frequency tremor with a mean amplitude of from 5 to 15 seconds of arc in the horizontal and vertical directions and up to 45 seconds of arc for torsional movement (Ditchburn, 1955). Others have estimated tremor to be 20 to 30 seconds of arc in amplitude (Riggs and Ratliff, 1951; Yarbus, 1967). Tremor frequency may range up to 100 cycles per second

(Riggs and Ratliff, 1951) however the major frequency component is 70 to 90 cycles (Yarbus, 1967) and the most powerful component is even lower in frequency (Fender, 1956).

All subjects make these three kinds of small fixation eye movements but the size and most frequent direction of the microsaccades may vary from subject to subject (Ditchburn and Foley-Fisher, 1967; Cunitz and Steinman, 1969). Although the eye is almost constantly moving it does not wander very far from its mean position during maintained fixation, permitting the retinal image to remain within the central 20 minutes of arc or so of the fovea. Variations in the luminance, size and color of the fixation target have statistically reliable but small effects on mean fixation position and stability -- effects not larger than 3 or 4 minutes of arc (Steinman, 1965; Boyce, 1967). Rattle (1969) found "unexpected fixation stability" when subjects maintained the line of sight at the imagined center of targets as large as 240 minutes of arc. Murphy et al., (1974) found that the line of sight can be well maintained anywhere within or at the edges of simple forms; the differences in mean fixation errors averaged only 3 minutes of arc and were not systematically related to the form or fixation position required. Steinman (1976) has concluded that whenever the target form is confined to the foveal floor (Polyak, 1941) the oculomotor system is capable of maintaining the line of sight in whatever region a subject is required to fixate free from stimulus constraints.

Small Eye Movements and Visual Acuity

In a fixation period of 4 seconds the fixated image may travel back and forth over as many as 30 to 50 foveal cone receptors (Keeseey,

1976). Therefore many cone receptors receive stimulation with a frequency and intensity that depend on both the characteristics of the motion and the spatial contrast properties of the image. Modern interest in the fine details of the maintained fixation pattern was provoked by dynamic theories of visual acuity (Weymouth, Anderson and Averill, 1923; Marshall and Talbot, 1942; Jones and Higgins, 1948) in which movement of the image back and forth across a number of receptors was thought to be responsible for the ability to resolve fine detail (as in a vernier task) of angular subtense considerably less than the diameter of the foveal cone. The cortex was thought to average messages from the population of receptors maximally stimulated, for example, during physiological tremor, allowing the perception of edges which were only shifting gradients of illumination in the optically blurred retinal image.

One of the first attempts to examine the role of eye movements in acuity was made by Ratliff (1952) who found that acuity for gratings was better when the eyes were relatively still. An optical method which fixes or "stabilizes" the location of the image on the retina, has been used to study visual acuity in at least three experiments (Riggs, Ratliff, Cornsweet and Cornsweet, 1953; Keesey, 1960; Fender and Nye, 1962). Keesey (1960) found that under both the stabilized image condition and the normal unstabilized viewing condition acuity for a single dark line was comparable improving to a maximum value as exposure duration was increased to 200 milliseconds. Only a slight improvement was indicated for longer exposure of the target. Similar results were obtained with vernier and grating targets suggesting that

the mechanisms subserving acuity were dependent on exposure duration but were not dependent on image motion in the manner suggested by the dynamic theories of acuity. Furthermore minute measurements of tremor amplitude permitted by the contact lens optical lever technique developed independently in the laboratories of Riggs, Ditchburn and Yarbus revealed that tremor itself was too small to sweep the image across an appreciable population of cones.

Eye Movement and Contour Visibility

Although target visibility is attenuated during a saccade (Ditchburn, 1955; Volkman, 1962; Latour, 1962; 1966; Volkman et al., 1968) there is a large body of literature which reveals that some retinal image motion is essential for persistent target visibility. Ditchburn and Ginsborg (1952) reported that when the horizontal components of eye movements were stabilized the vertical border between two areas of unequal luminance disappeared and the areas appeared equally bright for a few seconds each minute. Others have confirmed that when a simple line or border target is viewed as a stabilized image it rapidly loses contrast and disappears (Riggs, Ratliff, Cornsweet and Cornsweet, 1953; Yarbus, 1957). Moreover the image of such a simple figure tends to disappear and later reappear in its entirety (Pritchard, Heron and Hebb, 1960). Ditchburn and Ginsborg's (1952) suggestion that the contrast threshold of the stabilized image was higher than the normal threshold was confirmed by Riggs and Tulunay (1950) who found that visibility of a bipartite field was determined by contrast alone when the image was motionless on the retina.

A more complex target such as a geometrical figure viewed as a stabilized retinal image tends to fragment so that individual lines or combinations as well as the entire figure disappear and reappear in all-or-none fashion (Pritchard, Heron and Hebb, 1960; Evans and Piggins, 1963; Bennet-Clark and Evans, 1963; MacKinnon, Forde and Piggins, 1969). The length of time an image persists is also a function of its complexity. A single line may be visible for only 10 per cent of the total viewing time, however a more complex figure may remain visible in whole or in part up to 80 percent of the time (Pritchard, Heron and Hebb, 1960). Whereas earlier work in image stabilization had been done with a contact lens optical lever system which eliminated horizontal image motion Pritchard et al. (1960) used a tightly fitting contact lens on which was mounted a lightweight projection assembly, a device designed to eliminate image motion in any direction. Nevertheless it was suggested by Yarbus (1957) and by Barlow (1963) that the regeneration of "stabilized" images might be due to residual image motion resulting from lens slippage. Such image motion might account for the tendency of parallel lines to act as units (Pritchard et al., 1960). Indeed in studies of after-images (stabilized images which are not subject to the above criticism) there was less tendency for simultaneous disappearance and reappearance of parallel lines (MacKinnon, Forde and Piggins, 1969). Overall, however, the ways in which the patterns appeared to fragment under these two viewing conditions as well as under steady fixation are similar (Evans and Piggins, 1963; McKinney, 1963; Bennet-Clark and Evans, 1963). The latter investigators concluded that the partial and structured

reappearances reported in their study and others cannot be attributed solely to lens slippage.

Neither can the organized fading of such complex figures as the human profile, a pattern of curlicues or a capital letter 'B' obscured by hatching lines be attributed to random fluctuations of threshold in various parts of the retina (Pritchard et al., 1960b). The non-random nature of fragmentation (Evans and Piggins, 1963; Pritchard, Heron and Hebb, 1960; Bennet-Clark and Evans, 1963; Evans, 1965; 1967; Piggins, 1968; MacKinnon, Forde and Piggins, 1969) has been attributed to a suprarectal process (MacKinnon, Forde and Piggins, 1969). Further evidence of a central process is suggested by the cyclical nature of the fragmentation (Fiorentini and Ercoles, 1963; Piggins, 1968) and by demonstrated inter-ocular effects on target visibility (Krauskopf and Riggs, 1959; Ditchburn and Pritchard, 1960; Cohen, 1961).

Krauskopf and Riggs (1959) reported that the disappearance of a stabilized image presented to one eye was enhanced following (stabilized) stimulation to the corresponding retinal region of the other eye. The control situation involved previous stimulation of the other eye in a region symmetrically opposite (in the opposite hemifield) to the binocularly corresponding region in the other eye. The stimulus was a dark vertical bar presented in one half or the other of a lighted disk. A more appropriate control might have been to present the disk alone with no bar to the opposite eye. As it is, the control used may have actually facilitated visibility of the bar presented subsequently to the other eye.

Cohen (1961) had subjects view a stabilized black line target with the right eye. He found that patterned, unstabilized vision to the left eye resulted in more target visibility and less frequent disappearances than did diffuse light to the left eye. When no light was allowed to stimulate the left eye target visibility was lowest of all and disappearance was most frequent. As the apparent distance between the stabilized line and a parallel unstabilized line increased (the added line was 25, 75 or 150 minutes from the fixation point; the stabilized line appeared superimposed on the fixation point) the visibility of the stabilized image decreased. This apparent facilitation was attributed to neural interaction in the visual cortex. There was no indication of whether the subject might have perceptually superimposed the two stimuli or substituted the unstabilized line for the target line, for example through disjunctive eye movements or retinal rivalry. This result is consistent with the finding in the standard monocular stabilized viewing situation that parallel lines tend to act together (for example, Pritchard et al., 1960) supporting the suggestion of a central mechanism contributing to fragmentation phenomena. Curiously, one-eyed subjects (Goldstein, 1967) and subjects with strabismus (Piggins, 1972) report very little fragmentation.

Apparently temporal variation in retinal luminance plays a role in target visibility as fading of a stabilized image may be counteracted by flickering the target luminance (Pritchard, 1958) or by imposed motion of the target (Krauskopf, 1957; Ditchburn, Fender and Mayne, 1959). Keesey (1976) found that sinusoidal flicker of a stabilized bright line target (around a constant mean luminance) at

rates of less than 5 Hz sustained visibility almost continuously. When flicker rate exceeded 9 Hz visibility was determined solely by contrast but never reached the levels achieved when the image was flickered at low rates.

Ditchburn, Fender and Mayne (1959) found that imposed flicks (or saccades) as small as 2.5 minutes of arc (the smallest displacement tested) produced a marked increase in visibility of the stabilized image of a bar 3 minutes of arc in width. Regeneration always followed the flick giving a sharper image than that observed after spontaneous regeneration. A steep rise in target visibility also occurred for imposed tremor amplitudes exceeding 0.3 minutes corresponding to an overall displacement of 0.6 minutes which is roughly equal to the intercone spacing in the central fovea. The effect was practically independent of frequency. Imposed drifts restored visibility of a stabilized image to normality only when they were comparable in extent to the largest (relatively rare) drifts observed in normal vision. The authors concluded that no single component of normal eye movements is capable of maintaining optimal vision but rather that "additive interplay between components" would be necessary if normal eye movements were to serve this function.

Keeseey and Riggs (1962) found that a Mach band, clearly discernible for 15 seconds under unstabilized conditions disappeared readily within a few seconds when it was stabilized. Imposed sinusoidal motions of the image had to exceed 1 minute of arc in extent to sustain visibility at levels comparable to unstabilized vision. In contrast to Ditchburn et al. (1959) but in keeping with later work on

flicker (Keeseey, 1976) these investigators found that the frequency⁶ of the motion was critical as, at values of 8 Hz and higher, visibility was not lengthened regardless of the amplitude of image displacement. It was concluded that slow large drifts were essential for the maintenance of vision whereas tremor with frequencies higher than 10 Hz was judged ineffective. No saccade-like motions were tested. However, Keeseey (1976) reported Cornsweet's observation that when a large luminous disk on a dark background is stabilized on the retina it disappears; but if it is moved across the retina 1 minute of arc the whole disk reappears. The only parts of the retina that are receiving changing stimulation are two narrow crescents, one at the leading edge and the other at the trailing edge. A similar result has been described by Gerrits, deHaan and Vendrik (1966).

Yarbus (1967) found that for a sharp retinal image of a border, drift of the eye was sufficient to prevent formation of an empty field over the retina. Gerrits and Vendrik (1974) also concluded that vision was sustained by the slow and continuous motion of the image resulting from the drift component of eye movements, rather than from the tremor and saccadic motions that contain high-frequency components. The effectiveness of drift in maintaining visibility was attributed to the temporal variations in luminance it supplies to the receptors; an excursion over several receptors was considered of secondary importance in sustaining vision.

Apparently the type of stimulation supplied by image motion, while immaterial in determining maximum levels of acuity is essential

in maintaining clear visibility of targets. It has been suggested that the fragmentation which occurs under steady fixation and to some extent during stabilized viewing with a contact lens apparatus, particularly the greater frequency of joint action of parallel lines, may be attributable to scanning eye movements possibly arising from reading habits (MacKinnon, Forde and Piggins, 1969; MacKinnon, 1971). In particular MacKinnon (1971) proposed that variability between subjects under steady fixation as well as discrepancies between his results and earlier findings (MacKinnon et al., 1969) might be attributable to idiosyncratic scanning habits rather like those described by Cunitz and Steinman (1969). These investigators found that individual subjects differed considerably with respect to the direction and size of saccadic eye movements during both reading and steady fixation of the letter "T". (This work will be discussed in more detail shortly).

Cornsweet (1956) reported that neither the frequency of saccades nor the amplitudes of drifts correlated with the likelihood of fading of a stabilized target. Rather than determine the number of individual target disappearances which were accompanied by a saccade. Cornsweet flickered the targets at various rates which systematically affected the proportion of time that the target was visible and compared this proportion to the frequency of saccades. At the time of testing Cornsweet's subjects were likely quite experienced in viewing stabilized images as he noted that a good deal of practice was necessary to become accustomed to the procedure. Cornsweet's results may be questioned on the strength of the observation by Pritchard et al. (1960) that when a stabilized image disappeared or reappeared the

uninitiated subject first rotated his eyes in an effort to bring the image or center of attention back to the fovea. Soon, however, the subject learned to view the image passively and discovered that he could still transfer his attention from one point to another over the visual field.


Steinman, Haddad, Skavenski and Wyman (1973) have suggested that oculomotility probably evolved in the service of functions other than preventing stabilization of the image on the retina. They point out that normally retinal image motion is assured by the continuous and varied movements of the viewer and of his visual environment. In their view the function of eye movements is mainly to minimize retinal image motion due to instability of the eye, changes in orientation of the viewer's head and motion of the target itself as well as to move target images rapidly to a specialized retinal region where acuity is superior. The oculomotor system does not fully compensate for head motion indicating that there is a great deal of retinal image motion normally when the head is not supported on a bite board (Steinman, 1975; Winterson, Steinman and Skavenski, 1975; Steinman, 1976).

Eye Movements and Position Errors

Cornsweet (1956) proposed that saccades serve to correct visual position errors. According to his model the eye drifts because of an imbalance between antagonistic muscles. Increasing distance between the line of sight and the target centre serves as a visual error signal which triggers an involuntary saccade that moves the target back toward the centre of the foveal bouquet. The probability of a saccade

increases as the visual error signal grows larger and a visual error as small as 7 minutes of arc is virtually certain to trigger a position-correcting saccade. Others too have observed that micro-saccades are the main means by which a subject keeps the retinal image of a visual target in some "preferred" locus when he is asked to "fixate" (Nachmias, 1959, 1961; Fiorentini and Ercoles, 1966; Boyce, 1967).

However, Cornsweet (1956) noted that although fixation saccades tended to move the target toward the mean fixation position, on the average, they overshoot the mean fixation position by more than 1 minute of arc. Such "fixation errors" were confirmed by Nachmias (1961) who also showed (Nachmias, 1959, 1961) that drifts on some meridians correct visual errors introduced by other drifts and that increasing the drift rate of the eye did not increase the frequency of saccades. He concluded that the time since the last saccade was a better predictor of when the next saccade would occur than the deviation of the line of sight from the target. Nachmias' findings were confirmed by Fiorentini and Ercoles (1966) and by St. Cyr and Fender (1969). Boyce (1967) found that only 30 per cent of his subjects' saccades compensated for immediately preceding drift and concluded that although there was some compensation of preceding drift, the compensation was very inaccurate. Although the direction and magnitude of preceding drift had some influence on the direction and magnitude of the saccade they could not be regarded as the sole or even the main determinants of those quantities. Similar characteristics were reported in a larger sample of subjects by Proskuryakova and Shakhnovich (1968).



Other investigators have found that saccades are not required to keep the line of sight on a fixation target (Steinman et al., 1967; Filin and Mizinova, 1969; Matin, 1969). The variability of eye position under the instruction to "hold the eyes steady", when microsaccade frequency can go to zero over 9.8 seconds, is no greater than under "fixate" instructions when microsaccades occur at regular intervals. Drifts themselves do not carry the eyes further from an "optimal locus" than when they are interspersed with allegedly correcting microsaccades (Steinman et al., 1967). Another source of difficulty for Cornsweet's model was the report that target steps less than 15 minutes (that is, within the functional confines of the fovea) did not elicit saccades suggesting the existence of a saccadic "dead zone" (Rashbass, 1961; Young, 1966). The above findings suggest that both saccades and drifts produce, as well as correct, position errors during maintained fixation.

Pritchard and Heron (1960) recorded eye movements in the cat while the animal was presented such visual stimuli as a piece of cotton, a small stationary light, a candle, the experimenter's face and a rat in a jar. They recorded flick amplitudes (35 minutes of arc) larger than those recorded in human fixation eye movements (Fender, 1956) as well as larger drift amplitudes (about 35 minutes of arc). A particularly striking result was that flicks were rarely observed in the cat's eye movement record. At the time these rather puzzling results were attributed to the cat's having a retinal receptor density unlike that of the human. Whereas the human fovea centralis consists of a small area (about 20 minutes in diameter) of very closely packed

cones affording greatest acuity the area centralis of the cat retina has a lower cone density and essentially constant acuity over a relatively diffuse area.

The "involuntary" flicks which occur when the human subject is instructed to "fixate" may be an artifact of the instructional set. Apparently, saccades are not essential for the control of retinal image position as subjects can suppress saccades over an appreciable period of time with no increase in variability of eye position (Fiorentini and Ercoles, 1966; Steinman, Cunitz, Timberlake and Herman, 1967; Filin and Mizinova, 1969). Steinman et al. (1967) instructed their subjects to "hold" their eye in position in the presence of a stationary homogenous disk of white light, 5.4 or 31.2 minutes of arc in diameter, whose luminance was 1.0 millilambert. The saccade rate was markedly reduced from that observed under "fixate" instructions and subjects frequently suppressed saccades altogether throughout a 9.8 second trial.

Although saccades were very infrequent on "hold" trials compared to "fixate" trials the variability of eye position was comparable in the two conditions and subjects were not troubled by target fading even on trials when there were no saccades (Steinman et al., 1967). Low velocity drifts (about 6 min arc/sec) seemed sufficient to maintain target visibility. Murphy (1973) reported that the perceived form of a target which falls within the central 90 minutes of the fovea does not change when microsaccades are suppressed suggesting that saccades are not critical for form perception.

This saccade-free eye position control ("slow control") does not depend on the type or distance of the target nor does it result

defocusing (Steinman, Skavenski and Sansbury, 1969). Saccades can be suppressed with a variety of targets such as a point, a disk, a foveal annulus or an annulus in the periphery, whether they are steadily illuminated or flickering, however slow control is best and saccade suppression easiest with a steadily illuminated foveal disk about 0.5 degrees in diameter (Haddad and Winterson, 1975).

The eye drifts faster in the dark than when a fixation target is visible (Nachmias, 1959; Matin, Matin and Pearce, 1970; Skavenski and Steinman, 1970) and variability of eye position is much greater (Cornsweet, 1956; Nachmias, 1961; Steinman et al., 1967; Skavenski and Steinman, 1970). If targets are too feeble to be seen when they fall on the fovea a good deal of position control is lost. A feeble target placed near the periphery where it can be seen tends to be returned to the fovea where it disappears (Steinman and Cunitz, 1968). A fixation stimulus for one eye serves to hold the other eye in place provided the viewing distance is at least 2 meters to minimize variability arising from attempts to make convergent eye movements (Steinman, Haddad, Skavenski and Wyman, 1973).

Winterson and Robinson (1975), recorded two-dimensional eye movements in the cat by means of a scleral search coil in a magnetic field (Robinson, 1963) which permitted resolution of an eye movement of 1 minute. Body movements were restrained and the head was held in a fixed position while the cats looked about the room. Their field of view included a pegboard on which a variety of objects were suspended. Whenever the experimenters (in an adjacent room) "suspected that the subject had lost interest in the experiment" they made a variety of

noises intended to keep the cat awake and alert. It is not clear what criterion of arousal was employed.

Winterson and Robinson (1975) reported that the cats used slow control exclusively to maintain fixation on stationary objects of their own choosing in a lighted room. Eye drift was not corrected by microsaccades but by equal and opposite slow drifts which ensured that mean eye position did not change. The typical eye movement pattern consisted of one or more large saccades that shifted the line of sight a number of degrees, followed by slow control to maintain the line of sight. Saccades smaller than 10 minutes of arc were never observed. Occasionally small saccadic motions were observed on one meridian but such motions always proved to be a small component of a much larger saccade on the other meridian.

Although the cat's visual acuity (Smith, 1936; Blake, Cool and Crawford, 1974) might be expected to provide adequate error signals for shifts of eye position smaller than 10 minutes and there is a degree of anatomical specialization in the central retina (Stone, 1965) these conditions may not determine the occurrence of microsaccades in the cat or in the human. Human visual acuity is relatively uniform over a region 24 to 50 minutes in diameter (Millodot, 1966) yet human microsaccades are much smaller.

Winterson and Robinson noted that the stability of the cat's eye when it looked at an object of its choice was at least as good as the stability of the human eye when instructed to maintain eye position with slow control (Steinman et al., 1967; Murphy, Haddad and Steinman, 1974). Also, like humans, stability could be maintained over long

periods of time. Drifts exceeding 2 degrees were observed only in the dark or when the animal "dozed off". Drifts in one direction tended to be followed by similar drifts in the opposite direction resulting in an irregular oscillating pattern which kept the long term mean eye position from changing more than a few minutes of arc. Drift velocity in the cat was approximately twice that observed in man and drift oscillations were of higher frequency than in man. Uncompensated drifts and higher drift velocities were observed in the dark, indicating that slow control is visually activated in the cat as in man.

Characteristics and Functions of Small and Larger Saccades Compared

Visual thresholds are elevated by large saccades (Volkman, 1962; Latour, 1962; Volkman, Schick and Riggs, 1968). There is some evidence of a similar elevation when small saccades are made during fixation (Ditchburn, 1955; Beeler, 1967) though Krauskopf, Graf and Gaarder (1966) did not find that visual threshold was elevated when microsaccades occurred. The duration (Ron, Robinson and Skavenski, 1972) and maximum velocity (Zuber, Stark and Cook, 1965) of a saccade both increase with saccadic amplitude. For normal saccades executed at random around a structured visual field monkeys require an additional millisecond in duration for every degree of increase in amplitude and humans require 2 milliseconds per degree (Ron et al., 1972).

The maximum velocity achieved during a human saccade increases with amplitude up to 20° ; for larger saccades a velocity saturation occurs at between 500 and 700 deg/sec in the human and 1000 deg/sec in the monkey. The function relating maximum velocity and saccadic

amplitude is the same for voluntary saccades, corrective saccades and the microsaccades of fixation suggesting that the small rapid eye movements may be generated by the same neural mechanism or at least are limited by the same mechanics as the larger saccades (Zuber et al., 1965; Fuchs, 1976).

The finding that subjects can inhibit microsaccades (Steinman et al., 1967) led Cunitz and Steinman (1969) to suggest that fixation microsaccades may be under voluntary control and that they, like large saccades, are scanning eye movements, part of a visual search pattern. Their view presupposes that many "fixation" microsaccades serve to place various regions within or near the fixation target at the "optimal" locus where details can be most readily attended. Horizontal eye movements were recorded during fixation of a capital letter "T" which subtended 15 minutes of arc both horizontally and vertically and while subjects read a paragraph they had never seen before. Each letter or space subtended 7.7 minutes of arc horizontally and the entire text subtended 3.1 x 4.9 degrees. Both targets were presented on a white field 4.2 x 5.9 degrees with a luminance of 1 millilambert, sufficient for good legibility in an otherwise darkened environment. Subjects were instructed to "fixate" the letter target just as they had "fixated" points or discs of light in prior experiments and to "read" the paragraphs for comprehension.

Eye movements recorded during reading were similar to standard descriptions of normal reading (Yarbus, 1967; Woodworth and Schlosberg, 1954) with respect to the number of fixations per line, the number of regressions and the duration of reading pauses. The most striking

feature of the records was the low frequency of microsaccades observed during the reading pauses. Microsaccades occurred in fewer than 5 per cent of the reading pauses.

The distributions of time intervals between fixation microsaccades and between large reading saccades (reading pause durations) overlapped considerably for each subject. The difference between the mean log intervals was significant for one of the two subjects and was attributed to an appreciable number of long periods (more than 600 milliseconds) during which the subject made no microsaccades during fixation of the "T". The modal intersaccadic intervals and reading pause durations were very similar for both subjects. The median duration of all reading pauses that contained microsaccades was almost twice as long as the median duration of reading pauses without microsaccades. When a microsaccade was made during a reading pause it was made at about the same time that a large reading saccade would be expected. Therefore, the probability of a saccade occurring during reading was independent of the size of the saccade that was made. Reading pause duration was not significantly lengthened by increasing the difficulty of the reading material. When difficulty was increased the mean size of the reading saccade was reduced slightly and there were more pauses per line of text.

The individual subjects differed with respect to the number of regressions and variability in the size of forward movements during reading. Moreover they differed in the mean size of microsaccades during fixation. Each subject performed quite differently with respect to the direction and size of his saccades in the reading and fixation

conditions; however the temporal characteristics of these movements did not differ between the two conditions. The temporal distribution of saccadic eye movements was not related to their size and direction. This finding suggests that all saccades, large and small, are initiated by a single system (Cunitz and Steinman, 1969). Zuber, Stark and Cook (1965) have already provided evidence that a single physiological system controls the velocity-amplitude characteristics of all saccades up to approximately 3 degrees in amplitude.

Cunitz and Steinman (1969) propose that many "fixation" microsaccades serve the same purpose as large "voluntary" saccades in shifting the line of regard from one part of the visual array to another, even in a very circumscribed portion of the visual field. They further note the implication that the occurrence of microsaccades during fixation may be a relatively late development in the control of the visual search pattern requiring an ability to resolve small details as well as to execute accurately very small saccades. Steinman et al. (1973) have proposed that the eye movement pattern of maintained fixation is learned and that the observed similarity of the intersaccadic intervals during maintained fixation and reading supported the notion that fixation and reading may both be overlearned motor skills.

Large saccades, smooth pursuit and vergence movements of the rhesus monkey and man are qualitatively similar (Barmack, 1970; Fuchs, 1967; Keller and Robinson, 1972). Skavenski, Robinson, Steinman and Timberlake (1975) trained rhesus monkeys to perform a monocular visual discrimination task, involving both acuity and vigilance, which was

designed to elicit good fixation. Early in training monkey saccade rates were comparable to human rates of 1 to 2 saccades per second with occasional intervals of more than 2 seconds between saccades. However, monkey eye movement patterns differed from human fixation in two respects: (1) their saccades were generally large (greater than 30 minutes in amplitude) compared to human fixation microsaccades; and (2) their fixation positions were quite variable. Monkeys improved their fixation control remarkably when the entire visual display was made much smaller and for 3 of 4 monkeys variability in eye position as well as median saccade amplitude and median intersaccadic interval lay within the ranges reported for man (Ditchburn, 1973).

Small but consistent percentages of saccades of less than 10 minutes amplitude occurred during earlier discrimination training on larger visual displays indicating that microsaccades form part of the normal eye movement pattern in the two-year-old monkey. As the target separations were reduced and the targets were made smaller the distribution of saccade amplitudes shifted toward more microsaccades. When fixation patterns were under direct reward control all 4 monkeys eventually learned to keep their line of sight within 15 minutes of arc of the target for a period of 15 seconds, showing fixation accuracy comparable to that of man.

One monkey began to use slow control to keep his eye on target; this mode of control was very stable. Two other monkeys occasionally used slow control to effectively maintain eye position for 2 to 4 seconds. However, they also showed systematic drifts which carried the eye off target and were terminated by small return saccades. Monkeys,

like man, use slow control to markedly attenuate the drift that occurs in the dark. The presence of a single point of light was sufficient to permit reduction of the net drift rate by a factor of about 25. Skavenski et al. (1975) extended their results to a total of 7 monkeys and concluded that the rhesus monkey can control eye position as well as man (Skavenski and Steinman, 1970; Skavenski, 1971).

A major obstacle to the voluntary motor skill interpretation of the maintained fixation pattern was an experiment by Rashbass (1961) who concluded that there is a large saccadic "dead zone". His subjects did not track target steps smaller than 15 to 30 minutes of arc. If the fixation pattern is an overlearned habit based on a voluntary search made with saccades as small as 5 or 6 minutes of arc subjects should be able to voluntarily track target steps smaller than 15 minutes of arc. Bennet-Clark (1964) also reported a saccadic "dead zone" of the type described by Rashbass however some of his subjects were able to compensate for displacements of less than 10 minutes of arc. He concluded that the hypothesis of an oculomotor "dead space" proposed by Fender and Nye (1961) received some support but that the size of the dead space varied from subject to subject. Timberlake, Wyman, Skavenski and Steinman (1972) reported that the oculomotor 'dead zone' must be smaller than 10 minutes and might even be less than 5 minutes of arc.

Alpern (1969) pointed out that Cornsweet's (1956) finding that saccades frequently reduce small position errors argues against the broad "dead zone" described by Rashbass. Where Rashbass observed no saccade in 800 seconds for target steps of 15 to 30 minutes, Young

(1971) found that the probability of a corrective saccade decreased monotonically with step size below a displacement of about 30 minutes. Within 750 milliseconds after target displacement the probability of a corrective saccade decreased from 0.9 for target steps of approximately 50 minutes of arc down to 0.4 for target steps of about 5 minutes of arc. For an interval of 250 milliseconds after a target step of 5 minutes of arc the probability of a corrective saccade was less than 0.2. In Young's experiment subjects were not specifically instructed to make corrective saccades.

Wyman and Steinman (1973a) had subjects view monocularly a point of light less than 2 minutes in extent at a distance of 2.04 meters. Average eye position was measured for the 5 seconds preceding a target step and for the 5 second period beginning 1.5 seconds after the target step. They found that subjects instructed to do so tracked at least 98 per cent of unpredictable target steps, ranging from 3.4 to 13.8 minutes of arc, with an accuracy of within 0.5 minutes of arc. Subjects followed steps of 1.7 minutes of arc on approximately 65 per cent of the trials but even this was a statistically reliable proportion. For this small step the change in average eye position was about 60 percent too large. Average saccade latency increased from 200 milliseconds to nearly 450 milliseconds as target step size decreased from 28.4 minutes of arc to 3.4 minutes of arc (Wyman and Steinman, 1973b). These latencies are comparable to those of voluntary motor acts in standard reaction time experiments (Woodworth and Schlosberg, 1954). The latency and accuracy of the first tracking saccade were influenced by psychological variables in much the same way as has been

found in experiments on voluntary sensorimotor reaction times. A delay of 200 to 250 milliseconds is typically reported between a larger target step and the resulting saccade (Wheless, Boynton & Cohen, 1966; Komoda, Festinger, Phillips,; Duckman & Young, 1973). In a series of unpublished experiments Nachmias and Herman (reported by Steinman et al., 1973) showed that subjects tracked steps as small as those tracked in the work of Wyman and Steinman (1973a).

It has been demonstrated that human subjects are capable of suppressing saccades while maintaining eye position in the presence of a fixation target (Steinman et al., 1967). Moreover, subjects can reliably track target steps as small as 3.4 minutes of arc (Wyman and Steinman, 1973) however tracking is less likely for a step of 1.7 minutes of arc. An experiment by Haddad and Steinman (1973) revealed that humans can look away from a stationary fixation point in any direction with the same precision with which we can correct small eye position errors produced by drifts of the eye or changes in the position of the target. Subjects were required to make the 'smallest possible' saccade in a specified direction in the presence of a small stationary point of light. These saccades had a mean amplitude of 5.6 to 5.7 minutes of arc, comparable to the average fixation microsaccade (Ditchburn and Foley-Fisher, 1967) and a mean latency of 195 to 270 milliseconds comparable to simple reaction times. The saccades were always in the appropriate direction and could create as well as reduce visual errors, suggesting that the presence of a visual error was not necessary for the execution of a saccade. Saccades were three to four times as large in the dark as when the target was visible.

Haddad and Steinman (1973) noted that subjects required to maintain fixation of a target with slow control do make spontaneous saccades but these occur rarely and are about twice as large as the small voluntary saccades and typical fixation saccades. Spontaneous saccades do tend to move the eye opposite to its drift direction supporting the notion that they serve to correct the error introduced by drift (Cornsweet, 1956). Subjects are usually aware of having made a spontaneous saccade, but they are better able to detect target displacements (steps) and identify their direction than to detect and identify the direction of their spontaneous saccades. Target steps of 7.0 and 3.5 minutes were detected on virtually all trials but detection dropped to 65 percent of the trials when the target step was only 1.7 minutes of arc. The tiny saccades made during maintained fixation can be detected but their frequency is influenced by the attentional act and the maintained fixation pattern loses its typical characteristics (Steinman et al., 1973).

Haddad and Steinman (1973) concluded that their results were compatible with the speculation (Cunitz and Steinman, 1969) that the microsaccades made during maintained fixation serve the same function as the large scanning saccades: during maintained fixation the subject scans a small region near the fixation target just as during visual search he uses larger saccades to shift his line of sight.

From the eye movement literature at least two general questions emerge. The first question concerns the reportedly arbitrary nature of the experimental situation requiring a subject to fixate. It has been demonstrated that although the monkey normally makes relatively large

saccades the animal can be trained to fixate a small stationary target with microsaccades like those which typify maintained fixation in the humans. Both monkeys and humans can suppress saccades for several seconds maintaining eye position with slow control. Humans can track target steps as small as 3.4 minutes and voluntarily make saccades as small as the microsaccades observed during maintained fixation. Zuber et al. (1965) have found that the velocity-amplitude relationship for microsaccades is the same as that for larger saccades. The timing of saccade onsets is virtually the same in reading and fixation although the size of the average saccade differs. Even successful manipulation of saccade amplitude by varying difficulty of the reading material has no significant effect on the distribution of intersaccadic intervals according to Cunitz and Steinman (1969).

These data suggest that microsaccades and somewhat larger saccades (eg. scanning, reading) are all initiated by the same neurophysiological mechanism as hypothesized by Zuber et al. (1965) and by Cunitz and Steinman (1969). Further the data imply that the requirements of the viewing situation (fixation, reading, visual search) influence the size and direction of saccadic eye movements, perhaps through some well-practiced, voluntary action of the observer, but that the rate of saccade initiation is unaffected. It seems that the impulse for high velocity movement of the eye is generated at predetermined intervals and that the ultimate direction and size of saccadic eye movements is the result of some active modulation of this impulse to determine the specific action of the individual extraocular muscles and their combined effect. Apparently the only way the rate of

saccade initiation can be significantly altered is to suppress the impulse altogether or perhaps to balance the input to the extraocular muscle fibers capable of very rapid contraction so the net effect on eye position is essentially zero.

When the monkey is not required to minimize the variability of his eye position he makes relatively large saccades. The untrained cat rarely makes saccades and these are relatively large (Pritchard and Heron, 1960). Eye position is maintained with slow control, that is with drifting in one direction being compensated by drifting in the opposite direction resulting in a slow oscillation of eye position (Winterson and Robinson, 1975). Human eye movements have been recorded in situations characterized by some instructional set regarding where to look or what to seek in the visual stimulus (eg. fixation, reading, visual search). It might be expected that human eye movements recorded in a situation which places minimal constraints on looking behaviour would appear similar to the eye movements of the untrained monkey or perhaps even the cat. One might expect to see larger saccades and greater variability in eye position. If there were no specific requirements for attention to specific visual stimuli, for information extraction or for the maintenance of eye position one might expect to find a different distribution of intersaccadic intervals than are typical of maintained fixation. On the other hand if there is a neural mechanism which initiates saccades at particular intervals independent of the viewing situation one might expect to find no substantial difference in the distributions of intersaccadic intervals. The only occasion which would alter saccade rate would be an attempt by the

subject to suppress saccades. If the distribution of the intervals between saccade onsets does not vary substantially in situations where saccadic amplitudes differ, this would suggest that a neural generator sends out initiating volleys at certain intervals and that these volleys may be subsequently modified by other inputs to determine the specific muscle firing pattern and thus the direction and amplitude of saccadic eye movements.

There may be an effective area of inhibition along a contour extending a few minutes of arc from the contour. The metacontrast literature might predict that such inhibition would have both spatial extent and temporal extent. (Metacontrast varies not only as a function of the interval between the onsets of two immediately adjacent contours but also at any stimulus onset asynchrony metacontrast decreases with increasing spatial separation between the contours). Displacement of a target image to a point within such a temporary zone of interference would minimize the likelihood that the target would be perceived. This view is consistent with the finding that visibility of a stabilized image target is restored when the image is rapidly displaced by at least 2 minutes of arc or more slowly displaced over a greater distance (Ditchburn et al.; (1959). If drift rate were too slow to outdistance the inhibition it might not contribute to target visibility. A flick of sufficient size should assure visibility, not by virtue of the motion itself, but by moving the image to location where perception is unaffected. This notion of an inhibitory area along a contour is also consistent with the finding that target steps smaller than 3.4 minutes are less likely to be perceived and tracked

with corrective saccades (Wyman and Steinman, 1973). The drop in detection from essentially perfect performance to 65 per cent accuracy when step size is reduced from 3.4 minutes of arc to 1.7 minutes of arc suggests that sensitivity is reduced in an area a few minutes of arc in extent along a contour.

The spatial extent of interaction between contours has been described as a few minutes of arc (Flom et al., 1963). If there were an effective area of inhibition along a contour where perception of another contour was adversely affected, the second contour would have to lie beyond the zone of interference surrounding the first contour to be readily perceived. The location of a target contour within the zone of interference around a second contour might mimic the situation where a target is displaced so little that the step falls in the oculomotor "dead zone". When the subject is required to perceive the target stimulus in order to make some judgment about it he may flick his eye back and forth over the target with saccades which should be sufficiently large to move the image out of the relatively insensitive zone. However since the added contour is fixed in its distance from the target contour little if any improvement in perception should result from these eye movements. At a contour separation where perception of the target stimulus was significantly attenuated one might expect the subject to make a number of flicks of a size and direction appropriate to displacing the target image from the "dead zone".

CHAPTER THREE

CONTOUR EFFECTS IN VISUAL PERCEPTION

A contour, which is an abrupt change in luminance between two immediately adjacent areas, may enhance the perception of a difference in brightness between the two areas. The estimated size of the area affected by a contour varies considerably across studies. There are also some discrepancies in the reported nature of the effect. Most studies describe an interference (inhibition, suppression) effect but some describe a facilitation effect. A few studies demonstrate both effects, an interference effect over an area next to the contour and a facilitation effect at slightly greater distances. Further, anything which alters the perceptual effectiveness of a contour may influence the perception of brightness difference. Several studies suggest that the proximity of a second contour diminishes the perceptual impact of the first.

The experimental conditions employed in the different studies varied considerably with respect to luminance levels tested, target dimensions and viewing time or exposure duration of the target. Although the present work is concerned with relatively small, high contrast (black and white) stimuli viewed as long as the subject wishes, the problem may be set in context with a brief review of the typical studies suggesting contour effects. In general the studies fall into two major classes with respect to the subject's task: (1) the perception of a difference in brightness (in a broad sense this includes contrast sensitivity) and (2) the ability to resolve spatial

detail (a class which may be considered to include various measures of visual acuity as well as letter recognition tasks).

The independent variable which these studies have in common is some variation in the spatial extent of a target figure or, more particularly, in the separation between contours. Among the tasks involving brightness discrimination the dependent variable is the luminance difference (between adjacent areas) necessary for perception of a brightness difference on

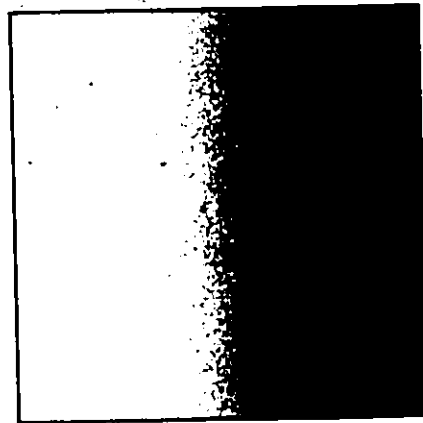
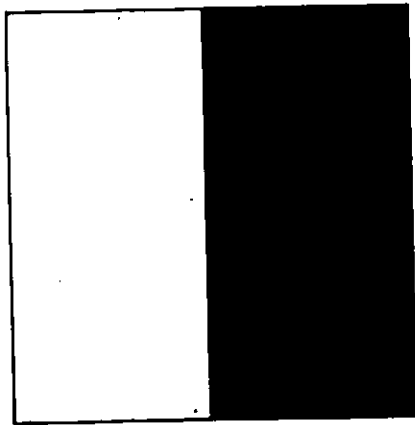
a criterion proportion of trials or the contrast ratio $\frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}}$

necessary for a criterion level of responding. When exposure durations are brief the exposure duration of the target necessary to achieve criterion performance may be the dependent variable. In the tasks concerned with spatial resolution the dependent variable is either the minimum separation perceived on a fixed proportion of trials or the probability of a correct response to a fixed separation between target contours. The distance to adjacent contours may determine performance in any of these situations.

Perception of Brightness Differences: Simultaneous Effects

Where there is an abrupt transition from a light area to a dark area, the edge of light area appears brighter than the remainder of the light area and the edge of the dark area next to the contour appears even darker than the remainder of the dark area (Figure 1). Objectively, there is no such variation in luminance. This subjective phenomenon, called 'Mach bands' (see Mach, 1914) requires a steep change in luminance if the bands are to be sharp (Bekesy, 1968).

Figure 1. Luminance gradients: A step change in luminance and a gradual transition. Mach bands appear in both situations but are sharper when the luminance gradient is steep.



Ratliff (1972) has described a physiological mechanisms in the compound eye of Limulus, the horseshoe crab, which may serve as a model of how Mach bands might be produced in the visual system. He found that along a transition from a light area to a dark area (an edge) the responses of visual cells exaggerate the luminance difference through a mechanism he called "lateral inhibition". The receptors at the edge of the light area are effectively subject to inhibition from only one side and are thus free to fire more rapidly than receptors in the rest of the light area. Conversely, the receptors at the edge of the dark area are subject to greater inhibition (from receptors in the light area) than are the other receptors in the dark area and therefore fire less rapidly.

This concept of lateral inhibition may be more readily understood by reference to Figure 2. The activity of a receptor cell (A) stimulated by light is reduced when a second nearby receptor (B) is also stimulated with light. The effect is a reciprocal one with each stimulated cell inhibiting the other, however the cell stimulated by the higher luminance inhibits the other more strongly. Stimulation of a third receptor (C) sufficiently distant that it has little or no direct effect on the firing rate of the first cell (A), but inhibits the second (B), disinhibits firing in the first cell (A)--its firing rate is increased again.

In a pattern of successively lighter stripes with a fixed increase in luminance from one stripe to the next there appears to be a slope in brightness within each stripe (Figure 3) even though individual stripe luminance is uniform (Hering, 1920). If both stripe

Figure 2. Lateral inhibition in the eye of Limulus (Ratliff, 1972). The activity of cells stimulated by light at A and B appear in records a and b, respectively. The time of light stimulation at A, B and C is indicated by the stippled bars below the activity record. In the uppermost record the rate of cell firing to stimulation at A is only slightly reduced by stimulation at C. In the lower records, firing to stimulation at A is clearly inhibited by simultaneous stimulation at B. Stimulation introduced at C inhibits firing to B thus disinhibiting firing to A. (See text).

LIGHT

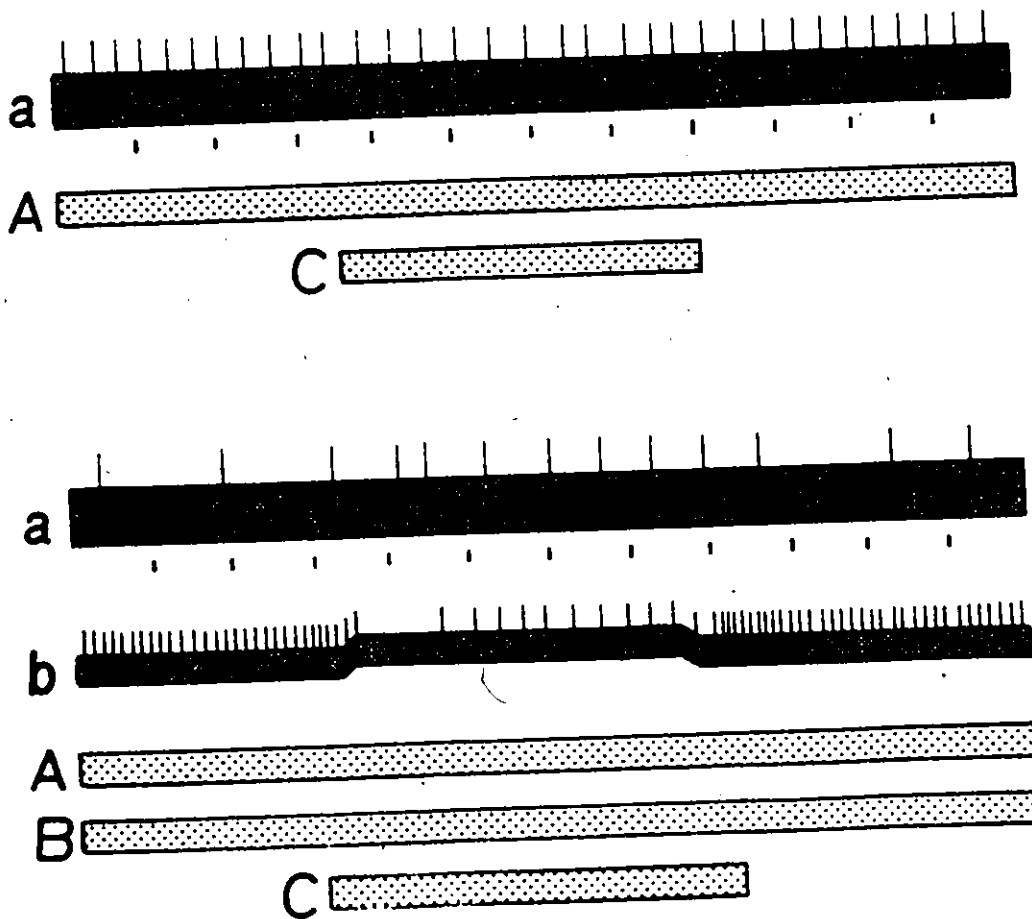
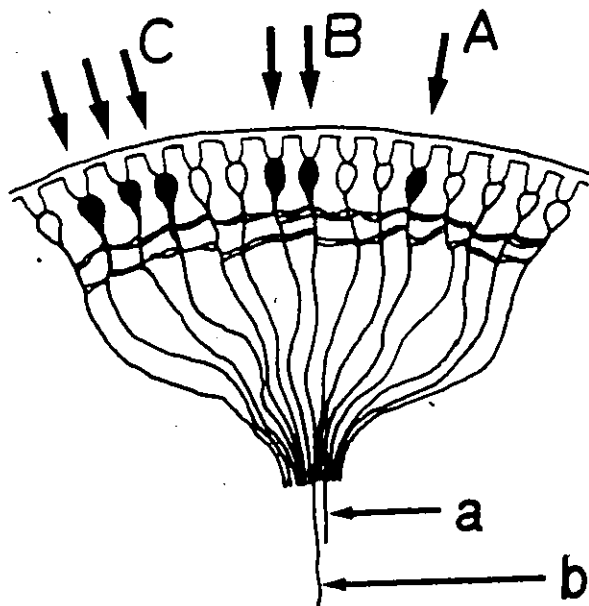
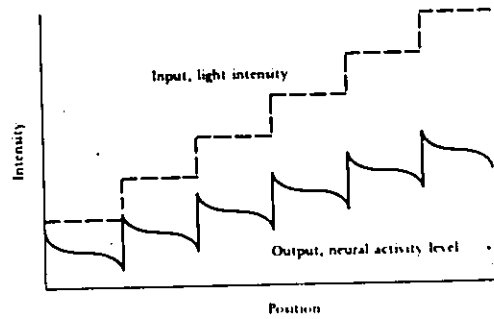
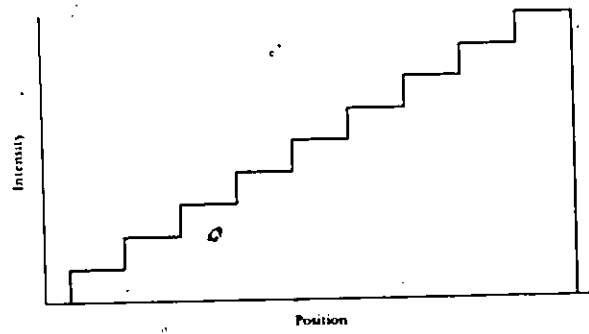


Figure 3. A pattern of successively lighter stripes, each of a uniform luminance, demonstrating Hering inhibition.



width and the luminance difference between stripes are reduced in a fixed ratio to each other the slope of the inhibitory effect is increased and its absolute extent is diminished.. On the other hand if the corners of the luminance step (the transition in luminance) are rounded or if the ascending part of the step is diffused by a rotating prism, both of which make the luminance change more gradual (as in Figure 1) the slope of the inhibitory effect is decreased (Bekesy, 1968).

In experiments to determine brightness difference threshold a small disc-shaped spot of light is viewed against a larger surround or background of uniform luminance. In the studies to be reported here, the area immediately surrounding the central spot is of fixed luminance. The brightness difference threshold is the increase in luminance of the test spot above that of its surround necessary for the spot to be perceived on a fixed proportion of trials.

Fry and Bartley (1935) have done a number of experiments which they believed demonstrated the effect of contour on the brightness difference threshold. They found that increasing the diameter of the central disk from 26 minutes of arc to 4.0 degrees reduced the brightness difference threshold but that further enlarging the disk to 8.0 degrees had no effect on threshold. The borders on opposite sides of the disk were thought to have interfered with each other and thus with perceiving the difference in brightness between the disk and its surround.

A similar result for rectilinear stimuli also demonstrated the specificity of the effect to contours of similar orientation. The

brightness difference threshold between two rectangular areas varied with the luminance of two squares one on either side of the rectangles. When the flanking squares formed common borders with the rectangles which were parallel to the border between the two rectangles, the brightness difference between the rectangles increased as the flanking squares became lighter or darker than either of the rectangles. However when the rectangles were oriented horizontally with their common border at right angles to the border formed with the squares, the brightness difference threshold between the rectangles fell continuously as the luminance of the flanking squares increased.

The brightness difference threshold for a disk, surrounded by an annulus whose inner diameter equalled that of the disk (47 minutes of arc) varied with the outer diameter of the annulus. As the distance between the edge of the disk and the outer edge of the annulus increased, the brightness difference threshold for the disk decreased asymptotically at 4.0 degrees, Fry and Bartley (1935) concluded that over short distances the contour at the outer edge of annulus prevented (perceptual) formation of the edge of the disk and thus prevented perception of a brightness difference.

Westheimer (1967) sought to determine whether the interaction effect on these thresholds occurred at the retina (the receptor surface of the eye) or somewhere higher in the visual system (in the brain) where input from the two eyes converged. The threshold target was a flashing spot which stimulated a retinal area 3.0 degrees from the fovea. The spot was viewed against a disk which was itself surrounded by an annulus. The diameter of the disc was selected to give the

minimum luminance difference threshold for the spot at that retinal eccentricity. When the disk and spot were surrounded by the annulus and viewed monocularly a marked reduction in spot threshold accompanied an increase in annulus luminance to equal that of the disk. However when the disk and spot were viewed by one eye and the surround annulus by the other eye (with the targets suitably aligned) the luminance threshold of the spot increased slightly when the annulus luminance was raised to equal the disk luminance. The interference exerted by the outer edge of the disk on spot threshold was apparently a retinal effect as presentation of the equally luminous annulus to the same retina counteracted the effect.

The threshold for a briefly flashed spot varies with its distance from a contour (Wildman, 1974). The threshold for detecting the spot is predictably higher on the high luminance side of an edge than on the dark side. However, on the light side right next to the edge (where a bright Mach band might appear) the luminance threshold for the spot rose to a sharp peak suggesting that there was an area of interference along the contour. The threshold declined fairly steeply on the dark side of the edge but the slope of the decline became more gradual further into the dark area away from the edge. The 'high side edge effect' was almost entirely absent at low intensities, developing with increasing intensity and remaining constant at even higher intensities.

Rather than vary the intensity of the target stimulus, Rousseau and Lortie (1970) briefly presented a thin vertical line at a fixed intensity and found that detection of the line varied with the

proximity of two flanking parallel dark bars. The test line was 25 seconds of arc wide and the bars were 31 minutes of arc in width. All were 1 degree 3 minutes ($1^{\circ}3'$) in height. When the bars were less than 31 minutes apart detection was inhibited compared to when the test line was presented alone. Line detections increased with bar separation to reach a maximum when the bars were about 62 minutes apart. At that point the number of detections exceeded that obtained with no bars present. With further increases in bar separation detections levelled off at a value comparable to detection of the test line when it was presented alone. The facilitation observed when the bars were 62 minutes apart was thought to reflect disinhibition like that described by Ratliff (1961, 1974).

Perception of Brightness Differences: Sequential Effects

The perception of a briefly presented visual stimulus may also be inhibited by the successive presentation of another stimulus, a phenomenon called backward masking. Masking of a letter or some other figure is effected when a bright flash of light is presented immediately after the target stimulus. Another effective masking stimulus is a pattern which overlaps the area occupied by the target figure. The probability of detecting the target stimulus increases as the interval between the target stimulus and the masking stimulus is made longer. An annulus which just surrounds the area occupied by a target letter also acts as a masking stimulus (Averbach & Coriell, 1961). At a given interstimulus interval the amount of masking decreases with increased diameter of the masking disk. While the curves for larger disk masks merge at an interstimulus interval of 100

milliseconds there is still considerable masking by a smaller disk (Kolers, 1962).

Maximum backward masking is obtained when a rectilinear target and mask have the same orientation. Sekuler (1965) found that the duration threshold for detection of a black vertical stripe decreased with increasing orientation differences up to 45 degrees. Although masking was still evident for orientation differences greater than 45 degrees the effect was independent of orientation. When the test stripe was horizontal the orientation effect extended to slightly larger orientation differences.

Backward masking with no spatial overlap between the target and mask stimuli is called metacontrast (Alpern, 1952). Pairings frequently used are a disk followed by an annulus or a vertical bar followed by two adjacent bars, one to either side of the target bar. The subject's task is usually related to the apparent brightness of the stimulus; he may be required to match the perceived brightness of the target to a standard or he may be asked to indicate whether or not the target was perceived. The amount of metacontrast may be inferred by the luminance or duration of the target necessary for it to be detected on a fixed proportion of trials.

Visibility of the target varies as a U-shaped function of stimulus onset asynchrony. Metacontrast masking increases as the interval between the onset of the target and the onset of the mask increases up to approximately 100 milliseconds, and then decreases with still longer intervals. Metacontrast is greatest when the border of the masking stimulus is contiguous with the border of the target

stimulus and diminishes with increasing separation between the borders (Alpern, 1953; Kolers, 1962). Metacontrast may still be obtained for separations of at least 1.0 degree when the target and mask are light stimuli (Alpern, 1953; Fry, 1934). When the target is presented to one eye and the mask to the other (dichoptic presentation) the effective separations are somewhat smaller (Kolers and Rosner, 1960).

Metacontrast is easier to obtain when the target and the masking images fall on a retinal area peripheral to the fovea (Alpern, 1953; Kolers, 1962; Fehrer and Raab, 1962). Kolers and Rosner (1960) were able to obtain foveal masking with dichoptic presentation but only if the edge of the disk target and the inner edge of the masking ring were exactly coincident. Normally, if the target and mask are presented simultaneously to the same eye (or to both eyes at once) the target is perceptible. However, simultaneous dichoptic presentation of the disk and the ring resulted in suppression of perception of the disk suggesting that binocular rivalry might be interacting with metacontrast effects. Binocular rivalry arises when the two eyes view targets which are sufficiently different that the images cannot be fused. In that event the input from one eye is suppressed and only the stimulus viewed by the other eye is perceived. Kolers and Rosner noted that although the disk might be discriminable at the shortest target-mask intervals it frequently appeared irregular. Even with foveal observation the disk appeared to have a faint grey border or to be slightly smaller than the ring.

The finding of metacontrast effects with dichoptic viewing indicates that this type of contour interaction can take place at some

supraretinal location in the visual system where the inputs from the two eyes converge. Any difference between the dichoptic effects and those obtained with either binocular or monocular viewing would suggest that, although there may be similar interactions at different levels in the visual system the mechanism of these effects may vary. Contour interactions obtained with binocular viewing may reflect a composite of monocular and dichoptic effects. Evidence of metacontrast effects at the fovea, albeit under dichoptic viewing conditions, indicate that this type of contour interaction is not unique to the visual cells receiving input from the peripheral visual field.

Manipulation of contour separations affects thresholds in a metacontrast paradigm as well as in the perception of a brightness difference in the studies reported previously. Kolers (1962) presented a black disk target, 30 minutes of arc in diameter, and a succeeding black annulus mask with an inner diameter of 42 minutes both at an intensity of 5.0 foot-Lamberts. The threshold duration of the disk increased as the wall of the annulus was increased from 2.0 to 20 minutes subtense and decreased slightly with further increases in the thickness of the wall. Even when the outer diameter of the black ring was extended to infinity, resulting effectively in a white disk mask, some inhibition of the target disk still occurred.

Relatively edgeless stimuli are less susceptible to metacontrast masking (Weisstein, Ozog and Szoc, 1975). When a target and a spatially flanking mask stimulus which were of equal luminous intensity and which shared the same figural properties were presented as random dot stereograms (Julesz, 1971) rather slight backward masking

was obtained but there were no metacontrast effects (Breitmeyer and Ganz, 1976); the amount of masking declined steadily as the interval between the onset of the target and the onset of the mask increased rather than rising to a maximum at some interval and then declining with longer intervals. Apparently continuous contours are necessary to obtain metacontrast effects.

Letter Recognition

While metacontrast masking is maximal when target and mask are separated in time by a fraction of a second, there is growing evidence that two adjacent contours presented simultaneously, whether briefly or for as long as the subject requires to respond, interfere with each other when they are spatially separated by a short distance. In some cases it is not clear whether this limitation is imposed by the visual system itself or whether it reflects constraints on cognitive processing. Nevertheless some regularities emerge from the various studies. For example, subjects may be asked to identify letters in a row which are available for unlimited viewing or for only a fraction of a second. These stimuli are frequently presented in a tachistoscope, a device which permits presentation of visual stimuli for a variety of exposure durations and also permits the superposition of two or three difference stimulus fields in the subject's line of sight. The subject typically views a fixation target, such as a small dot, centered in an adapting field prior to presentation of the stimulus array.

The presence of additional letters adjacent to a letter to be identified interferes with perception of the target letter. The combined effect of two flanking letters (one on either side of the test

letter) is more deleterious than that of one adjacent letter. The spacing between letters is an important factor as recognition of the target letter improves with increased spacing between it and any flanking letters. Moreover, the replacement of a letter with a blank facilitates recognition of the letters nearby.

When exposure duration is limited to 50 milliseconds and demands on memory are minimized a letter easily recognized by itself is much more difficult to identify in an array particularly in positions intermediate between fixation and the ends of a row (Averbach and Coriell, 1961; Merikle et al., 1971; White, 1971). Even with an exposure duration of 200 milliseconds recognition of a single letter presented to a retinal area just outside the fovea is greatly reduced by the addition of one adjacent letter and is even further reduced by the addition of another letter on the other side of the test letter. With increasing separation between the two flanking letters and the test letter recognition returns to the level obtained when the test letter is presented alone (Bouma, 1970).

Even with unlimited viewing and fixation to the left of a row of 9 letters, each 20 minutes wide, letters at the ends of the row are more readily identified than those a few positions from the right end of the row. Nevertheless, single letters presented in these more central (row) positions are identified as accurately as the end letters in the row. When a letter in one of these row positions is replaced with a blank, recognition of nearby letters improves (Townsend, Taylor and Brown, 1971).

Eriksen and Rohrbaugh (1970) exposed single letters approximately 12 minutes of arc wide for a duration which permitted 85 percent accuracy in identifying the letters. The exposure duration ranged from 11 to 17 milliseconds across subjects. When the target letter was flanked by two other letters, disks or X's of comparable size and at each of three different spatial separations, target identification was reduced only at the smallest spacing of 4.8 minutes of arc. Similarly, forced-choice reaction time to a foveally viewed target letter flanked on either side by three noise letters (forming a row) increased as the spacing between the letters reduced from 60 minutes to 30 minutes to 3.6 minutes (Eriksen and Eriksen, 1974). The subjects were required to press one lever if the target letter was H or K and to press another lever if the letter was S or C. The differential effect of angular versus curved noise letters was most apparent at the smallest letter spacing tested.

The plausibility of the assumption that perception of an individual letter is adversely affected by the presence of adjacent letters (Woodworth, 1948) has been strengthened by the finding that the higher probabilities of identifying end letters in a row are reduced by the addition of parentheses to the ends of the array (Haber and Standing, 1969). This finding that the spacing between a letter and adjacent contours (whether letters or disks) affects letter recognition suggest that there is interference between adjacent letters.

Curiously, one lab has reported that nearby contours facilitate letter recognition. Matthews and Henderson (1971) found that a target letter centered in a row of eight letters was more readily recognized

than when it appeared alone. The letters were 22 minutes high and ranged in width from 16 to 22 minutes. Depending on the letter combinations used the angular separation between the closest contours of the target letters and the two flanking letters varied from 1.5 to 4.25 minutes of arc. The exposure durations were short (3 to 9 milliseconds), and background luminance was relatively high at 28 foot-Lamberts. In a subsequent experiment (Matthews, 1974), the same single letters were presented for a few milliseconds simultaneously with a surrounding annulus which had an internal diameter of 30 minutes and an external diameter of 52 minutes (therefore, the wall of the annulus was 11 minutes wide). The separation between the inner edge of the annulus and the nearest edge of the various letters ranged from 8.0 to 14 minutes of arc. The magnitude of the facilitation effect of the annulus varied markedly across subjects. When ring thickness was held constant at 11 minutes and the inner diameter of the annulus was varied over values of 36, 54, 72, 90 and 108 minutes the letter recognition scores of two subjects peaked at 54 minutes while the performance of a third, which was lower overall, peaked at 36 minutes. Such variable results raise the question of whether the subjects wore lenses to correct optical errors of vision during the experiment or if such variability may be typical of experiments in which exposure duration is limited to a few milliseconds.

Interpreting his results in terms of visual cell receptive field organization Matthews suggested that facilitation was greatest when the dark target and the dark annulus covered the inhibitory flanks of a cell whose receptive field centre lay between the target and the

annulus. Increasing the inner diameter of the annulus would result in stimulation of the inhibitory flanks by the white area, decreasing firing to stimulation of the centre. Ultimately the inhibitory area would be sufficiently affected to completely offset the centre response.

Contrast Sensitivity

A luminance grating is a target of alternating parallel light and dark bands of equal width. A square wave grating is one in which the luminance changes abruptly from one band to the next. The absolute value of the luminance difference between bands is constant and the luminance across a single band is uniform. In a sinusoidal luminance grating luminance varies at right angles to the target plane as a sine function of distance along the plane. The luminance of the bands changes more gradually from light to dark and back again. A light band and an adjacent dark band are referred to as one cycle of the grating. The spatial frequency of a grating is the number of cycles contained within a fixed distance along the grating expressed as one degree of visual angle. The greater the number of cycles per degree, the higher is the spatial frequency and the finer is the grating pattern. The half-cycle width refers to the width of one light or dark band in the grating pattern.

One major difference between the paradigm for determining the contrast threshold for a grating target and that for determining a brightness difference threshold is that the contrast of the grating is varied about a constant mean luminance. The only circumstance under which the overall luminance of the target would vary is if the viewing

situation did not permit presentation of an integral number of cycles at all spatial frequencies tested. Such a variation would be of greater concern at lower spatial frequencies. Contrast is usually expressed as a ratio of the difference between the maximum

and minimum luminance $\frac{(L_{max}-L_{min})}{L_{max}+L_{min}}$. As the minimum luminance

approaches zero the ratio goes to 1.0 whereas when the minimum luminance approaches the maximum luminance the ratio goes to zero. The greater the contrast the closer the ratio is to 1.0.

The presence of adjacent contours may affect the contrast threshold for a grating target. Estevez and Cavonius (1976) determined contrast sensitivity for sinusoidal luminance gratings presented on a homogenous field equal in luminance to the mean grating luminance and found that sensitivity (the inverse of the contrast threshold) peaked at intermediate spatial frequencies. When the grating was surrounded by dark lines (six or 12 minutes wide) and presented against the homogenous field, sensitivity did not reach a peak at intermediate frequencies and was somewhat attenuated at higher spatial frequencies. When the grating was presented against a dark background sensitivity was lower at all spatial frequencies than it was when flanked by the dark lines, with the greatest drop in sensitivity at the lower spatial frequencies.

Nachmias (1968) superimposed a grating pattern 3.75 degrees high and covering a constant area or a pattern consisting of one and a half cycles of the grating (two light bands flanking one dark band) on a circular background 9.0 degrees in diameter. The half-cycle widths

tested were less than 43 minutes of arc. The patterns were oriented diagonally on the background which had a luminance of approximately 9.0 foot-Lamberts. At both exposure durations tested (11 and 500 milliseconds) contrast sensitivity was higher for the extended grating pattern than for the one-and-a-half cycle pattern. This apparent facilitation may reflect an interaction rather like the disinhibition described by Ratliff (1961) in the Limulus eye. It is also reminiscent of the disinhibition described in a backward masking paradigm by Dember and Purcell (1969) who demonstrated that a letter masked by a disk could be effectively unmasked by a ring which followed the disk.

Contour Effects Over Small Areas

Studies employing small targets viewed foveally suggest that contour effects may extend over a very few minutes of arc. These effects are apparent in both brightness difference thresholds and measures of spatial resolution. Westheimer (1967) found that the threshold luminance of a briefly flashed circular spot, 1.0 minute of arc in diameter, first rose as the background diameter increased up to 5.0 minutes of arc and then fell with further increases in background diameter. Viewing was foveal and background luminance was 0.40 log millilamberts. When the threshold was highest the outer edge of the background was 2.0 minutes of arc from the edge of the central spot. The effect on spot threshold was prominent over background diameters of 4.0 to 6.0 minutes of arc, which would entail contour separations of 1.5 to 2.5 minutes of arc. The result was the same whether the background was exposed for 250 milliseconds or for an indefinite period and regardless of whether the threshold was tested at the beginning or

end of the background exposure. When the background was flashed simultaneously with the spot and for the same duration (10 milliseconds) there was only a small effect of background area over a range of background luminances. Miller (1954) found that the brightness difference threshold of a light bar increased with increasing bar widths up to 4.0 to 6.0 minutes of arc where it levelled off. The effective bar widths are the same as the effective background diameters in Westheimer's study.

An interpretation of this result in terms of receptive field organization (to be discussed shortly) would be that at the diameter providing the greatest inhibition of perception of the spot (that is, where the luminance threshold was highest) the background just fills the inhibitory surround of a receptive field with an excitatory centre. In the receptive fields of many cells at various levels of the visual system there is summation of surround stimulation so that inhibition is greatest when the entire surround is just filled. Spillover onto an area larger than the surround might be expected to disinhibit responding to the central spot as there is some neurophysiological evidence of a disinhibitory extra-surround area. As the threshold luminance curve varies as an inverted U-shaped function of background diameter the probability of detecting a spot of fixed size and luminance would be expected to vary as a U-shaped function of background diameter suggestive of a trough-like area of interference along a contour.

Rentschler and Hiltz (1976) found that the threshold intensity of a vertical line 1.0 degree high by 1.0 minute wide may be raised in

presence of a parallel subthreshold line nearby and lowered when the second line is at a distance of at least 8.0 or 9.0 minutes of arc. The range of the inhibitory interaction and the distance at which facilitation was first evident decreased with increasing luminance of the added line. When the added line was slightly below threshold it remained invisible when the test line was bright and when the test line itself was below threshold. However, the added line was visible when the test line was dimly visible. Reciprocal facilitatory interactions were evident at the line separations where the presence of the second line lowered the threshold for the test line. This finding of interference giving way to facilitation with increasing distance from a contour recalls the observations of Rousseau and Lortie (1970) however, the dimensions of the added lines and the extent of the apparent zone of interaction were both much larger in the earlier study.

Visual Acuity

Visual acuity tasks and letter recognition tasks typically require spatial resolution of high contrast target patterns. A chart frequently used as well as other typical targets appear in Figures 4 and 5. Contour interaction may play a role in these situations where the effect of a contour appears to extend over just a few minutes of arc. A long black line may be detected when it subtends a visual angle as small as 0.5 seconds of arc (Hecht and Mintz, 1939). A misalignment of two line segments (vernier acuity) can be perceived when the displacement is as small as 2.0 seconds of arc (Berry, 1948). Both of these values are considerably smaller than the 15 to 30 seconds of arc minimum separation between two spots or lines which can be perceived

Figure 4. Snellen acuity chart.

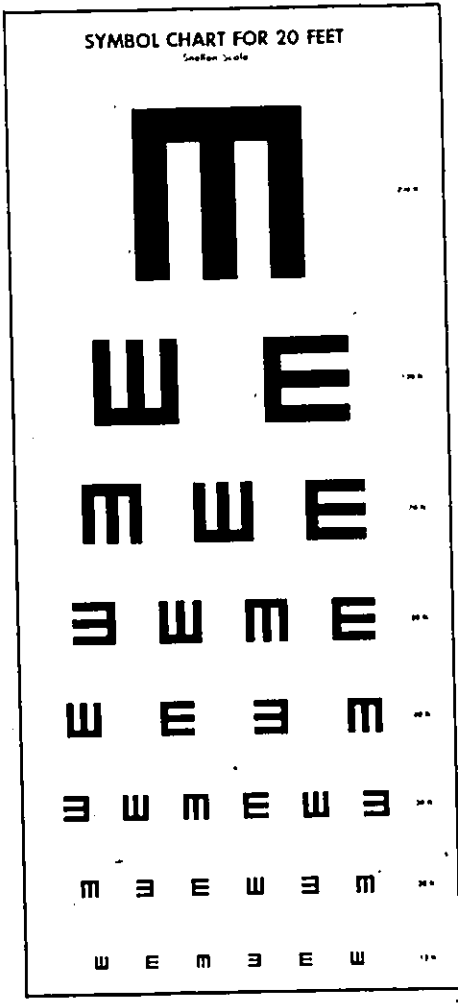


Figure 5. Examples of acuity targets.
(A) Snellen E, also known as
the "Illiterate E" (B)
Landolt ring, (C) Snellen
letters and (D) vernier
target.

E W E M

A

C O O O

B

E
M B N C
R F A G P L T
U V D H J O S K Q W
D A E B R C X C F N Z V U P

C

| | | |

D

(Adler, 1959). Kulikowski and Tolhurst (1973) found that contrast sensitivity for stationary sinusoidal luminance gratings was greatest for a half cycle width of 8.5 minutes but they confirmed Westheimer's (1960) earlier finding that the smallest half-cycle width which permits detection of a grating is about 36 seconds of arc.

Persons with normal visual acuity can reliably read a row of letters which are each 5.0 minutes high by 4.0 minutes wide with individual lines and spaces each 1.0 minute wide. As some letters are more difficult to recognize than others (Sloan et al., 1952), acuity may be tested with Landolt rings instead. The latter are rings with a break in one of four or eight symmetrical locations. A break of 1.0 minute of arc can be located by someone with normal visual acuity.

The more difficult letters S, R, O, and B, may be likened to a complex pattern of lines such as a grating whereas the easier letters, L and J, are comparable to a single line target (Hartridge and Owen, 1922, Sloan, Rowland and Altman, 1952). The same factor which limits acuity for individual lines in a grating pattern may also limit acuity for the individual elements of a more complex letter.

Even when viewing time is unlimited a letter correctly identified when it is viewed singly may be more difficult to identify among other letters (Burian, 1969) whether in a row (Wagner, 1918; Taylor and Brown, 1972), in an array (Stuart and Burian, 1962) or on a Snellen acuity chart (Davage and Sumner, 1950).

Stuart and Burian (1962) found that in a 7 x 7 array of letters the four corner letters were identified most readily, however with increasing separation more peripheral letters were identified until

finally the most central letters were recognized. Similarly letters at either end of a row are identified more readily than those occupying less extreme positions regardless of whether viewing is monocular, binocular or dichoptic (Wagner, 1918; Taylor and Brown, 1972). When letters are presented dichoptically it makes no difference whether each eye is shown letters occupying sequential or alternating positions suggesting that there is a strong suparetinal component in the interaction between adjacent letters. Further evidence that adjacent letters interfere with each other comes from the finding that replacement of one of the letters in a row with a blank improves recognition of the adjacent letters (Townsend, Taylor and Brown, 1971).

Letters are relatively complex stimuli which may demand considerable cognitive processing over and above the initial analysis provided by the visual system. There are a few studies of contour interaction and visual acuity which make a minimum of cognitive demands and provide targets which more closely resemble the visual stimuli employed in the electrophysiological study of the visual system. These studies demonstrate that visual acuity for a particular target is affected by the presence of nearby contours.

Vernier resolution for two light vertical line segments is affected by the proximity of two horizontal line segments located one to each side of the vernier target (Westheimer and Hauske, 1975). The vertical line segments each 6.4 minutes high by 7.0 to 10.0 seconds wide, and the horizontal line segments, each 3.2 minutes long, were exposed for 50 milliseconds at a target luminance of 100 millilamberts. As the horizontal line segments were separated they interfered more

with vernier acuity than when they abutted the vertical lines. Beyond a separation of a few minutes of arc vernier acuity rapidly improved. Similarly the interfering influence of a pair of vertical lines, moved from virtual superposition on the target at 0.0 degrees displacement, increased to a maximum at a separation of several minutes of arc and then decreased at larger separations. Dichoptic presentation of the vernier pattern and the flanking vertical lines also resulted in a reduction of monocular vernier acuity indicating that interference with vernier resolution occurred at a central level. When the vernier pattern with and without vertical lines was presented at a longer exposure duration of 1.0 second, vernier thresholds were lower but the interfering effect persisted.

Monocular visual acuity for a gap in a Landolt ring, as well as accuracy in locating a gap of fixed size, is greatly reduced when the ring is surrounded by four bars, each parallel to an imaginary tangent and at a distance of about 1.0 minute of arc. Impairment is usually attenuated at smaller separations. With increasing separations acuity, or accuracy, improves and beyond 4.0 minutes' separation the bars have virtually no effect on gap perception (Flom, Weymouth and Kahneman, 1963). Resolution is similarly impaired regardless of whether the Landolt ring and peripheral bars are presented dichoptically or monoptically for 0.5 seconds (Flom, Heath and Takahashi, 1963). Surrounding the Landolt ring (or 'C' as it is sometimes called) with an array of C's and E's in various orientations also impairs visual resolution of the gap in the ring (Flom, Weymouth and Kahneman, 1963).

Binocular acuity as measured by Landolt rings, gratings, and Snellen charts is superior to monocular acuity (Horowitz, 1949; Davage and Sumner, 1950; Kahneman, Norman and Kubovy, 1967). Acuity is typically measured with high contrast test objects and expressed in terms of the minimum separable distance or the probability of seeing. Campbell and Green (1965) found that over a wide range of spatial frequencies the binocular contrast threshold for detection of a sinusoidal grating pattern was consistently lower than the monocular threshold.

Although more letters on an acuity chart are identified when viewing is binocular the improvement with row-by-row presentation of the letters compared to exposure of the entire chart is less marked than for monocular viewing (Davage and Sumner, 1950). Eriksen, Greenspon, and Lappin (1966) and Eriksen and Greenspon (1968) have found binocular summation in the recognition of a briefly presented letter. The work of Townsend (1968) however suggests that the binocular advantage may be limited to the case where forms are presented in a homogenous field, at least in a forced-choice recognition task. The subjects were required to report which of two target letters appeared within a 4 x 4 array of letters briefly presented to the fovea. The target letter was randomly located in the array among 15 nontarget letters. The binocular hit rate was best described by the average of the monocular hit rates indicating that binocular vision added nothing to the accuracy of letter recognition in this task.

A similar pattern of results were obtained in unpublished experiments by Blake, Fox and McIntyre (see Blake and Fox, 1973) on forced-choice recognition of target letters presented alone or in an array of nontarget letters. There was binocular summation for single letters, replicating Eriksen's results. However, when the target letter was surrounded by seven or thirteen nontarget letters, binocular performance was no better than monocular performance even though under both conditions the hit rates were above chance. Casperson and Schlosberg (1950) found that detection of dot numerosity could be described by the binocular probability summation model when the number of dots did not exceed four, otherwise binocular performance declined to the monocular level.

These findings all raise the possibility that the superiority of binocular performance is limited to rather simple displays with relatively few contours or perhaps to situations where the contours are widely spaced. Fry and Bartley (1933) hypothesized that the binocular response was a function of a summation process and an inhibitory process in combination. Consistent with this hypothesis are the experiments demonstrating interocular interference effects (for example, Flom, Heath and Takahashi, 1963). In complex displays containing numerous contours the contribution of interference may equal or even exceed that of summation thus eliminating any superiority of binocular viewing (Blake and Fox, 1973).

Contour Effects on Activity of Visual Cells

Contour interaction effects have been observed in the activity of single visual cells in the cat and in the monkey, whose visual

system and visual capacity resemble that of man (DeValois, Morgan and Snodderly, 1974). For example, a cortical cell which is maximally excited by a line of particular dimensions, orientation and location may be inhibited when the line is displaced somewhat laterally (Hubel and Wiesel, 1962; 1968). Recording in the visual cortex of the cat, Burns and Pritchard (1971) found that when a cortical cell responded optimally to a test line of a particular orientation and location, adding a second line at various distances from the first affected the cell's rate of responding. At some separation between the lines, the response rate fell below that obtained when the first line was presented alone.

The area of the visual field (and by implication the corresponding retinal area) which affects the electrical activity of a visual cell is termed the receptive field of the cell. Hubel and Wiesel (1962, 1968) recorded from cortical cells whose receptive fields consisted of an elongated excitatory region next to an elongated inhibitory region with the two sharing a linear boundary. These cells were most responsive to edges, stimuli consisting of a light, rectangular area immediately adjacent to a dark, rectangular area. The approach of an edge of opposite contrast (the mirror image of the optimal stimulus), effectively producing a bar of decreasing width, inhibited cell firing to the optimal stimulus.

The receptive fields of some cortical cells were found to have an elongated excitatory centre flanked by two inhibitory regions more or less symmetrical in area and in their effect on cellular activity. Hubel and Wiesel (1962) observed spatial summation in these cells, in

that the greater the area of an inhibitory flank covered by a stimulus, the greater was the reduction in the rate of cell firing. Moreover, simultaneous stimulation of both flanks had a greater effect on cell firing than did stimulation of one flank. Binocular summation of excitatory effects has also been reported. When a suitable stimulus is located in the excitatory region of each of the two corresponding monocular receptive fields of a binocularly driven cortical cell, the recorded response is greater than to stimulation of either eye alone and may even exceed the sum of the monocular responses (Hubel and Wiesel, 1962; 1968; Pettigrew, Nikara and Bishop, 1968; Burns and Pritchard, 1968).

It is tempting to speculate on the relationship between the perceptual experience of contour interaction for the human and the electrophysiological response of single visual cells in the cat and monkey. Generalization from the latter to the former cannot be justified at this time however as we cannot directly compare the electrophysiology of human and non-human species nor do we know much about the relationship between the activity of individual cells and the integrated function of the visual system. Moreover, the electrophysiological work generally requires paralysis of the eyes whereas contour interaction in humans has typically been demonstrated in a free-viewing situation.

CHAPTER FOUR

SMALL EYE MOVEMENTS AND CONTOUR EFFECTS

Experiment One. Are the Small Eye Movements of Fixation Unique?

Typically, microsaccades have been recorded while an observer has been fixating a small stationary target. Relatively little is known about the occurrence of microsaccades when no specific fixation instructions are provided. In a less constrained situation a different pattern of saccadic eye movements might well be expected. If there were some structure to the visual scene one might anticipate the occurrence of relatively large saccades as the line of sight was shifted from one area to another. Whether or not very small saccades would be observed in such a situation is a matter of some conjecture.

Skavenski et al. (1975) found that saccades less than 10 minutes of arc occur normally in the eye movement repertoire of rhesus monkeys. Reduction of target dimensions and separations in a discrimination task resulted in a shift of the distribution of saccade amplitudes toward more of these very small saccades. When fixation eye movement patterns were specifically rewarded, all 7 monkeys tested learned to keep their line of sight within 15 minutes of arc of the target for a period of 15 seconds, demonstrating fixation accuracy comparable to that of man.

Historically, fixation eye movements and the larger 'scanning' eye movements have been studied separately and there was some suggestion that microsaccades and 'scanning' saccades were generated by different neural mechanisms. Zuber, Stark and Cook (1965) found that a

single function described the velocity amplitude relationship for all saccades up to 3 degrees (whether they be classified as 'voluntary' saccades, 'corrective' saccades, or the microsaccades of fixation) suggesting that saccades of varying amplitude were generated by a common neural mechanisms or were at least limited by the same mechanics.

Cunitz and Steinman (1969) hypothesized that if saccades of varying amplitude were initiated by a single neural system the distribution of time intervals between saccades should not vary with saccade amplitude. They recorded eye movements while subjects steadily fixated the intersection of the arms of the letter 'T' and while they read a paragraph for comprehension. The saccades recorded during reading as the eye moved along the text, were relatively large. Microsaccades occurred in fewer than 5 per cent of the pauses between 'reading' saccades.

Although the direction and size of saccades differed substantially in the reading and fixation conditions, the distributions of time intervals between fixation microsaccades and between large reading saccades overlapped considerably. The difference between the mean log intervals was significant for one of the two subjects tested and was attributed to an appreciable number of long periods (more than 600 milliseconds) during which the subject made no saccades during fixation of the "T". The modal interval between microsaccades during fixation and the modal interval between 'reading' saccades were described as 'very similar'.

The median duration of all reading pauses containing microsaccades was almost twice as long as the median duration of reading pauses without microsaccades. According to the authors, when a microsaccade was made during a reading pause, it was made at about the same time that a large reading saccade would be expected. They concluded that the temporal distribution of eye movements was not related to their size and direction and that all saccades of varying amplitude were initiated by a single system.

Human microsaccadic eye movements may be the product of a rather arbitrary viewing situation and atypical of human eye movements in general. The present experiment was intended to determine whether microsaccades might occur in situations other than maintained fixation and to obtain a general idea of the possible variation in the amplitude and frequency of small saccadic eye movements in different situations. It was decided to record eye movements during maintained fixation of a small stationary spot of light and during conversation, a situation seemingly less constrained as no specific fixation instructions would be provided. Differing distributions of saccade amplitudes were expected in the two situations.

If Cunitz and Steinman (1969) were correct in their reasoning, no significant difference in the temporal distributions of saccades should be observed even though amplitude distributions might differ in the 2 situations. Cunitz and Steinman spoke of a common initiating mechanism and used the interval between saccades as the appropriate temporal variable. In the present study the interval between saccade onsets was taken as the variable indicative of the functioning of an initiating mechanism for saccades.

METHOD

Subjects. Three volunteers served as subjects in this study.

Apparatus. Eye movements were recorded by means of an optical lever system (Figure 6). The subject wore a tight-fitting helmet (Figure 7) on which were mounted a light source, a system of lenses for collimating the light emitted by the source (Figure 8), an adjustable mirror from which the column was reflected and an aluminum rod to which was attached a translucent screen (Figure 6 and 7). The weight of the helmet was counterbalanced by means of a flexible coil spring suspended above the subject's head. A scleral contact lens was placed on the subject's right eye (Figure 9). The lens was irrigated with physiological saline introduced through a hollow stalk which protruded from the lens. Affixed to the stalk was a tiny mirror chip. Collimated light was reflected by the adjustable mirror to the mirror chip and then brought to a focus on the translucent screen. The distance from the mirror chip to the screen was approximately 600 millimeters. The subject's left eye was occluded.

The reflected and focussed light spot could not be seen by the subject but was visible on the far side of the screen where a television camera was located. The image of the light spot on the screen and the output of a digital timer were simultaneously recorded on videotape (Figure 10). The smaller graduations of the grid on the screen each registered an eye movement amplitude of approximately three minutes of arc while the larger divisions corresponded to a displacement of approximately 30 minutes of arc. The eye movement records were uncontaminated by head movements because the optical system was carried on and moved with the head.

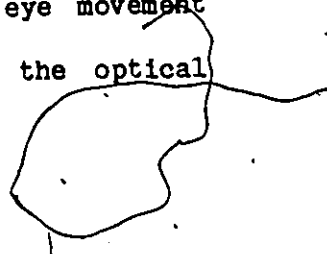


Figure 6. Scheme of the optical lever system for recording small eye movements.

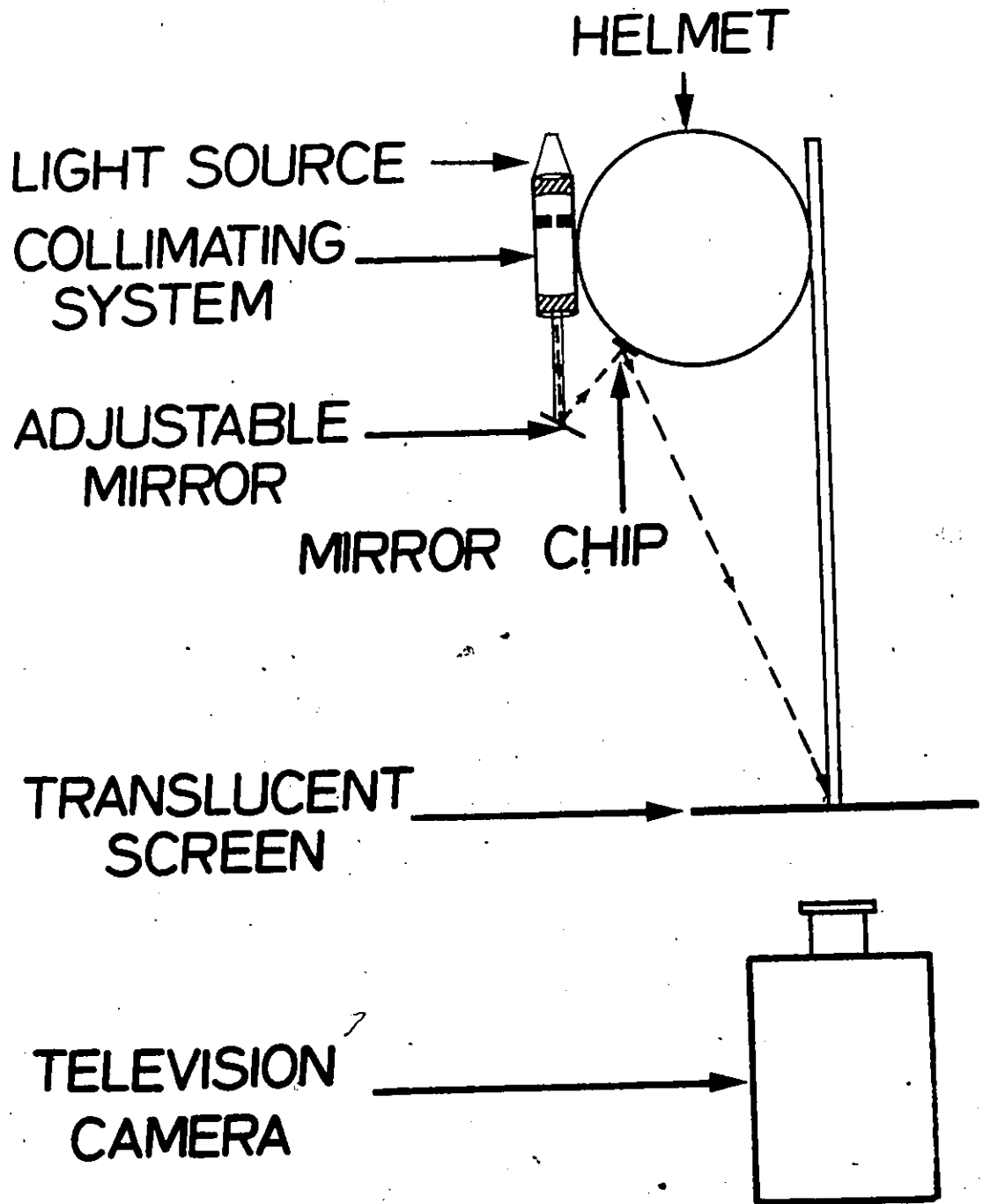
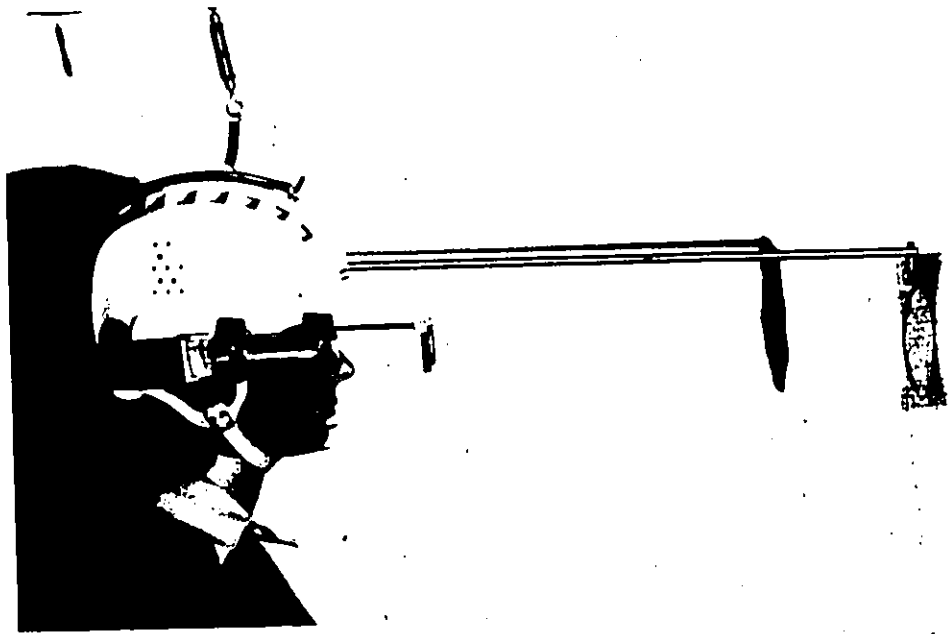
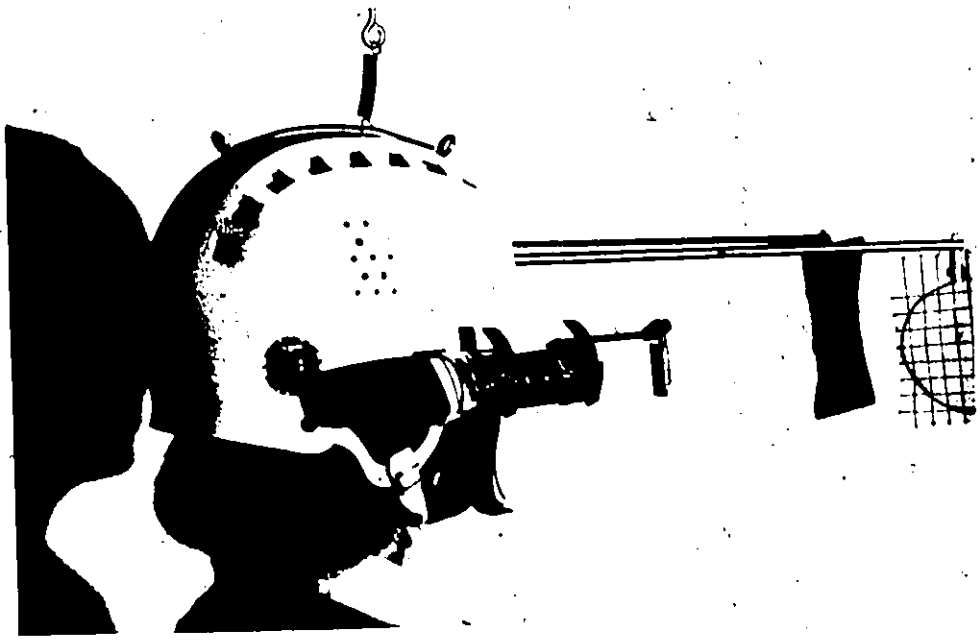
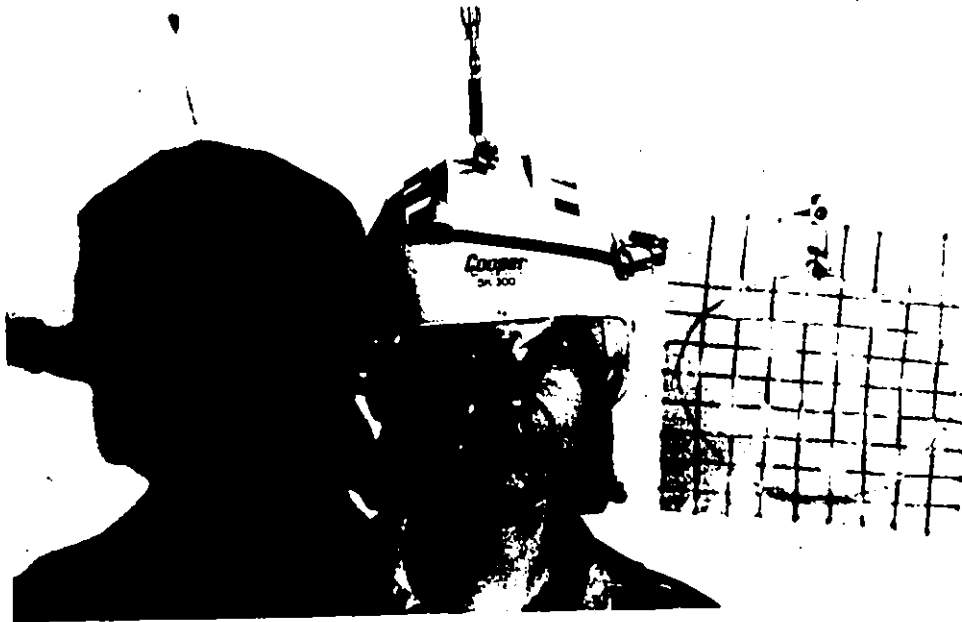


Figure 7(a-d). Subject wearing the helmet bearing the system for projecting and collimating the light, the adjustable mirror and the translucent screen.







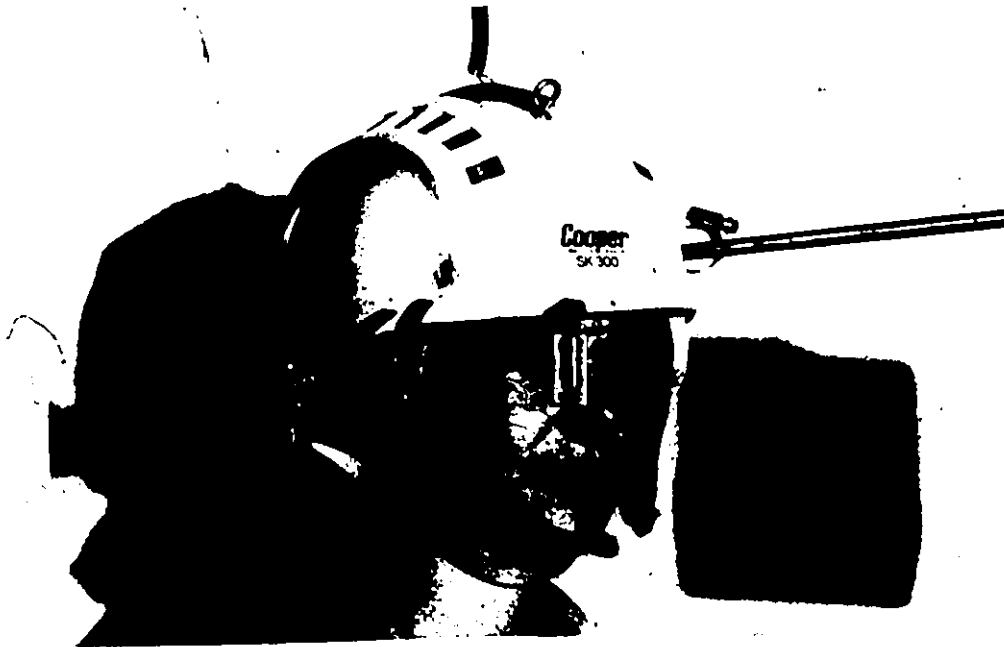
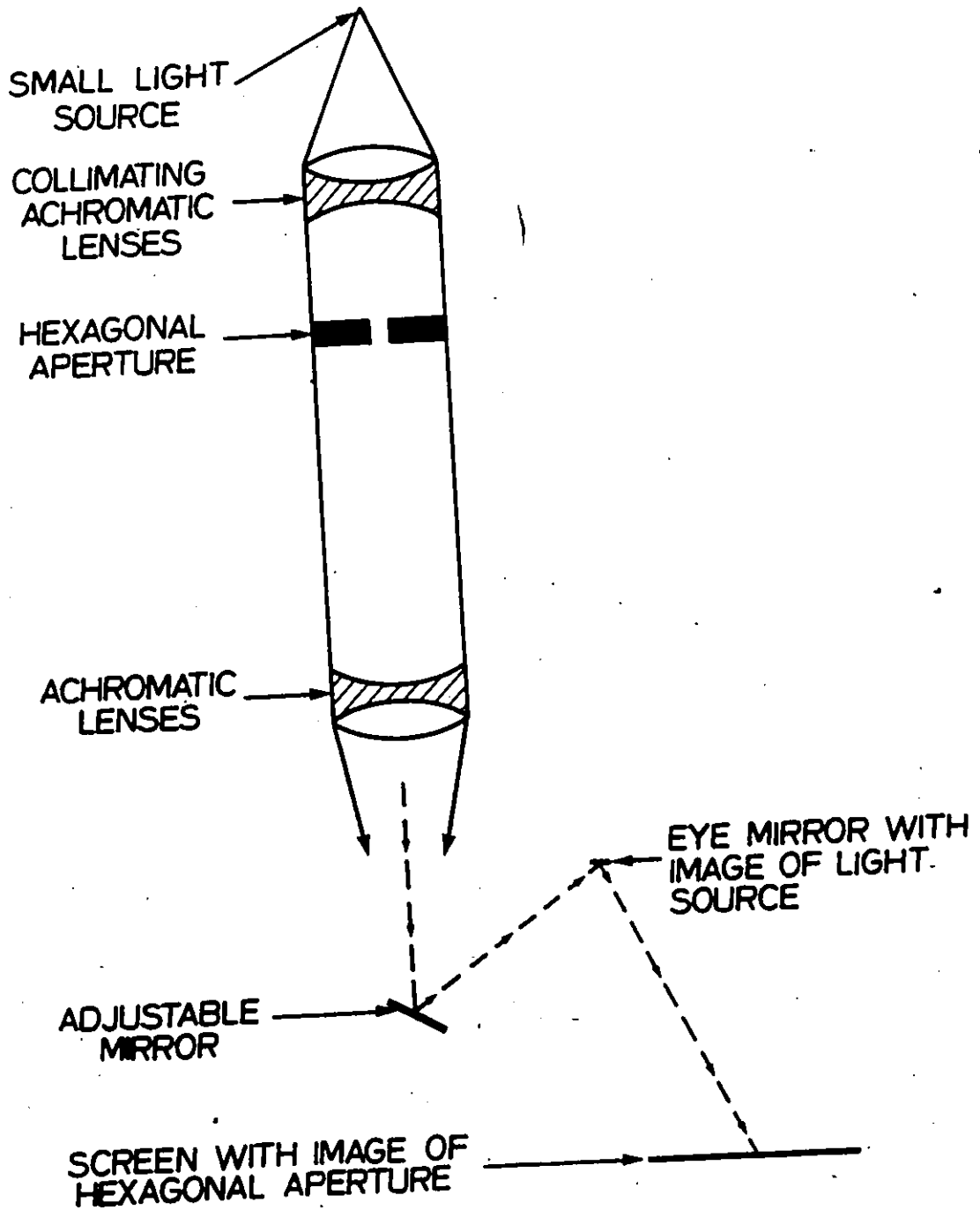


Figure 8. The system of lenses to collimate the light used to produce the spot on the screen.



NOT TO SCALE

Figure 9. Subject wearing the scleral contact lens with the attached hollow stalk, mirror chip and flexible tubing.



Figure 10. Image of the light spot on the translucent screen as it appeared on the video monitor, with superimposed output of the digital timer.



Procedure. The subject was seated in the laboratory where the background luminance was approximately 10 millilamberts. Over a short interval 2 drops of a topical anaesthetic (Ophthetic) were applied to the surface of the right eye. Once anaesthesia was achieved the lens and attached tubing were irrigated with physiological saline, the lids were gently retracted and the lens was placed on the eye. The lens adhered to the eye by means of the slight negative pressure created by gravity acting on the solution in the tubing. The eyelids were free to close over the lens as only the stalk carrying the tubing and the mirror chip protruded from the eye. The tubing was loosely looped over the ear and lightly taped in place so as not to interfere with movement of the eye.

The subject was then seated in front of the television camera and the helmet was placed on his head. While one experimenter aligned the mirror so that a clear reflected image appeared on the translucent screen and television monitor the other experimenter controlled the video recorder and continued to talk with the subject. The second experimenter was seated about 2 meters in front of the subject. While the eye movements of the subjects were recorded the first experimenter continued to apparently align and focus the various components of the eye movement system. As the subjects were unable to see the reflected image on the translucent screen they were unaware of this ruse. After several minutes of conversation the second experimenter announced that all was ready and the experiment could begin. In this manner eye movements were recorded without any or certain knowledge of the subject.

In the second part of the experiment a small light spot (less than 2 minutes of arc in diameter) was introduced in the subject's line of sight and he was asked to fixate the spot on a given signal. The subject was advised that there would be five 15-second periods of fixation alternating with 15-second rest periods. At the termination of the experiment the eyelids were retracted and the tubing was elevated, eliminating the negative pressure under the lens so that it virtually fell off the eye. Immediately upon removal of the lens a drop of Cetamide, an antibiotic, was topically applied to the eye.

The eye movement record obtained during conversation was sampled in five 15-second segments approximately 15 seconds apart. The segments for both conversation and fixation were viewed on the television monitor a frame at a time. The time difference between frames was approximately 16.7 milliseconds. Any displacement of at least 3 minutes of arc observed from one frame to the next (velocity at least 180 minutes of arc per second) was treated as a saccade (Figure 11). More gradual displacements were classified as drifts. Saccade amplitudes and the intervals between saccade onsets were computed for each subject and their respective frequency distributions were plotted for conversation and for fixation.

RESULTS

The eye is more mobile during conversation than it is during fixation (Figure 12). Eye movements recorded during conversation and during maintained fixation differed in several respects: (1) drift of the eye, (2) the relative frequencies of various saccade amplitudes, (3) the number of saccades occurring over a fixed period of time and (4) the distribution of intervals between saccade onsets.

Figure 11. Appearance of a saccade as viewed on the video monitor.

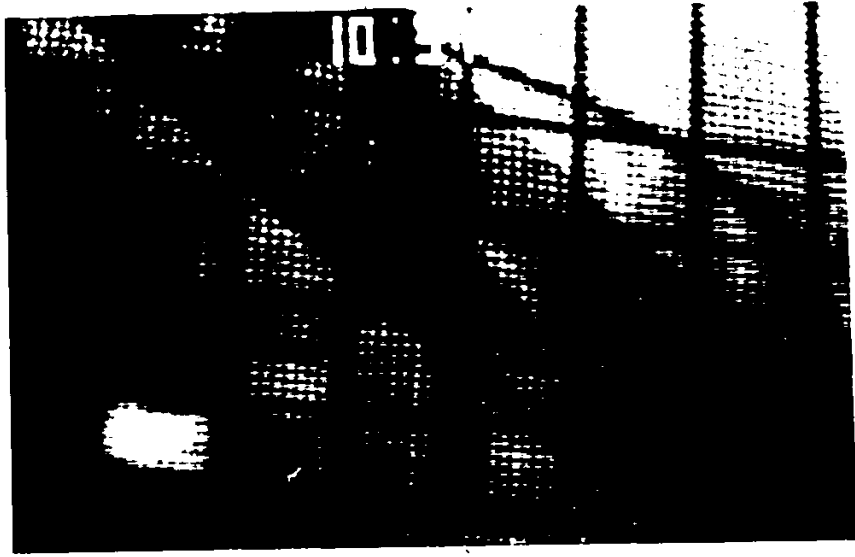
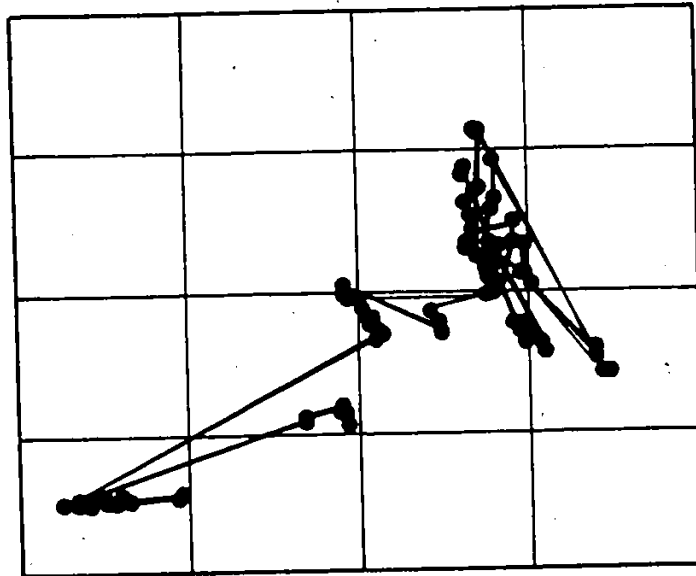
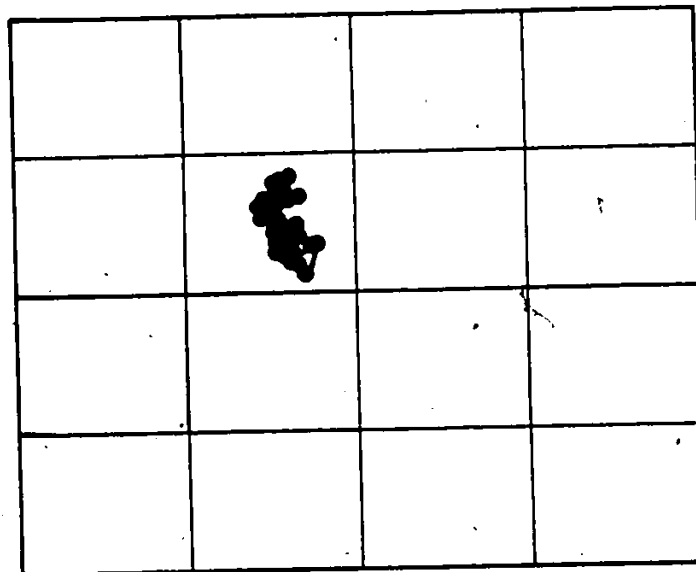


Figure 12. Variation in eye position
over 7 seconds of
conversation and over 15
seconds of maintained
fixation.

CONVERSATION 7 SECONDS



FIXATION 15 SECONDS



←30'→

There is a much greater tendency for the eye to drift when the subject is engaged in conversation than when he has been instructed to fixate a light spot. The eye may drift twice as far during conversation as it does during an equivalent period of fixation.

Most of the saccades which occur during fixation are less than 15 minutes of arc in amplitude; few are larger than 30 minutes (Figures 13 to 15). This is consistent with amplitudes reported previously for the microsaccades of maintained fixation (Fender, 1956). A wider range of saccadic amplitudes is evident during conversation as the distribution is skewed toward larger amplitudes. The eye may move up to 60 minutes of arc in one saccade. Displacements larger than 60 minutes are frequently (though not exclusively) associated with blinking. The distributions of saccade amplitudes recorded during conversation and fixation differed significantly for all three subjects (Table I).

More saccades occur during conversation than during an equivalent period of fixation. This difference is generally reflected in the greater frequency of intervals (between saccade onsets) of 100 milliseconds or less (Figures 16 to 18) recorded during conversation. The frequency distributions of intervals under the two viewing conditions differed significantly for all three subjects (Table II) with a shift toward shorter intervals between saccade onsets.

DISCUSSION

The amplitudes of saccades recorded during maintained fixation compared favourably with the range of amplitudes reported by previous investigators (Riggs and Ratliff, 1951; Fender, 1956; and Steinman et

Figure 13. Frequency of occurrence of various saccade amplitudes during five 15-second periods of conversation (A) and of fixation (B). Subject A.H.

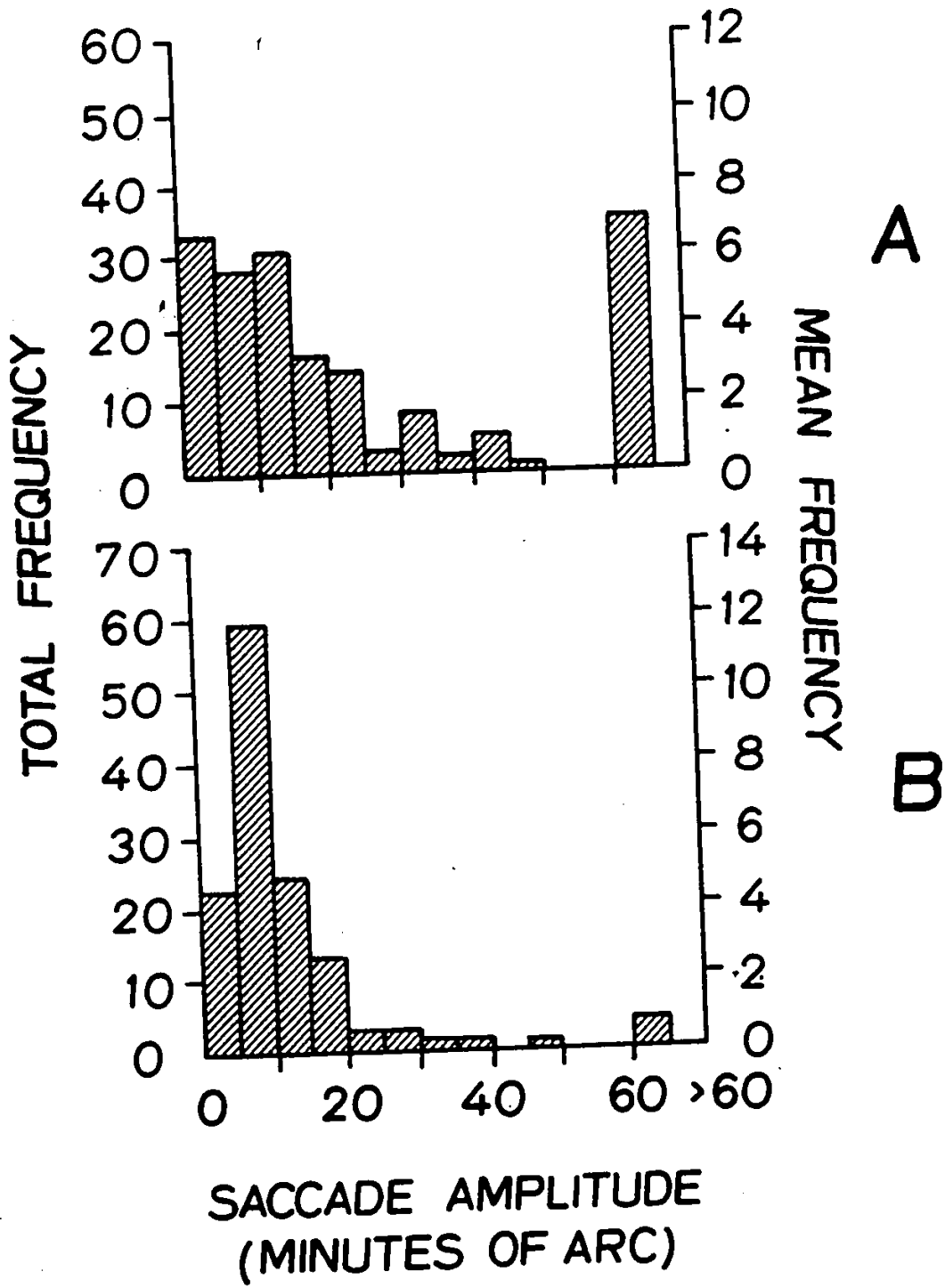


Figure 14. Frequency of occurrence of various saccade amplitudes during four 15-second periods of conversation (A) and fixation (B). Subject N.P.

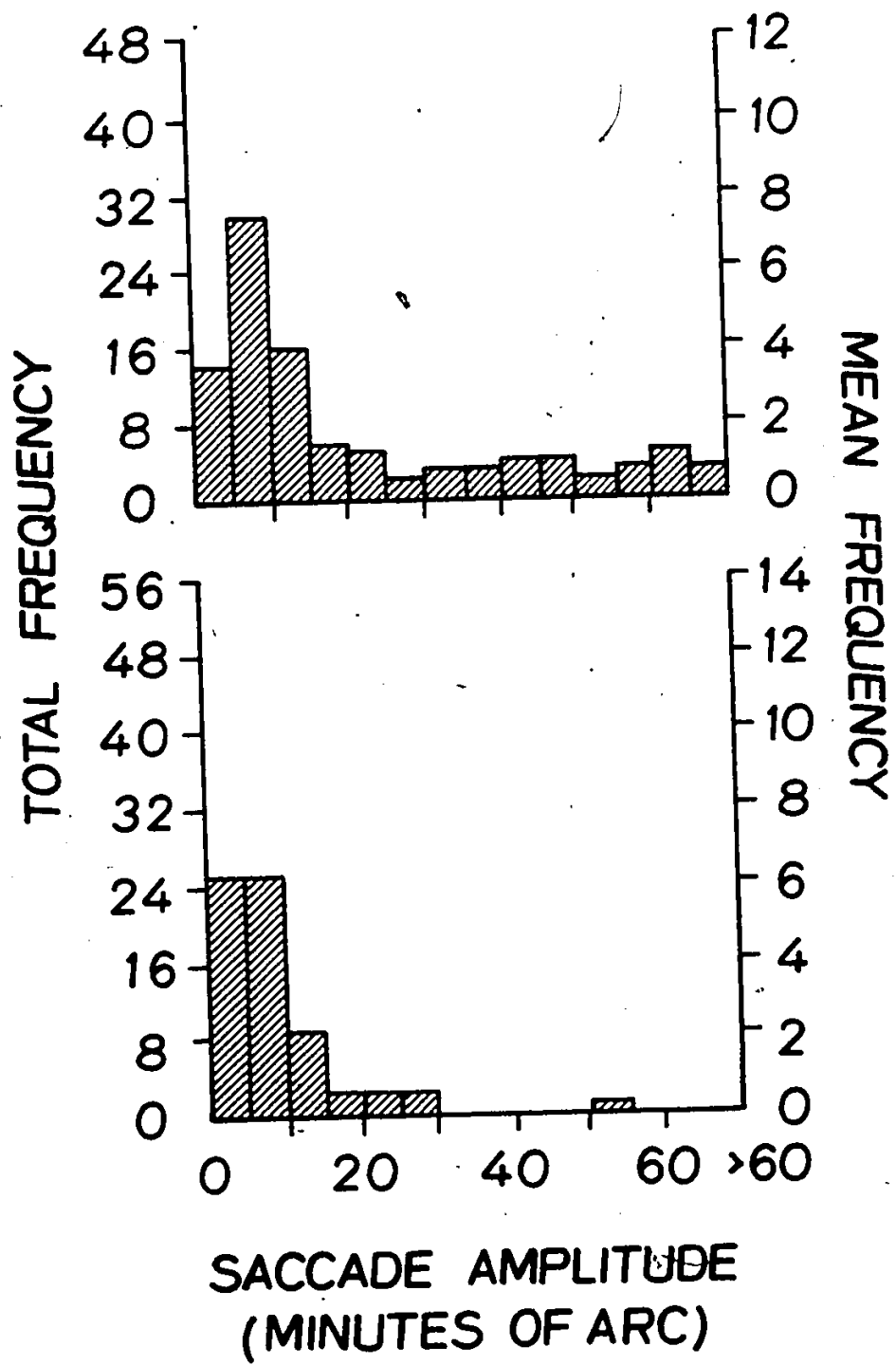
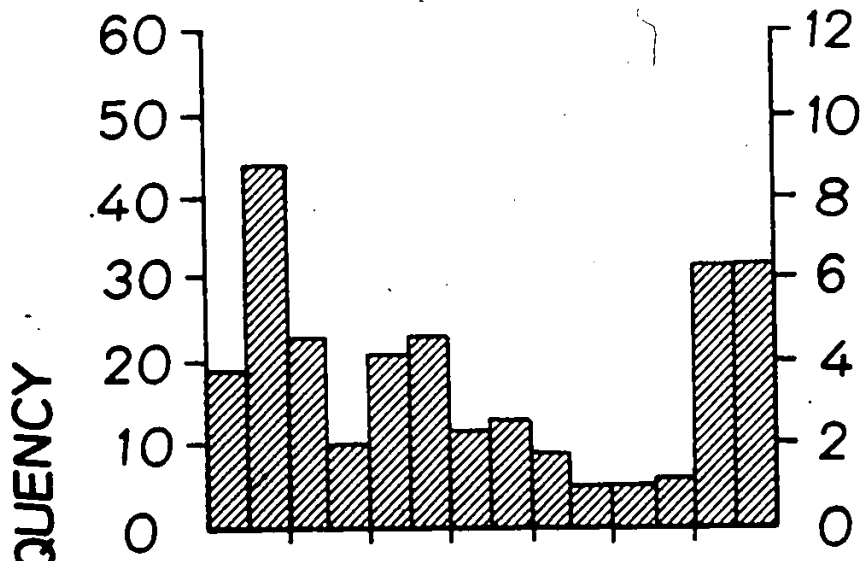
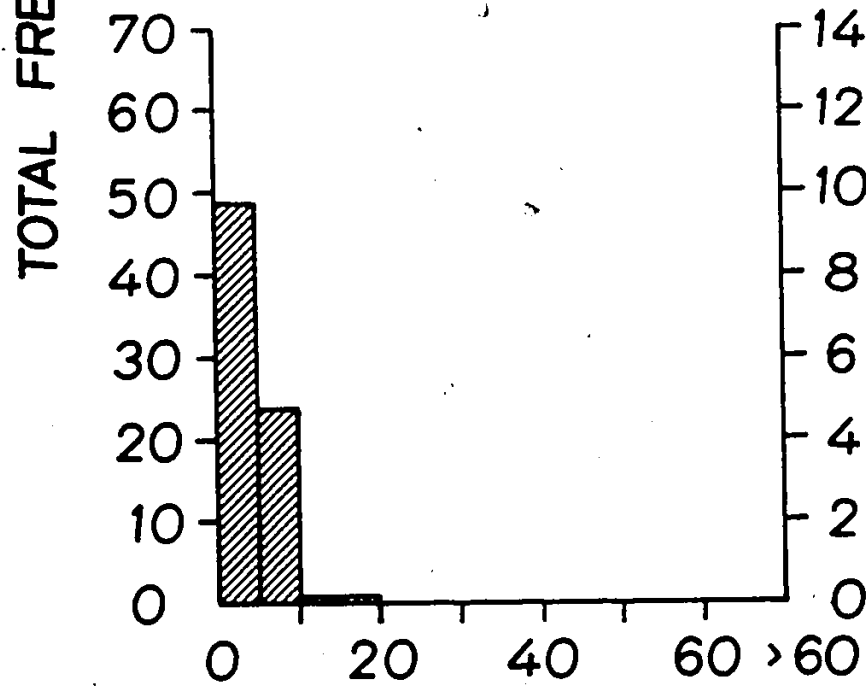


Figure 15. Frequency of occurrence of various saccade amplitudes during five 15-second periods of conversation (A) and fixation (B). Subject W.H.



A



B

**SACCADE AMPLITUDE
(MINUTES OF ARC)**

Table I. χ^2 test for significance of difference between the distributions of saccade amplitudes during conversation and during fixation.

Subject	χ^2_n	
A.H.	$\chi^2_7 = 48.64$	$p < 0.001$
N.P.	$\chi^2_5 = 23.63$	$p < 0.001$
W.H.	$\chi^2_9 = 144.29$	$p < 0.001$

Figure 16. Frequency of occurrence of various intervals between saccade onsets during five 15-second periods of conversation (A) and of fixation (B). Subject A.H.

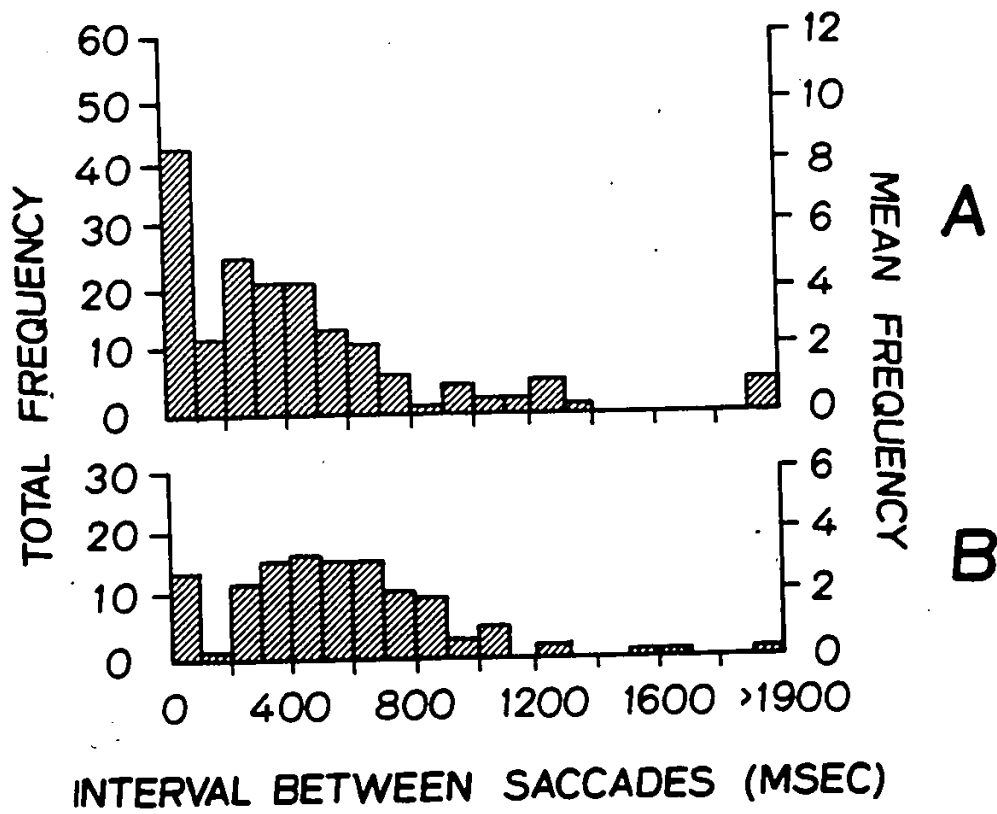


Figure 17. Frequency of occurrence of various intervals between saccade onsets during four 15-second periods of conversation (A) and fixation (B). Subject N.P.

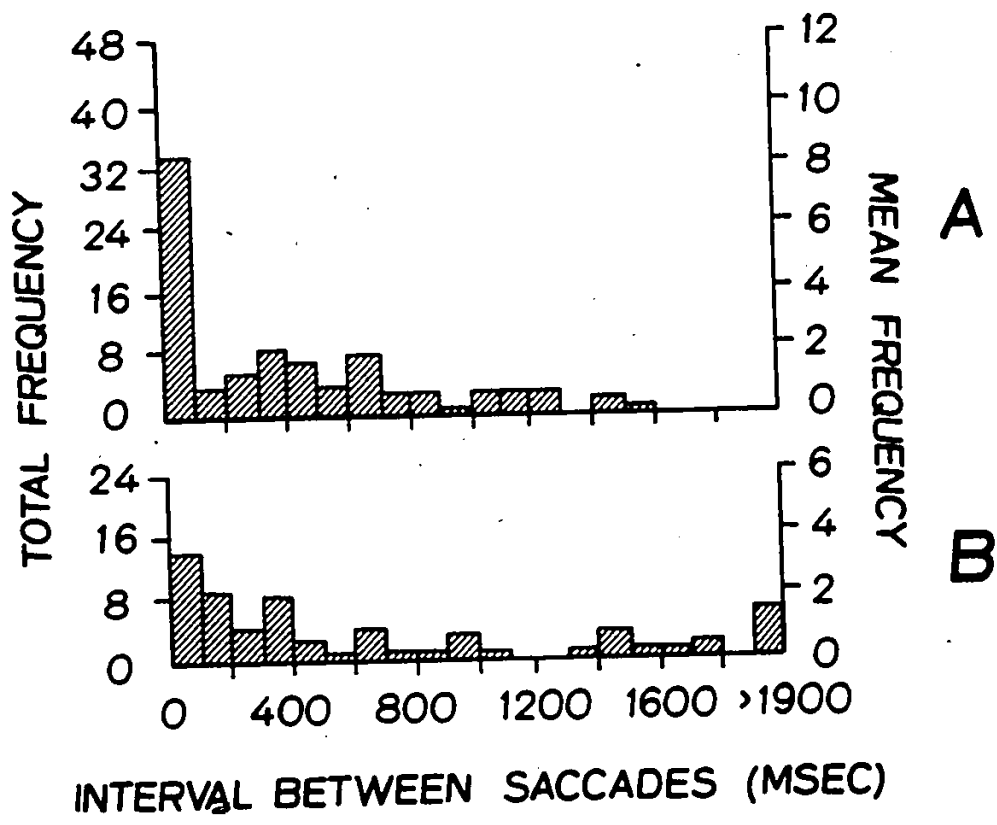


Figure 18. Frequency of occurrence of various intervals between saccade onsets during five 15-second periods of conversation (A) and fixation (B). Subject W.H.

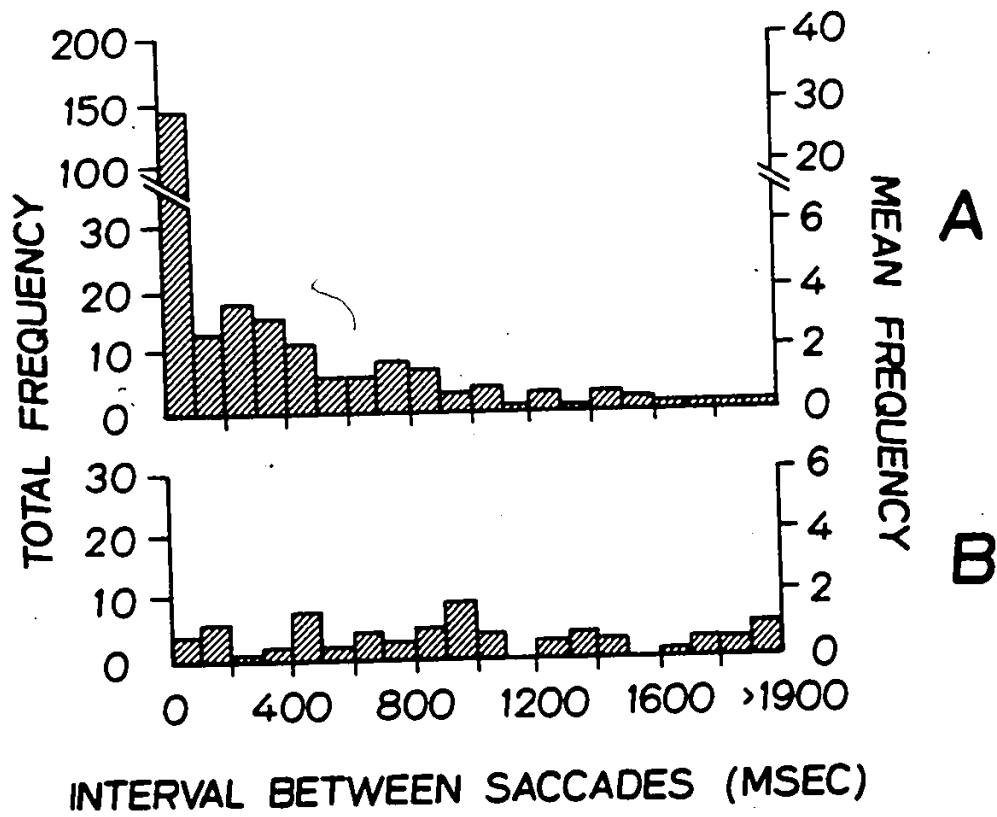


Table II. χ^2 test for significance of difference between the distributions of intervals between saccade onsets during conversation and during fixation.


Subject	χ^2_n	
A.H.	$\chi^2_{11} = 36.40$	$p < 0.001$
N.P.	$\chi^2_8 = 28.37$	$p < 0.001$
W.H.	$\chi^2_5 = 97.67$	$p < 0.001$

al., 1967). As anticipated, there were proportionately more large saccades (exceeding 30 minutes of arc in amplitude) during conversation than during maintained fixation. The occurrence of smaller saccades during conversation and their virtual predominance during fixation parallels the findings in naive and trained rhesus monkeys (Skavenski et al., 1975) and invites speculation that humans also learn to vary the pattern of their eye movements with situational demands.

Cunitz and Steinman (1969) conceded that the temporal distribution of saccades did not differ substantially between fixation and reading and that the probability of a saccade occurring during reading was independent of its amplitude. In the present study, the distributions of intervals between saccade onsets differed significantly in the 2 situations tested with a tendency toward proportionately more short intervals (up to 100 milliseconds) during conversation than during fixation. While at first glance it appears that the large eye movements recorded during conversation maybe associated with shorter intervals between saccade onsets, no direct correlation between saccade amplitude and time since the onset of the previous saccade could be established. In fact perusal of the data suggested that the relationship between these variables differed in the 2 situations and that short intervals were more likely to be associated with small saccades during conversation than was the case during fixation.

The present findings support Cunitz and Steinman's conclusion that there is no general relationship between the timing of saccades and their amplitude. However, the present data demonstrate that the

timing of saccades may vary in different situations. Whether this is sufficient to dispute the notion of a common initiating mechanism for all saccades is not clear. At least some proportion of the small saccades observed during conversation may be 'corrective', that is minor adjustments to the main saccade. It may not be appropriate to regard corrective saccades as initiated by a separate neural event. Instead they may represent a drastic (in process) alteration in the transmission path of the impulse initiating the main saccade. Although all saccades may be limited by the same mechanics (Zuber et al., 1965) the question of a common neural initiating mechanism appears to be more complex than was supposed by Cunitz and Steinman (1969).



Experiment Two. Small Eye Movements and Contour Interaction

Along a contour there is apparently an area of perceptual interference. The metacontrast literature suggests that this is a graded effect with both spatial and temporal extent. A small target lying a short distance from a contour may fall entirely within the interfering zone along the contour, with the result that the target is less likely to be perceived than would be the case otherwise. Similarly, a small displacement of a solitary target contour may fail to carry the target beyond the temporary zone of interference established by the contour in its previous location and the target step may go undetected and untracked by the eye, essentially falling within an oculomotor "dead zone".

By analogy an eye movement sufficiently large and rapid to move the image of a target contour beyond the transient area of insensitivity would contribute more to perceptibility of the contour than would a slower or smaller displacement. Location of a target contour within the zone of interference adjacent to another contour would be the spatial equivalent of a target step sufficiently small that the target contour fails to cross beyond the area of transient insensitivity.

If one were to manipulate the likelihood of perceiving a target in a free-viewing situation (as opposed to stabilized viewing) one might demonstrate a concomitant change in the pattern of small eye movements. Perhaps contour interaction could be demonstrated at spatial separations comparable to the amplitudes of microsaccadic eye movements. If so, by contriving to reduce the perceptibility of a

target contour with the addition of a nearby contour, one might provoke a predictable change in the pattern of small eye movements.

At a contour separation where perception of a target contour is significantly attenuated, requiring an observer to make some judgment about the target might result in his flicking his eye back and forth over the stimulus as if to displace the target from the area of perceptual insensitivity. The saccades would be sufficiently large that displacement of the target image would be greater than the area of relative insensitivity.

The present experiment sought to demonstrate whether such a relationship between the area of contour interaction and the amplitude of saccadic eye movements could be demonstrated. It was expected that at a contour separation where target perception was considerably attenuated there would be an increase in the frequency of saccadic eye movements slightly larger than the apparent zone of interference.

METHOD.

Subject. One observer experienced in wearing the contact lens served as a subject in the present study.

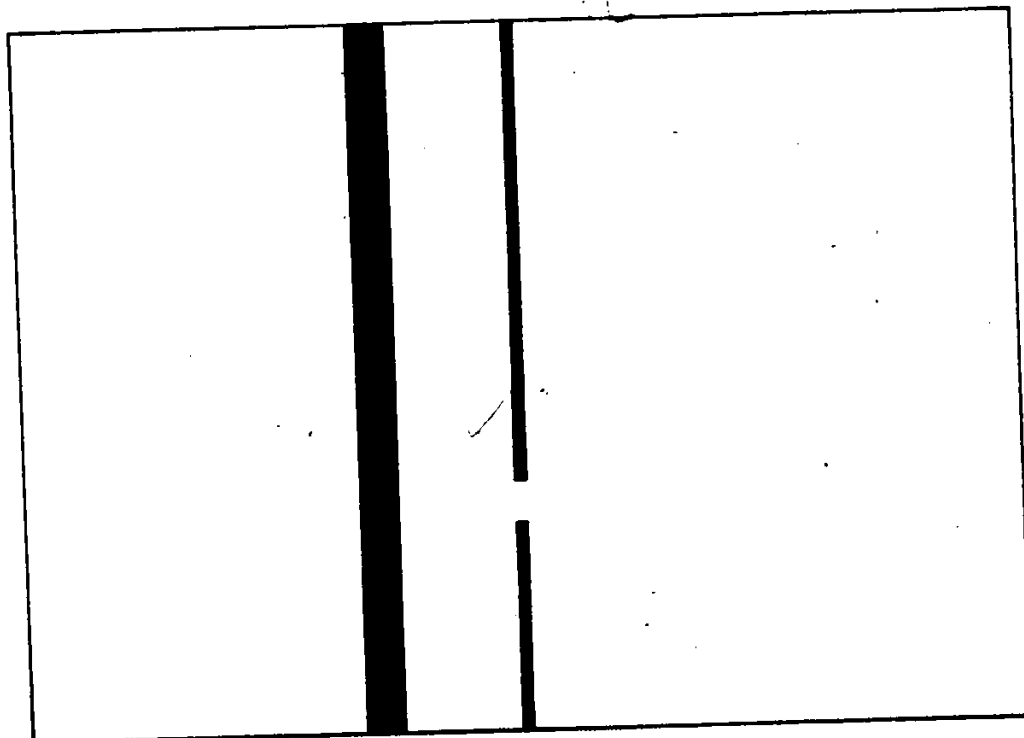
Apparatus. The subject sat at a table and rested his chin and forehead against a contoured support. Against a dark background 10 meters in front of the subject there was a white (bristolboard) field which subtended an area 4.05 degrees wide by 3.20 degrees high. White cards bearing the stimulus figures on the front surface and paper clips on the back were centred on the white field and held there by embedded magnets. The luminance of the cards and of the field was approximately 10 foot-Lamberts. In the tenth experimental session the chin rest was

replaced with the helmet and contact lens apparatus described in Experiment 1 so that small movements of the right eye could be recorded. An occluder worn over the right eye throughout each session permitted unhampered movement of the eye, with or without the contact lens, and provided no obstruction to the column of light reflected by the mirror chip.

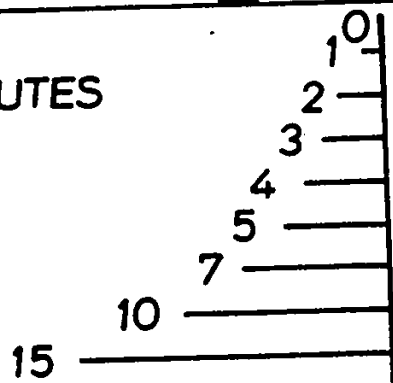
Stimuli. Centred on each stimulus card was a vertical black line 64.5 minutes of arc high and 0.5 minutes of arc wide. One-third of the way from the top or bottom of the "test" line there was a gap approximately 0.5 minutes of arc in size. There were 9 other line configurations each consisting of the test line and parallel to it a wider line of equal height and 2.2 minutes of arc in width. The added line was located to the left of the test line either touching it or at a distance of 1,2,3,4,5,7,10 and 15 minutes of arc (Figure 19). There were 2 possible gap locations for each of the 10 line configurations giving 20 different stimuli in all.

Procedure. The subject viewed the targets with his dominant left eye. The stimuli were mounted by hand and left in position until the subject had responded. Viewing time was unlimited. Preliminary testing with the test line alone and a range of gap sizes suggested the size best suited to the subject. One size was then selected and tested in a baseline session of 100 trials of the test line presented alone. Within each block of 20 trials the gap's location was varied randomly being equally frequent near the top and bottom of the test line but with no more than 3 successive trials the same. The subject's task was to respond "top" or "bottom" on every trial to indicate the location of

Figure 19. Schematic diagram of the stimulus in position on the white background with the various line separations indicated below.



MINUTES



the gap. Feedback was provided throughout the experiment and initially included the experimenter's pointing to the gap until the subject had become familiar with the two possible gap locations. A brief rest was permitted between blocks of trials. The gap size which permitted the subject to correctly locate the gap on approximately 75 to 85 per cent of the baseline trials was used for all stimuli subsequently viewed by the subject. This procedure provided a background against which any effect of the added line on gap perception would be apparent.

The baseline session was followed by 9 experimental sessions during which the 20 different stimuli were presented in random sequence within each of 5 blocks of trials. The data were scored for the number of times the gap was correctly located under each of the experimental conditions, that is, for each spacing between the lines as well as for the test line presented alone. In each session there were 5 occurrences of each of the experimental conditions. The data were expressed as the proportion of trials correct under each condition, corrected for slight variations in gap size (see Appendix).

During the tenth experimental session the movements of the right eye were recorded. As microsaccades are binocularly synchronous (Ditchburn and Ginsborg, 1953) the movements of the right eye were taken as representative of both eyes. Data were collected on 2 blocks of 20 trials each giving 4 eye movement records for each line configuration. The individual records were analysed for the frequency of various microsaccade amplitudes. Total and mean frequencies of various amplitudes were computed for horizontal saccades recorded while the subject viewed each line configuration.

RESULTS

The gap was correctly located on 81 of the 100 baseline trials. In the first 9 experimental sessions accuracy in locating the gap was found to drop from 90 per cent, when the added line was 7 minutes of arc from the test line, to 81 per cent when the lines were separated by 2 minutes of arc (Figure 20). The gap was least likely to be located when the added line touched the test line (0 minutes of arc separation) effectively forming a wide band with a small notch in one side. Over an area extending at least 4 minutes of arc from the edge of the added line there appeared to be an area of interference with perception of the gap substantially affected when the lines were separated by a distance of approximately 2 minutes of arc.

In the tenth experimental session the relative frequency of small horizontal saccades 5 to 10 minutes of arc in amplitude increased when the added line was 2 minutes of arc from the test line (Figure 21). Although all of the horizontal saccades recorded during this visual task were within the range of amplitudes typical of fixation eye movements the general predominance of saccades less than 5 minutes of arc in amplitude shifted to slightly larger displacements when the lines were two minutes of arc apart. When the test line was viewed alone saccadic activity increased and this was reflected in high frequencies of various saccade amplitudes.

DISCUSSION

The zone of interference along the edge of the added line appears to be at least 4 minutes of arc in extent. Perception of the gap was less likely when the lines were separated by 2 minutes of arc

Figure 20. Accuracy in determining gap location with varying distances between the test line and the added line. Subject N.P. (n = no added line; X = baseline score). Each data point represents 90 trials.

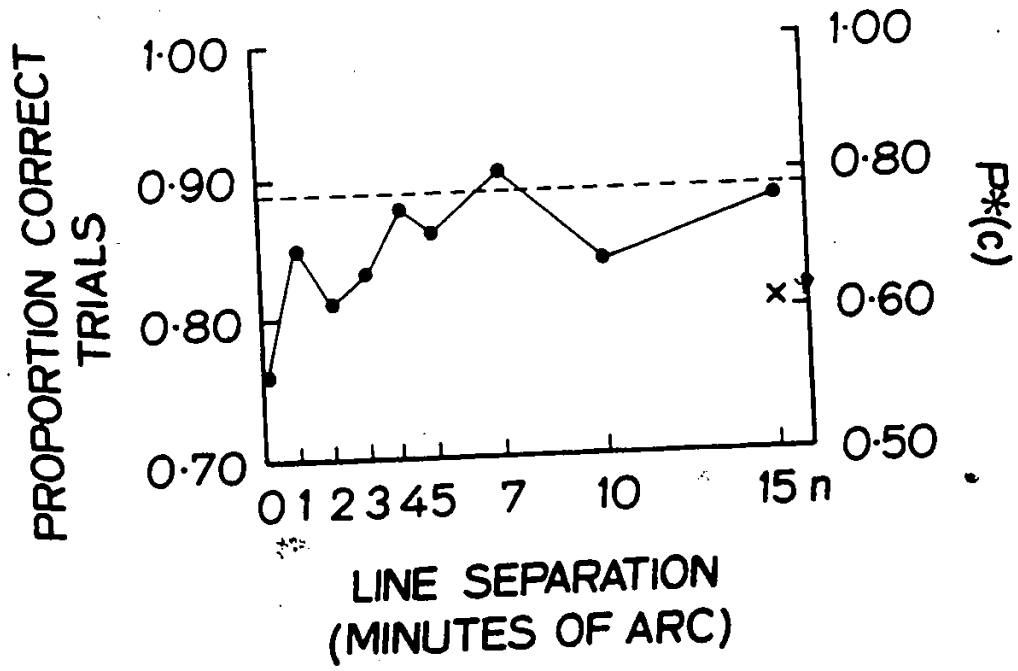
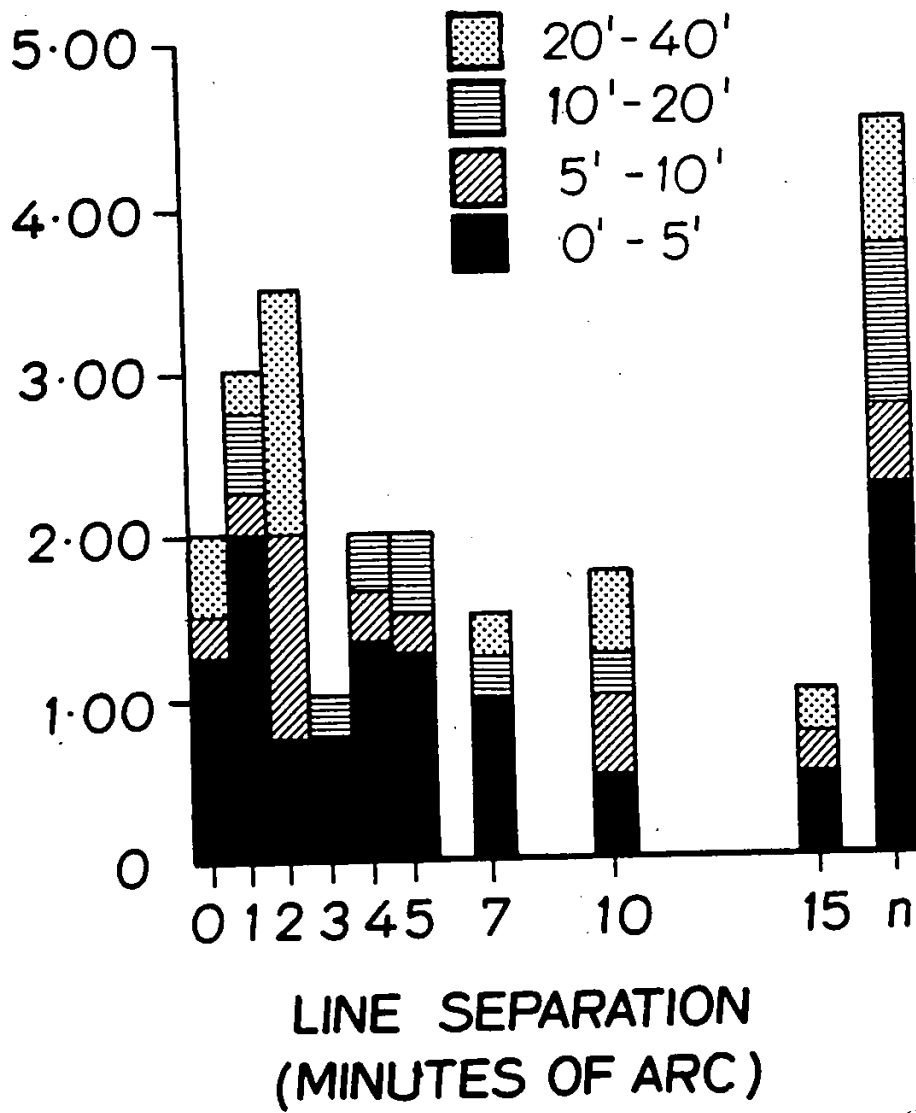


Figure 21. Frequency of various saccade amplitudes as a function of line separation: horizontal saccades (n = no added line). Subject N.P.

MEAN NUMBER OF SACCADES PER TRIAL



than at the other separations tested. Perception of the gap was least likely when the added line touched the test line; however, with this particular target the subject's task may not be truly comparable to locating a gap in a line. The test line, rather than lying within an area of interference along the edge of the added line, is joined to the added line thus eliminating the contour at the edge of the added line.

It was hypothesized that when a target contour fell within the perceptually insensitive area along another contour there would be an increase in the number of saccades of amplitudes appropriate to displacing the target from the insensitive zone. Perception of the gap was substantially affected when the test line was 2 minutes of arc from the added line and the zone of interference along the added line appeared to extend at least 4 minutes of arc laterally. As anticipated there was an increase in the number of horizontal saccades 5 to 10 minutes of arc in amplitude when the subject viewed stimuli in which the lines were 2 minutes of arc apart.

The provocation of a predicted shift in the distribution of saccadic amplitudes by manipulation of the perceptibility of a target contour in an unstabilized viewing situation augments evidence that microsaccadic eye movements act to maintain perception of a visual target.

The data suggest that the oculomotor "dead zone" is the spatio-temporal equivalent of the zone of interference demonstrated with the simultaneous presentation of 2 contours and support the notion that the area of insensitivity along a contour has both spatial and temporal extent. It appears that the distribution of saccadic

amplitudes may be affected by variations in the demands of the viewing situation subtler than those demonstrated in Experiment 1. Moreover, the subject may be able to voluntarily alter saccade amplitudes in an attempt to restore or maintain perception of a visual target.

Experiment Three. Contour Interaction: Perception of a Target Contour
in the Presence of an Adjacent Contour

Among the studies of contour effects there is considerable variation with respect to the nature and dimensions of the target figures, the spatial separations between contours tested and the subject's task. It is not surprising therefore that contour interaction effects have been described variously as interference, facilitation or both and that the estimated spatial extent of the contour effect differs across studies. One point of agreement however is that the magnitude of the effect on perception of a target contour varies with the spatial separation between the target and a nearby contour.

It is difficult to interpret apparent contour interactions between letters as, individually, some letters are more difficult to recognize than others. This may be due in part to the distinctiveness of the overall letter shape and therefore to the number of structurally similar letters with which it may be confused. To distinguish among possible alternatives it may be necessary to determine whether there is a break in the contour of the letter, the number of elements in the letter or the relative orientations of the elements. The perceptually more difficult letters such as S, R, O and B tend to be more complex structurally than are the easier letters such as L and J and may thus be subject to more internal interference between the closely spaced elements of the letter.

Substitution of a Landolt ring target overcomes some of the possible sources of variance in using letters to assess the nature and extent of contour interaction effects. Nevertheless the Landolt ring may still be sufficiently complex that internal contour interaction effects are possible. Consequently the present work concerns the effect of a single vertical line on perception of a gap in a second vertical line, conceptually a Landolt ring of infinite diameter next to a second ring of infinite diameter. Potential interactions between segments of an individual ring are essentially eliminated and any effects at the ends of lines would be held constant.

The use of such a target provides for minimal confounding of contour interaction and permitted prediction of a specific shift in the amplitude distribution of horizontal microsaccades in Experiment Two. The present and subsequent studies represent further investigation of contour interaction effects over distances falling within the range of amplitudes of microsaccadic eye movements. The present experiment is essentially a replication and extension of the first part of Experiment Two and was expected to confirm the general finding that the presence of a second contour may adversely affect perception of a target contour over distances of a few minutes of arc.

METHOD

Subjects. Five psychology students with normal or corrected-to-normal visual acuity served as subjects.

Apparatus. The apparatus used in this study was that employed for the investigation of contour interaction effects in Experiment 2.

Stimuli. As in the previous experiment, the basic stimulus consisted

of a vertical black test line with a gap approximately one-third of the distance from the top or bottom of the line. There were 18 other line configurations each consisting of the test line and an added line located at various distances (the maximum was 15 minutes of arc) to the left or to the right of the test line. In all a subject viewed 2 sets of 20 stimuli. In one set the added line was located to the left of the test line at each of 9 different distances and there were two possible locations of the gap giving 18 different stimulus cards. To these were added two cards bearing only the test line, each with the gap in a different location. The second set of stimuli were made up in the same way but the added line was located to the right of the test line.

Procedure. All subjects were refracted and wore appropriate lenses during the study. The study was conducted in essentially the same way as was Experiment 2. Three subjects viewed the stimuli with the dominant eye only and two viewed alternately with the dominant eye or the non-dominant eye on successive days. One baseline session was run for each eye tested.

Each of the subsequent experimental sessions consisted of four blocks of 20 trials. One set of stimuli (i.e. with the added line to the left or to the right only) was presented in a random sequence in each block. The location of the added line to the left or right of the test line varied across the 4 blocks in any of 6 possible orders. Each subject participated in 1 session a day, at a fixed hour, for 16 days if only the dominant eye was tested or for 20 days if each eye was tested. In the latter case viewing with the dominant or non-dominant eye alternated across days.

The data for individual eyes were separately scored and trials in which the added line was located to the left of the test line were scored separately from those in which it was added to the right. In every session there were 4 occurrences of each of the experimental conditions. The data analysis was carried out in the manner described in Experiment 2.

RESULTS

The gap size appropriate to individual subjects ranged from 0.3 to 0.8 minutes of arc (Table III). As the location of the added line to the left or right of the test line had no differential effect on gap perception ($\chi^2_{10} \leq 3.63$ in all cases - see Table IV) these data were combined for each subject giving 128 trials per data point in Figure 22 and 80 trials per point in Figure 23. With relatively small distances between the added line and the test line the proportion of correct trials declined to levels 5 to 30 per cent below those achieved in the absence of the added line. When the data were corrected for chance accuracy according to the formula,

$$P^*(C) = \frac{P(C) - 1/m}{1 - 1/m}$$

where $P(C)$ is the proportion of correct trials and m is the number of alternatives, the interfering effect of the added line was even more apparent indicating a decline in accuracy of from 10 to 60 per cent across subjects. At the spatial separations tested there was no evidence that the presence of the added line facilitated perception of the gap in the test line.

Table III. Gap sizes and baseline scores for subjects in Experiment Three.

Subject	Eye	Gap size (minutes)	Baseline (score)
J.Z.	Right	0.3	85%
C.H.	Left	0.8	79%
M.F.	Right	0.5	75%
L.K.	Left	0.3	81%
	Right	0.3	92%
M.T.	Left	0.3	78%
	Right	0.3	75%

Table IV. A comparison between location of the added line to the left and to the right of the test line in Experiment Three.

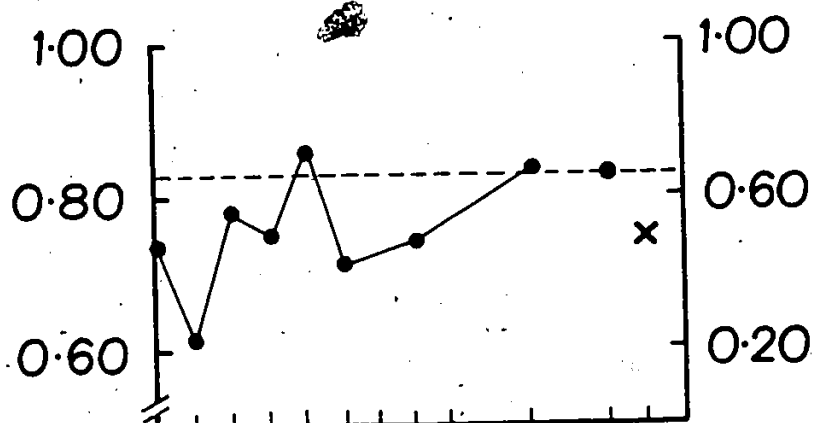
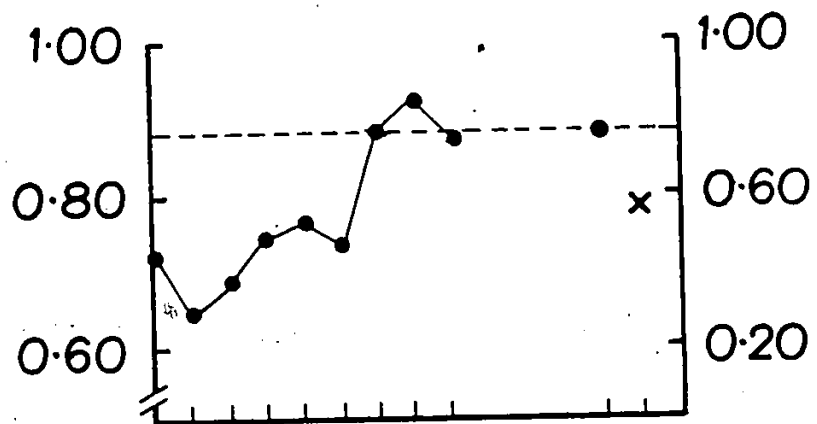
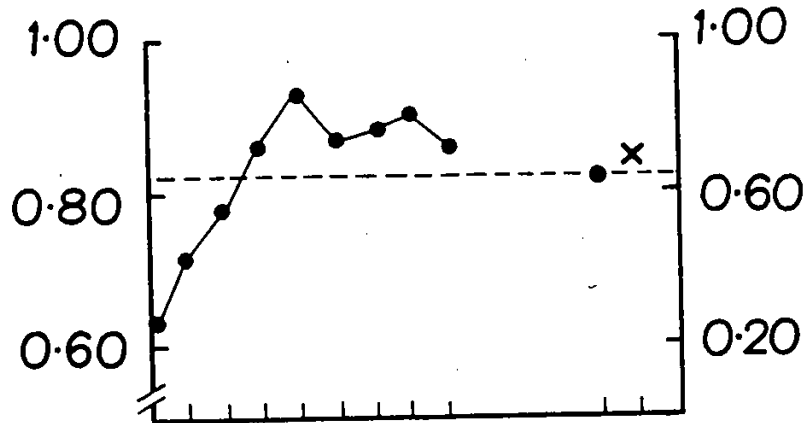
Subject	Eye	χ^2_{10}
M.F.	Right	3.63
J.Z.	Right	1.78
C.H.	Left	3.44
L.K.	Left	0.53
	Right	1.11
M.T.	Left	1.04
	Right	0.89

None of the values is significant.

Figure 22. Accuracy in determining gap location with varying distances between the added line and the test line. Subjects J.Z., C.H. and M.F. (no = no added line; b = baseline score). Each data point represents 128 trials.

10%

PROPORTION CORRECT TRIALS



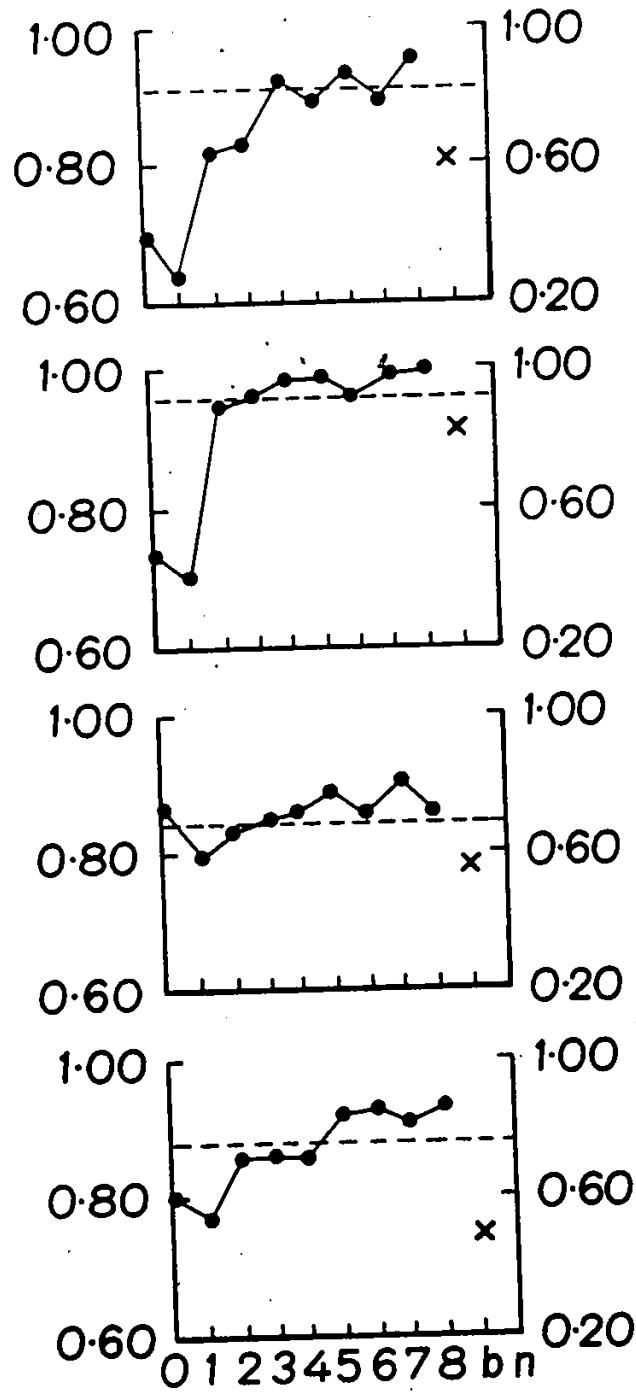
P*(c)

0 1 2 3 4 5 6 7 8 10 n b

LINE SEPARATION (MINUTES)

Figure 23. Accuracy in determining gap location with varying distance between the added line and the test line. Subjects L.K. (L.E. and R.E.) and M.T. (L.E. and R.E.). Each data point represents 80 trials. (n=no added line; b=baseline score).

PROPORTION CORRECT TRIALS



P*(c)

LINE SEPARATION (MINUTES)

DISCUSSION

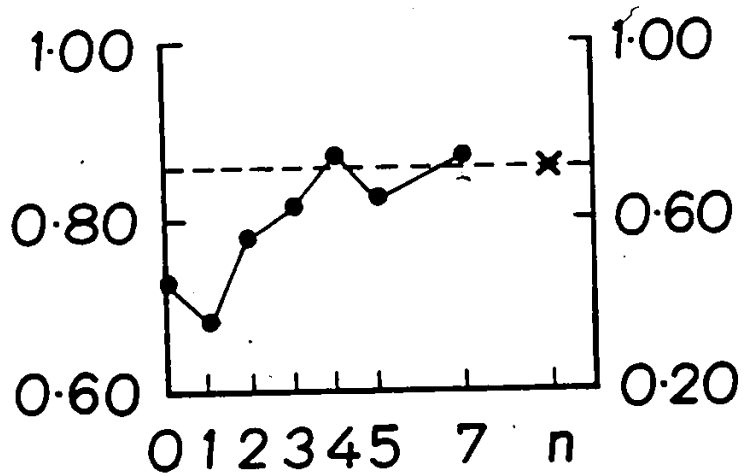
The data confirm that along a contour there is an effective area of perceptual interference extending a few minutes of arc from the contour (Figure 24). The implication of this result is that a target contour which falls within an area a few minutes of arc from another contour is less likely to be perceived than at a slightly greater distance from the second contour or in the absence of the second contour. The effect of the added contour is essentially nullified at a distance of 2 to 6 minutes of arc depending on the subject.

The demonstration of an interference effect in a free viewing situation is reminiscent of the spatial brightness summation typical of some visual cell receptive fields. By analogy, if the gap is thought to lie over the excitatory centre of a receptive field then increasing the distance between the test line and the added line (i.e. increasing the width of the light area between the two lines) may be thought to increase the stimulated area of the inhibitory surround to a point where the surround maximally inhibits the centre response to the gap. Further increasing the width of the light area between the lines might be likened to the stimulation encroaching on a disinhibitory extra-surround area with the result that the effect of the inhibitory surround is increasingly counteracted and the centre response to the gap is restored.

At the luminance level used in this experiment, 10 foot-Lamberts, Ricco's law (of spatial summation of brightness) breaks down at about 2 minutes of arc when exposure duration is limited. The comparable result obtained in this experiment with unlimited viewing

Figure 24. Postulated effect of one contour on perception of another nearby contour. Model derived from an arbitrary averaging of the 5 dominant eye functions in Experiment 3.

PROPORTION CORRECT TRIALS



CONTOUR SEPARATION (MINUTES)

$P^*(c)$

time suggests that some factor (perhaps rapid small eye movements) limits either the effective exposure duration or the functional area of spatial summation.

It should be noted that this discussion is of general principles of the functional organization of the human visual system. It is by no means assumed that the response of a single receptive field is being tapped. Rather, the functional organization of mammalian visual cell receptive fields is used as an heuristic model of the integrated function of the human visual system and the emergent principles of its organization are simply represented by analogy to the level of single cell response. The spatial dimensions described in this context are meant to approximate the limiting case under the specific conditions tested and are not to be construed as reflecting an absolute limit of human visual function under ideal conditions.

Experiment Four. Summation In Contour Interaction

Letters at either end of a row of letters are identified more readily than those occupying less extremem positions regardless of whether viewing is monocular, binocular or dichoptic. In the latter case it makes no difference whether each eye is shown letters occupying sequential or alternating positions (Taylor and Brown, 1972). These findings suggest that the interfering effects between letters summates and that there is a strong suparetinal component in the interaction between adjacent letters. Bouma (1970) confirmed that the deleterious effect of 2 flanking letters on perception of a target letter was greater than that of a single adjacent letter.

Evidence for suparetinal contour interaction has been provided with non-letter targets as well. Vernier resolution for 2 bright, vertical line segments is adversely affected by adjacent vertical lines with either monoptic or dichoptic presentation of the target and flanking lines (Westheimer and Hauske, 1975). Visual acuity for a gap in a Landolt ring is similarly impaired regardless of whether the ring and four surrounding bars are presented dichoptically or monoptically (Flom, Heath and Takahashi, 1963).

The above findings indicate that a contour presented to one eye can have a deleterious effect on perception of a contour presented to the other eye. In addition to evidence of binocular interference one may find examples suggestive of binocular summation. Binocular acuity is superior to monocular acuity (Horowitz, 1949; Savage and Sumner, 1950; Kahneman, Norman and Kubovy, 1967) an effect frequently attributed to physiological summation of monocular inputs.

More letters on a Snellen chart are identified with binocular viewing than with monocular viewing. Row-by-row presentation of the letters results in a higher proportion being correctly identified than when the entire chart is exposed. Curiously this improvement is not so marked with binocular viewing as with monocular viewing (Savage and Sumner, 1950). This finding suggests that there may be binocular summation of interference between rows of letters which offsets any advantage confined by binocular summation of excitatory effects. Similarly, Blake, Fox and McIntyre (reported in Blake and Fox, 1973) found binocular summation for forced-choice recognition of a target letter presented alone. However, when the target letter was surrounded by several nontarget letters, binocular performance was no better than monocular performance.

Fry and Bartley (1933) hypothesized that the binocular response represented a summation process and an inhibitory process in combination. The above findings do suggest that the superiority of binocular performance is limited to displays with either few contours or widely spaced contours. In displays containing numerous or closely spaced contours the contribution of interference may equal or exceed that of summation effectively eliminating any superiority of binocular viewing.

The present experiment was addressed to the question of whether contour interaction effects would be similar regardless of whether viewing was binocular or monocular.

METHOD

Subjects. Four psychology students with normal or corrected-to-normal visual acuity participated in this study.

Apparatus. The apparatus used in this investigation was the same as that used in Experiment 3.

Stimuli. The stimuli were similar to those described in the previous experiment but two lines were added one on either side of the test line, parallel to it and equidistant from it. There were 10 different line patterns: one consisted of the test line alone while the others consisted of the test line with two lines flanking it either touching it or at distances of 1, 2, 3, 4, 5, 7, 10 and 15 minutes of arc. For each line pattern the gap occurred once in the upper portion of the test line and once in the lower part of the line.

Procedure. This study was conducted in the same way as the previous experiment. All subjects viewed the baseline target with the dominant eye (that used for sighting when both are open). Subsequently three subjects (J.S., S.D. and M.L.) viewed the stimuli with the dominant eye over 15 sessions and two (J.S. and R.C.) viewed the stimuli binocularly over 5 days. Binocular testing of J.S. was carried out after the 15 monocular sessions. In the experimental sessions the 20 different stimuli were presented in a random sequence in each of 5 blocks of trials giving 10 presentations of a given line pattern per session.

RESULTS

The gap size used in this experiment was 0.5 minutes of arc. All 4 subjects correctly located the gap in the test line on approximately 80 per cent of the baseline trials (Table V).

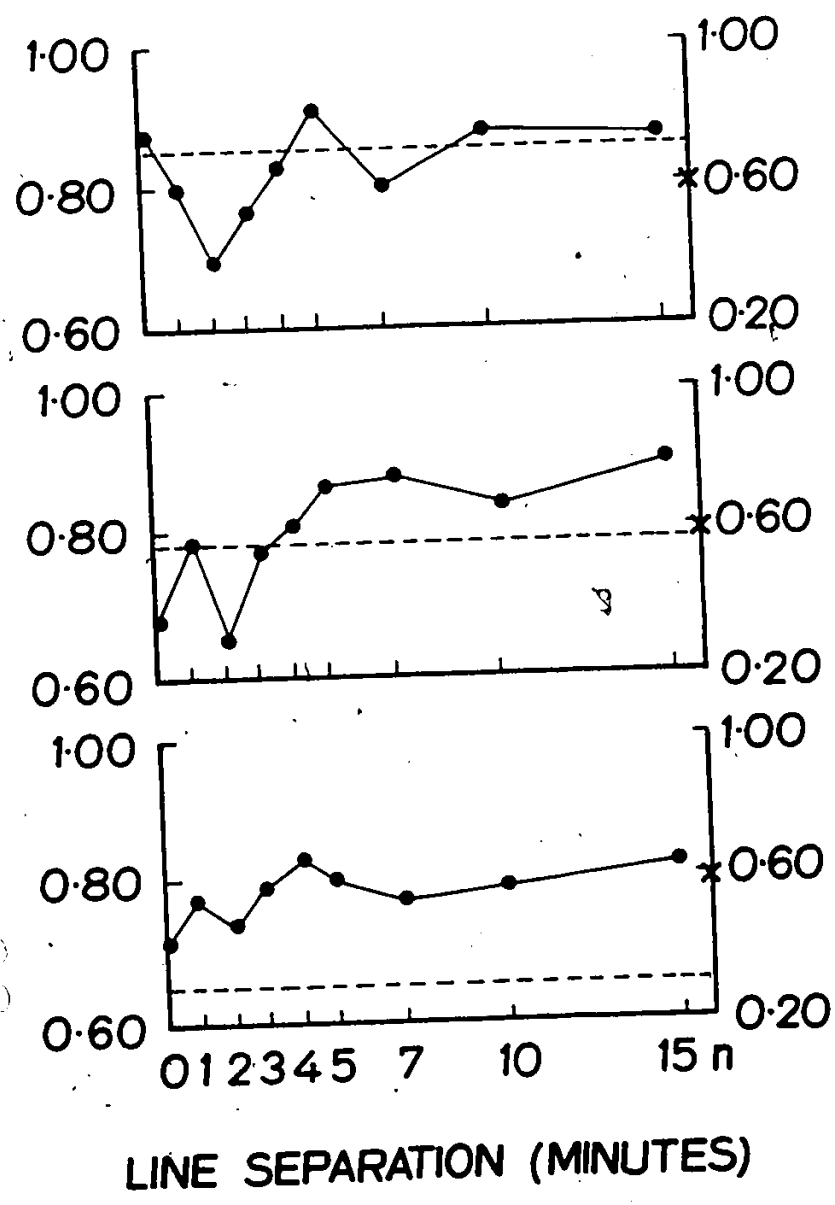
Of the subjects who viewed the stimuli monocularly 2 maintained their baseline accuracy for the no added line (n) condition over the experimental sessions (Figure 25). M.L. however indicated that

Table V. Selected gap size and baseline scores of subjects in Experiment Four.

Subject	Dominant eye	Gap size (minutes)	Baseline score
J.S.	Left	0.5	80%
M.L.	Right	0.5	80%
S.D.	Left	0.5	81%
R.C.	Right	0.5	80%

Figure 25. Accuracy in determining gap location with varying distances between the test line and two lines added one to either side of the test line. Subjects J.S., S.D. and M.L. (X-baseline score). Each data point represents 150 trials.

PROPORTION CORRECT TRIALS



P*(c)

although he performed adequately in the baseline sessions he had difficulty focussing on the test line in the absence of the two added lines during the experimental sessions. Allowing for that particular difficulty the three subjects showed similar variations in accuracy of gap location with differing distances of the added lines. Accuracy declined as the spacing between the lines diminished from 4 to 2 minutes of arc and improved somewhat at a separation of 1 minute. Each data point in the figure represents 150 trials. Figure 26 summarizes the general effect taken as an average of the three individual plots.

When the stimuli were viewed binocularly accuracy dipped when the lines were separated by about 3 minutes of arc (Figure 27). When J.S. viewed the targets binocularly the "V"-shaped interference effect shifted slightly toward larger line separations compared to monocular viewing.

DISCUSSION

Perception of a gap in a line is similarly affected by variations in the distance of additional lines flanking the first under both monocular and binocular viewing. In light of intersubject variation, however, it is not clear whether one should describe the effect at separations of 2 to 3 minutes of arc as interference or that at somewhat greater separations as facilitation of gap perception. The stimulus configuration in which the flanking lines make contact with the test line (0 minutes of arc separation) may well constitute a different task than the other configurations judging by subjective reports and the unpredictable direction which the accuracy function takes in the transition from 1 to 0 minutes separation between the

Figure 26. Postulated effect of two added lines on perception of a gap in a line between them. The model is derived from averaging the functions of the subjects who viewed the targets monocularly.

PROPORTION CORRECT TRIALS

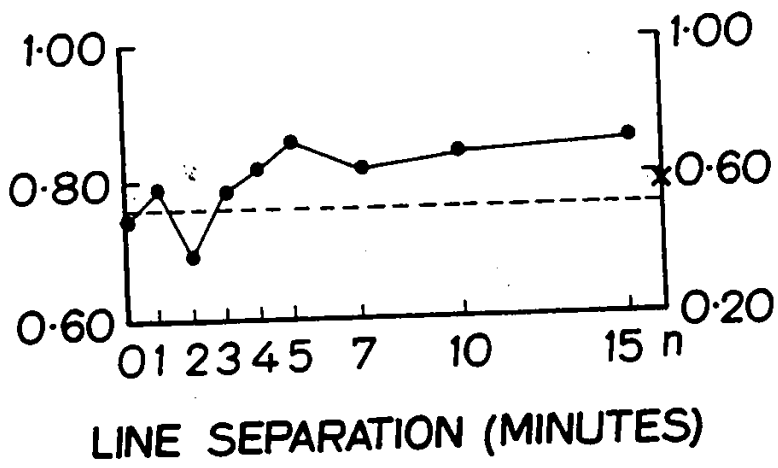
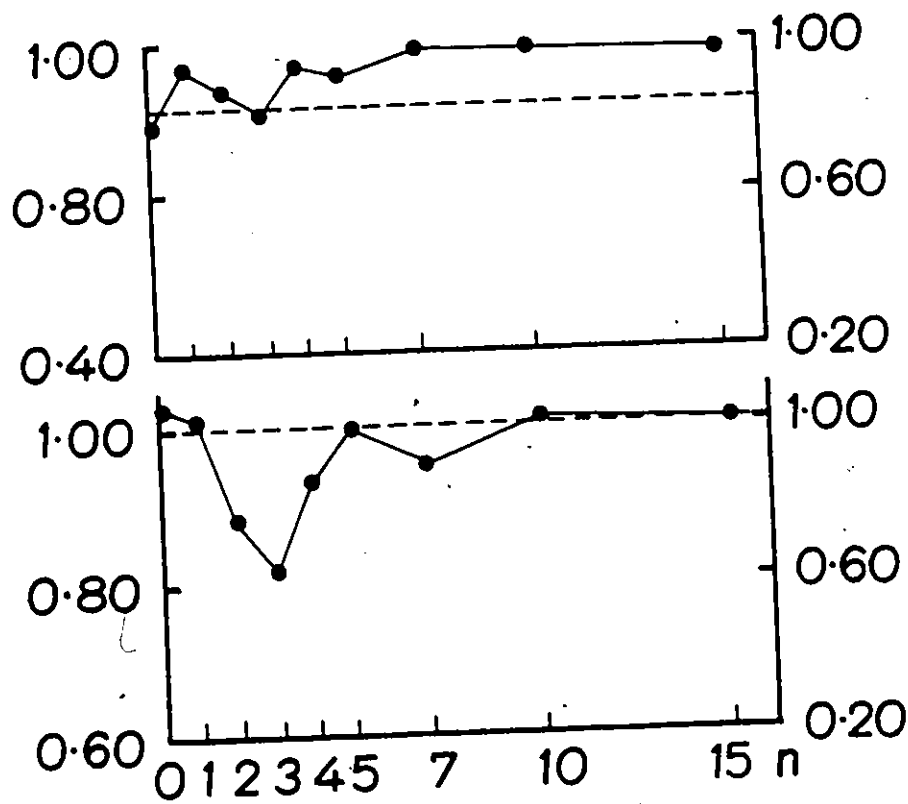


Figure 27. Accuracy in determining gap location with varying distances between the test line and two lines added one to either side of the test line. Subjects R.C. and J.S. viewing binocularly. Each data point represents 50 trials.

PROPORTION CORRECT TRIALS



LINE SEPARATION (MINUTES)

P*(c)

lines. Although J.S. obtained relatively higher scores for binocular viewing than he did for monocular viewing, these may reflect a practice effect rather than binocular summation, as binocular testing followed the sessions of monocular testing.

Experiment Five. The Shape of the Interference Function

Flom et al. (1963) found that perception of the break in a Landolt ring was most adversely affected when tangential bars were removed to a distance of about 1 minute of arc. As the spacing between the bars and the ring varied from that value, accuracy in locating the gap improved resulting in a "U"- or "V"-shaped function over a range of small contour separations. A similar effect has been suggested in Experiments 3 and 4 and the present study was designed to explore the shape of the contour interaction function more carefully. As the bars in the Flom et al. (1963) study were the same width as an arc of the Landolt ring, the width of the added lines used in this experiment was reduced to equal the width of the test line.

METHOD

Subjects. Two students with normal or corrected-to-normal visual acuity served as subjects in this experiment.

Stimuli. The test line was of the same dimensions as that used in the previous experiments, that is, approximately 0.5 minutes of arc wide by 74.5 minutes of arc high. Two lines of the same dimensions as the test line were located, one on either side of it and equidistant from it, at distances of 0.3, 0.5, 0.7, 0.9, 1.1, 1.2, 1.4, 1.6 and 1.8 minutes of arc. One set of stimuli had a solid test line whereas in another set the test line was broken in the middle by a gap 0.3 minutes of arc in size. The two sets of stimuli were combined giving one solid test line and one broken test line for each three-line configuration.

Apparatus. The apparatus used in this study was that described in the previous experiments.

Procedure. The procedure followed in this experiment was similar to that in the preceding studies. The stimuli were viewed monocularly. There were two baseline sessions, one to test each eye. Solid and broken test lines were presented equally often in a random sequence in each of 5 blocks of 20 trials. The subject was to respond "yes" to indicate that a gap was judged to be present and "no" to indicate the absence of a gap in the test line. In each of the 20 experimental sessions which followed, the various 3-line stimuli were presented in a random sequence within each of 5 blocks of trials giving a total of 10 trials for each line separation per session. Only one eye was tested in a given session. The data for each eye were analyzed separately and scored for the proportion of correct trials at each line separation so that 100 trials contributed to each data point.

RESULTS

The gap size chosen permitted each subject to correctly report either the presence or the absence of a gap on at least 70 percent of the baseline trials regardless of which eye viewed the target (Table VI). As the spacing between the lines was reduced accuracy declined then rose again (Figure 28). Over the line separations tested the lowest point fell at about 1.2 minutes of arc and represented more than a 20 per cent decline in accuracy from the highest point of the function. If the scores were corrected for chance success (P^c) the difference in accuracy was over 40 per cent.

DISCUSSION

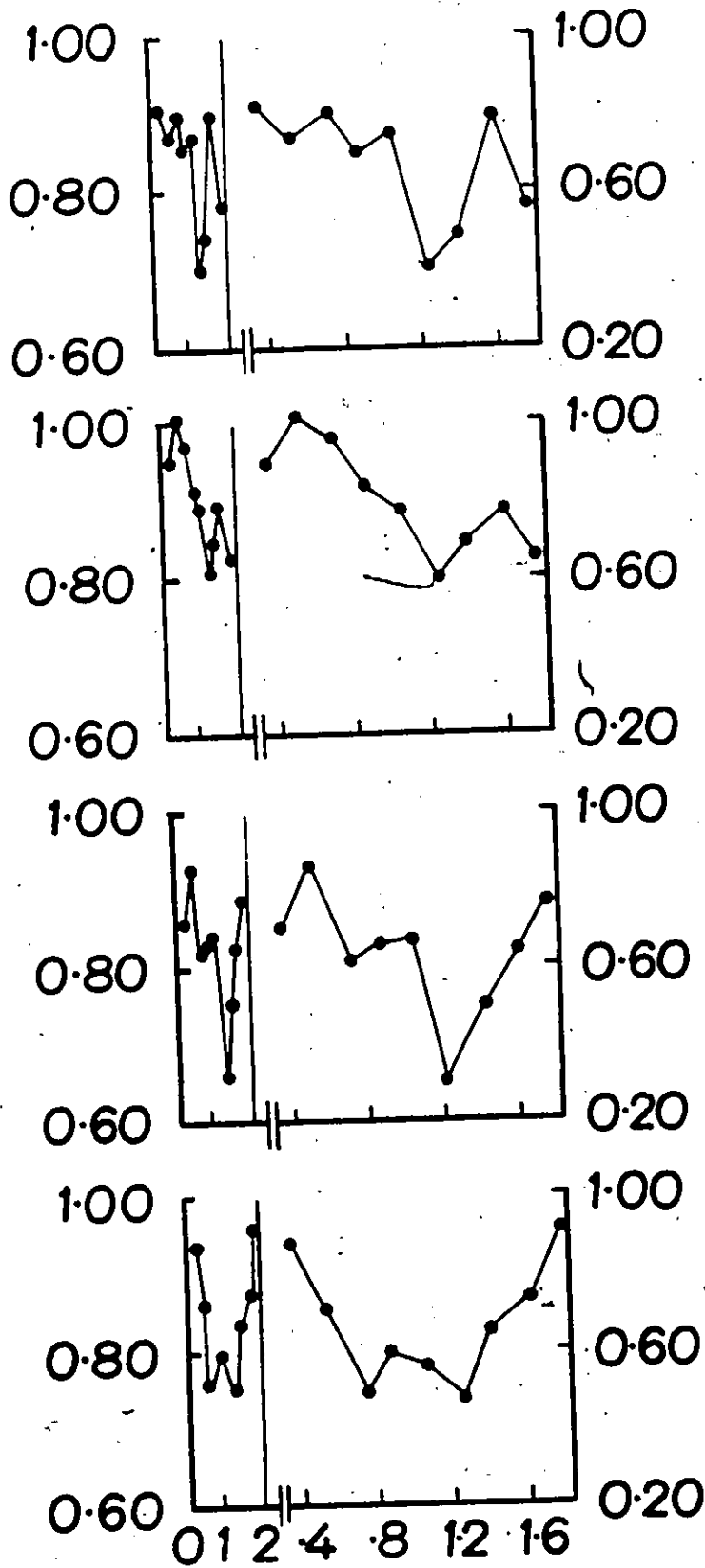
These results extend the notion that along the edge of a contour there is effectively a trough-like area of interference in which perception of (a discontinuity in) another contour is relatively impaired (Figure 29).

Table VI. Gap size and baseline scores for the subjects in Experiments Five.

Subject	Eye	Gap size (minutes)	Percent correct trials	
			Gap present	No gap
M.H.	Left (dom.)	0.3	75%	70%
	Right	0.3	86%	71%
L.deS.	Left	0.3	70%	90%
	Right (dom.)	0.3	84%	98%

Figure 28. Accuracy in discriminating presence or absence of a gap in the test line with varying distance of two symmetrically flanking lines. Subjects M.H. (L.E. and R.E.) and L. de S. (L.E. and R.E.). Each data point represents 100 trials.

PROPORTION OF CORRECT TRIALS

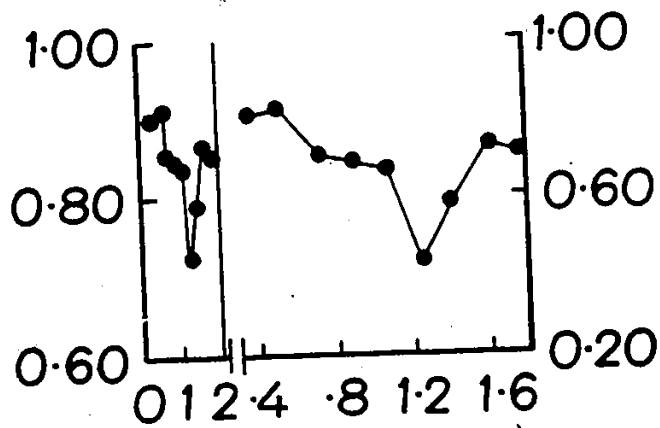


$P^*(c)$

LINE SEPARATION (MINUTES)

Figure 29. Postulated effect of two narrow added lines on discrimination of the presence or absence of a gap in a line between them. The model is derived by averaging the functions in Figure 28.

PROPORTION CORRECT TRIALS

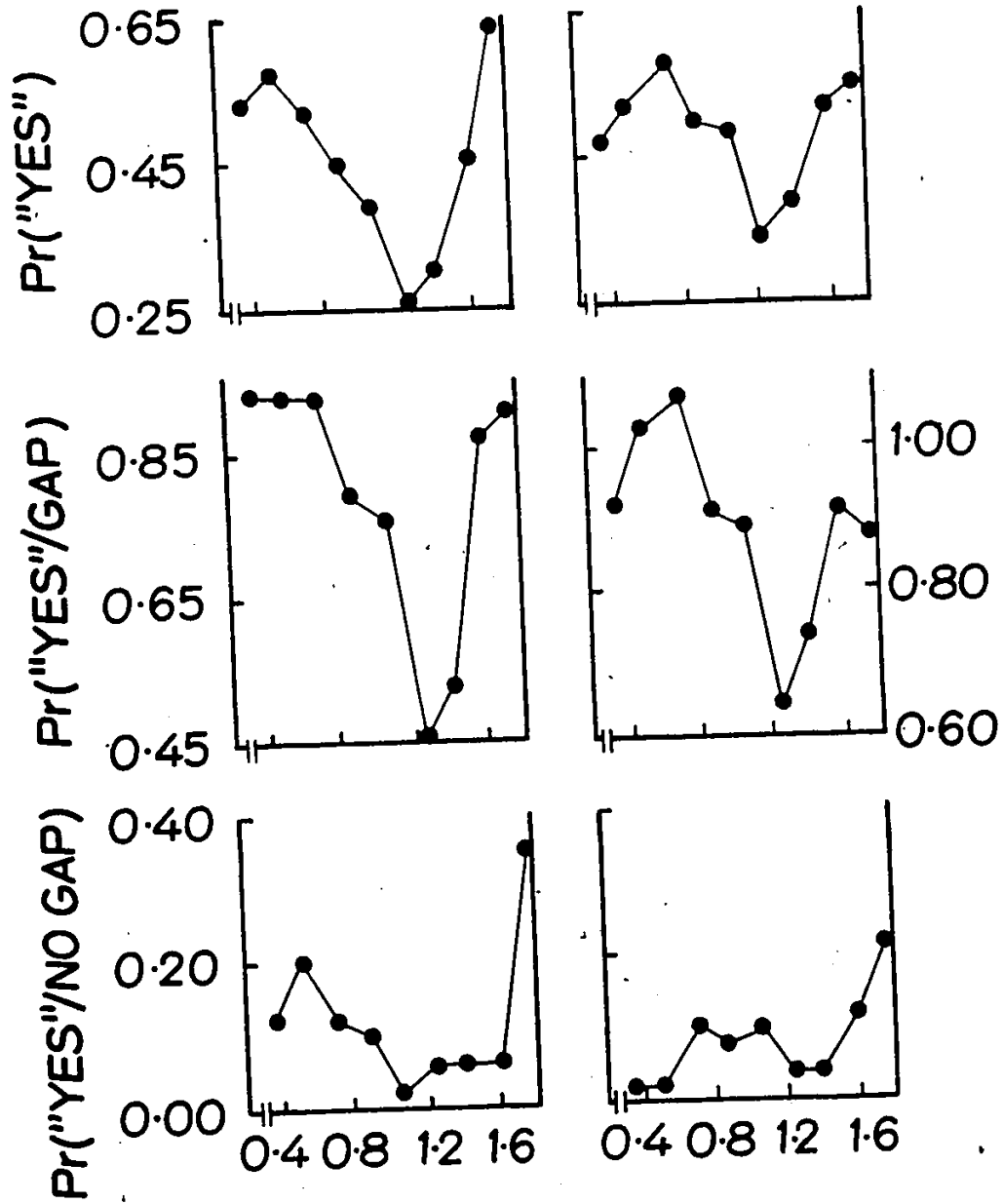


P* (c)

LINE SEPARATION (MINUTES)

If the probability of saying "yes" when there is a gap present is plotted against line separation and the probability of saying "yes" when there is no gap in the test line is similarly plotted, it is apparent that the tendency to report the presence of a gap varies with line separation in a manner comparable to the response of a visual cell with an antagonistic centre-surround-extra-surround receptive field organization (Figures 30, 31 and 32). By analogy, the gap may be conceived of as effectively overlying the "on" centre of the hypothetical receptive field. When the symmetrically flanking lines are very close to the test line one may imagine that they overlie the inhibitory surround. As the centre is effectively stimulated and the surround is not the net response of a cell in the visual system possessing a receptive field so stimulated would be to fire. As the black flanking lines are removed to greater distances from the test line the light area between the lines is extended laterally so that the inhibitory surround is stimulated over increasing areas. As the size of the stimulated surround area increases a stronger inhibitory effect is exerted so that the net response of the visual cell is diminished reaching a minimum when the total width of the surround is stimulated. As the flanking lines are moved still further from the test line the light area between the lines begins to encroach on the "disinhibitory" extra-surround. As more of the extra-surround area is stimulated its antagonistic influence on the inhibitory effect of the surround increases and the net response of the cell is a gradual recovery of firing in response to stimulation of the receptive field centre by the bright gap in the test line.

Figure 30. Probability of indicating the presence of a gap in the test line (A) overall, (B) when there was a gap present, and (C) when there was no gap present: Subject M.H. In the 3 pairs of graphs individual data points represent 100, 50 and 50 trials, respectively.



LINE SEPARATION (MINUTES)




Figure 31. Probability of indicating the presence of a gap in the test line (A) overall, (B) when there was a gap present and (C) when there was no gap present. Subject L.deS. In the 3 pairs of graphs individual data points represent 100, 50 and 50 trials, respectively.

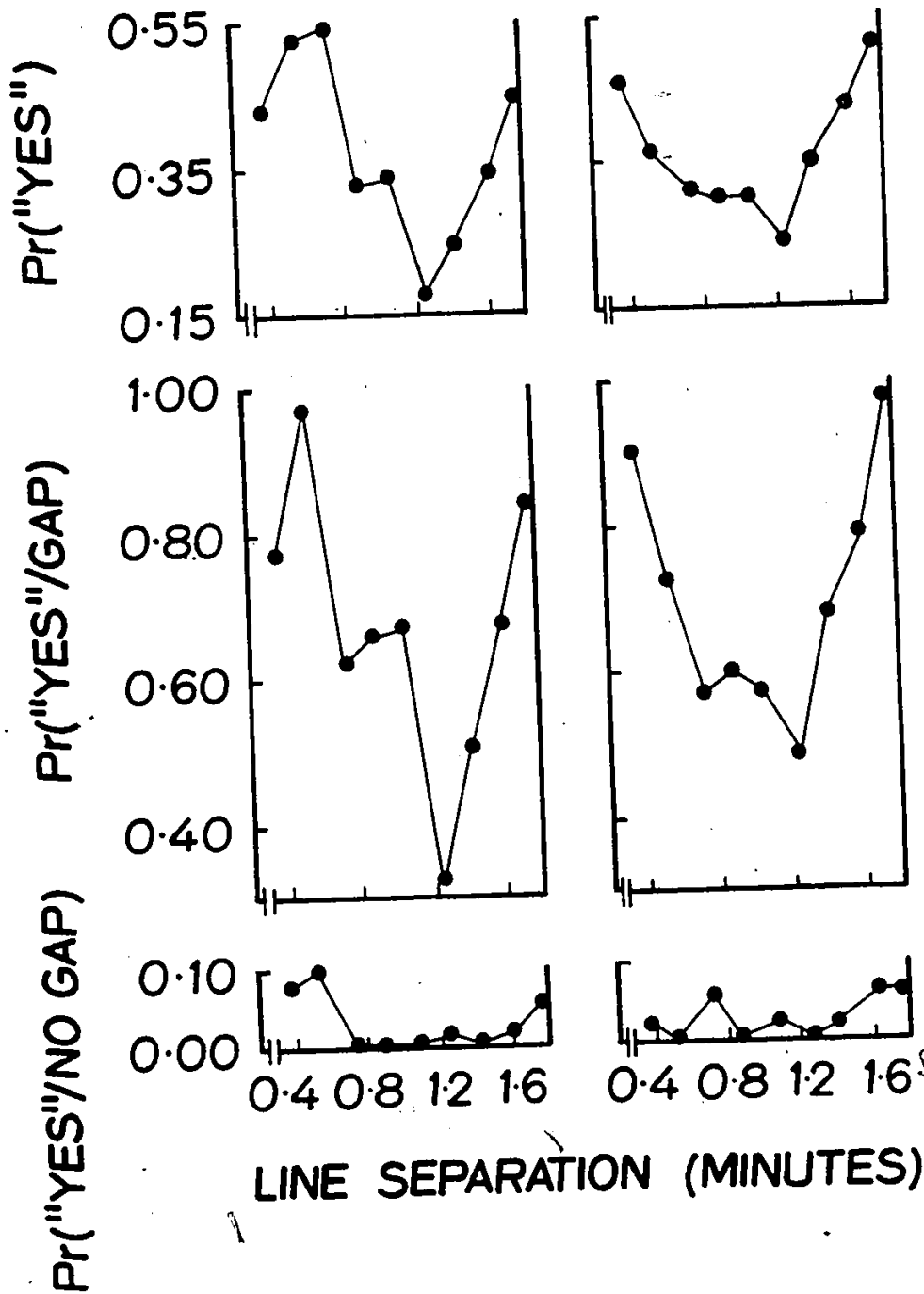
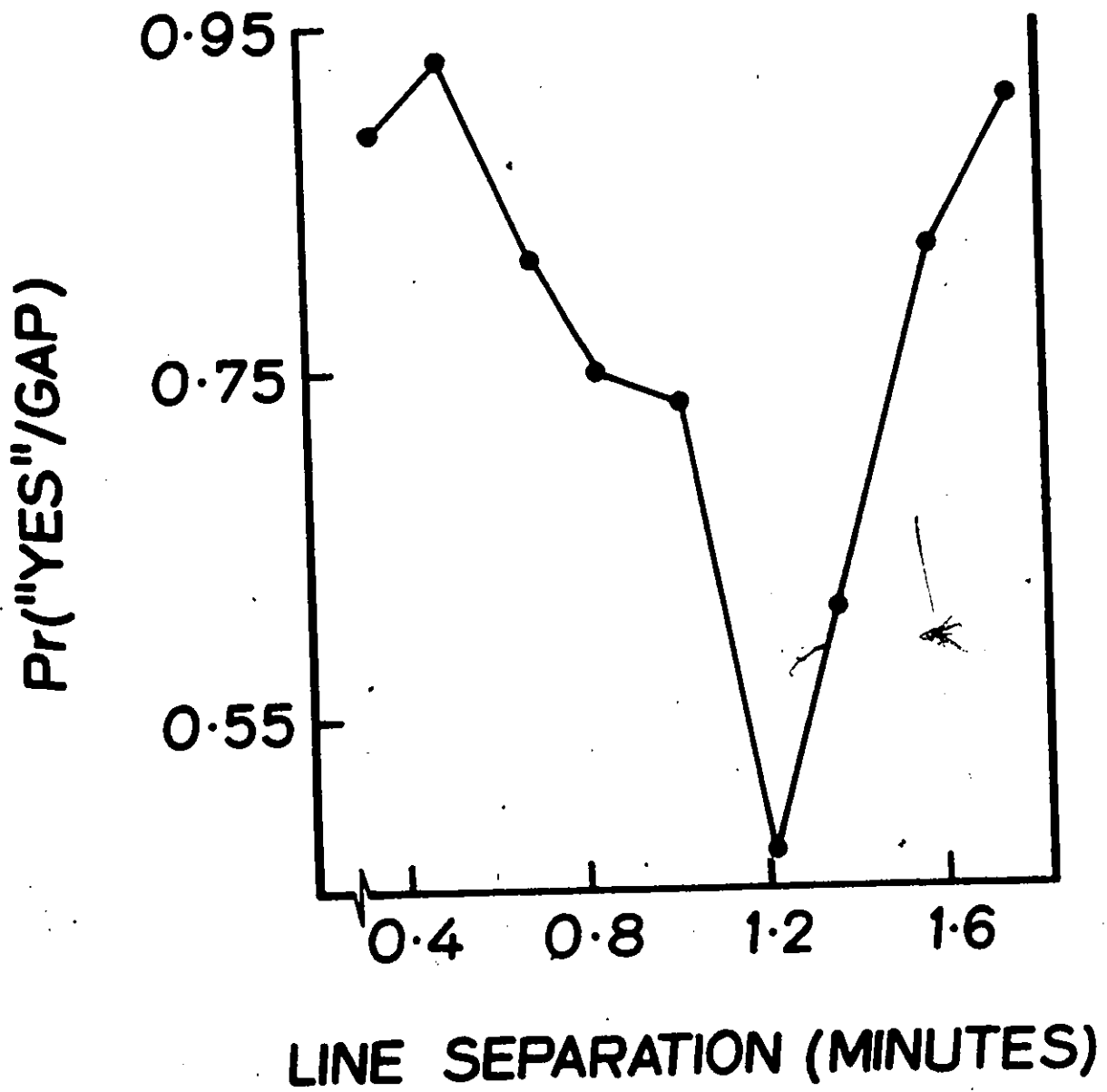


Figure 32. Postulated effect of 2
flanking lines on perception
of a gap in the test line.
Model is derived by averaging
the 4 (B) functions in
Figures 30 and 31.



This comparison to single cell function is appealing as it suggests a model for the seemingly paradoxical finding that perception of a gap in a test line is less likely when additional lines are a short distance (approximately one minute of arc) away from the test line than when these lines are either closer to or further from the test line. While this analogy draws on one of the pervading organizing principles of the mammalian visual system, antagonistic centre-surround-extra-surround effects, it cannot be offered as an appropriate model of the integrated function of the human visual system with the present state of our knowledge. As noted earlier, the electrophysiological data are derived from non-human species usually with immobilization of the eyeball, so generalization to the freely-viewing human is not necessarily warranted. Moreover, little is known about the relationship between single cell activity and the activity of populations of cells, much less the relation of either to perceptual experience. Consequently this appealing analogy between perception and single cell activity is purely speculative.



CHAPTER FIVE

GENERAL DISCUSSION AND CONCLUSIONS

The work reported here constitutes a rather broad, empirical study of the general relationship among small eye movements, spatial interaction between visual contours and the perception of (a discontinuity in) a target contour. As had been found by others (Riggs and Ratliff, 1951; Fender, 1956; Steinman et al., 1967), saccadic eye movements recorded during steady fixation of a small stationary target rarely exceeded 30 minutes of arc in amplitude and were frequently less than 10 minutes of arc. Recording during conversation, a less structured situation with no explicit fixation instructions, suggested the possible variation in the amplitude and frequency of these small eye movements. More saccades occurred during conversation and there was an increase in the relative number of saccades exceeding 30 minutes of arc in amplitude. The distributions of saccade amplitudes differed significantly in the two situations.

Historically fixation eye movements were regarded as unique and as possibly being generated by a different neural mechanism than were the larger 'scanning' saccades. Zuber, Stark and Cook (1965) found that a single function described the relationship between velocity and amplitude for all saccades up to 3 degrees suggesting that saccades of varying amplitudes were generated by a common neural mechanism or were at least limited by the same mechanics. Cunitz and Steinman (1969) hypothesized that if saccades of varying amplitude were initiated by a single neural system, the distribution of time intervals between

saccades should not vary with saccade amplitude. They found that although the size of saccades differed substantially during reading as compared to maintained fixation, the distributions of time intervals between fixation microsaccades and between large reading saccades overlapped considerably and the modal interval between saccades was 'very similar' in the two conditions. They concluded that the temporal distribution of eye movements was not related to their size and that all saccades of varying amplitude were initiated by a single system.

In the work reported here, the interval between saccade onsets was taken as the variable indicative of the functioning of an initiating mechanism for saccades. The distributions of intervals between saccade onsets during conversation and during fixation differed significantly with a tendency toward proportionately more short intervals (up to 100 milliseconds) during conversation. Despite the initial impression that the larger eye movements recorded during conversation might be associated with shorter intervals between saccade onsets no linear relationship between saccade amplitude and time since the onset of the previous saccade could be established. In fact, the relationship between these variables appears to differ in the 2 situations with association between short intervals and small saccades more likely during conversation than during fixation.

Although these data support Cunitz and Steinman's conclusion that there is no general relationship between the timing of saccades and their amplitude, they indicate nevertheless that the timing of saccades may vary in different situations. It is not clear whether this is sufficient to refute the notion of a common initiating

mechanism. At least some proportion of the smaller saccades observed during conversation may be 'corrective', that is, minor adjustments to the main saccade. As such, they may not be appropriately regarded as initiated by a discrete neural event equivalent to that initiating the main saccade. Rather, corrective saccades may represent an alteration superimposed on the main saccade and thus (by their occurrence before another main saccade) contribute to the proportion of relatively short intervals between saccade onsets. It appears that the question of a single initiating mechanism for saccadic eye movements cannot be simply resolved with data on the timing of saccades.

Abolition of the relative motion between a visual image and the retina results in intermittent perceptual fading of part or all of the image (see work by Ditchburn, Riggs, Yarbus, Pritchard, Evans, Piggins and others). Small eye movements apparently play a role in sustained perception of a visual target (Ditchburn, Fender and Mayne, 1959). Indeed when a subject first views a 'stabilized' retinal image the eye moves about in an exaggerated fashion as if to restore perception of the target. In the present work, it was hypothesized that successful manipulation of the likelihood of perceiving a target in a free-viewing situation (as opposed to stabilized viewing) might precipitate a concomitant change in the pattern of small eye movements suggestive of an attempt to restore perception.

Perception of a target contour may be adversely affected by the presence of a nearby contour (Rentschler and Hiltz, 1976; Flom, Weymouth and Kahneman, 1963) over separations as small as a few minutes of arc. As this is within the range of amplitudes of fixation microsaccades one

might expect to see a concomitant change in the pattern of small eye movements. To facilitate prediction in the present work, a vertical line target was utilized and the amplitude distribution of horizontal saccades varied as expected. The area of interference along the added line appeared to be a few minutes of arc in extent. When the distance between the target contour and the added contour was such that perception of the target was disrupted there was an increased number of horizontal eye movements slightly larger than the apparent area of interference. Were it not for the fixed location of the added line relative to the test line these eye movements might have been adequate to restore perception of the visual target.

Apparently, the distribution of saccadic amplitudes may be affected by subtle variations in the viewing situation which affect perception of a feature of interest. The provocation of a predicted shift in the distribution of saccadic amplitudes by manipulation of the perceptibility of a target contour in an unstabilized viewing situation augments evidence (albeit indirectly) that microsaccadic eye movements act to maintain perception of a visual target.

Among the studies of contour effects there is considerable variation with respect to the shape and dimensions of target figures, the spatial separations between contours tested and the subject's task. Contour interaction effects have been described as interference, facilitation or both and the estimated spatial extent of the contour effect differs across studies. In general however, the magnitude of the effect on perception of a target contour varies with the spatial separation between the target and a nearby contour.

13

The present work concerned the effect of 1 or 2 vertical lines on perception of a gap in another vertical line. The use of such a target provided for minimal confounding of contour interaction and permitted prediction of a specific shift in the amplitude distribution of horizontal microsaccades. The data confirm that along a contour there is an effective area of perceptual interference extending a few minutes of arc from the contour. Perception of a target contour which falls within an area a few minutes of arc from another contour is likely to be adversely affected.

Interfering effects between letters summate so that the deleterious effect of 2 flanking letters on perception of a target letter is greater than that of a single adjacent letter (Taylor and Brown, 1972; Bouma, 1970). Moreover there appears to be a strong suparetinal component to the interaction between adjacent letters (Taylor and Brown, 1972) as well as between other types of target contour and one or more additional contours (Westheimer and Hauske, 1975; Flom, Heath and Takahashi, 1963). These studies all demonstrated that a contour presented to one eye may have a deleterious effect on perception of a contour presented to the other eye.

Simultaneous presentation of a target contour to both eyes frequently facilitates perception of the target (Horowitz, 1949; Savage and Sumner, 1950; Kahneman, Norman and Kubovy, 1967). When a target contour is surrounded by other contours, the advantage (to perception of the target) conferred by binocular presentation may be so attenuated as to be negligible, suggesting that interference effects summate binocularly as well (Davage and Sumner, 1950; Blake and Fox, 1973).

136

In the present work perception of a gap in a line was similarly affected under both monocular and binocular viewing conditions by variations in the distance to 2 flanking lines. Though perception deteriorated and improved over the same range of separations for all subjects under both viewing conditions, compared to perception with no added lines, the contour effect appeared to be interference in some cases and facilitation in others - a rather puzzling situation. The experiment was not conducted in such a way as to permit assessment of the contribution of binocular summation whether facilitative or interfering. The experiment simply demonstrates contour interaction effects in both monocular and binocular viewing.

The data of Flom et al. (1963) as well as results reported here suggested that the effect of contour interaction on target perception might conform to a "U-" or "V-" shaped function of contour separation, at least over an area of a few minutes of arc. Restricting the line separations tested to just a few minutes of arc confirmed that the likelihood of perceiving the gap in the test line varied as a trough-like function of line separation.

The tendency to report perception of a gap varied with contour separation in much the same way as does the response of certain monkey visual cells to a similar stimulus. Although the similarities between the human perceptual experience and the response of single cells in the visual system of the monkey invite generalization from one to the other they must be regarded cautiously as an interesting coincidence, given the present state of our knowledge.

The effect of an adjacent contour on gap perception is most parsimoniously explained on the basis of spatial summation within antagonistic areas of concentrically organized receptive fields. Thus it is unnecessary to resort to a model based on line detectors or edge detectors (Tolhurst, 1972). Spillman, Fuld and Gemits (1976) proposed a similar model to account for the brightness phenomenon in the Ehrenstein illusion. These authors ascribed the effect to both retinal and supra-retinal components though the latter was regarded as being considerably weaker. Although the present data do not permit discrimination between retinal and post-retinal effects, the results of Experiment Four raise the possibility of binocular receptive fields characterized by spatial summation and by concentrically organized and antagonistic areas of somewhat greater dimensions than in monocular fields. The latter may range from 2 to 5 minutes of arc in diameter according to the present results, a value somewhat smaller than the 5 minute estimates by Westheimer (1967) and Baumgartner (1960).

In recent years the visual system has been likened to a spatial frequency analyser responding to the Fourier components of the luminance distribution across the visual field (for example, See Westheimer, 1960). According to this notion different visual channels respond to sinusoidal luminance distributions of certain frequencies and these channels interact in various ways. The results of Experiment Five in particular may be interpreted according to a model of spatial frequency channels. Gap perception is relatively unaffected when the spacing between the lines is either one or three times the width of an individual line. In both cases the central (test) line would coincide

with the locus of a dip in a sinusoidal luminance distribution based on the width and location of the 2 added lines. The actual luminance distribution across the stimulus area containing the gap carries an effective spatial frequency of half that across stimulus areas containing 3 solid line segments. This frequency difference of one octave has been found to be of significance in other psychophysical studies. In a composite luminance grating the individual Fourier components are perceived independently when their spatial frequencies differ by at least an octave (i.e. by a factor of 2).

In the stimulus configuration providing for substantial interference with gap perception the spacing between the lines was such that the lines would not coincide with the dark phases of a sinusoidal luminance grating whose half-cycle width equalled the width of the target lines. This result suggests that this particular line configuration failed to optimally activate a particular spatial frequency channel rendering discrimination of the presence or absence of a gap (i.e. a difference in spatial frequency) much more difficult. This model has appeal, however the data do not uniquely favour either a spatial frequency channel model or a receptive field model. As the latter is simpler and requires fewer assumptions it is here endorsed in the interests of parsimony. Extending the width of the added lines to virtual infinity would permit one to determine whether a receptive field model based on spatial summation in concentrically organized antagonistic areas adequately accounts for the present findings.

The likelihood of perceiving a visual target is typically lower during a saccadic eye movement. Saccadic suppression is much greater

when a target is viewed against a patterned background than when viewed against a featureless ground. This suggests that the effect may be principally attributed to interference or masking from contour sweeping across the retina. In Experiment Two it was found that attenuated perception of the gap was associated with a particular line separation as well as with a shift in the pattern of saccadic eye movements to somewhat larger amplitudes. The likelihood of perceiving the gap varied with line separation. The shift toward larger saccades was recorded only at the separation associated with a substantial attenuation of gap perception. As discussed in the experiment, the altered pattern of eye movements is probably secondary to a spatial contour effect. Nevertheless, it is possible that saccadic suppression served to further depress gap perception at that point, with the added line acting as a masking contour.

This research provides normative data and an approach which may be utilized in the study of such perceptual disorders as amblyopia ("lazy eye") and certain reading disabilities. Either of these conditions might be fruitfully investigated with a model based on the general relationship between contour interaction, small eye movements and visual perception suggested by these data.

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APPENDIX

ESTIMATION OF THE EFFECT OF GAP SIZE ON GAP PERCEPTION

After Experiment 3 was completed, the gap on each stimulus card was measured with a travelling microscope. As there were slight variations in gap size on the stimuli viewed by a subject (the total range of variation was less than 0.5 millimeters or 0.35 minutes of arc viewed at 10 meters) the effect of these variations was estimated and the data adjusted accordingly. Preliminary work suggested that the proportion of correct responses increased linearly over a small range (possibly 0.6 millimeters) of gap sizes and levelled off at higher or lower values. As only 2 of the original 5 subjects were available for testing on variations in gap size specifically, the effect was inferred for the other subjects from their original data.

METHOD

Subjects. Two of the subjects whose data are reported in Experiment 3 participated in this study. Each viewed with the dominant eye wearing the same optical correction as in the original experiment.

Apparatus and stimuli. The apparatus was that used in Experiment 3. The subject viewed a series of 10 cards each bearing a single vertical test line but having gaps of 5 different sizes, each size being presented once near the top and once near the bottom of the line. The range of gap sizes tested exceeded the range of gap sizes viewed by the subject in the original experiment. JZ was tested on gap sizes of 0.80 to 1.60 millimeters (0.28 to 0.56 minutes of arc) and C.H. was tested on gap sizes of 1.65 to 2.45 millimeters (0.58 to 0.86 minutes of arc).

Procedure. As in the original experiment the stimulus cards were mounted by hand and the subject's task was to indicate the location of the gap. The 10 stimuli were presented in random order and the entire set was presented 10 times a session. There were 10 daily sessions in all. The number of correct responses per session for each gap size was recorded and the overall probability of a correct response for each gap size was computed. Correction of the data for response bias under the signal detection model (Green and Swets, 1974) produced no significant change in the number of correct responses for the various gap sizes (Walsh test \circ Siegel, 1956) so the uncorrected data were used.

RESULTS

For JZ the probability of a correct response increased linearly with gap size up to 1.4 millimeters and then levelled off (Figure 33). The linear regression of frequency of correct responses on gap size (0.8 to 1.4 millimeters) was

$$Y'_1 = 10.2X + 4.93 \quad (\text{Eq. 1.1})$$

and the correlation between the two variables, r , was +0.84. For each position of the added line in the original experiment there were 2 possible gap sizes, 1 at the top of the test line and 1 at the bottom. Each of these was presented twice in a session giving a total of four presentations of the added line in a particular location with respect to the test line. To predict the likelihood of correctly locating a gap in the original experiment simply on the basis of its size the regression equation was divided by 10:

$$\frac{Y'_1}{10} = 1.02X + 0.49 \quad (\text{Eq. 1.2})$$


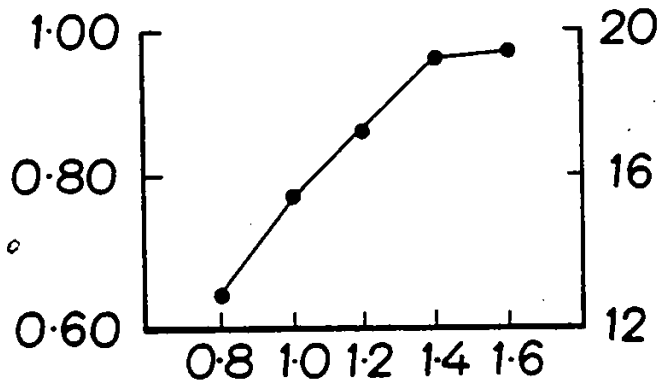


Figure 33. Accuracy in gap location as a function of gap size.
Subject J.Z. Each data point
represents 200 trials.

PROPORTION CORRECT TRIALS



GAP SIZE (MILLIMETERS)

MEAN FREQUENCY CORRECT TRIALS

The predicted number of correct trials for the gap size at the top of the line plus that for the bottom of the line were subtracted from the actual score to obtain an estimate of the experimental effect, that is, the effect of the added line in a particular location relative to the test line. The difference score thus computed for presentation of the test line alone was subtracted from the original score to obtain a number which was then added across conditions to all of the difference scores. The effect of this procedure was to standardize the scores to the original score on the test line alone. These scores, representing the number of correct trials for each location of the added line relative to the test line, were expressed as the proportion of trials correct under each condition.

The linear regression of the number of correct responses on gap sizes of 1.85 mm. to 2.45 mm for subject CH was

$$Y'_1 = 4.8X_1 + 4.68 \quad (\text{Eq. 1.3})$$

Dividing this by 10 gave

$$\frac{Y'_1}{10} = 0.48X_1 + 0.47 \quad (\text{Eq. 1.4})$$

This predictor was applied to CH's data in Experiment 3 in the same manner as had been done for JZ.

For the remaining subjects a linear regression analysis was carried out on the original data to derive a function relating correct location of the gap to gap size for each eye tested. The values predicted by the obtained linear function were subtracted from the actual scores (as was done for the previous subjects) to give an

estimate of the experimental effect. These differences in turn were standardized to the test line alone condition and converted to proportions.