

RAPID CHANGES AND HYSTERESIS IN SPATIAL INTEGRATION FOR HUMAN ROD VISION

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SUMMARY

1. Two previous papers (Hallett, 1969*a*, *b*) were concerned with the visual threshold appropriate to a peripheral retinal point and in particular with the rapid changes in point threshold produced by illuminating the dark-adapted eye with large brief duration backgrounds. This paper extends this approach to testing signals of larger subtense.

2. Spatial integration for the rods can rapidly diminish and recover within a few hundred milliseconds.

3. A brief duration background which raises the threshold at a retinal point as much as some steady background is more effective than the steady background in reducing the extent of spatial integration.

4. Hysteresis can be substantial; the extent of spatial integration varies, even for a given point threshold, according to whether the threshold is rising or falling, or temporarily or permanently steady.

5. A possible type of non-linear model is discussed in the next paper (Hallett, 1971).

INTRODUCTION

When motoring through a storm at night a lightning flash will reveal the road in useful detail and there is no particularly noticeable loss of visual sensitivity following the flash. In the laboratory it is found that the dark-adapted observer can detect peripheral dark objects of about 14 min subtense against brief duration backgrounds which deliver only 1 quantum absorption per rod (Hallett, 1962) and this is relatively close to the visual acuity limit for the same light-adapted retinal region (about 6 min, see Mandelbaum & Sloan, 1947, for references).

Now it is a long standing idea in human visual physiology that the eye can increase its acuity by using a 'retinal emulsion' of finer functional grains (receptor aggregates) – certainly the extent of spatial integration does shrink at higher levels of adaptation (e.g. Craik & Vernon, 1941;

Barlow, 1958) – and experiments on animals have always attached importance to the functional reorganization of the retina that occurs with light adaptation (e.g. Granit, 1955; Barlow, Fitzhugh & Kuffler, 1957). Is vision during a flash mediated by more finely organized rod pools than those apparent in the dark-adapted eye or are any changes of spatial integration too slow and too late to be of any consequence? The answer given in this paper is definite: from the viewpoint of the incoming light signals it is as if the extent of spatial integration is small at the instant of the background flash.

METHODS

The apparatus, techniques and some of the physiological characteristics of observers R.F.W., H.V.S. and E.K.S. are fully described in two previous papers (Hallett, 1969*a*, *b*).

The fifty experiments reported here were spread over the long period from 1966 to 1969 so that the accuracy of the absolute photometric calibrations is probably only ± 0.05 log. Conversions from photometric to energy units are given where necessary in the legends to the figures and depend, as in the previous papers, on 0 log scotopic td being equivalent to 5.65 quanta (507 nm, cornea) $\text{deg}^{-2} \text{sec}^{-1}$ (e.g. Scheibner & Baumgardt, 1967) and on the figure of 0.1 for the fraction of corneal quanta (507 nm) absorbed by the rods (Rushton, 1956).

The thresholds were found by the method of constant stimuli and are the mean log thresholds derived from k experiments of five series per point on a stimulus scale of 0.087 log (Hallett, 1969*c*). The accuracy is indicated by the scatter in the graphs, which roughly amounts to a s.d. of ca. $0.18 \times k^{-0.5}$ log. In the Figures that follow the ordinate $O \log_{10}$ threshold intensity means the absolute threshold intensity of the smallest subtense test and this corresponds, when allowance is made for test area, to a threshold energy of magnitude 100 ($\lambda = 507$ nm) quanta at the cornea.

The observer's field of view is shown in Fig. 1. The testing signal T falls on the temporal retina of the left eye, 18 deg away from the fovea. It is a brief duration flash (1.5–10 msec duration) and its angular subtense is either the independent variable or a fixed parameter of the given experiment. The large homogeneous 18 deg subtense background B is also centred on the same point. It may be steadily illuminated or briefly illuminated (usually for the same duration as the testing signal) and if briefly illuminated the testing signal may either precede ($t < 0$), be synchronous with ($t = 0$) or follow the background flash ($t > 0$), where t is the time interval between the beginnings of the signal and background flashes.

The signal and background beams in experiments at low intensities have the same spectral distribution (Schott PAL Interference Filter, peak 507 nm, half-width 20 nm) and enter at the centre of the dilated pupil. When the background is bright, or the threshold disturbance is of large magnitude, the rod mechanism has been isolated by the method of Aguilar & Stiles (1954): the signal beam is then green (530 nm, half-width = 28 nm) and enters the pupil 2 mm towards the nasal edge, the background beam is red (635 nm, half-width = 30 nm) and enters at the centre of the pupil (Schott Veril B 60 filters with red cut-off filters to eliminate tails). Under these conditions the signal flash is seen only by the rods, and the elevation of rod threshold is due to the rod (not the cone) response to the background flash (Hallett, 1969*a*; Alpern & Rushton, 1967).

The subjective appearance of a moderately bright 507 nm brief duration background is that of a more or less homogeneous white field which rapidly brightens and

somewhat more slowly dies away. The appearance of a bright 635 nm background flash is that of red field that brightens and dies away but it is not particularly homogeneous; the central portion seems paler and tends to persist somewhat as a white point and there may be some ill-defined tracery in the peripheral part.

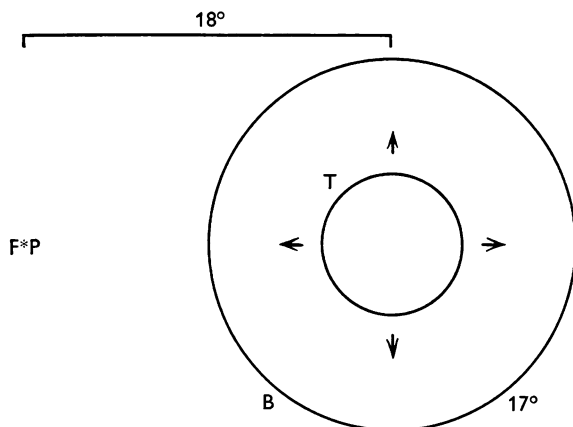


Fig. 1. The observer's field of view (left eye). T is a brief duration testing signal of various sizes presented at time interval t with respect to a large (17 or 18 deg) brief duration background B. FP is the fixation point.

RESULTS

Threshold of the dark-adapted eye

As is well known the visual threshold appropriate to some point on the dark-adapted retina can be measured by the method of fixation and flash (e.g. Pirenne, 1967), combined with some sound psychophysical procedure such as the method of constant stimuli. When he is ready, the dark-adapted observer looks at a small dim red fixation point and triggers the apparatus. A small brief signal flash of fixed timing and position is then delivered and the observer reports whether or not he sees it. After a number of repetitions of the manoeuvre with signals of various randomly selected intensities, including zero ('blanks'), it is easy to find the mean threshold and ascertain the scatter and fallibility of the measurements (Hallett, 1969c).

Time course of a threshold disturbance

Now suppose that we are interested in the time course of the threshold disturbance produced by a brief illumination of the uniform background. One can scarcely measure signal threshold as a function of 'real time' because the time interval between the beginning of the background flash and the moment of decision cannot be measured. It is quite easy, however, to measure threshold as a function of 'stimulus time', t . The apparatus is arranged so that when triggered it delivers a brief duration large subtense

background of fixed energy, Q , after some fixed time (normally 200 msec). A signal flash is also delivered, at time t relative to the background, and after the usual repetitions the mean threshold energy, $q_Q(t)$, scatter and fallibility are found. The apparatus is then adjusted to a new value of t , the manoeuvres repeated, and eventually one obtains the whole function, $q_Q(t)$, which relates the threshold disturbance of the signal to the time interval t between the signal and background.

This is what has already been done (Hallett, 1969*a, b*) for small brief duration testing signals and some further examples of these threshold-time interval functions ('impulse functions') for large, homogeneous, brief duration backgrounds are shown as the top curves for the observers of Figs. 2-4. These curves, for small (13-24 min) and brief (1.5-10 msec) duration signals, are representative of the results previously published. Signal threshold energy begins to rise at $t = ca. -150$ msec along a slightly sigmoid line to a peak at $t = 0$ and then eventually returns to the value typical of the dark-adapted eye (*ca.* 100 quanta 507 nm). This is the pattern which is to be expected if the signal and background flashes enter a 'single terminal' quasi-linear network and generate responses which last a few hundred msec. The response to the background alone will be noisy because of the random variation in the number of quanta in each background flash. The response to the signal plus background may be distinguished from the response to the background alone if it exceeds the confidence limits appropriate to the background response. The signal will be most difficult to distinguish from the background if it is coincident with the background ($t = 0$) because then the two responses completely overlap. Recognition will be easier, and threshold energy lower, if only partial overlap occurs ($t \neq 0$). Much the same argument applies to many *non-linear* networks of possible physiological interest; the peak of the threshold-time interval function will usually be at $t = 0$ (unless the signal travels via a different path or is sufficiently strong to bias the shape of the response) because then the response to signal and background will completely overlap and be hardest to distinguish.

Threshold-time interval functions $q_Q(t)$ for small brief duration signals and large brief duration backgrounds ('impulse functions') have already been analysed (Hallett, 1969*b*) in terms of linear signal/noise theory. In all experiments it has been possible to relate the function to the classic integration time of the eye and in sixty-nine of ninety-one experiments (five observers out of nine) it has also been possible to calculate accurately the thresholds of the steadily illuminated eye. In the remaining twenty-two experiments (four observers) the calculated 'steady-state' thresholds are consistently high because the impulse function is of excessive magnitude. Three of the five observers of the present paper (E.S.H., H.V.S. and

R.F.W.) belong to this latter group. The results and analysis which follow do not depend upon the magnitude of the observer's 'impulse function'.

Impulse functions for small and large subtense signals

In this paper the term 'impulse function' will be used for convenience to mean the time course of the threshold disturbance created by a brief duration ('impulse') background, whatever the signal subtense, it being understood that the background is large and homogeneous. This is consistent with previous usage (Hallett, 1969*b*) which regards the background as the forcing function and the signal threshold as the observed response.

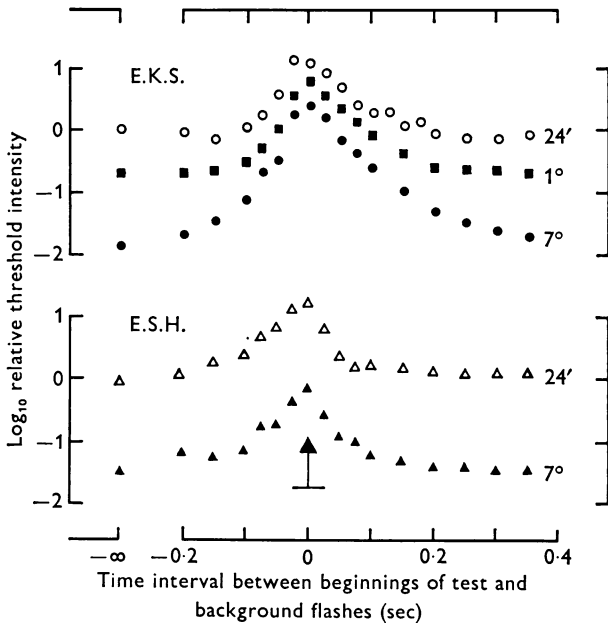


Fig. 2. The threshold disturbance due to a large brief background at time zero as measured by different sizes of test.

Top: observer E.K.S. Background intensity of 3.56 log quanta per deg² (1 quantum absorbed per 35 rods).

Bottom: observer E.S.H. Background intensity of 2.66 log quanta (507 nm at the cornea) per deg² (1 quantum absorbed per 280 rods).

10 msec duration blue green (507 nm) test and 17 deg subtense 10 msec duration background. Each curve is the average of 3 days' sessions.

Figs. 2-4 show impulse functions for signals of small (< 1 deg) and large (ca. 7 deg) subtense. In all cases the function peaks at time interval $t = 0$, which is as expected, since then the nervous responses to signal and background must overlap completely and be most difficult to separate. What is not necessarily expected is that the difference Δ between log

thresholds for the small and large signals should also change with t , being smallest at $t = 0$. This log threshold difference is a measure of the extent of *spatial integration*. If the visual system were able to integrate all the far spread quanta in a 7 deg signal then the threshold *energy* for this large signal would be the same as for a 24 min (0.4 deg) signal and the threshold *intensity* would be $\log(7/0.4)^2 = 2.5 \log$ lower. This is clearly not the case for even the dark-adapted eye ($t = -\infty$, Fig. 2) and the extent of the integration is reduced even further during the response to an impulse background.

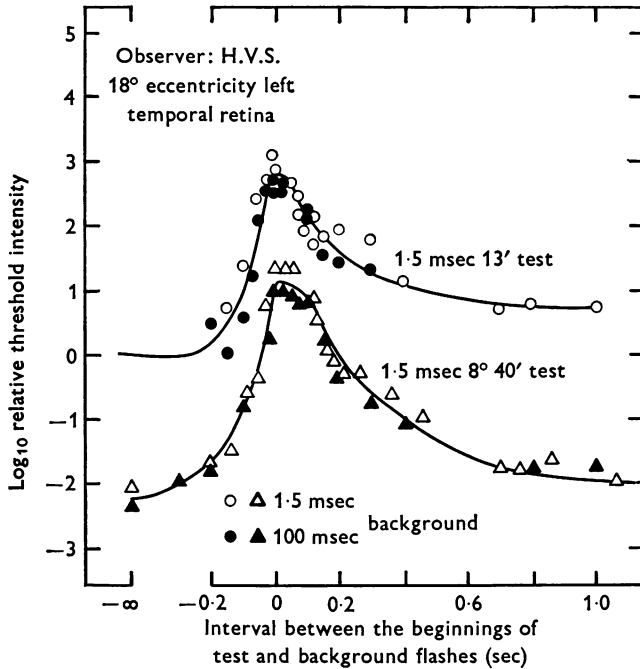


Fig. 3. Observer H.V.S. The time course of the threshold disturbance created by a large brief duration background as measured by two sizes of test. This experiment shows that the extent of spatial integration may be changed very rapidly by a brief duration background.

Background intensity is 4.65 log quanta (507 nm at the cornea) per deg² (1 quantum absorbed per 3 rods). Rod isolation conditions.

If one inspects Figs. 2-4 carefully it will be seen that the log threshold difference Δ between the small (13 or 24 min subtense) and large (7 or 8.7 deg subtense) signal flashes is initially large but that the threshold disturbance of the large test begins sooner, is of bigger amplitude and outlasts the response to the small signal. Thus the extent of spatial summation, as measured by Δ , diminishes and recovers again in the course

of a few hundred milliseconds in the time scale t . Now the observer's eye-hand reaction time is of the order of 1–2 sec from the occurrence of the background so that it is clear that the full cycle of functional reorganization of the visual system (whatever this may be at the cellular level) is completed within a few hundred msec of the impulse background.

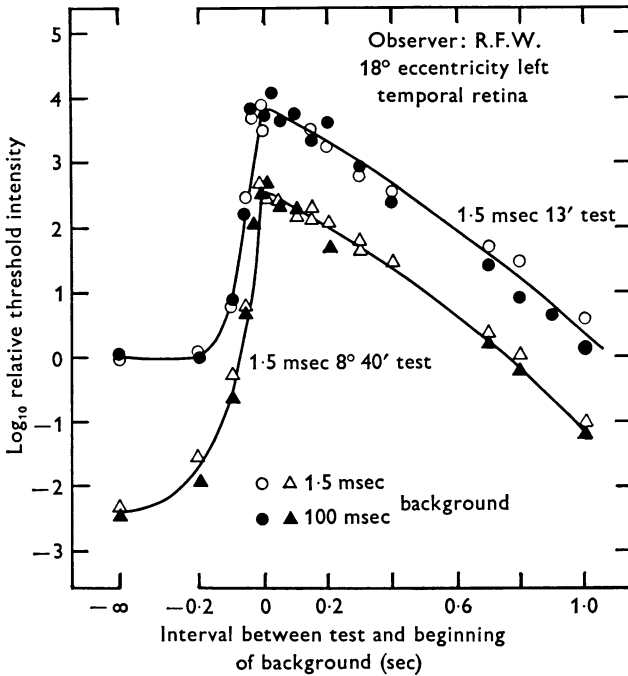


Fig. 4. Observer R.F.W. The time course of the threshold disturbance due to a large brief duration background as measured by two sizes of test. A similar experiment to that of Fig. 3, except that the red background is brighter: 6.25 log quanta (507 nm at the cornea) per deg² (14 quanta absorbed per rod).

Fig. 5 reveals these changes in a different way. Here the log threshold of the large test is plotted against the log threshold of the small test at the same time interval t . The diagonal lines represent loci of constant log threshold difference Δ , corresponding to the dark-adapted value of Δ . The plots are subject to a fair amount of variation but a great deal of work would be required in order to improve on them. A few points are clear. Spatial integration, as reflected by Δ , initially shrinks but the rest of the relation is in the form of an anticlockwise hysteresis loop. For a few hundred millisecond range of t (starting at $t = -75$ msec) Δ , and thus the extent of spatial integration, assumes two different values according to whether $t < 0$ or $t \geq 0$. By and large it seems that at $t < 0$ Δ , and thus

spatial integration, is closer to that seen in the dark-adapted eye, whereas for $t \geq 0$, the situation is like that of a more light-adapted eye. This crude picture will be confirmed. The vertical heights of the hysteresis loop for the various observers are respectively E.S.H. 0.1, E.K.S. 0.2, H.V.S. 0.75, and R.F.W. 0.5 log, so it is clear that the effect can be of fair magnitude.

Spatial integration functions at various time intervals t

Fig. 6 shows experiments in which the full area-threshold intensity curve, or spatial integration function, has been measured for a few values of t , the time interval between signal and background. The functions have been displaced for clarity and in actual fact the left-hand parts are within 0.4 log of each other.

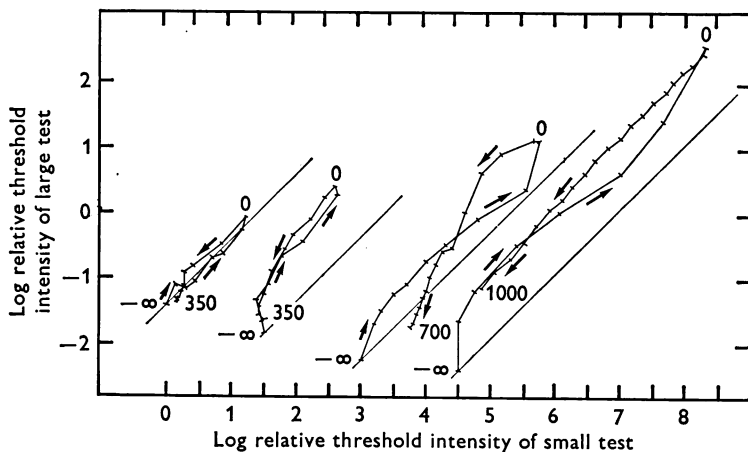


Fig. 5. Hysteresis effects in spatial integration. The data of Figs. 2, 3 and 4, replotted as log small test threshold versus log large test threshold in units of the small test threshold intensity.

From left to right respectively the data are for observers E.S.H. (Fig. 2) properly placed, E.K.S. (Fig. 2) displaced laterally by +1.5 log, H.V.S. (Fig. 3) displaced by +3 log and R.F.W. (Fig. 4) displaced by +4.5 log. The arrows show the direction of increasing time interval t and the numbers by the graphs indicate certain values of t . The time marks represent intervals of 25 msec (E.S.H.), 25 msec (E.K.S.), and 25 msec for $t < 0$ and 50 msec for $t > 0$ (H.V.S. and R.F.W.).

The top curve, for $t = -50$ msec, is very similar in form to the expected integration function of the fully dark-adapted eye ($t = -\infty$). The curve is, however, generally about 0.7 log higher than it would be in the absence of the impulse background and in the case of the largest tests the elevation is probably a little greater than 0.7 log. Complete spatial integration of energy extends to 1 deg, as has been previously found for the dark-

adapted eye in the absence of impulse backgrounds (Hallett, Marriott & Rodger, 1962).

When $t = 0$ the situation is quite different. The point threshold (8 min subtense signal) is now only 0.3 log higher than it was in the top Figure but complete spatial integration only extends to 0.5 deg and the thresholds for the larger tests have risen considerably. By $t = +50$ msec

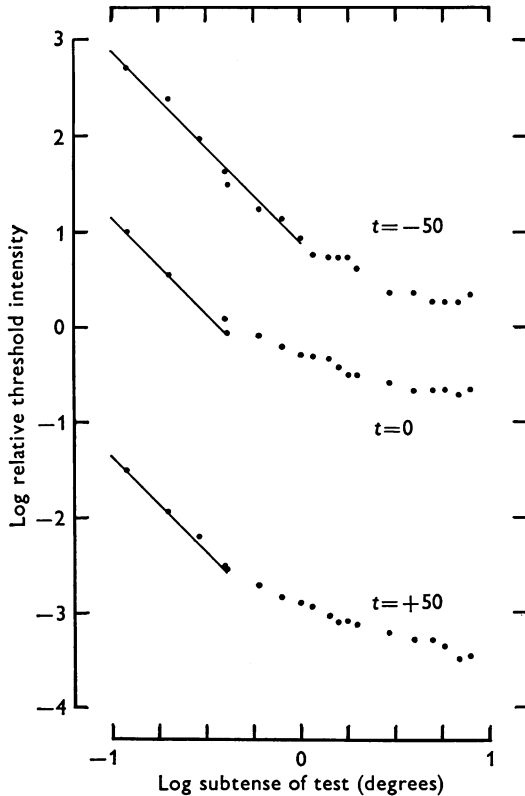


Fig. 6. Observer J.A.M. Changes of spatial summation produced by a very brief illumination of the dark-adapted eye.

The three curves show the dependence of the threshold intensity of a 2 msec duration testing flash on its angular subtense and on its timing with respect to a large 2 msec duration background. The testing flash occurs 50 msec before ($t = -50$) or synchronously ($t = 0$) or 50 msec after ($t = +50$) the brief background flash. The 45 deg line shows the extent of complete spatial summation. It is important to note that the three curves have been displaced vertically by $+2 \log (t = -50)$, $0 \log (t = 0)$ and $-2 \log (t = +50)$ for clarity; in their true positions the left hand parts of the curves nearly overlap.

Both test and background are blue green (507 nm) and the background is of intensity 3.67 log quanta (cornea) per deg² (1 quantum absorbed per 27 rods). Each curve is the average of two sessions.

the point threshold has recovered by 0.5 log to approximately the value observed at $t = -50$ msec, but the $t = +50$ curve (bottom) differs very much from that at $t = -50$ (top): complete spatial integration of energy extends only to 0.5 deg and although the thresholds for the larger signals have fallen from their elevated position at $t = 0$ they are not so low as was the case at $t = -50$ msec.

Fig. 6, then, amply confirms the previous conclusions – at time intervals $t < 0$ the shape of the spatial integration function is not much different to the dark-adapted form but by $t \geq 0$ the shape of the function is strongly reminiscent of the light-adapted eye, even though the point threshold may be the same as at $t < 0$. From the viewpoint of the stimulus the eye is apparently light-adapted at the instant of a lightning strike, although from the viewpoint of the electrophysiologist the action has yet to begin.

Interpretation of the events in real time

It is of course hazardous to argue from threshold disturbances in the time interval scale t to nervous responses in real time, but according to the following simple argument the experiments in Figs. 2–6 do *not* provide any grounds for believing that testing signals delivered at $t < 0$ are processed by a network with changing space constants. On this simple view the nervous response to a testing signal at $t < 0$ is related to the prevailing spatial integration function at the instant of delivery, i.e. that of the fully dark-adapted eye, but the later parts of the nervous response to the testing signal are lost in the early parts of the response to the suprathreshold background, and consequently the threshold is raised by a nearly constant factor for all sizes of testing signal. (This factor may be a little greater for the larger testing signals. The integration of the effects of the far spread quanta in the larger tests may take a somewhat longer time than for small tests and thus rather more of the eventual nervous response to a large test may be obscured by the early parts of the response to the background.)

At time interval $t \geq 0$ the simplest view is that spatial integration functions, such as those of Fig. 6, do reflect something like the changes in real time: the s.d. of the background response would be related to the spatial integration function of the dark-adapted eye and the mean response to the testing signal delivered at time t would be related to the spatial integration function prevailing at time t after the background impulse. Interpretation may be more complicated, however, e.g. if the latency of the test response varies with the size of the test, etc.

Increment threshold functions for steady and brief duration backgrounds

So far in this tentative exploration of the vast ‘*threshold \times signal area \times time interval \times background energy*’ space we have considered the *threshold \times time* plane in a little detail (Figs. 2–4) and also the *threshold \times area* plane (Fig. 6) but not the *threshold \times background energy* plane or for that matter different background waveforms. Figs. 7 and 8 partly remedy this and show increment threshold curves for small and large tests which are presented either against large steady backgrounds or else presented synchronously ($t = 0$) with large brief duration backgrounds.

The pattern of the results is much the same as has been seen in the previous experiments. The interval Δ between the log thresholds of small and large tests increasingly narrows, indicating a reduction in the extent of spatial integration, as the brief duration background increases in brightness from levels of about 1/3000 (observer H.V.S.) or 1/10,000 (observer R.F.W.) quanta absorbed per rod per flash.

The dashed lines in Figs. 7 and 8 show that steady and brief duration backgrounds, which are matched so as to elevate the 'point' threshold equally, are dissimilar in their threshold raising actions on large subtense

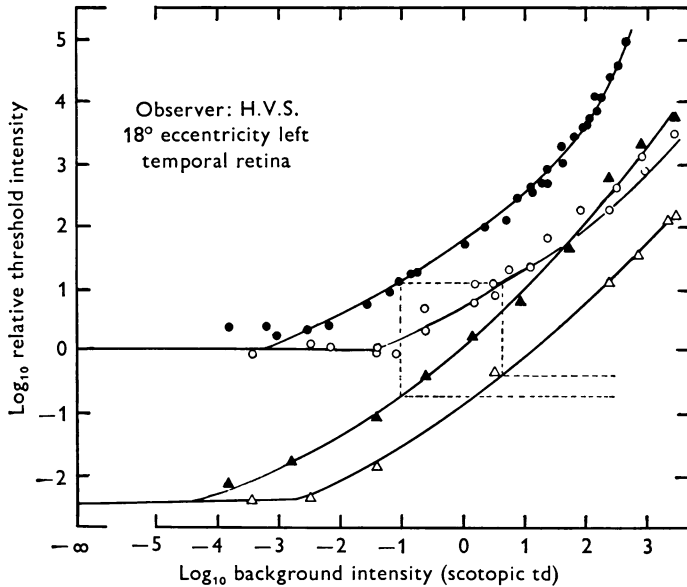


Fig. 7. Observer H.V.S. Increment thresholds for small (13 min; ●, ○) and large (8 deg 40 min; ▲, △) subtense test centred on a large 18° subtense background. The background is either steadily illuminated (filled symbols) or else briefly illuminated during the same 1.5 msec that the test is exposed (open symbols). The dashed lines show that steady and flashed backgrounds which have equivalent threshold raising power for a small test are not equivalent for a large test. Rod isolation conditions: green (530 nm) test entering at the nasal edge of the pupil of the left eye; red (635 nm) background entering centrally.

signals. The effect is quite considerable, of the general order of 0.5 log. It is an obvious conclusion that the spatial integration functions for steady and impulse backgrounds ($t = 0$) are different even when the point thresholds of the two sets of functions are equal.

Spatial integration functions for steady and brief duration backgrounds

This conclusion has been confirmed in experiments in which the spatial integration function has been measured for tests synchronous with flashed backgrounds or

superimposed on steady backgrounds. If one matches a flashed and steady background to produce the same threshold elevation for small tests then the remaining parts of the spatial integration functions for the two backgrounds do not coincide: the flashed background is much more effective in raising the thresholds of the larger tests than is the steady background.

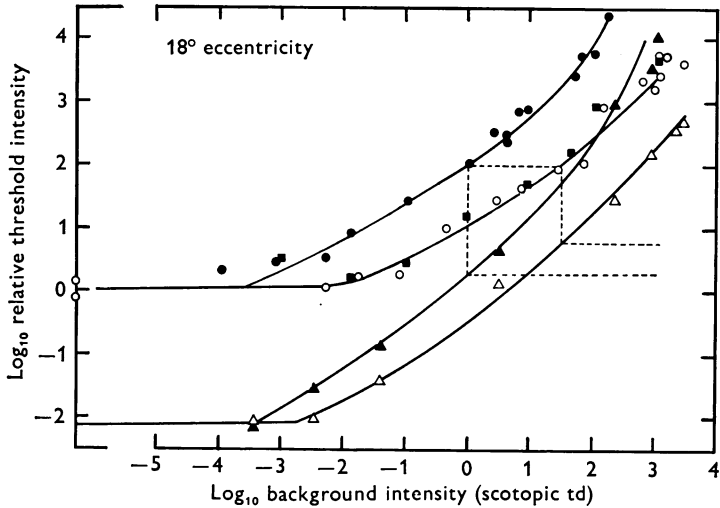


Fig. 8. Observer R.F.W. A similar experiment to that of Fig. 7. ●, 1.5 msec duration 13 min subtense test on steady background; ○, ■, same test on a coincident 1.5 msec duration background; ▲, 1.5 msec duration 8 deg 40 min subtense test on steady background; △, same test on a coincident 1.5 msec duration background. Rod isolation conditions. 18 deg eccentricity left temporal retina.

DISCUSSION

The experimental findings of this paper are threefold: (1) in the very practical time scale t of interval between signal and background it is clear that the extent of spatial integration can diminish and recover in a few hundred msec, the duration of the disturbance depending on the energy of the impulse background – and by implication the neural substrate of spatial integration can change and recover within a few hundred msec of the background flash; (2) for $t < 0$ (signal before background) the form of the spatial integration function is rather like that of the fully dark-adapted eye whereas for $t \geq 0$ it is more like that of the light-adapted eye; (3) the threshold for a point signal fixes, by definition, the position of the integration function but does not determine its shape, which is related to the history of illumination. These results are very relevant to current work on human vision and the electrical responses of the retina.

The equivalent background principle

The value of this approach has been appreciated for many years (e.g. Crawford, 1947, and earlier work on glare) and more recently this approach has been extended, notably by Rushton (e.g. Blakemore & Rushton, 1965; Rushton, 1965). It is a trivial matter formally to eliminate threshold from both increment threshold functions (for steady backgrounds) and dark adaptation curves (for substantial bleaches) and thus obtain a single function of equivalent background (or 'dark light') *vs.* time. The fact that this resultant function is the same for various spatial forms of testing signal lends support to the conclusion that both the position *and* form of the spatial integration function are linked and are determined by the sum of real background light and the dark light of bleaching. Although this linkage of position and form is true for the relatively steady-state situation in Rushton's experiments it clearly breaks down for the conditions of transient uniform illumination studied in the present paper.

The rapidity and nature of the changes in spatial integration

Are the rapid changes in spatial integration mediated by reorganization of a fixed processor or is the task of detection switched from one existing processor to another whenever the situation demands it?

A number of electrophysiological studies (e.g. Granit, 1955; Barlow *et al.* 1957) have stressed the plasticity of organization at the retinal ganglion cell level although no particular comment has been made about the rapidity of these changes – if anything the work of Barlow *et al.* would seem to indicate that brief duration flashes do not produce much inhibitory effect. On the other hand the histological structure of the retina (e.g. Pirenne, 1961) and the whole thrust of recent studies of pattern recognition (e.g. Levick, Oyster & Takahashi, 1969) is to stress the fact that the visual system contains a hierarchy of processors amongst which the labour of pattern recognition is subdivided. If this is so then in analysing pattern detection by whole man one may be dealing with a problem far worse than that encountered in Stiles's analysis of trivariant colour vision (e.g. Wyszecki & Stiles, 1967). It does seem that one size of neuronal receptive field is tuned optimally to one size of target (e.g. Blakemore & Campbell, 1969; Campbell, Cooper & Enroth-Cugell, 1969) but if such is the case any small change in signal size, or for that matter in background lighting, may switch the signal detection task to another of the many varieties of processor.

Hopefully this pessimism is not justified. The following paper contains experiments in which the threshold-raising effects of a luminous line seem to be qualitatively the same for both line and spot-shaped testing stimuli.

Also McKee & Westheimer (1970) have stressed that some aspects of lateral inhibitory effects in human vision have features reminiscent of processing at the horizontal and bipolar cell level; possibly the varieties of spatial processing at these early stages are relatively few.

$h(t)$

In a previous paper (Hallett, 1969*b*) the impulse functions for point testing signals were analysed in terms of linear signal/noise theory and a pragmatic quasi-linear unit impulse function $h(t)$. The approach relates the impulse functions to the classic integration time for the eye, enables the dark light of the eye or the steady-state increment threshold relationship to be calculated with good accuracy, and gives a fair account of the threshold disturbance due to small or moderate steps of background intensity, but the approach does not yield the threshold overshoots caused by very large *on* and *off* steps. Since the impulse function of a linear system contains all the information about system dynamics, and since the quasi-linear impulse functions of the dark-adapted eye can be used to predict some aspects of the light-adapted (rod) behaviour it would seem a reasonable expectation that brief illumination drives the visual system in roughly the same way as steady adaptation. This paper shows that this is true to the extent that both brief illumination of the dark-adapted eye and steady illumination reduce spatial integration, but the two forms of illumination are certainly not equivalent since it is quite clear that brief and steady backgrounds which equally raise the thresholds for small tests do not do so for large tests. In summary a linear signal/noise approach to rod vision can be very useful but may fail for at least two reasons: (*a*) it seems possible that the signal/noise ratio K , or some similar constant, may vary with the illumination conditions (at least in the case of some observers or some experiments: Hallett, 1969*a*); (*b*) changes in spatial integration (and no doubt lateral inhibition) are different for different temporal forms of illumination.

Spatial integration and lateral inhibition

The experiments of Figs. 7 and 8 show that for a given point threshold spatial integration is always much less for an impulse background ($t = 0$) than for a steady background. Does this mean that the energy of large tests is largely cancelled out because the light falls on mutually antagonistic retinal regions which are especially antagonistic when triggered by brief illumination of the dark-adapted eye? In the following paper it will be shown that brief illumination of the dark-adapted eye does, in fact, cause substantial inhibitory effects similar to those found by Westheimer for the steadily light-adapted eye.

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