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# DISTURBANCES OF ROD THRESHOLD FORCED BY BRIEFLY EXPOSED LUMINOUS LINES, EDGES, DISKS AND ANNULI

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SUMMARY

1. When the dark-adapted eye is exposed to a brief duration (2 msec) luminous line the resulting threshold disturbance is much sharper (decay constant of *ca.* 10 min arc) than would be expected in a system which is known to integrate the effects of light quanta over a distance of 1 deg or so.

2. When the forcing input is a pair of brief duration parallel luminous lines the threshold disturbance falls off sharply at the outsides of the pattern but on the inside a considerable spread of threshold-raising effects may occur unless the lines are sufficiently far apart.

3. The threshold disturbance due to a briefly exposed edge shows an overshoot reminiscent of 'lateral inhibition'.

4. If the threshold is measured at the centre of a black disk presented in a briefly lit surround then (*a*) the dependence of threshold on time interval between test and surround suggests that the threshold elevation is due to a non-optical effect which is not 'metacontrast'; (*b*) the dependence of threshold on black disk diameter is consistent with the notion that the spatial threshold disturbance is progressively sharpened as the separation of luminous edges increases.

5. If the threshold is measured at the centre of briefly exposed luminous disks of various diameters one obtains the same evidence for an 'antagonistic centre-surround' system as that produced by other workers (e.g. Westheimer, 1965) for the steadily light-adapted eye.

6. The previous paper (Hallett, 1971) showed that brief illumination of the otherwise dark-adapted eye can rapidly and substantially change the extent of spatial integration. The present paper shows that brief illumination leads to substantial 'inhibitory' effects.

7. Earlier approaches are reviewed: (*a*) the linear system signal/noise theory of the time course of threshold disturbances (Hallett, 1969*b*) is

illustrated by the case of a small subtense flash superimposed on a large oscillatory background; (*b*) the spatial weighting functions of some other authors are given.

8. A possible non-linear model is briefly described: the line weighting function for the receptive field centre is taken to be a single Gaussian, as is customary, but the line weighting function for the inhibitory surround is bimodal.

## INTRODUCTION

Reduction of the extent of spatial integration seems to be associated with an increase in the manifestation of inhibitory processes. Thus in the case of human rod vision Barlow (1958) has used various sizes of test presented on large steady backgrounds to show that the extent of complete spatial integration is reduced by increase in the ambient level of illumination, while Westheimer (1965) has used various sizes of steady background and a small test to show that the antagonism of mutually adjacent retinal regions is increased. Similarly at the level of the retinal ganglion cell of the cat Barlow, Fitzhugh & Kuffler (1957) have shown that increase in the ambient level of illumination reduces spatial integration and increases the antagonism between the centre and surround of the receptive field. Now the previous paper (Hallett, 1971) showed that relatively weak, brief illumination of the dark-adapted eye causes a pronounced reduction of the extent of spatial integration, so one may reasonably suppose that appropriate variations in the stimulus pattern will reveal co-existing inhibitory effects. This paper presents a variety of such experiments.

## METHODS

### *Apparatus*

The optical apparatus (fig. 1 of Hallett, 1969*a*) consists of two independent optical trains (one for the testing signal and the other for the background), each with its own shutter, neutral wedges, interference filter and field diaphragm. The two blue-green beams (Schott PAL filters, peak 507 nm, half-width = 20 nm) are superimposed by means of a half-aluminized plate glass mirror and enter the centre of the dark-adapted pupil. The effective entrance pupil is the image of a $3 \times 1$ mm vertical slit, largely filled by an image of the coiled filament of the apparatus lamp.

When the shutters are open and the field diaphragms large the observer sees at infinity two superimposed fields of 17 deg subtense – one for each apparatus beam. These can be masked so as to produce test and background patterns (Fig. 1). By changing the masks one can arrange, say, that the test moves relative to the background pattern, and threshold measurements made during such a traverse yield a transect of the visual threshold disturbance in space created by the luminous background pattern.

Fig. 1 shows the observer's field of view for the various experiments. A small dim red fixation point ensures that the patterns are centred on a point 18 deg from the fovea. One apparatus beam is used to provide various suprathreshold stimulus patterns B. The luminous pattern is obtained by using one of a variety of specially cut B-field apertures (slits or holes in aluminium disks, or small brass disks mounted on thin Perspex disks) with the optically important edges levelled. These apertures rest against stops in the apparatus and are easily oriented and changed. The test flash T is obtained by masking the second beam with one of a series of T-field apertures. Each T-aperture is a disk perforated by a single-bevelled hole at various

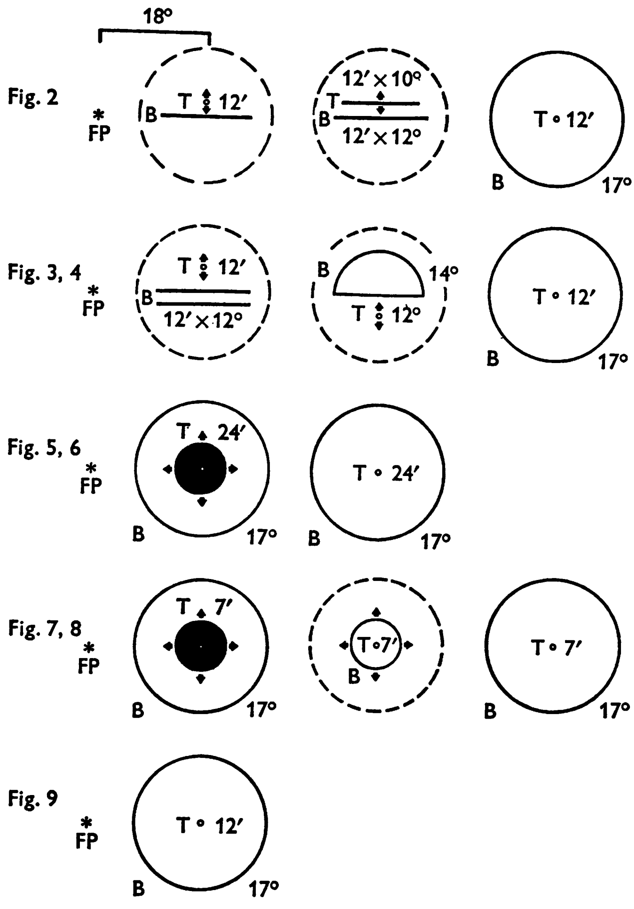


Fig. 1. The observer's field of view (left eye) for the various experiments of this paper. FP, fixation point; T, testing signal, and B, suprathreshold stimulus, both centred on a point in the temporal retina at 18 deg from the fovea. The vertical pairs of arrows in experiments of Figs. 2–4 indicate that the test T is presented at a variety of vertical positions relative to the suprathreshold background pattern B. In all the other experiments the test T is at the centre of the background pattern. The sets of four arrows in Figs. 5–8 indicate that the black disk or luminous disk is presented at a variety of angular sizes.

eccentricities from the disk centre. By changing the T-disks, then, the test flash may be moved point by point in a vertical traverse of the background pattern B.

*Weak secondary images*

Internal reflexion in the half-aluminized mirror (selected $\frac{1}{4}$ in. plate glass) which is used to combine the T and B fields (mirror M′ in fig. 1 of Hallett, 1969*a*) produces secondary images at about 5 % of the intensity of the main image and at about 1 deg *horizontal* displacement. Happily these secondary images can be disregarded. (1) Even if complete physiological summation does occur between the main and secondary image of the small test T the error in threshold is small (0·02 log), and one may reasonably expect that the error will often be less. (2) No complications arise with the line and edge patterns (Fig. 1) because these are oriented horizontally so that the important horizontal edges of the main and secondary images coincide. (3) In the case of the black disk or annular patterns (Fig. 1) the matter is less simple because the main annulus is overlapped by a weak secondary annulus at 1 deg horizontal displacement. For this reason the physical intensity at the very centre of the main image of the black disk (prior to image formation by the eye) is 1·3 log less than that of the main background (i.e. 0·95 contrast) for disks less than 2 deg subtense and zero (i.e. contrast 1) for disks of greater than 2 deg subtense. There are no indications that this weak secondary annulus determines the threshold for the test T under the *present* experimental conditions (eye fully dark-adapted between flashes; generally low intensity background flashes). In fact at the intensities used black disks of less than 1 deg subtense are not visible at all and behave as if their contrast is about zero, and disks of 2 deg diameter, or more, are clearly visible and behave as if their contrast is about 1.

*The fundal image*

The spatial spread of the physiological effects of a luminous target is so much greater, in the present experiments, than the likely spread due to optical blurring that the latter process may be largely ignored. Thus physiological summation at 18–20 deg from the fovea extends to 1–2 deg (for circular targets) for the completely dark-adapted eye, and the threshold-raising effect of a 12 min wide luminous line falls off in a roughly exponential fashion with a space constant of *ca.* 10 min. By contrast, the optical line spread function in the present experiments can plausibly be approximated by a process of exponential decay with a space constant of about 1·4 min. This is the value suggested by the researches of Flamant (1955), Westheimer & Campbell (1962) and Krauskopf (1962) for a 3 mm diameter circular artificial pupil and foveal vision. On the one hand one might argue that the conditions of peripheral vision require that this space constant be increased a little, and on the other hand one can argue for a smaller value, because (i) Campbell & Gubisch (1966) have shown that the earlier estimates of optical blur are excessively large, and (ii) the effective entrance pupil in the present experiments (a $3 \times 1$ mm image in the plane of the iris) is no doubt closer to the optimal pupil size than is a 3 mm artificial pupil.

The mildly myopic observers (E.S.H., M.K.S. and J.M.L.) wore their normal distance correction; this increased the sharpness of the fixation point but did not seem to have much effect on the subjective appearance of the background pattern. Observers J.A.M., E.K.S. and S.A.L. were emmetropes.

*Other details*

(*a*) The present results represent about 130 experimental sessions on six observers during the period from May 1968 to August 1969. Thresholds were found by the method of constant stimuli and are mean log thresholds derived from $k$ experiments of five series per point on a stimulus scale of 0·087 log. The S.E. of the experimental points is roughly 0·18 $k^{-0.5}$ log (Hallett, 1969*c*).

(*b*) The completely dark-adapted observer fixates and when ready he triggers the apparatus and observes the small subtense, brief duration testing signal and the given forcing input (e.g. a brief duration suprathreshold line, Fig. 1) with his peripheral vision. He reports as to the presence or absence of the test and is usually ready to trigger the apparatus again after 15 sec or so. Many such trials with various randomly chosen intensities of test, including blanks, permit the calculation of the mean log threshold for that set of stimulus conditions (e.g. Hallett, 1969*a*, *c*). About twenty changes of the independent variable are made in the course of an experimental session and it is usually necessary to average the results of three or more sessions.

(*c*) Conversions from photometric to energy units are given where necessary in the legends to the Figures and depend, as in previous papers, on 0 log scotopic td being equivalent to 5·65 log quanta (507 nm, cornea) deg$^{-2}$ sec$^{-1}$ or 0·55 log quanta (507 nm) absorbed/rod/sec (e.g. Scheibner & Baumgardt, 1967; Rushton, 1956).

## RESULTS

As is well known the fully dark-adapted eye is able to integrate the nervous effects of weak lights over considerable distances. In the retinal region of present interest (about 20 deg from the fovea) spatial integration is complete for brief circular flashes of diameter $D = 1$ deg subtense (e.g. Hallett, Marriott & Rodger, 1962) which deliver only about ten quanta to some 10,000 rods, larger flashes requiring more energy for the same probability of detection. Since these inputs are exceedingly weak one might hope that the spatial integration function (which relates log test threshold intensity to log test area) could be analysed in terms of linear signal/noise theory, e.g. the condition for visibility might be that

$$\text{peak amplitude }\{(\text{stimulus intensity profile}) * (\text{point spread function})\}$$
$$\geqslant K \times \{\text{S.D. of the background noise process}\}, \qquad (1)$$

where the asterisk represents the operation of convolution and $K$ is the chosen signal/noise ratio.

Unfortunately there is a wide variety of solutions to the point spread function in eqn. (1) and the distinction between the solutions, and the fitting of constants, depends very largely on the thresholds of the larger area tests, for which eqn. (1) is not likely to be true since it disregards (*a*) the important possibility ('probability summation') that threshold may be reached if the response exceeds the noise level at only one or few of all possible places (Pirenne & Marriott, 1959; Harris & Duntley, 1966), (*b*) the likely heterogeneity of larger retinal areas.

In view of these difficulties, then, the simplest statement is that the extent of spatial integration in the peripheral dark-adapted retina is compatible with a point spread function which falls to ½ in about $\pm D/2 = 30$

min – this value being, if anything, an underestimate. How does this extensive spread compare with that of the threshold disturbance caused by various suprathreshold patterns?

## *Lines and edges*

### *One line*

Fig. 2 shows the threshold disturbance in space created by a single briefly exposed line of various brightnesses, measured with a testing signal presented at the same instant (time interval $t = 0$). The testing signal is either a brief duration luminous spot (Fig. 2*a–d*) or a luminous line (Fig. 2*e*). Peak threshold increases roughly as the 0·6 power of the input and the fall in threshold energy is very roughly described by an exponential space constant of about 10 min of arc (in fact in the case of the brightest input there is an additional more widely spread disturbance extending over several deg). To a first approximation, then, one is apparently dealing with results which can be treated in terms of linear signal/noise theory (e.g. Hallett, 1969*b*), for which the expectations are that threshold increases as the 0·5 power of the input and that the form of the line spread function is independent of input magnitude.

The narrowness of the line spread functions in Fig. 2 is, however, strikingly less than expected.

The eye is essentially dark-adapted and is exposed to these very weak stimuli only every 15 sec or so; bleaching of rhodopsin is infinitesimal and any disturbance of the threshold lasts less than 1 sec. In these circumstances one might reasonably expect that the spatial disturbance would be wide, e.g. of width 1 deg or greater at 0·3 log below peak if $D$, the diameter of the complete integration area, is 1 deg, not *ca.* 14 min width as is actually observed. Nor can one assume that $D$ has been substantially reduced by illumination – when the eye is briefly illuminated by a *large* background of intensity very close to that used in Fig. 2*c* (e.g. Hallett, 1971, fig. 6, $t = 0$, intensity of one quantum absorbed per thirty rods) then $D$ is found to be 30 min. The discrepancy between expectation and observation is very marked and would no doubt be even worse if the luminous line were narrower than 12 min.

One hypothesis for the surprising narrowness of these line spread functions is that the testing signal and the forcing line are being processed by independent detectors (cf. Stiles' analysis of colour vision). According to prevailing electrophysiological notions the labour of pattern recognition is subdivided between different cells. It is therefore conceivable that the testing signal (a spot) in Fig. 2 (*a–d*) is detected by a 'spot sensing' device and that the threshold raising effects of the forcing line are actually widely spread but largely confined to the 'line sensing system'. Fig. 2*e* disposes of this suggestion: the space constant of threshold spread is not much different when the forcing input and testing signal are lines. A very similar result has also been obtained for a second observer (M.K.L.).

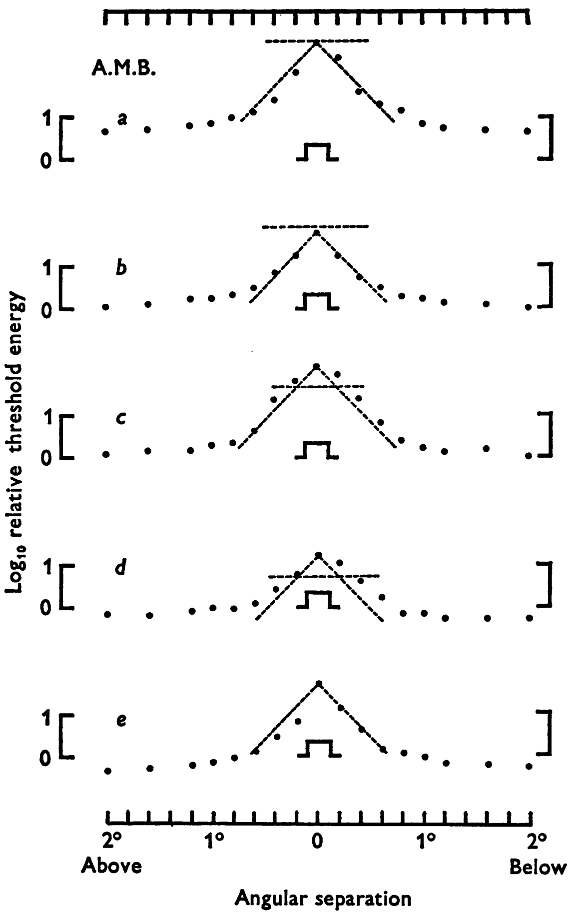


Fig. 2. Observer A.M.B. The threshold disturbance in space created when the hitherto dark-adapted eye is briefly exposed to a luminous line of various brightnesses. The luminous line is of 2 msec duration and 12 min × 12 deg subtense and its brightness (from top to bottom in the Figure) is 6, 5, 4, 3 and 4 log quanta (507 nm) quanta per deg$^2$ respectively (i.e. one quantum absorbed per 0·12, 1·2, 12, 120 and 12 rods).

For the top four curves the testing signal is a luminous spot of 12 min subtense and 2 msec duration. For the bottom curve the testing signal is a 12 min × 10 deg line of 2 msec duration. Both testing signals and forcing inputs are blue green (507 nm) and are exposed synchronously. The sloping lines correspond to a 10 min space constant. The horizontal lines indicate the threshold when the forcing input is a large (17 deg subtense) 2 msec duration background synchronous with the test.

Conceivably the sharpness of the line spread functions in Fig. 2 arises from a process of lateral inhibition analogous to that seen in *Limulus* eye (e.g. Hartline & Ratliff, 1958). It is interesting to note that sharper responses are possible; if there is no noise or non-linear filtering and the inhibitory coefficients are properly chosen the model of linear recurrent inhibition ensures that the neural response is a faithful copy of the original stimulus, despite optical spread, etc.

$L(x, y)$ be the intensity profile of the suprathreshold stimuli and testing signal in $x$, $y$ space,
$P(x, y)$ be the point function, for optical and excitatory spread,
$K(x, y)$ be the weights of the inhibitory coefficients,
$R(x, y)$ be the response of the ommatidium at $x$, $y$,

then

$$R(x, y) = \sum_{\substack{\text{all } x' \\ \text{all } y'}} L(x', y') P(x'-x, y'-y) - \sum_{\substack{\text{all } x' \neq x \\ \text{all } y' \neq y}} K(x'-x, y'-y) R(x', y')$$

expresses the well-known idea that the response at $x$, $y$ is equal to the excitatory response at $x$, $y$ minus the inhibitory effects of all neighbouring ommatidia. If

$$P(x, y) = K(x, y) \quad \text{and} \quad P(0, 0) = 1$$

then all $R(x, y) = L(x, y)$, i.e. the response is a faithful copy of the input. This process is analogous to the use of a *RC* 'probe' for eliminating the distortion due to a cable.

Fig. 2 (*a–d*) and also Figs. 3 and 4 do provide evidence for processes of inhibitory type (the threshold for a testing signal on a luminous line is usually equal or greater than that on a large uniform background of the same luminance). On ordinary linear theory (for which peak threshold *ought* to increase in proportion to input) this is explained by postulating that the line spread functions underlying Fig. 2 include a widespread but weak undershoot. Figs. 2–4 are not, however, exact enough to argue either for or against weak undershoot.

*Two lines*

Fig. 3 shows experiments in which the threshold disturbance in space is created by a pair of briefly exposed suprathreshold parallel luminous lines. Under the conditions of Fig. 3 the observer sees the pair of lines as a single blur when they are relatively close together but becomes more confident as to the existence of two separate lines as their separation is increased. Measurement confirms this impression in a more objective way. The threshold disturbances are completely fused when the separation of the lines is 30 min of arc but become progressively less fused as the angle of separation is increased. This pattern of results is quite unexpected. The sharpness of the experimental line spread function for this observer (*ca.* 10 min space constant, Fig. 3) suggests two virtually separate threshold

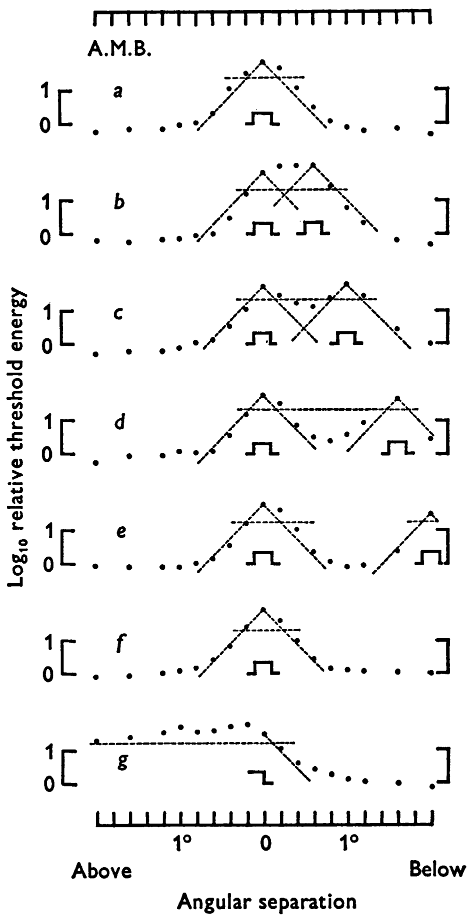


Fig. 3. Observer A.M.B. Top six curves. The threshold disturbance in space created either by a single briefly exposed luminous line or by two briefly exposed luminous lines of various separations.

The threshold is measured with an effectively 'point impulse' testing flash of 12 min subtense and 2 msec duration delivered at the same time as the 'line background' composed of one or two 12 deg × 12 min subtense and 2 msec duration lines. The lines are indicated by square waves in the illustration and from top to bottom in the figure are respectively (*a*) a single line or two lines of (*b*) 0·5 deg, (*c*) 1 deg, (*d*) 1·5 deg, (*e*) 2 deg and (*f*) 3 deg average separation.

Both test and lines are blue green (507 nm) and the lines are of intensity 4·0 log quanta (cornea) per deg$^2$ (one quantum absorbed per 12 rods). The sloping lines correspond to an exponential space constant of 10 min. The horizontal lines indicate the threshold when the forcing input is a large (17 deg subtense) 2 msec duration background synchronous with the test.

Bottom curve (*g*). An exactly analogous experiment except that the forcing input is an edge.

disturbances for 30 min separation of the two forcing lines, not the fusion actually observed. In fact if one develops eqn. (1), using the superposition of exponential line spread functions of 10 min space constant, the threshold

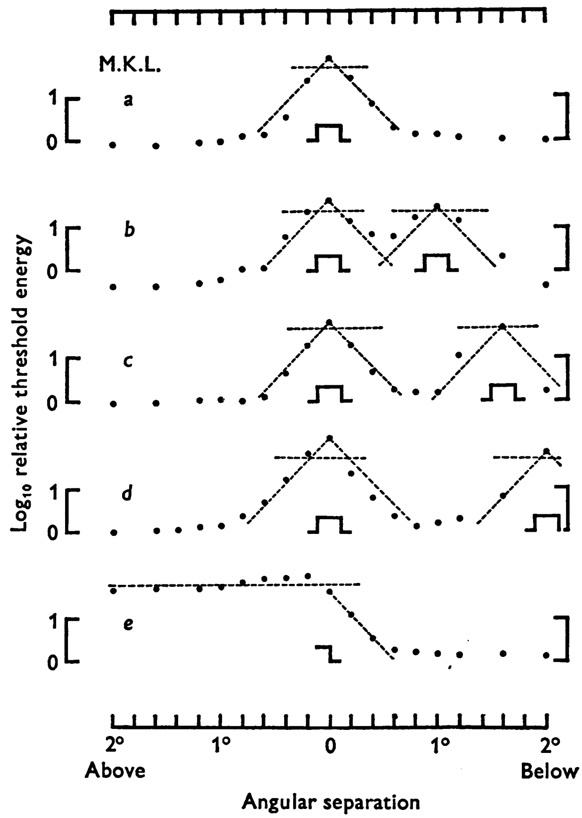


Fig. 4. Observer M.K.L. Top four curves. The threshold disturbance in space created by two briefly exposed lines of various separations. From top to bottom respectively the inputs are either (*a*) a single line or two lines of (*b*) 1 deg, (*c*) 1·5 deg, and (*d*) 2 deg separation. Bottom curve (*e*). An analogous experiment except that the forcing input is a step. The experimental conditions are similar to those of Fig. 3, except that the suprathreshold stimuli are somewhat brighter: 4·5 log quanta (cornea) per deg$^2$, i.e. one quantum absorbed per 4 rods.

should almost follow the sloping lines drawn in Fig. 3 – the calculated threshold midway between the forcing lines being 0·15 log above the intersection of the sloping lines, not the 0·85 log unit observed.

Fig. 4 is a similar experiment to that of Fig. 3 but at an intensity 0·5 log higher and for a different observer. Subjectively the forcing lines were recognizable as being separate and the threshold measurements show that the threshold disturbance at the inside of the forcing pattern is nearly as sharp as that at the outsides. Figs. 3 and 4 taken together, then, are analogous to the common experience that the ease of resolving the gap between two lines increases with both angular separation and brightness.

*One edge*

Figs. 3*g* and 4*e* show experiments in which the forcing input is a briefly exposed edge; threshold begins to rise before the edge is reached and there is a diffuse overshoot at the edge reminiscent of the inhibitory interactions seen so clearly in *Limulus* eye. The present effect is quite unexpected. Although Mach bands can be seen in brief flashes, using central vision (e.g. Mach quoted in Riggs, Ratliff & Keesey, 1961), other work on the steadily light-adapted periphery (e.g. Barlow *et al.* 1957; Westheimer, 1965; Novak & Sperling, 1963) would tend to suggest that persistent bright illumination is a requirement for inhibitory effects.

Finally, Figs. 2–4 suggest two other observations. First, although the threshold disturbances are in some respects much sharper than one would expect, given the extensive spatial integration of the dark-adapted eye, the disturbances are nevertheless restricted to roughly $\pm 1$ deg of the line or edge stimulus. This possibly points to the idea that there is an extensive initial spread of the nervous effects of quantum absorptions but that a subsequent sharpening process restricts the spread of threshold raising effects, perhaps within limits imposed by quantum fluctuations, 'graininess' and other non-linearities. Secondly, if the data of Fig. 4 are replotted as log threshold at the midpoint between the lines *versus* separation one obtains nearly the same form as that for the threshold at the midpoints of black disks of various diameters, namely after 30 min separation the threshold energy falls with an exponential constant of 16 min. Although this observation is based on only five experimental points it is of interest since it suggests that the profile of the threshold surface that corresponds to a black disks (*v.i.*) is also progressively sharpened as diameter, and no doubt brightness, is increased.

*Black disks (luminous annuli)*

Figs. 5 and 6 (top curves) show experiments in which the threshold for a small brief duration testing signal is measured as a function of the time interval $t$ between the test and a large subtense, brief duration background. As has been previously shown (e.g. Hallett, 1969*b*) the threshold disturbance peaks at $t = 0$ and subsequently declines with an exponential time constant of about 80 msec. This is what would be expected if the brief duration testing signal and background enter the same electrical network and produce protracted responses, because when test and background flashes are synchronous ($t = 0$) their responses are also synchronous and the problem of signal detection is likely to be greatest. The remaining curves of Figs. 5 and 6 show the effect of sparing the retinal region on which the testing signal falls by blocking out the background light with a

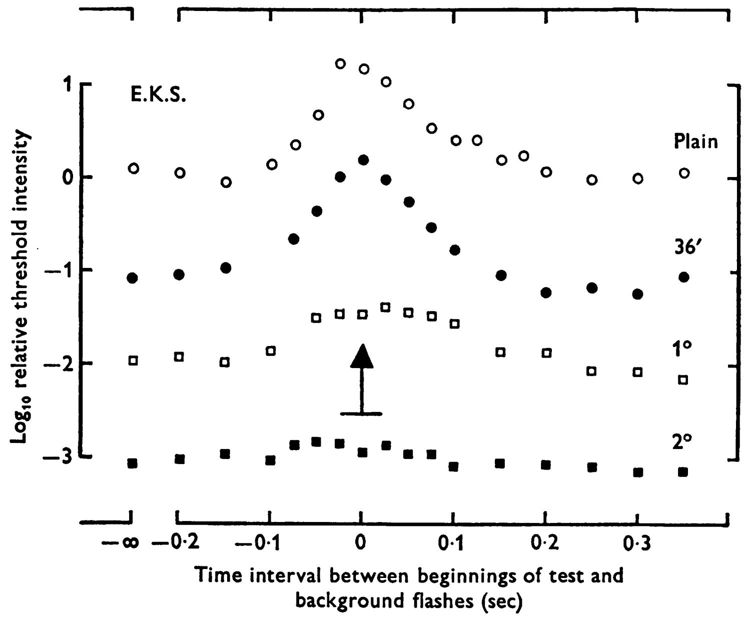


Fig. 5. Observer E.K.S. Time course of the threshold disturbance created by background light spatially and temporally separate from the testing light.

A background of 18 deg subtense is exposed for 10 msec at time zero. The top curve (○) is the threshold disturbance created by the uniform plain background. Much the same disturbance occurs if the central part of the background is blocked out by a 36 min subtense black disk (●), despite the fact that the retinal region on which the test falls is never exposed to direct background light. This lateral action of the background light is, however, reduced by blocking out the central 1 deg (□) to 2 deg (■) of the background.

Conditions: 10 msec duration 24 min subtense blue green (507 nm) test centred on a 10 msec duration 18 deg subtense blue green (507 nm) background of intensity 3·56 log quanta (cornea) per deg² (one quantum absorbed per 35 rods). Each curve is the average of 2–3 days' sessions. All four curves have the same base line (ordinate zero) but the lower three curves have been displaced by whole numbers of log units for clarity.

black disk. Disks of less than roughly 1 deg diameter are not visible at this intensity and their presence does not affect the threshold disturbance. Disks larger than 2 deg diameter are clearly visible and protect the testing

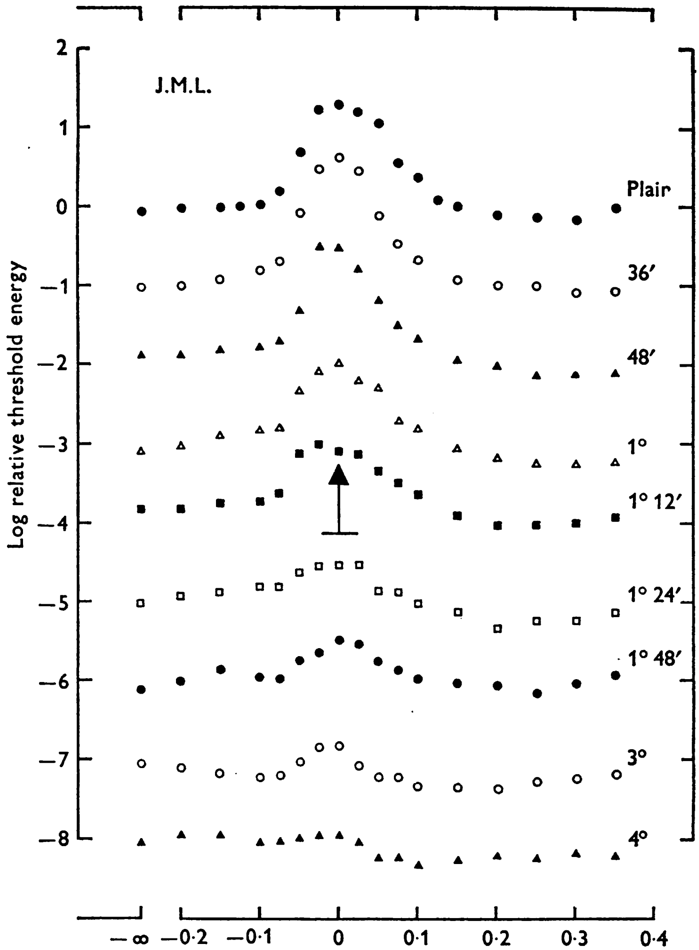


Fig. 6. Observer J.M.L. An experiment similar to that of Fig. 5. Top ('plain', ●), the threshold disturbance created by a large uniform background of 10 msec duration at time zero. Other curves, the disturbance is reduced by blocking out a sufficiently large part of the background with a disk so as to increase the lateral distance between the test and background light. Values to right indicate the subtense of the black disk (if any) which protects the retinal region of the test from the direct action of the background light. The curves are displaced vertically by whole numbers of log units for clarity. Background intensity is 3·67 log quanta (507 nm at cornea) per $deg^2$ (1 $h\nu$ absorbed per 27 rods). Conditions otherwise identical to those of Fig. 5. Each curve represents one experimental session.

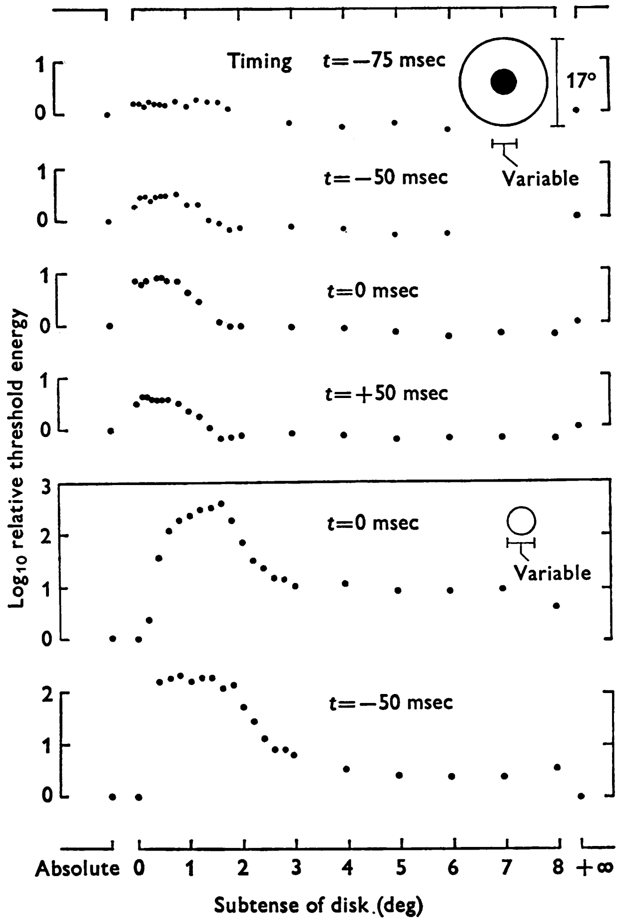


Fig. 7. Observer J.M.L. The threshold disturbance created by two patterns of background illumination. The 'timing' $t$ denotes the time interval between the beginnings of the test and background flashes in msec, e.g. $t = -75$ msec means that the test precedes the background, and so on.

Top four curves. Black disks of 48 min of less subtense do not protect the retinal region on which the test falls from the action of background light; the threshold would be the same if the disk were not there (subtense = 0). Black disks larger then 100 min subtense protect very well and the threshold is close to the absolute threshold for the dark-adapted eye.

Lower two curves. Backgrounds of 30–100 min subtense elevate the threshold far more effectively than the full 18 deg subtense background which delivers 300 times as many quanta to the retina.

Each curve is the average of 2–8 days' sessions. 2 msec duration 7 min subtense blue green (507 nm) test and 2 msec blue green background. Background intensity is 3·67 log quanta at the cornea per deg$^2$ (one quantum absorbed per 27 rods).

signal completely. Intermediate disks of 1–2 deg diameter reduce the peak threshold disturbance and apparently increase the time constant of recovery, which means that the protective action of the black disk is not purely an optical effect, because attenuation of light level alone does not affect this time constant (Hallett, 1969*b*). Finally, it should be noted that the responses peak, when present, at $t = 0 \pm 20$ msec, which suggests that the 'metacontrast' effect (peak at $t = -100$ msec, Alpern, 1953) and its subsequent analysis (e.g. Alpern, Rushton & Torii, 1970) is not directly relevant to the present problems.

Figs. 7 and 8 (filled circles) show similar experiments with black disks but the experiments have been devised so as to examine the dependence of the threshold disturbance at the centre of the disk on disk diameter. Apart from a variation in height the shapes of the experimental functions do not depend upon the time interval between testing signal and background. Black disks of 48 min diameter or less are not visible at this intensity of background flash and do not lower the threshold. For larger disks the threshold falls off with an exponential constant of about 16 min (diameter) so that clearly visible disks of 2 deg or greater subtense protect completely. The threshold at the centre of the disk then remains at the absolute threshold value of *ca.* 100 quanta (507 nm, cornea) despite the periodic exposure of the annular background.

It seems quite possible that the effectiveness of black disks in lowering the threshold of a retinal point is related to a process of 'edge sharpening'. There are two arguments. First, the intensity of the annuli in the experiments of Figs. 7 and 8 (filled circles) is quite close to that of the pair of luminous lines in Fig. 3. As previously mentioned when the black gap between the lines is not resolved there is extensive spread of threshold raising effects into that region, and as the black gap is resolved better the threshold spread becomes more restricted or 'sharper'. In fact the relation between the threshold at a point midway between the luminous lines in Fig. 3 and the separation of the lines parallels the relation between the threshold at the centre of a black disk and the diameter of the disk – threshold likely remains constant to at least 30 min line separation and then falls with an exponential constant of 16 min (the corresponding values for black disks are about 48 min diameter and 16 min respectively). Secondly, by analogy with the straight edge in Figs. 3*g* and 4*e*, a black disk can be regarded as being a 'circular edge'. If reasonable symmetry holds it is likely that the surface of the corresponding threshold disturbance in space is in the form of a flat plain in which is a crater with sloping sides (of 'exponential constants, possibly somewhat greater than the 10 min observed in Figs. 3*g* and 4*e*) and heaped edges.

### *Luminous disks*

Figs. 7 and 8 (open circles) show the complementary experiments to those just discussed: the threshold at the centre of a suprathreshold luminous disk as a function of disk diameter, with time interval $t$ between testing flash and disk as parameter. A fair amount of experimental repetition was required as an unusual amount of day to day variation (up to 0·5 log) was shown by these usually excellent observers.

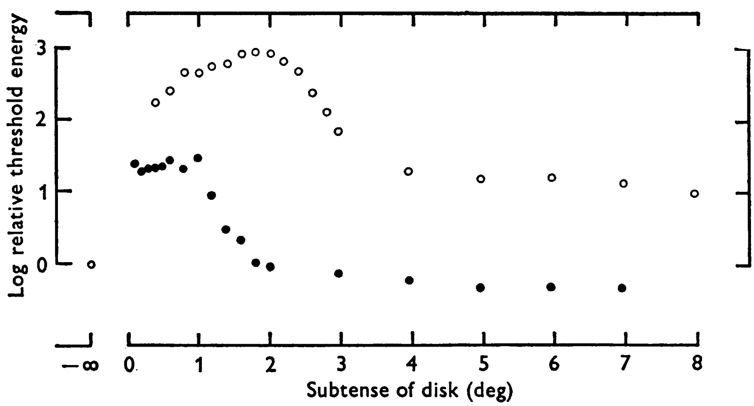


Fig. 8. Observer J.A.M. Threshold disturbance created by two spatial patterns of background illumination. A similar experiment to that of Fig. 7.

Top curve. The threshold is highest if the background is about 2 deg subtense.

Bottom curve. The background is of 17 deg subtense but its centre is blocked out by a black disk of variable size. Black disks of 1 deg subtense or less do not protect the retinal region on which the test falls from the action of the background light. Disks larger than 2 deg protect very well and the threshold is then close to that of the dark-adapted eye.

Each curve is the average of 5 days' sessions. 2 msec duration 7 min subtense blue green (507 nm) test synchronous with a 2 msec duration large blue green background. Background intensity is 3·67 log quanta (cornea) per $deg^2$ (one quantum absorbed per 27 rods).

As expected threshold intensity initially rises with increase in disk diameter, at least for $t = 0$, in plausible accord with the extent of spatial integration of either the dark-adapted eye ($D \simeq 1$ deg) or the dark-adapted eye briefly illuminated by a large background of this intensity ($D \simeq 30$ min, *v.s.*). There is a maximum, however, at 2 deg disk diameter and threshold then falls 1–2 log to reach at 3 deg disk diameter the value expected for large subtense backgrounds. These results are very similar to those first investigated by Crawford (1940) and more recently by Westheimer and others (e.g. Westheimer, 1965). The present effects are just as dramatic despite the brevity and low level of illumination, which are factors usually believed to diminish inhibitory interactions (e.g. Barlow *et al.* 1957; Westheimer, 1965; Novak & Sperling, 1963). The pattern of results suggests 'centre-surround antagonism', such as is seen in electrophysiological studies of the retina and lateral geniculate (e.g. Bishop, 1967), because illumination of the region immediately adjacent to the testing signal increases the threshold, but as the luminous disk is made larger the threshold eventually falls, even though more light is entering the eye.

There is another, slightly different, aspect of these results. The analogies between the results with lines, edges and luminous disks suggest that the threshold surface corresponding to a small luminous disk is a small hillock with sloping sides. This hillock no doubt initially increases in all dimensions as disk size increases up to 2 deg diameter and then develops a limited central depression with heaped edges as disk size increases from 2 to 3 deg.

*Black disks and white disks compared*

Further interesting features of the present results are apparent on comparing the thresholds at the centres of black disks (filled symbols) and white disks (open symbols) of similar diameters in Figs. 7 and 8. Although such inputs are complementary, inasmuch as black and white disks of the same diameter add to make an extensive uniform background, the resulting threshold functions in Figs. 7 and 8 are far from being complementary in any sense.

The experiments with white disks (open symbols) suggest that at this retinal eccentricity the diameter of the 'centre' of the 'antagonistic centre-surround system' is about 2 deg subtense, because that is the size of the most effective background, and that of the whole system about 3 deg, or more, because that is the approximate size above which no further changes occur. But the filled symbols show that a black disk large enough to cover the 'centre' (2 deg subtense) completely spares the threshold of the central point from the effects of the light in the surround! Clearly the process of lateral inhibition must be one that allows suprathreshold light in the 'antagonistic surround' to interfere with the effects of the same intensity of suprathreshold light in the 'centre', although suprathreshold light in the antagonistic surround alone does not disturb the threshold of the central testing flash. This is possibly reminiscent of some aspects of the behaviour of the antagonistic centre-surround of the bipolar cells of *Necturus* (Werblin & Dowling, 1969; Norton, Spekreijse, Wagner & Wolbarsht, 1970). Parallels between the present type of human data and visual receptive fields of retinal neurones have been suggested by McKee & Westheimer (1970).

DISCUSSION

When attempting to analyse biological systems there is a tendency to take as analogies physical systems which are fairly well understood and susceptible to linear analyses. A typical model for human rod vision would be some optical copying device, such as a camera, image converter or certain xerographic procedures, in which the resolution of some details and the integration of others can be related, with varying degrees of difficulty, to the point spread and impulse functions of the system (Higgins & Perrin, 1958; Clark Jones, 1958; Neugebauer, 1967; Bouwers, 1966). We will consider linear approaches first and then indicate the features of a possible non-linear model.

*Linear theory for temporal disturbances*

Linear methods may be perfectly adequate if the experimental conditions are appropriately selected. If attention is restricted to intensities of not much more than 10 quanta absorbed $rod^{-1}$ $sec^{-1}$ one minimizes one source of non-linearity – the stage of photoelectric conversion in the receptors (Fuortes & Hodgkin, 1964; Werblin & Dowling, 1969), and if the background is large and uniform and the testing signal of small subtense and brief duration one partly minimizes the effects of changing lateral interactions. This is what has been done in studies of the way in which the rod threshold is forced by brief duration ('impulse'), step and steady backgrounds (Barlow, 1957; Hallett, 1969*a*, *b*). Fig. 9 extends the approach of Hallett (1969*b*) to large continuously oscillating backgrounds and serves as an illustration of the usefulness of linear system signal/noise theory.

In Fig. 9 the testing signal is presented every 15 sec or so at some fixed point with regard to the background cycle and its threshold intensity measured. The timing is then changed, another measurement made and so on until the complete cycle of threshold disturbance has been measured (●). The threshold disturbance 'follows' the background waveform fairly well at the longest cycle periods but scarcely follows at all at periods (of 0·1 sec or so) which are comparable to the time constants of the system. The theoretical approach is that the observer behaves as a detector of constant fallibility and is limited by the quantum fluctuations in the background; the testing signal and background enter a linear network and the signal is seen if it causes the confidence limits of the temporal response to the background alone to be exceeded at any instant. The theoretical points (○) are in good agreement with the experimental ones (●), using an empirical impulse function $Kh_Q(t)$ and constants very close to those found for five other observers (e.g. Hallett, 1969*b*).

Clearly this linear system signal/noise approach to small signals and

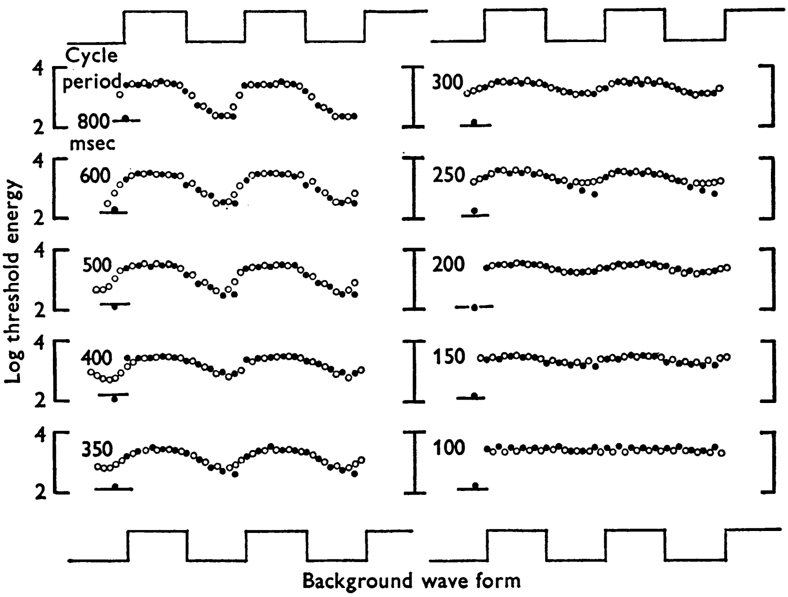


Fig. 9. Observer S.A.L. The threshold disturbance created by large continuously oscillating backgrounds of various periods.

Vertical scale: $\log_{10} q_{B.X}(t)$ quanta (507 nm, cornea). The filled circles (●) are experimental points. The filled circle near 100 quanta is the absolute threshold of the completely dark-adapted eye. The remaining filled circles are the perturbation of threshold by a square-wave background of $10^{5 \cdot 63}$ quanta (cornea) $\deg^{-2}\sec^{-1}$ (3 quanta absorbed per rod per sec).

At the longest cycle periods the threshold is steady during most of the illumination phase and falls to the absolute threshold during the dark phase. At the shortest cycle period the threshold is undisturbed by the brightening and darkening of the background.

The theoretical points (○) and the short horizontal lines near 100 quanta are the linear signal/noise prediction (Hallett, 1969*b*),

$$q_{B,X}(t) = K\left(X\int_{-\infty}^{+\infty} h_Q^2(t')\,dt' + \int_{-\infty}^{+\infty} B(t')\,h_Q^2(t-t')\,dt'\right)^{0 \cdot 5} \tag{2}$$

for the empirical 'impulse function' $Kh_Q(t) = g_Q \exp - (\text{mod } t/\tau_t)$ where $\tau_t$ is 0·04, ∞ and 0·08 sec for $t < -0{\cdot}02$, $-0{\cdot}02 < t < +0{\cdot}02$, $t > 0{\cdot}02$ respectively. The left-hand curves are for 'dark light' $X = 10^{3 \cdot 05}$ quanta (507 nm, cornea) $\deg^{-2}\sec^{-1}$ and 'gain constant' $g_Q = 10^{1 \cdot 2}\deg^2$. The right-hand curves use very similar values ($10^{2 \cdot 85}$ and $10^{1 \cdot 3}$ respectively). These values for $X$ and $g_Q$ are close to those derived from the impulse functions of other observers (e.g. Hallett, 1969*b*).

Blue green (507 nm) 2 msec duration 12 min subtense test. Blue green temporal square-wave 17 deg subtense uniform background. Each curve is the average of 2 or more days' sessions.

large backgrounds is useful but there are certain limitations (Hallett, 1969*b*). (i) The rising phase of the empirical impulse function changes its exponential growth constant with input, so that the prediction of the responses to on-steps is actually a little arbitrary. (ii) The gain constant $g_Q$ deg$^2$ (in the legend to Fig. 9), which determines the height of the empirical impulse function (and which lumps together the constants $K$ (signal/noise criterion), $F$ (quantum efficiency) and $\alpha$ deg$^2$ (summation area) of Barlow's (1957) theory for small signals and steady backgrounds) is not a true constant but grows rather slowly with the energy density (Q quanta deg$^{-2}$) of the impulse background. (iii) For some observers and on some occasions $g_Q$ is excessively large so that predicted thresholds are too high. (iv) The theory cannot predict the overshoots in threshold which are produced at the *on* and *off* of very bright square waves (e.g. Crawford, 1947; Baker, 1963). Of these limitations (i) and (ii) simply require that one use small amplitude impulse functions to predict small threshold changes, moderate to predict moderate, and so on. Limitation (iii) can be a large effect (0·8 log) and has been attributed (Hallett, 1969*a*) to the fact that the criterion $K$ of some observers may be very high when the illumination conditions are transient or difficult. Limitation (iv) applies to threshold disturbances of 3–4 log magnitude.

What can be done to improve this sort of analysis? There are two possible approaches. The first is to make some different set of assumptions about the nature of the signal/noise decision (e.g. Papoulis, 1965). The simple linear signal/noise approach to Fig. 9 presupposes a very stable system with good memory that is able to store all the confidence limits to the temporal waveform of the neural response to the background alone, and this approach leads to the formulation (2) in the legend of Fig. 9 which has the analytical disadvantage that the threshold disturbance due to temporal square waves, $q_{B,X}(t)$, cannot show overshoots even if the system impulse function $h(t)$ undershoots, since $h^2(t) = [-h(t)]^2$ (Hallett, 1969*b*). These matters will not be further considered here. The second approach is to drop the restriction that the 'neural response' must be a linear function of the stimulus and also to try to consider the way in which the threshold-elevating effects of a quantum absorption grow and decay, not only in time, but also in space as well.

### *Allowances for spatial effects*

The work of Granit (1955) and Kuffler (1953) showed that there is a complicated interplay at the retinal level between excitation and inhibition, depending upon the nature and history of illumination, and the experiments of the present two papers provide an ample range of effects which cannot be accounted for by simple linear signal/noise theory. How may these effects be treated?

*A linear approach to spatial disturbances*

Enroth–Cugell & Robson (1966), following Schade (1956) and Rodieck (1965), used a point spread function equal to the weighted difference between two Gaussian density functions of different variance in order to calculate the contrast sensitivity of cat retinal ganglion cells to small amplitude sine-wave gratings of constant over-all luminance. This spread function shows negative undershoot and is not unlike the spread function of the xerographic process (Neugebauer, 1967). Daitch & Green (1969) extended the use of this function to describe the relation between luminance and contrast sensitivity for human rod vision at 12 deg eccentricity from the fovea, using sine-wave gratings presented in 0·2 sec flashes once every sec. They found that a 4 log increase in intensity reduced the spread constant of the point spread function by a factor of 2.

The point spread function,

$$P(r) = \text{const.}\,\{\exp(-r/R)^2 - 0{\cdot}1\,\exp(-r/3R)^2\}, \qquad (3)$$

is a good approximation to the results of Daitch & Green (1969), if $R \simeq 0{\cdot}2$ deg at low levels of luminance, and to some of the results of Enroth–Cugell & Robson (1966). $P(r)$ undershoots at $1{\cdot}6\,R$ and returns to within 2 % of zero at $4R$, and in this connexion it is of interest to look at Fig. 2 of Fiorentini & Maffei (1968). These workers measured small changes in threshold at the centre of a variable subtense subliminal luminous ring, superimposed on a weak background, for human rod vision at 10 deg eccentricity from the fovea: one may comment that their results seem to be nicely compatible with the idea that the subliminal ring adds to the brightness of the test, according to a point spread function which undershoots at $r = 0{\cdot}5$ deg and returns again to zero at $r = 1$ deg, and that if this function is (3) above then $R = 0{\cdot}25 - 0{\cdot}3$ deg, in good agreement with the value of 0·2 deg applicable to the experiments of Daitch & Green (1969).

Unfortunately this sort of spread function is a poor fit to the present data no matter what value of $R$ one uses. The line spread function corresponding to (3) above,

$$L(x) = \text{const.}\,\{\exp(-x/R)^2 - 0{\cdot}3\exp(-x/3R)^2\}, \qquad (4)$$

falls to 1/2, 1/4 and 1/8 at approximately $0{\cdot}7R$, $0{\cdot}85R$ and $R$ respectively and undershoots at $1{\cdot}2R$. This form is far too 'blunt' at small $x$ to account for the threshold disturbance due to a single luminous line, even if one makes supplementary assumptions (e.g. 'the absolute threshold of *ca.* 100

quanta (cornea) is the lowest possible threshold') in order to explain the absence of a undershoot. In fact it is difficult, as we saw earlier (pp. 454–458), to reconcile the sharp fall in threshold on either side of a single line, or on the outsides of a pair of lines, with the extensive spread between the lines, using any linear theory.

*Towards a non-linear approach*

Sperling & Sondhi (1968) have presented a model designed to treat data for temporal integration and flicker, and more recently Sperling (1970) has indicated how this model might be modified to treat spatial phenomena as well. The model is not derived analytically from data, in the way that Kelly (1969, and unpublished) has treated sine-wave flicker, but is rather an analogue imitation of a possible neuronal network. The essential idea is that a neurone can be mimicked by an ordinary low pass *RC* filter; excitatory messages are dissipated by the filter in the usual way and inhibitory messages linearly reduce the resistance of the filter, thereby reducing its gain and increasing its speed of response. The action of the model occurs in two stages. In the first stage light falling on the centre and surround of the receptive field is spatially weighted by Gaussian density functions of different spread (functions similar to the first and second terms on the right of eqn. (3) above), converted to voltage and then passed through one or two active *RC* lag filters which feed-back to their own resistances. This parametric feed-back compresses the dynamic range of the signal. In the second stage the signal from the *centre* passes to another active *RC* filter, the resistance of which is *reduced by the signal from the surround*, and then via a few passive *RC* lag stages to a level discriminator. Thus the surround attenuates the message from the centre and increases the speed with which it is dissipated.

Models of this sort are very relevant to the present data: (1) the scaling of the message can be arranged so that the S.D. of the message (which originates from quantum chaos in the light stimuli) is constant, or almost so, and thus if the signal/noise decision is one of fixed confidence it can be approximately implemented as the recognition of a fixed change in level (compare Barlow & Levick, 1969); (2) since the inhibitory action of the surround on the centre is essentially a process of analogue division negative-going signals do not occur and this avoids the problems which negative undershoots present to simple linear signal/noise analysis (p. 468; Hallett, 1969*b*); (3) the fact that the model's temporal response to a large impulse background is skewed as background intensity increases, coupled with the fact that the inhibitory message from the surround is subject to one more *RC* lag than the message from the centre, suggests that it should be possible to account for at least some of the ways in which the time course of the threshold disturbance is modified by changes in background brightness and signal area (Hallett, 1969*b*, 1970).

Although Sperling (1970) has used his model to illustrate a number of well-known aspects of human visual physiology (e.g. Mach bands, edge effects and changes in the extent of spatial integration with target duration and background brightness, etc.) the approach is not without its difficulties. The labour of calculating thresholds for a wide variety of spatio-temporal patterns, and of investigating the dependence of the calculations on various parameters, is not trivial, particularly since the 'neuronal network' is intuitive and no doubt modifiable to some extent if one wishes to incorporate the ideas of other workers (e.g. Devoe, 1966; Ratliff, Knight & Graham, 1969), but the principal problem is the best form of the spatial weighting functions. With Gaussian functions it is easy to show that the 'neural responses' to steady luminous lines are always rather 'blunt', the 1/2, 1/4 and 1/8 widths being in the rough ratios 1:1·4:1·6 (or worse if the input or feed-back weights are large). Matters are considerably improved, however, if one assumes instead a *bimodal* function for the inhibitory surround. This is reminiscent of the bimodal distribution of the coefficients of lateral inhibition in *Limulus* eye (R. B. Barlow, 1967; Ratliff *et al.* 1969), and the possible virtues of such a function will now be considered.

*Provisional line spread functions*

The simple line spread functions,

$$L_{\text{centre}}(x) = \exp-(x/R)^2, \tag{5a}$$

$$L_{\text{surrounded}}(x) = \exp-\{(x-\pi^{0\cdot5}R)/R\}^2+\exp-\{(x+\pi^{0\cdot5}R)/R\}^2 \tag{5b}$$

are contrived to give an inhibitory field three times as wide as the excitatory one, in conformity with previous approaches (Schade, 1956; Enroth-Cugell & Robson, 1966; Daitch & Green, 1969; Sperling, 1970). The 'centre function' (5*a*) is a simple Gaussian with space constant $R$ and peak at $x = 0$ but the 'surround function' (5*b*) is a bimodal distribution formed, for simplicity, from the sum of two widely separated Gaussians, also of space constant $R$, but with peaks at $x = +1\cdot77R$ and $-1\cdot77R$. The 'neural responses' of Sperling's model, modified by equations (5*a*) and (5*b*), have been calculated for the case where there is no compression in the first stage (weak steady inputs and low feed-back weights) and where there is extensive inhibition of the centre message by the surround in the second stage.

This can be simply done by calculating the response pattern of the receptive field centres (the convolution of (5*a*) with the spatial distribution of the luminance of the suprathreshold forcing pattern) and dividing this by the response pattern of the receptive field surrounds (which is the convolution of (5*b*) with the forcing pattern). The following results have been obtained: (i) the 'neural response' to a single thin luminous line is nicely sharp and falls off rapidly with an exponential constant of 0·3*R* (cf. Fig. 1 in which the constant is *ca.* 10 min); (ii) the response to a *pair* of luminous lines falls off rapidly at the outsides, as expected, but the response shows no signs of bimodal peaks (one for each line input) unless the separation of the luminous lines is 1·9*R* or greater (cf. Fig. 3, resolution of the gap plausibly begins at a line separation of 0·75 deg at the intensity used); (iii) the height of the 'neural response' midway between a pair of luminous lines falls off asymptotically with an exponential constant of 0·5*R* on increasing the separation of the lines (cf. 16 min (p. 459) for the similar constant that describes the height of the dips in Figs. 3 and 4); (iv) the response to an edge shows overshoot and falls off asymptotically with an exponential constant of 0·35*R* (cf. a constant of *ca.* 10 min for Figs. 3 *g* and 4*e*); (v) the response to a luminous stripe shows depression at the centre and overshoot, or 'heaping', at the edges if the stripe is of width 4·1*R* or greater (the experimental parallels between linear and circular edged targets, pp. 463–465, and the maxima at 2 deg subtense in Figs. 7 and 8 (open circles), suggest the possibility that depression and overshoot occur at a stripe width of *ca.* 2 deg). Comparison of the calculated with the experimental values in (i–v) shows that, with $R = ca.$ 30 min, the logarithmic shapes of the 'neural responses' of the model are reminiscent of the log threshold disturbances shown in the various Figures of this paper.

The value of this provisional approach is that it illustrates the way in which an essentially coarse system with widespread spatial integration (eqns. 5*a*, *b*, $R = 30$ min) can nevertheless be associated with sharpening (the 'neural response' to a line or at an edge is not nearly so diffuse as one might have expected), and the interaction of centre and surround is such that the 'neural response' to lines and edges does not show negative undershoot. In these respects the 'neural responses' of the model parallel the experimental threshold disturbances.*

Unfortunately this approach must remain provisional because there seem to be at least two objections. The first is that the value of $R = 30$ min should be large enough to be compatible with the extensiveness of spatial integration at the absolute threshold (dark-adapted observer, zero background). If the contribution of the inhibitory surround is assumed negligible, so that only eqn. (5*a*) need be considered, then calculation shows that the threshold energy of a luminous disk of diameter 2*R* should be 0·2 log

* See note added in Proof.

greater than the minimal threshold energy for very small disks. This conflicts with the experimental fact (e.g. Hallett *et al.* 1962) that the threshold energy of a 1 deg subtense flash is not greater than that of much smaller flashes. Thus one is forced to additional postulates, e.g. *either* the complicated postulate that $R$ is reduced from a dark-adapted value of *ca.* 1 deg to a value of 30 min by brief illumination of the intensities used in the present experiments, *or* the simpler idea that the surround is actually excitatory at the lowest intensities of rod vision, augmenting the integrating power of the centre. The second objection is that by no means all aspects of the log 'neural response' of the model imitate the experimental log threshold disturbances. If the model and results are to be rigorously compared, one should attach confidence limits to the response of the model and from these calculate the *thresholds* of the model; this has yet to be done.

### *Conclusions*

Relatively weak, brief illumination of the dark-adapted eye leads to a reduction of spatial integration and to other threshold changes that are attributable to lateral inhibition.

A striking feature is that threshold disturbances do not extend much beyond the edges of the background pattern, despite the known extensiveness of spatial integration at the lowest intensities of rod vision. It is suggested that a possible model is one in which the response of the receptive field centre (Gaussian line weighting function) is divided by the response of the inhibitory surround (bimodal line weighting function). The advantages and disadvantages of this approach are briefly indicated.

### *Note added in Proof*

With a posterior nodal distance of 16·68 mm the spread constant $R = 30$ min of arc is equivalent to 0·15 mm at the human retina and the quantity $\pi^{0\cdot5}R$ to 0·26 mm. This latter value, from eqn. (5*a*), is the effective width of the excitatory centre, and if one allows that eqn. (5*b*) need not be exact, and that there exists a corresponding point spread function $P(r)$ with spread constant *ca.* $R$ and centre of gravity at $r =$ *ca.* $\pi^{0\cdot5}R$, then 0·26 mm is also the most effective radius for lateral inhibitory interaction. The effective width of the whole field is $3\pi^{0\cdot5}R$ or 0·78 mm.

It is generally speaking difficult to compare various physiological and anatomical estimates of retinal organization – there may be species or retinal position factors as well as the difficulties peculiar to the different measurements and the following comparison is necessarily brief. Recent electrophysiological measurements in *Necturus* by Werblin (1970) give 0·3 mm or so (perhaps 0·2–0·3 mm after correction for the size of the scanning stimulus) for the diameter of the centre of the receptive fields of bipolar and subsequent retinal cells and 0·25 mm as the most effective radius for lateral inhibition at the bipolar cell level. The over-all receptive field size is in the region of 0·7–1·0 mm. The agreement between these electrophysiological measurements and the above provisional estimates from human rod vision is rather good.

One should note that the point weighting function for the horizontal cell in Fig. 3 of Werblin (1970) peaks at the origin and this may seem to argue against the present view that the point spread function for the inhibitory surround has an eccentric peak. Such a point spread function would depend on (i) the spatial distribution of synaptic inputs, (ii) the cable properties of the cell membrane, and (iii) the spatial distribution of synaptic outputs. The weighting function in Fig. 3 of Werblin (1970) reflects only the first two of these so the possibility that the point spread function of inhibition has an eccentric peak cannot be excluded.

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A list of errata in previous papers is given at the beginning of this volume.

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