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THE VISIBILITY AND FADING OF THIN LINES VISUALIZED BY THEIR CONTROLLED MOVEMENT ACROSS THE RETINA

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SUMMARY

1. The entoptic shadows of the retinal blood vessels were visualized by temporal modulation of their contrast.

2. For perception of fine detail, the shadows must move successively from one photoreceptor to the next. To see coarser detail the contrast need only be temporally modulated.

3. The contrast threshold of the pattern of shadows rises steadily as they are viewed until the shadows can no longer be seen even with the highest contrast available.

4. This elevation of contrast threshold is partially binocularly transferred, suggesting that the perceptual fading has a central origin.

5. The fading of the shadows is specific for their orientation, direction of movement and their width.

6. Image movements like those produced by fixational eye movements have been simulated. The shadows still fade; the results can be explained in terms of spatial adaptation (Blakemore & Campbell, 1969) of spatial frequency and orientation channels.

INTRODUCTION

Images stabilized with respect to the retina quickly fade (Ditchburn & Ginsborg, 1952); some workers (Pritchard, Heron & Hebb, 1960) report that they reappear and fade repeatedly, while others (Campbell & Robson, 1961; Yarbus, 1967) observe no reappearance. Barlow (1963) has studied the various methods of image stabilization and has suggested that reappearance may be due to faulty stabilization.

Flickering the stabilized image prolongs the time for which it is seen

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(West, 1968). Similarly, moving the image with respect to the retina in a controlled fashion can keep it visible for a longer time (Ditchburn, Fender & Mayne, 1959). Nevertheless, the image still fades.

Brindley (1970, p. 149) has suggested that the fading of detail and contrast of accurately stabilized images may occur at the retinal level as 'retinal ganglion cells are known to adapt in an appropriate way'. Gerrits, de Haan & Vendrik (1966), on the other hand, cite evidence to suggest that stabilization effects occur in a 'higher centre' of the visual system, i.e. central to the retina and lateral geniculate nucleus. The site of fading of temporally modulated images in the human is even less certain. Enroth (1952) shows records of cat retinal ganglion cells that do not cease responding to flickering light even after extended periods of stimulation; presumably the perceptual habituation in humans must occur central to the retina.

Many of these conflicting results and interpretations may have their origins in faulty stabilization. This study of stabilized images and controlled movement of them is based on the most nearly perfectly stabilized system: the entoptic shadows of the retinal blood vessels. As the retinal blood vessels lie in front of and extremely close to the photosensitive elements of the retina and move with the retina, stabilization is almost perfect. While the patterns the subject views are necessarily limited, it is, nevertheless, possible to suggest answers to the following questions:

(i) which parameters of image presentation are necessary to make the images visible continuously?, e.g. types of temporal modulation and movement, contrast levels, etc.

(ii) at what level in the visual system does fading of temporally modulated images occur?

It should be pointed out that this is essentially a study of parafoveal and near peripheral vision, as no blood vessels lie over the fovea.

METHODS

The technique for making the blood vessels visible has been described by Campbell & Robson (1961) and extended by Sharpe (1971) using a PDP-8 digital computer (Digital Corp.).

In brief, when a spot of blue light from an oscilloscope (P-11 phosphor), focused in the plane of the pupil of one eye with a converging lens (Maxwellian View), is made to scan the subject's dilated pupil, he sees the lens uniformly illuminated, with the shadows of the blood vessels superimposed. The focal length of the lens used was 60 mm; at this distance from the plane of the pupil the uniformly illuminated field subtended 27 deg. A small spot at the centre of the lens was fixated. The subject's pupil was dilated and accommodation paralysed with either cyclopentolate hydrochloride (Mydrilate) or Homatropine. His other eye was covered and his head was held rigid with a bite bar.

Simple patterns of movement were executed by the oscilloscope beam, causing

the shadows of the vessels to move over the retina in a controlled fashion. The coordinates for the successive positions of the spot of light were generated on the computer in FOCAL (a simple interpretive computer language) and displayed by means of a machine code programme whose speed was set by an oscillator. The relative contrast of the moving shadows could be controlled by varying the proportion of time the spot spent moving rather than stationary in the centre of the pattern. This kept the mean luminance constant.

The experiments were performed on one subject (C.R.S.) quantitatively and checked qualitatively on several others.

RESULTS

Anatomical considerations

Michaelson & Campbell (1940) claim that the retinal blood vessels which cast shadows upon the photoreceptor layer of the retina are situated in two layers. The superficial capillary net and large vessels lie in the optic nerve fibre layer, while the deep capillary net lies between the inner nuclear and the inner plexiform layers. A more recent study, however, by Toussaint, Kuwabara & Cogan (1961) using an improved histological technique to preserve three-dimensional structure claims that such a laminar structure does not exist. 'The lamination of capillary plexuses which has not been thought to be characteristic of the retina was not, in general, confirmed. One exception to this is a plexus in the nerve fibre layer about the disk and arising from the disk. Another possible exception is the periphery where the thinness of the inner layers of the retina is accompanied by a comparable thinness of the vascular zone. Elsewhere, capillaries anastomose throughout all layers without any tendency to lamination.'

Helmholtz (1909, vol. I, p. 220) quotes H. Müller's figure of 0·2–0·3 mm for the distance between the blood vessels and the photoreceptor layer in the region of macula lutea based on histological evidence. Müller also estimates this distance by matching the apparent displacement of the vessels to a visual angle in the outside world when the light shone trans-sclerally to visualize them was moved. For three subjects he obtained the values 0·19, 0·26 and 0·36 mm. Brindley (1970, p. 139) has pointed out that this agreement between the anatomical evidence and the psychophysical experiment is the most direct evidence to support the hypothesis that the rods and cones are the light receptors. Implicit in this reasoning is the assumption that the vessels upon which the comparison is based do lie in definite layers.

This experiment was repeated with a spot of light moving up and down a line 6 mm long focused in the plane of the pupil. The vessels made visible were horizontally oriented (normal to the direction of movement of their shadows); at 8 Hz and 15 Hz the subjects saw capillaries and larger vessels respectively. Their angular widths were estimated and found to correspond to thicknesses of 7 and 67 μ, which are consistent with the vessels being capillaries and arterioles (Hogan & Feeney, 1961).

Assuming distances of 17 mm between the nodal plane of the eye and the retina and 20 mm between the plane of the pupil and the retina (Helmholtz, 1909, vol. III, p. 39), the vessels were calculated to lie 0·12 mm (S.D. $\pm$ 0·03, N = 10) in front of the photoreceptors for subject C.R.S. and 0·16 mm (N = 2) for subject J.G.R. (No correction was made for the reduction in length of the line caused by the refracting elements of the eye; ray tracing shows that this correction would be very small.) The larger vessels appeared to move slightly more than the smaller ones, although this was virtually impossible to quantify. Both this observation and the anatomy

point to the fact that the larger vessels lie farther away from the retina than the others. In future calculations the value 0·1 mm will be used as an approximation for the vessel to receptor distance for all types of vessel.

The large difference between this figure and Müller's is not surprising. As Müller visualized the vessels by trans-scleral illumination, there was probably a large degree of uncertainty in the geometry of his calculations. He almost certainly was viewing the largest vessels alone; if one illuminates the eye trans-sclerally by sunlight brought to a focus on the sclera, the field seen is reddish yellow (Helmholtz, 1909, vol. I, p. 212). The capillaries are only visible with green or blue light (Behrendt & Wilson, 1965).

These drawbacks to Müller's experiment are mentioned in a similar study by König & Zumft (1894), and apparently he himself was aware of them. König & Zumft cast double shadows of the vessels upon the receptors by moving in front of the eye a surface through which two narrowly separated pinholes were made to act as point sources for monochromatic light. They compared the distance between the double shadows to a scale viewed through the other eye. They obtained values of about 0·4 mm for the vessel to receptor distance.

If the capillaries anastomose throughout all layers of the retina as Toussaint *et al.* (1961) suggest, then one would expect the capillaries closest to the photoreceptors to cast the sharpest shadows. The shadows of the larger vessels are not nearly as sharp, presumably because they lie farther away from the photoreceptors than the capillaries. The largest vessels, viewed either ophthalmoscopically or trans-sclerally, which converge on to the optic disk were not seen in this study. Unfortunately, neither Müller nor König and Zumft specify exactly which vessels they viewed.

Visualizing the vessels

(*a*) *Effects of movement*

As Campbell & Robson (1961) have pointed out, the most effective way of visualizing the retinal blood vessels is to scan the plane of the pupil with a spot of bright light brought to a focus. Blue light is optimal, probably due to the absorption properties of haemogolobin. The shadows of the branching vascular network that are seen are highly detailed and disappear *immediately* their movement is stopped. Movements of the eye with no movement of the spot of light are not sufficient to make the vessels visible. Even when the shadows are moved continuously, their apparent contrast decreases until they disappear completely; they then never reappear spontaneously.

Fig. 1 shows the disappearance times for the vessels that are seen when the pupil is scanned with a spot moving in a circle of diameter 6 mm as a function of temporal frequency. This kind of movement causes the shadows of the vessels to slide continuously over the photoreceptors through a total excursion of about 7 min arc. Circular scanning visualizes all orientations, whereas linear scanning reveals only those vessels whose shadows lie normal to their direction of movement.

As the velocity of the movement is increased, the larger vessels become visible. As Fig. 1 indicates, at 10 Hz with 7 min arc excursion, both

capillaries and larger vessels can initially be seen simultaneously; the capillaries are the first to disappear. The fact that the larger vessels lie superficial to the capillaries means that their shadows always move slightly faster across the rods and cones than those of the capillaries. Hence their lying in different planes does not explain why the larger vessels are seen only at higher velocities.

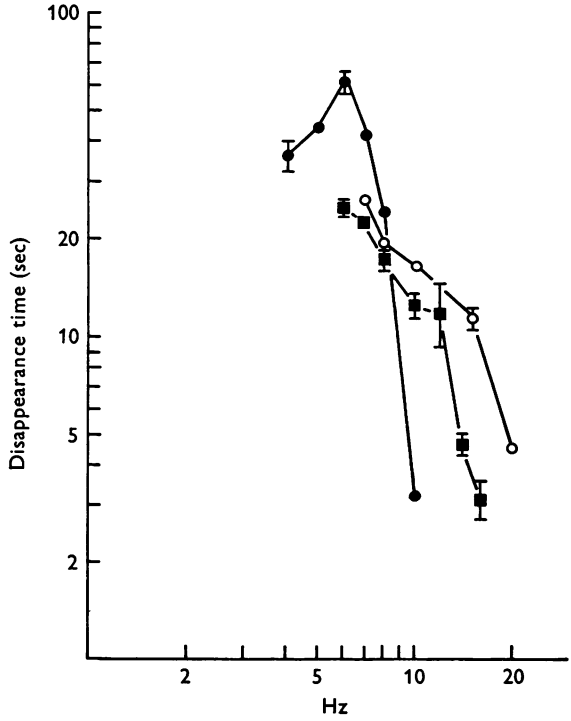

Fig. 1. Disappearance times for circular scanning producing total shadow excursion of 7 min arc: capillaries, ●; larger vessels, ○. (Capillaries were visible down to 2 Hz but the apparent contrast was so low that measuring disappearance times was difficult.)

Vessels visualized by flashing shadows on and off the same area of retina, ■.

Each point is the mean of five readings and S.E. is indicated when large enough, in this and subsequent Figures unless indicated otherwise.

If the spot of light is made to jump from one position to another and back again repeatedly, causing the shadows to jump across the retina, the larger vessels can be seen. The fine detail of the capillaries, however, is not visible. The most that is seen of the capillaries is a faint blur. Fig. 2 shows the range of temporal frequencies over which this method works as a

function of the displacement of the shadows across the retina. The minimum displacement to see anything at all (the faint blur) is about 1·2 min arc.

These results suggest that to see the fine detail of the capillaries their shadows must slide more or less continuously over the retina. Fig. 3 shows the results of an experiment to determine the maximum 'step length' compatible with seeing the capillary detail. The spot of light was made to move

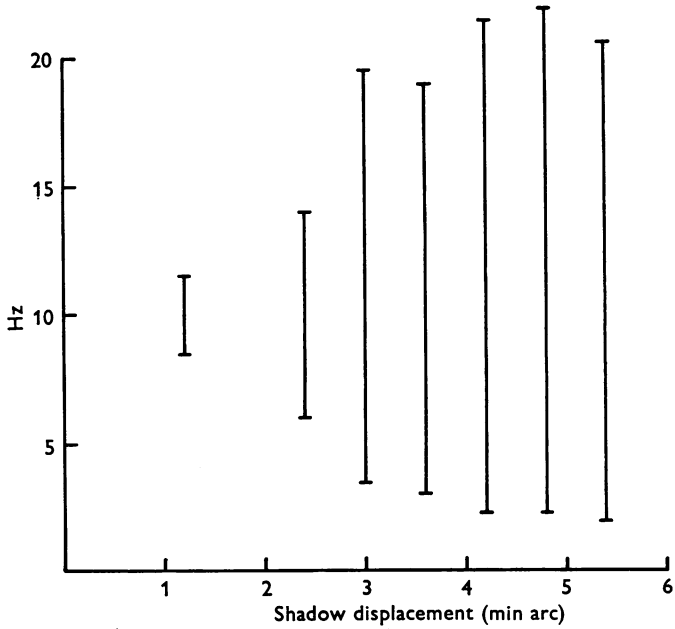

Fig. 2. The range of temporal frequencies over which vessels can be seen when visualized by a step displacement of their shadows. For a 1·2 min arc displacement only a faint blur is seen.

along a line in one direction, flying back to the beginning at the end of each traverse. The total excursion of the shadows across the photoreceptor layer was 7 min arc and the repetition rate was kept constant at 8 Hz. The number of successive positions of the spot in each scan was varied between 100 and 5; this varied the step length from one position of the shadows to the next from very nearly 0 to 1·4 min arc. The disappearance times for seven different step lengths are plotted. The maximum step length which can cause the shadows to be seen at all can be obtained by extrapolating the linear regression line to the horizontal axis. This suggests that for the shadows of the capillaries to be seen, they cannot move in steps larger than about 2 min arc across the photoreceptor layer.

Polyak (1941, Fig. 99) gives 1 and 2 min arc as the intercone separation for 1 and 8 degrees into the periphery, respectively. These figures and the above results would seem to suggest that to perceive very fine detail, the image has to move successively from one receptor to the next.

Are the velocities of shadow movement in this study necessary to visualize the vessels comparable to the image velocities during normal fixational eye movements? Ditchburn & Foley-Fisher (1967) quote a value

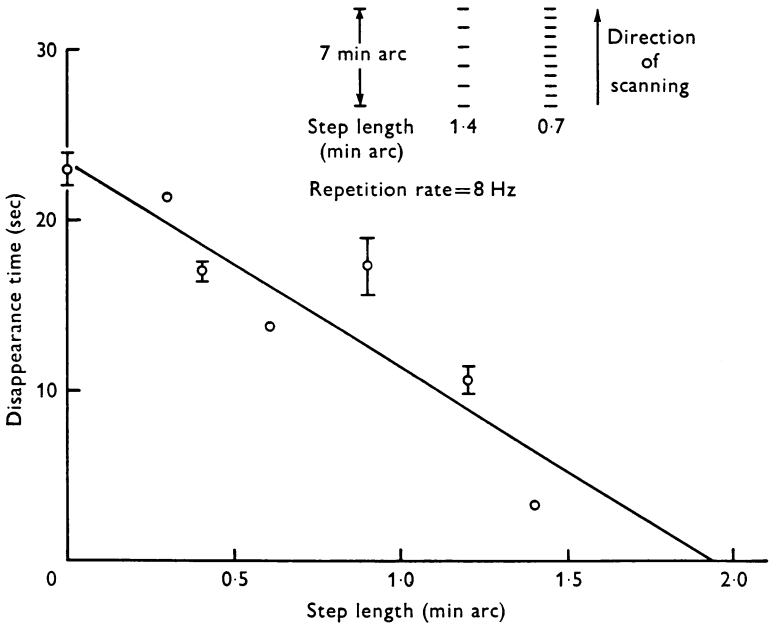

Fig. 3. Disappearance time as a function of step length for linear unidirectional scanning producing a shadow excursion of 7 min arc. Repetition rate kept constant at 8 Hz. Each point is mean of three readings and a straight line has been fitted to the points by the method of least squares.

Inset: horizontal bars indicate successive positions of a shadow in this experiment for two different step lengths.

of 4·3 min arc/sec as an approximate median drift velocity for the eye during fixation; this figure was calculated by pooling data from a number of subjects from several studies.

For a linear to and fro motion of the scanning spot of light with 7 min arc total shadow excursion, the slowest frequency at which the capillaries are visible is 1·5 Hz 1; the apparent contrast is low. This corresponds to a velocity of 10·5 min arc/sec. This is rather larger than the drift velocity of fixational eye movements. As the frequency is increased to about 8 Hz, the

apparent contrast of the shadows increases. The maximum velocity at which the arterioles were visible was 2·1 deg/sec (18 Hz).

Presumably the shadows become visible at 10·5 min arc/sec rather than at the fixational drift velocity because of temporal summation of on and off signals from the centres and surrounds of the receptive fields of cells at the various levels in the visual system. Hubel & Wiesel (1959) have shown 'synergistic' responses from neighbouring inhibitory and excitatory regions of orientation selective 'simple' cells in the visual cortex of the cat. The 'complex' units, which respond specifically to moving stimuli, only respond to movements of rather higher velocities; Noda, Freeman, Gies & Creutzfeldt (1971) give 10 deg/sec as a minimum in the awake cat. Similar results have been obtained in the awake monkey (Wurtz, 1969*a*,*b*). The necessity of temporal summation can be demonstrated by causing the spot of light to stop at a point on the circumference of a scanning circle for a fraction of each cycle – this keeps the velocity of shadow movement constant but decreases the repetition rate. If the delay is greater than about 0·8 cycles, then the shadows are no longer seen.

(*b*) *Effects of contrast*

Fig. 1 also shows the disappearance times for the situation in which the shadows of the vessels are flashed on and off on the same area of retina, the mean level of illumination being kept constant. This is equivalent to modulating the contrast of the images in a stepwise fashion. This was accomplished by alternately displaying for equal amounts of time an extremely fast circular motion (6 mm diameter circle in the plane of the pupil at 100 Hz) to dilute the contrast of all the shadows and a bright spot at the central position of the pattern to flash the shadows briefly on the area of retina directly behind the vessels. Below 10 Hz only fragments of precapillaries could be seen at very low apparent contrast; the highly detailed branching pattern of the capillaries was not seen. Above 10 Hz the larger vessels could be seen, but only poorly and with very low apparent contrast. Fig. 1 shows that the disappearance time for this method of visualization was always less than for the continuous movement method. Presumably only the wider vessels are visible when flashed on and off because they stimulate more than one receptor, resulting in spatial summation. The arterioles were estimated to subtend about 14 min arc, whereas the capillaries subtend only about 1·5 min arc.

If the uniform field is flashed on and off no shadows are seen at all. Presumably, the change in mean illumination is enough to mask any detail. If the subject, however, is initially dark adapted and then faces a bright surface and rapidly blinks his eyes, some of the vessels become visible fleetingly (Cornsweet, 1970, pp. 406–407).

Fig. 6 plots disappearance time as a function of the initial suprathreshold contrast of various patterns of shadows for circular scanning. The abscissa values represent the percentages of the maximum contrast available for a particular pattern which were set at the beginning of each test (see Methods). Up to a certain point the disappearance time increases with the contrast set initially for a particular pattern. To some extent, then, the disappearance time is a measure of the initial suprathreshold contrast that the subject perceived.

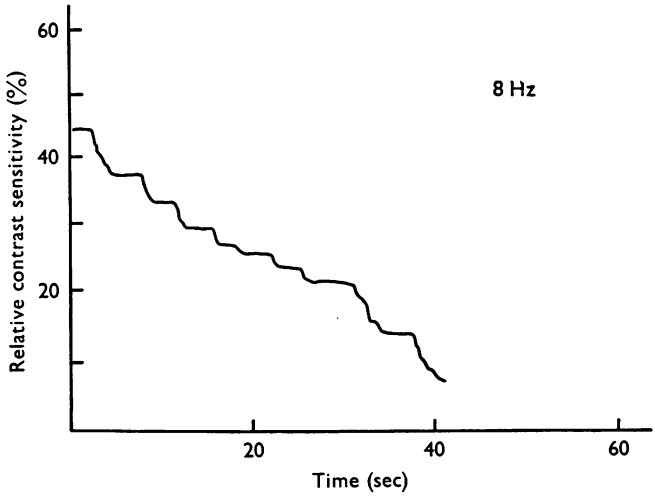

Fig. 4. Relative contrast sensitivity as a function of time for circular scanning producing a shadow excursion of 6 min arc. The subject viewed the patterns at threshold throughout the test. Ordinate values indicate the percentage of total light flux coming from the contrast diluting spot at the centre of the pattern. Ordinate values of 100 and 0 % imply contrast sensitivities of infinity and zero, respectively.

Fading of the vessels

(*a*) *Time courses of fading and recovery*

By using the contrast dilution technique described in the methods, it was possible to measure relative contrast thresholds as a function of time for the various patterns of shadows. Fig. 4 shows these measurements for the patterns seen by circular scanning which produced a total shadow displacement of 6 min arc. The ordinate values represent the percentage of total light flux entering the eye coming from the spot at the centre of the pattern; this light dilutes the contrast of the shadows cast by the spot of light as it moves around the edge of the scanning circle. Thus ordinate values of 100 and 0 % imply contrast sensitivities (the reciprocals of

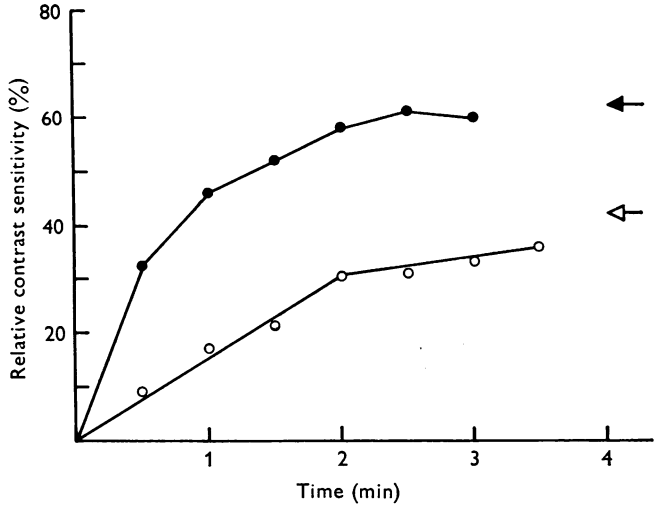

Fig. 5. Rate of recovery of contrast sensitivity after complete fading. Ordinate as in Fig. 4. Shadow excursion 6 min arc. Scanning frequencies of 8 Hz (○) and 14 Hz (●). Arrows indicate initial contrast sensitivities.

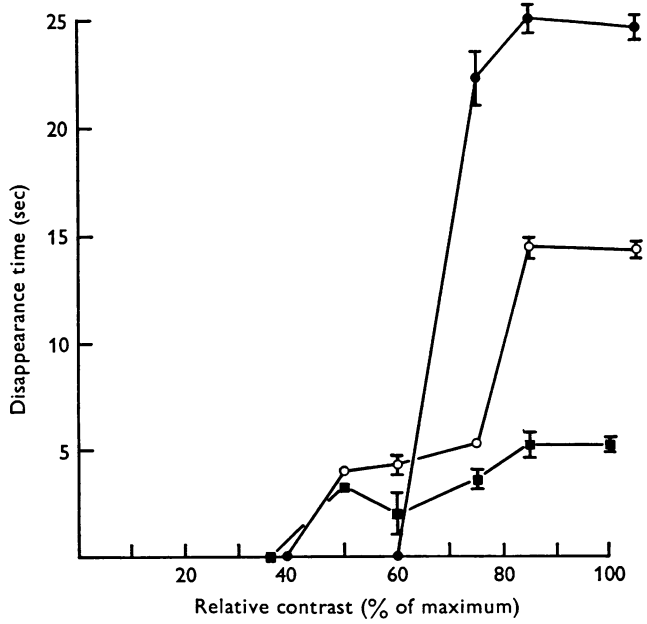

Fig. 6. Disappearance time as a function of the initial suprathreshold contrast at different scanning frequencies. Circular scan with shadow excursion 6 min arc. Contrast measured in terms of percentage of the maximum contrast available. Scanning frequencies: 8 Hz, ●; 11 Hz, ○; 14 Hz, ■.

contrast thresholds) of infinity and zero, respectively. Strictly speaking, one cannot compare values for different sets of vessels, as there is no guarantee that they cast shadows of equal contrast upon the photoreceptor layer of the retina. As can be seen from Fig. 4, the contrast sensitivity for a particular pattern falls steadily as the subject views the shadows at threshold, until the shadows can no longer be seen even with the highest contrast available. The rate of fall of sensitivity is greater for the higher scanning velocities, i.e. when the subject is viewing the larger vessels.

Fig. 5 plots the rate of recovery of contrast sensitivity after complete fading for several patterns. Thresholds were measured at 30 sec intervals; between readings the diluting spot was turned up to maximum brightness and the scanning pattern shut off. In all cases complete recovery to control threshold took about 3 min.

TABLE 1. Relative contrast sensitivities

Contrast sensitivity* before fading		Contrast sensitivity* immediately after complete fading in contralateral eye		Contrast sensitivity* 2 min later	
R	L	R	L	R	L
67·3	65·8	—	52·3	—	62·0
65·3	63·3	—	—	—	—
68·7	71·3	—	—	—	—
60·6	60·6	—	55·0	—	67·8
61·9	65·6	—	—	—	—
63·7	67·5	—	—	—	—
72·7	74·0	55·3	—	71·3	—
70·0	71·3	—	—	—	—
68·7	71·7	—	—	—	—
68·0	69·3	58·3	—	71·2	—
68·0	66·7	—	—	—	—
69·3	68·0	—	—	—	—

* Contrast sensitivity is expressed in terms of the percentage of the total light flux coming from the diluting spot at the centre of the pattern. See text.

(*b*) *Binocular transfer of elevation of contrast threshold*

Is the elevation of contrast threshold, caused by extended viewing of a particular pattern of shadows, binocularly transferred? If it is, this would suggest that the site of perceptual fading lies at or beyond the visual cortex, assuming there is a no binocular interaction among lateral geniculate nucleus neurones; there has been shown little or no such excitatory interaction in monkeys (Brindley, 1970, p. 103; Wiesel & Hubel, 1966), although an inhibitory interaction has been shown in cats (Sanderson,

Darian-Smith & Bishop, 1969). To test for binocular transfer of the effect the subject determined contrast thresholds in each eye for the patterns of shadows seen at 8 Hz, the velocity at which the most dense network of capillaries was seen. He then viewed the shadows at the maximum available contrast through one eye until they completely faded and measured the contrast threshold in the other eye immediately afterwards. After 2 min the measurement in the second eye was repeated. Table 1 shows the results. The control thresholds in each eye were always very similar. Immediately after fading in one eye, the contrast threshold in the other was elevated, returning to the control value by 2 min later. The transfer of threshold elevation is only partial; this may be because the patterns viewed through the different eyes are not exactly the same and it may indicate that part of the effect may occur in the LGN or the retina, or that all cells in the human visual cortex are not binocularly driven. In any case, these results do indicate that at least some of the effect occurs at or beyond the visual cortex.

(c) *Orientation specificity*

If part of the perceptual fading occurs at the level of the visual cortex, then the fading ought to be orientation specific, as it has been shown that visual cortical cells respond best to contrast gradients of specific orientation (Hubel & Wiesel, 1959).

In testing for orientation specificity, controls were obtained by determining disappearance times for the shadows seen by scanning the pupil with the spot of light moving along lines of various orientations in one direction, flying back to the beginning of the line at the end of each traverse. The length of each line was 4 mm, producing a shadow displacement of 5 min arc, and the repetition rate was 10 Hz; the shadows seen were those of capillaries. This method of visualizing the shadows produces an interesting and important illusion. The shadows seen have their orientation normal to the orientation of the scanning line. They appear, however, to move *continuously* in the direction opposite to that of the scanning spot, with no apparent displacement in the other direction. This shows that the 'drift' component is effective in visualizing the shadows, whereas the 'flick' back is not. The results are shown in Fig. 7. Now if the subject views the horizontal shadows until they fade (by scanning with a vertical line, 0 deg) and then closes a switch changing the orientation of the scanning line, the shadows visualized at the new orientation disappear after a time dependent on the magnitude of the orientation change. When the orientation is changed by 90 deg the disappearance time is not significantly different from the control value; smaller orientation changes reduce the disappearance time. If, however, the direction of scanning is reversed, i.e. an

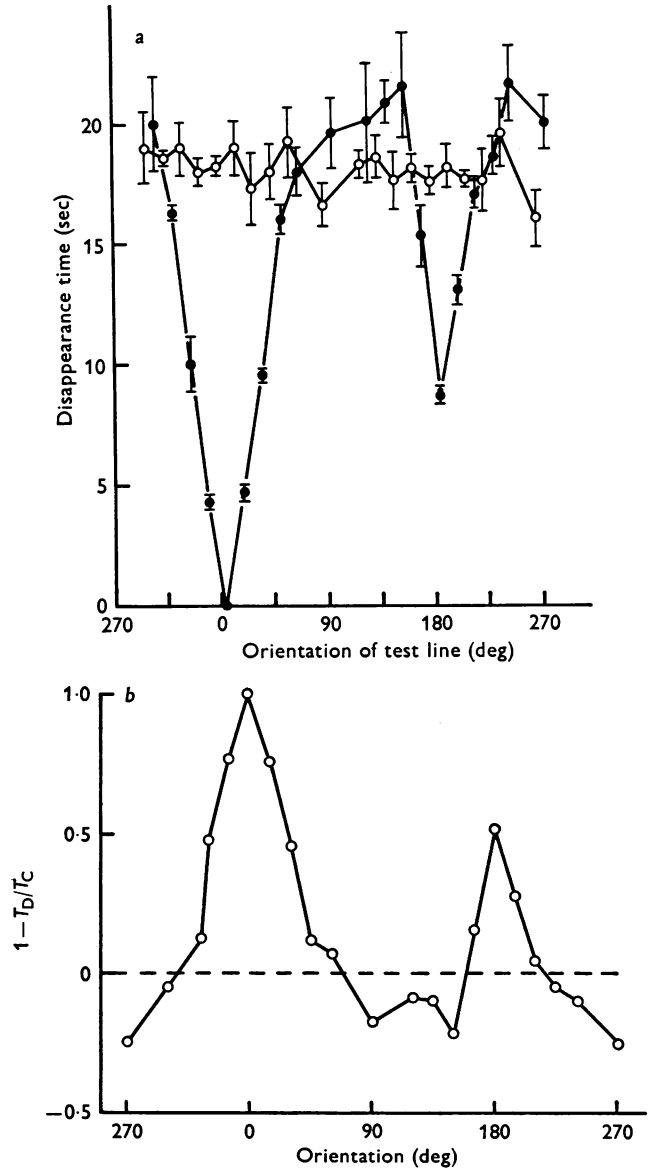

Fig. 7. *a*, disappearance times for various orientations of scanning time before (○) and immediately after (●) viewing a vertical (0 deg) scanning line until the vessels faded. The scan was linear and unidirectional, producing a shadow excursion of 5 min arc at 10 Hz; 0 deg refers to continuous movement of the scanning spot upwards, and 180 deg to continuous movement downwards. Each point is the mean of three readings; standard errors are indicated. The closed points (●) have been displaced slightly to the right.

b, $1-T_D/T_C$ versus orientation (see text).

orientation change of 180 deg, the subject sees horizontal shadows again, moving in the opposite direction, but for less time. The results are quantified by plotting $(1 - T_D/T_C)$ *vs.* orientation, where T_C is the control disappearance time and T_D the disappearance time after switching to another orientation – a value of 1 corresponds to seeing nothing after switching. These results are further evidence for the existence of channels in the human visual system selective for the orientation of spatial patterns (see also Campbell & Kulikowski, 1966, and Blakemore & Nachmias, 1971), and their direction of movement (see also Barlow & Hill, 1963 and Barlow & Brindley, 1963).

(*d*) *Width specificity*

As the fading has been shown to be at least partly cortical, then the fading ought to be width specific as well. Campbell, Cooper & Enroth-Cugell (1969) have shown that visual cortical cells in the cat respond best to gratings of specific bar width.

To show that the fading is width specific, advantage was taken of the fact that higher scanning velocities visualize wider vessels. Fig. 8 shows as controls the disappearance times for the vessels seen with circular scanning producing a 6·5 min arc total shadow excursion for frequencies for 6–20 Hz. The subject viewed the capillaries at 6 Hz until they faded, switched to another scanning velocity and then measured the disappearance time at this new velocity. Arterioles appeared after switching to frequencies above 9 Hz. The reverse experiment was also performed: the subject viewed arterioles at 12 Hz until disappearance and then measured disappearance times for the other patterns seen at different velocities. The results are quantified by plotting $(1 - T_D/T_C)$ *vs.* scanning frequency, where T_C is the control disappearance time and T_D the disappearance time after switching to another velocity. The fading, then, appears to be width specific. Strictly speaking, the experiment is poorly controlled as there is no guarantee that a certain area of retina has vessels of various widths but of the same orientation over it. These results are consistent with the existence of channels in the human visual system selective for width, i.e. spatial frequency (see also Blakemore & Campbell, 1969 and Campbell & Robson, 1968).

Simulation of image movements similar to those of normal vision

From the results already described it ought to be possible to predict the type of movements necessary to produce continuous vision. As the fading is orientation and width specific, the required type of movement must distribute the excitation over as many different orientation and spatial frequency channels as possible. This can be done by varying the direction

and velocity of image movement continuously. Normal eye movements accomplish this to a large extent. Nachmias (1959) and Boyce (1967) have shown that drifts and saccades occur in all directions and, although the distributions are often weighted, they often point in opposite directions for the two different components.

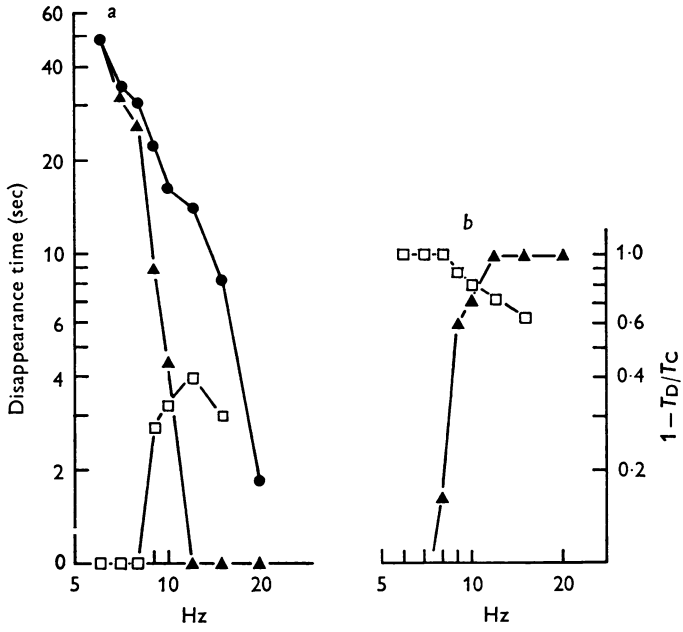

Fig. 8. *a*, Control disappearance times *vs.* Hz ●; disappearance times for vessels seen after complete fading of capillaries at 6 Hz, □; disappearance time for vessels seen after complete fading of larger vessels at 12 Hz, ▲. *b*, Results replotted as $1-T_D/T_C$ *vs.* Hz. See text.

To attempt this one assumes that moving an image across the stationary retina is equivalent to moving the retina past a stationary image. Several investigators have challenged this equivalence (Latour, 1962; Volkman, 1962; Beeler, 1967); they demonstrated rather small increases in brightness thresholds during and just before voluntary and involuntary saccades and have suggested that these may be the result of an inhibitory corollary discharge from the oculomotor system. More recently, however, MacKay (1970*a*, *b*) has produced evidence that these threshold elevations are the result of saccadic movement across the retina of the image of the whole visual field causing a great enough neural disturbance to reduce the sensitivity to small transient signals. The oculomotor system need not be implicated to account for these effects.

There also exists the possibility that the drift component of normal fixational eye movements is *more* effective in stimulating the visual system than the corresponding image movements *per se*. Wurtz (1969*a*), in discussing the role of fixational eye movements with respect to visual cortical cells in the awake monkey, claims that 'because adapting and non-adapting units are found in the presence of eye movements in the awake animal, and because non-adapting units are found in the absence

of eye movements in the paralysed animal, it does not seem likely that eye movements alone are the mechanism for maintaining unit discharge'. Whether non-adapting units are found in the absence of eye movements is open to question; Burns, Heron & Pritchard (1962) claim that only intermittent illumination of a cell's receptive field can alter the mean frequency of discharge. Hubel & Wiesel (1959), however, show responses in paralysed cats to stationary stimuli turned on for 1 sec which last for the duration of the stimuli. Perhaps, a much stronger excitatory than inhibitory input to a cortical cell could be the mechanism Wurtz is suggesting. Nobody has yet measured the eye movements of physiological nystagmus and cortical unit responses simultaneously. For more rapid rates of movement, however, Wurtz (1969*b*) found the neuronal responses to stimulus and eye movements to be the same.

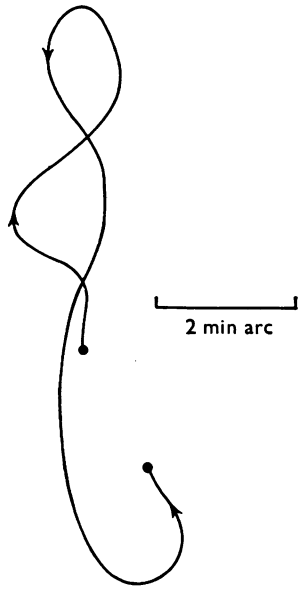

Fig. 9. Sketch of first-order pseudo-random walk (■) of Table 2.

Ditchburn *et al.* (1959) attacked this problem by separately simulating the flick, drift and tremor components of fixational eye movements by moving the image of a thin line across the retina in a controlled fashion and determining the effects on its visibility. As no single component would keep the line visible continuously, they concluded that the capacity of normal eye movements to maintain clear vision 'must depend upon additive interplay between the different components'. Gerrits & Vendrik (1970) made a similar study in which an object was rotated eccentrically by a small electric motor mounted on a contact lens stabilizing system and concluded that 'the drift is essential for preservation of perception' and that the saccadic and tremor movements were probably much less impor-

tant. They too, however, were unable to combine the three components together.

Using the computer it was possible to generate displays that would cause the shadows of the vessels to move over the retina in patterns of motion combining the characteristic tremor, drift and saccadic components of fixational eye movements. The simplest pattern was for the spot of light focused on the plane of the pupil to execute a first-order pseudo-random walk. This was accomplished by making the spot move in a series of steps in one direction by adding equal increments to its 'x' Cartesian co-ordinate and either adding or subtracting the same value from its 'y' co-ordinate or leaving it the same, according to values produced by a random number generator. Thus, the step lengths for this pattern were either 1 or $\sqrt{2}$ times a chosen amount. The spot started its walk at the centre of the pupil and if it came within a certain distance from the edge of the iris, the direction of drift was reversed. After a certain number of steps, the spot jumped back to the centre of the pupil. Fig. 9 is a sketch of such a walk. The correspondence between this pattern of movement and normal fixational eye movements is as follows: the individual steps which make the movement discontinuous represent the tremor component, the frequency of which is set by the oscillator driving the display programme. The drift component is composed of the series of steps, leading in one general direction. The jump back to the centre of the pupil corresponds to the saccade. The computer printed out the total length of the drift, the length of the 'saccade' and the mean step length, all in terms of the visual angle through which a point on a shadow moved over the photoreceptors. From the oscillator setting the mean drift velocity and 'saccade' frequency could be calculated.

As the length of the random walk increases, the probability of the direction of the drift passing through and visualizing all possible orientations becomes greater. Now if distributing the neural excitation into as many different orientation channels as possible will prevent fading, then the disappearance time for a given type of random walk ought to increase with its length. Fig. 10 shows this to be the case for three different first-order pseudo-random walks of the same mean step length. Table 2 shows the parameters describing each walk. Although all three components of normal fixational eye movements were present, fading still occurred. As mentioned before, the drift velocities necessary to visualize the shadows were much greater than the physiological values. Matching the parameters of the random walks to those mentioned by Ditchburn & Foley-Fisher (1967) for normal fixational eye movements was completely ineffective in visualizing the shadows. The contrast of the shadows is low, and temporal summation is needed.

Also plotted on Fig. 10 are the data from Fig. 1, in terms of 'drift

speed'. It can be seen that the disappearance times for a circular scanning motion are comparable to those for a random walk, the drift length of which is about comparable to the circumference of the circle traced out on the retina by a point on one of the shadows. This is to be expected as a circular pattern of motion passes through all possible orientations. These results imply that the various components of normal fixational eye movements do not promote vision in an additive fashion as suggested by Ditchburn *et al.* (1959).

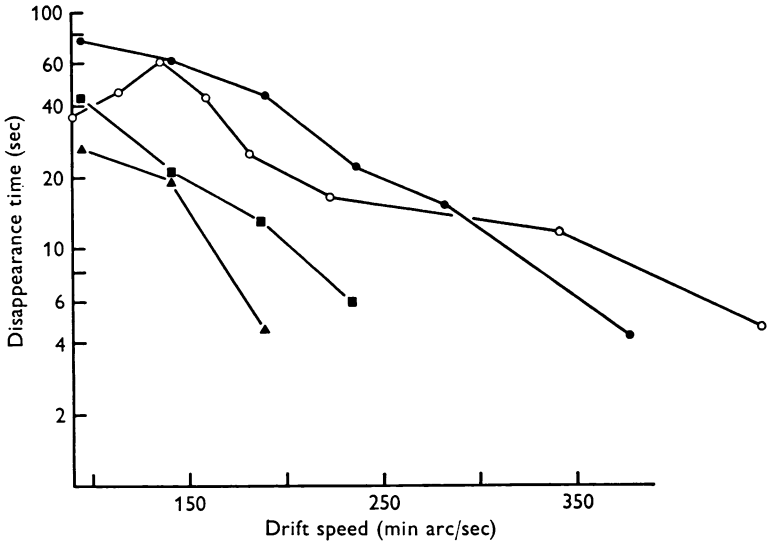

Fig. 10. Disappearance times at various drift speeds for three different random walks, closed symbols; for a circular scan, ○, with circular excursion of 22·3 min arc. The relevant parameters for each random walk are indicated in Table 2.

TABLE 2. Random walk parameters

Random walk*	No. of steps	Mean step length (min arc)	Length of drift (min arc)	Angle of flick (min arc)
▲	55	0·2	10·4	0·2
■	100	0·2	18·8	2·0
●	220	0·2	41·5	1·7

* See Fig. 10.

DISCUSSION

The conclusions drawn from this study may not be entirely general, as the images viewed were necessarily limited to patterns of wiggly thin lines. The images seen by causing controlled movement of the shadows of the

retinal blood vessels fade and do not reappear. This does not necessarily imply that reappearance of images of larger area stabilized with contact lens techniques is due to destabilization – Barlow (1969) says 'a more likely explanation is that the retina does not adapt completely, and continues to signal the illumination of each portion of the image.' This might also explain why stabilized images of larger area fade more slowly – in a few seconds (Gerrits *et al.* 1966) as opposed to the immediate disappearance of the blood vessel shadows when their motion is stopped.

Part of the fading of the images visualized by controlled movement of the shadows almost certainly occurs at the level of the visual cortex, in view of its orientation and width specificity and the binocular transfer of threshold elevation. This fading has similar characteristics to 'spatial adaptation' (Blakemore & Campbell, 1969). Blakemore, Muncey & Ridley (1971) have shown that prolonged viewing of a high contrast sinusoidal grating causes a reduction in the apparent contrast of a similar test pattern; the degree of reduction varies with the contrast of the test pattern. The time constant of this process is about 30 sec. The reduction in apparent contrast of the test grating is greatest at low contrast levels, suggesting that spatial adaptation renders the affected part of the visual system more sensitive to changes in contrast. Blakemore & Campbell (1969) found that the threshold elevation caused by spatial adaptation is limited to a spectrum of spatial frequencies with a band width of just over an octave at half amplitude, centred on the adapting frequency, and that the elevation of contrast threshold in the unadapted eye was slightly less than that in the adapted eye. Blakemore & Nachmias (1971) measured the orientation specificity of spatial adaptation in terms of elevation of contrast threshold and found that the half width of the effect at half amplitude was 6·75 deg.

These investigations of spatial adaptation using sinusoidal gratings have all dealt with foveal vision. The results reported in this paper suggest that spatial frequency and orientation channels operate for parafoveal and near peripheral vision as well. There is also evidence presented for the existence of channels selective for the direction of image movement.

The finding that the shadows must be moved successively from one photoreceptor to the next (about 1–2 min arc) to be seen agrees well with other workers' results. Keesey & Riggs (1962) found that image movement must be greater than 1·3 min arc for enhancement of seeing time and Ditchburn *et al.* (1959) obtained a figure of 0·6 min arc which is within the intercone separation (0·6–1·8 min arc) for the area of retina they were studying. These results suggest that the fine tremor component of fixational eye movements is not essential for maintaining perception, as the amplitude is too small – Ratliff & Riggs (1950) give a median value of 17·5 sec arc.

The drift component is likely to be much more important (Gerrits & Vendrik, 1970). The velocities of this type of motion necessary to produce perception in this study are high due to the low contrast of the shadows being viewed.

There is now considerable evidence that the involuntary saccadic component is *not* particularly important in maintaining perception. It has been shown that continuous relatively slow image movement is necessary for the perception of fine detail; saccadic movement is much too rapid. Important in this regard is the illusion of continuous movement in one direction with no apparent displacement in the other direction when the vessels are visualized by scanning with a spot of light which moves continuously along a line in one direction, flying back to the beginning of the line at the end of each traverse. This result suggests that the drift component is responsible for perception, whereas the saccade is ineffective. Similarly, Beeler (1967) found that subjects were unable to detect any stimulus movement just before and during involuntary saccades, for a suprathreshold spot of light moved through 15 min arc in a stepwise fashion. In addition, visual brightness thresholds are slightly elevated before and during both involuntary and voluntary saccades (Latour, 1962; Volkman, 1962; Beeler, 1967; MacKay, 1970*a*). Finally, image movements incorporating the saccadic component are no more effective in producing continuous perception than movements lacking it (see Fig. 10).

The importance of the larger voluntary saccades in maintaining perception should now be clear. As the apparent contrast of a visual scene decreases due to spatial adaptation, changing the fixation point will limit this process by shifting spatial frequency harmonics and orientations to regions of the visual field unadapted to these specific features.

Presumably, if the shadows of the retinal blood vessels were of greater contrast and if they could be moved through larger visual angles, then simulating the type of image movements of normal fixation would make them visible continuously. Their maximum excursion, which is limited by the pupil diameter, is about 8 min arc. According to Riggs, Ratliff, Cornsweet & Cornsweet (1953), even normal fixational eye movements are insufficient to keep some test-objects visible continuously; with good fixation, fine lines tend to fade and reappear.

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REFERENCES

BARLOW, H. B. (1963). Slippage of contact lenses and other artifacts in relation to fading and regeneration of supposedly stable retinal images. *Q. Jl exp. Psychol.* **15**, 36–51.

BARLOW, H. B. (1969). Stabilized retinal images. In *Proc. of the International School of Physics 'Enrico Fermi'*, Course XLIII, Processing of Optical Data by Organisms and by Machines, pp. 431–441.

BARLOW, H. B. & BRINDLEY, G. S. (1963). Inter-ocular transfer of movement after-effects during pressure blinding of the stimulated eye. *Nature, Lond.* **200**, 1347.

BARLOW, H. B. & HILL, R. M. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature, Lond.* **200**, 1345–1347.

BEELER, G. B. (1967). Visual threshold changes resulting from spontaneous saccadic eye movements. *Vision Res.* **7**, 769–775.

BEHRENDT, T. & WILSON, L. A. (1965). Spectral reflectance photography of the retina. *Am. J. Ophthal.* **59**, 1079–1088.

BLAKEMORE, C. & CAMPBELL, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* **203**, 237–260.

BLAKEMORE, C., MUNCEY, J. P. J. & RIDLEY, R. M. (1971). The perceptual fading of a stabilized cortical image. *Nature, Lond.* **233**, 204–205.

BLAKEMORE, C. & NACHMIAS, J. (1971). The orientation specificity of two visual after-effects. *J. Physiol.* **213**, 157–174.

BOYCE, P. R. (1967). Monocular fixation in human eye movement. *Proc. R. Soc.* B **167**, 293–315.

BRINDLEY, G. S. (1970). *Physiology of the Retina and Visual Pathway*, 2nd edn. London: Edward Arnold.

BURNS, B. D., HERON, W. & PRITCHARD, R. (1962). Physiological excitation of visual cortex in cat's unanaesthetized isolated forebrain. *J. Neurophysiol.* **25**, 165–181.

CAMPBELL, F. W., COOPER, G. F. & ENROTH-CUGELL, C. (1969). The spatial selectivity of the visual cells of the cat. *J. Physiol.* **203**, 223–235.

CAMPBELL, F. W. & KULIKOWSKI, J. J. (1966). Orientational selectivity of the human visual system. *J. Physiol.* **187**, 437–445.

CAMPBELL, F. W. & ROBSON, J. G. (1961). A fresh approach to stabilized retinal images. *J. Physiol.* **158**, 11–12*P*.

CAMPBELL, F. W. & ROBSON, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *J. Physiol.* **197**, 551–566.

CORNSWEET, T. N. (1970). *Visual Perception*. New York: Academic Press.

DITCHBURN, R. W., FENDER, D. H. & MAYNE, S. (1959). Vision with controlled movements of the retinal image. *J. Physiol.* **145**, 98–107.

DITCHBURN, R. W. & FOLEY-FISHER, J. A. (1967). Assembled data in eye movements. *Optica Acta* **14**, 113–118.

DITCHBURN, R. W. & GINSBORG, B. L. (1952). Vision with a stabilized retinal image. *Nature, Lond.* **170**, 36–37.

ENROTH, C. (1952). The mechanism of flicker and fusion studied on single retinal elements in the dark adapted eye of the cat. *Acta physiol. scand.* **27**, suppl. 100, 1–67.

GERRITS, H. J. M., DE HAAN, B. & VENDRIK, A. J. H. (1966). Experiments with retinal stabilized images. Relations between the observations and neural data. *Vision Res.* **6**, 427–440.

GERRITS, H. J. M. & VENDRIK, A. J. H. (1970). Artificial movements of a stablized image. *Vision Res.* **10**, 1443–1456.

HELMHOLTZ, H. VON (1909). *Physiological Optics*, ed. SOUTHALL, J. P. C. (1962). New York: Dover Publications.

HOGAN, M. & FEENEY, L. (1961). Election microscopy of the human choroid. III. The blood vessels. *Am. J. Ophthal.* **51**, 1084–1097.

HUBEL, D. H. & WIESEL, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *J. Physiol.* **148**, 574–591.

KEESEY, U. T. & RIGGS, L. A. (1962). Visibility of Mach bands with imposed motions of the retinal image. *J. opt. Soc. Am.* **52**, 719.

KÖNIG, A. & ZUMFT, J. (1894). Über die lichtempfindliche Schicht in der Netzhaut des menschlichen Auges. *Sber. preuss. Wiss.* **1894**, 439–442.

LATOUR, P. L. (1962). Visual threshold during eye movements. *Vision Res.* **2**, 261–262.

MACKAY, D. M. (1970*a*). Elevation of visual threshold by displacement of retinal image. *Nature, Lond.* **225**, 90–92.

MACKAY, D. M. (1970*b*). Mislocation of test flashes during saccadic image displacements. *Nature, Lond.* **227**, 731–733.

MICHAELSON, I. C. & CAMPBELL, A. C. P. (1940). Anatomy of finer retinal vessels and some observations on their significance in certain retinal diseases. *Trans. ophthal. Soc. U.K.* **60**, 71–112.

NACHMIAS, J. (1959). Two dimensional motion of the retinal image during monocular fixation. *J. opt. Soc. Am.* **49**, 901–908.

NODA, H., FREEMAN, R. B. JR., GIES, B. & CREUTZFELDT, O. D. (1971). Neuronal responses in the visual cortex of awake cats to stationary and moving targets. *Expl Brain Res.* **12**, 389–405.

POLYAK, S. L. (1941). *The Retina.* Chicago: University of Chicago Press.

PRITCHARD, R. M., HERON, W. & HEBB, D. O. (1960). Visual perception approached by the method of stabilized images. *Can. J. Psychol.* **14**, 67–77.

RATLIFF, F. & RIGGS, L. A. (1950). Involuntary motions of the eye during monocular fixation. *J. exp. Psychol.* **40**, 687–701.

RIGGS, L. A., RATLIFF, F., CORNSWEET, J. C. & CORNSWEET, T. N. (1953). The disappearance of steadily fixated test-objects. *J. opt. Soc. Am.* **43**, 495–601.

SANDERSON, K. J., DARIAN-SMITH, I. & BISHOP, P. O. (1969). Binocular corresponding receptive fields of single units in the cat dorsal lateral geniculate nucleus. *Vision Res.* **9**, 1297–1303.

SHARPE, C. (1971). A fresh approach to stabilized retinal images. Part 2. *J. Physiol.* **217**, 9–10*P*.

TOUSSAINT, D., KUWABARA, T. & COGAN, D. G. (1961). Retinal vascular patterns. Part II. Human retinal vessels studied in three dimensions. *Archs Ophthal., N.Y.* **65**, 575–581.

VOLKMAN, F. C. (1962). Vision during voluntary saccadic eye movements. *J. opt. Soc. Am.* **52**, 571–578.

WEST, D. C. (1968). Flicker and the stabilized retinal image. *Vision Res.* **8**, 719–745.

WIESEL, T. N. & HUBEL, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *J. Neurophysiol.* **29**, 1115–1156.

WURTZ, R. H. (1969*a*). Visual receptive fields of striate cortex neurones in awake monkeys. *J. Neurophysiol.* **32**, 27–42.

WURTZ, R. H. (1969*b*). Comparison of effects of eye movements and stimulus movements on striate cortex neurones of the monkey. *J. Neurophysiol.* **32**, 987–994.

YARBUS, A. L. (1967). *Eye Movements and Vision* (translation editor: L. A. RIGGS). New York: Plenum Press.