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# IMPULSE FUNCTIONS FOR HUMAN ROD VISION

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## SUMMARY

1. This paper presents accurate increment threshold data for human rod vision for a small number of experimental parameters. The test is small and brief and the large background is either steady or transient.

2. The linear threshold disturbance due to an impulse background consists of an input dependent exponential growth phase and an exponential recovery phase of more or less fixed time constant (*ca.* 0·08 sec).

3. The data are treated by applying signal/noise decision theory to a hypothetical filter with two shot noise inputs, viz. the testing signal and the background. The gain and time course of the impulse function of the filter are slightly affected by the magnitude of the input.

4. A linear approach is useful since the impulse functions for dark or light-adapted rod vision yield independent information about quantities which have previously only been used to describe the increment thresholds for small tests on steady backgrounds, viz. the integration time and dark light of the fully dark-adapted eye and the gain changes (or changes in the signal/background ratio) which occur on progressive light adaptation.

## INTRODUCTION

It is common knowledge that the ability of a man to detect a light signal is reduced as the brightness of his surroundings increases, for the planets and stars that are visible at night disappear, beginning with the dimmest, as dawn breaks. This loss of sensitivity is accompanied by the advantage that the details of forms and movements become more visible. In part these observations are explained by the fact that the retinal image becomes richer in detail as the density of quantum absorptions increases and that the strength of luminous signal added to the background must significantly exceed the quantum fluctuations of the background, which *increase* as the square root of the background intensity, if the signal is to be seen.

The experimental observations on the signal/background relation have been reviewed by some of the workers (Pirenne, 1956; Barlow, 1957;

Rushton, 1965*a*) who have made substantial contributions in this field, and have been analysed in terms of quantum fluctuations, integration of the effects of light energy over space and time, dark noise of the eye, rod saturation by bright backgrounds and lateral inhibition. There has, however, been no way of predicting human visual performance in one situation, given data for some other situation, until recently, and only a little of the consequences of a quantum absorption in space and time could be guessed from the laws of temporal and spatial integration. These suggest that for the present region of interest (18 degrees from the fovea) the effects of a quantum absorption travel for *ca.* 1 degree and last for *ca.* 0·1 sec, but whether the spatial spread is still large after 0·1 sec or has begun to die away is not clear, since it depends upon one's opinion as to the precise nature of the laws of summation (Barlow, 1958; Baumgardt, 1961).

A linear method of predicting the threshold for a small brief duration signal added to a large steady background, given the time course of the threshold disturbance created by impulse illumination of the dark-adapted eye, was recently demonstrated as a curiosity since it was obvious that human rod vision was non-linear and the method of calculation led to overprediction of the threshold for some observers and correct prediction for others (Hallett, 1967). A full account of this work has been given in the previous paper (Hallett, 1969*a*). This approach has since been extended to six new observers and as a result of recent experiments involving $7 \times 10^4$ presentations of the signal something more definite is now known of the time course of the threshold elevating effects of quantum absorptions.

*Previous work on steady backgrounds.* Barlow (1957) studied the relation between the threshold energy of a small brief testing signal added to a steady background and the brightness of the background. If the background count of quantum absorptions is sampled over space and time then the count of a sample must fluctuate as the square root of the background intensity $B$ and the mean increase in the count due to signal must be significantly larger than the fluctuations due to the background alone if the signal is to be detected. Provided allowance is made for the contribution to these fluctuations by the dark light of the eye, mean signal energy is proportional to $g_B B^{0\cdot5}$ over a range of $B$, where $g_B$ is the gain of the system (v.i.). Barlow's analysis does not give an independent estimate of $g_B$ and in fact as $B$ increases the mean signal needs to be increasingly stronger than is required by a constant signal/noise ratio. It is as if $g_B$ increases with $B$, slowly at first but more rapidly as rod saturation is approached.

The present paper is largely concerned with methods of minimizing the effects of variation in the gain $g_B$. For this reason only small, brief duration signals will be discussed. If the testing signal is long and large the effects of quantum absorptions will tend to cancel each other out ('lateral inhibition loss', Barlow, 1957); at any rate $g_B$ (as defined here) increases very rapidly with $B$ for large tests, just as lateral inhibition is more prominent at high $B$ (e.g. Barlow, Fitzhugh & Kuffler, 1957).

## METHODS

The apparatus and calibrations have been described in other papers (Hallett, 1969*a*, *c*, *d*). The testing signal is of 12′ subtense and is centred on the 18 degree subtense background at 18 degrees eccentricity from the fovea in the nasal field of the left eye. The pass band of the test is centred at 530 nm and the test light enters at the nasal edge of the dilated pupil. The pass band of the background is at 635 nm and enters at the centre of the pupil. The duration of the test is 1·5 msec in nearly all experiments; in the experiments (●) in Fig. 1 the test was 15 msec in one third of the impulse background sessions, but otherwise 1·5 msec; the test was 15 msec in two thirds of the step background sessions (●) and 60 msec in the remainder. These changes in test duration were made so as to increase the available test energy but there is no reason to suppose that these changes make much difference to the time course of the threshold energy disturbance.

Figure 1 represents about 180 hr of observation ($6 \times 10^4$ exposures of the test) by three observers. The points on the impulse functions are the average of the results of the observers and are therefore each based on nine sessions or forty-five series of the method of constant stimuli. The points on the step functions are based on twice that number of series.

The errors in the thresholds are considered in the next paper but the standard error of the mean log threshold for $h$ sessions is about $0{\cdot}17k^{-0{\cdot}5}$ log. The error in the background scale is about 0·1 log.

## RESULTS

The time course of the threshold disturbance $q_Q(t)$ due to an impulse background of energy $Q$ may be measured as follows. The properly adapted observer fixates and when ready he triggers the apparatus, which delivers a large 1·5 msec background flash at time $t = 0$ and a small brief testing signal at some other time $t$. These stimuli are centred at a point 18 degrees nasal to the fixation point and so the retinal images are on the rod-rich area of temporal retina. The observer says 'yes' or 'no', as to whether he thinks the testing signal is visible or not and the result is recorded by the experimenter. The trial is then repeated at some new strength of the testing signal, which is sometimes zero, and after a considerable number of trials with full psychological precautions it is possible, using well known methods (Pirenne, Marriott & O'Doherty, 1957; Hallett, 1969*a*, *c*), to determine the mean log signal energy log $q_Q(t)$ which allows the signal to be detected, with a probability of 0·5 in a single trial, when the signal occurs at time $t$ relative to a background of energy $Q$. The time $t$ at which the signal occurs is then changed to some new value, the whole process repeated and eventually the form of the impulse function $q_Q(t)$ is satisfactorily sampled. The dimensions and spectral composition of the test and background are chosen to ensure the closest approach to linear system signal/noise expectations for isolated rod vision.

Impulse functions for small brief testing signals have been measured in various states of adaptation in ninety-one sessions on ten observers. The results of twenty-two sessions (four observers) have been included in the previous paper (Hallett, 1969*a*). This paper deals with sixty sessions (three observers) but the experimental parameters are varied less and the results are consequently more accurate. A small difficulty arises because the impulse functions are excessively high in twenty sessions (five observers) out of the total of ninety-one. This discrepancy is considered in the previous paper, is likely due to a different signal/noise criterion and does not affect the demonstration of the relation of the integration time of the eye $\tau$ to the impulse function (Hallett, 1969*a*). The experiments presented in this paper are not complicated in this way, indeed the three observers were afforded every opportunity of agreeing on a common criterion by consulting each other's records, etc., between experimental sessions, though naturally strict precautions were taken to ensure that the presence or absence of the test was judged only on legitimate visual information, even to the extent of denying the *experimenter* the use of the results of previous sessions as 'guide lines'. The method of constant stimuli was used, with randomization and blanks, and the variations in the threshold measurements are analysed in the next papers (Hallett, 1969*c*, *d*).

Figure 1 summarizes the average log thresholds of sixty experimental sessions on the three observers.

The filled symbols at the top of Fig. 1 indicate the way in which the log threshold of the hitherto dark-adapted eye is disturbed by an effectively impulse background of energy $Q$ delivered at $t = 0$. The 3 log threshold disturbances due to impulse backgrounds of 3 different energies show (i) a

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Legend to Fig. 1.

Fig. 1. The mean log thresholds for the three observers of this paper as a function of the time interval between the beginnings of the testing signal and the background.

*Top.* Impulse functions $q_Q(t)$ for various impulse backgrounds of energy $Q$. Filled symbols mean that the impulse background illuminates the hitherto dark-adapted eye: value of the impulse is $-2{\cdot}8$ (▲); $-1{\cdot}2$ (■); and 0·6 (●) log scotopic troland sec. Open symbols mean that the shutter is transparent (density 2·8) so that the eye is steadily illuminated before and after the delivery of the impulse background: impulse of $-1{\cdot}2$ log scotopic troland sec added to steady background of $-1{\cdot}2$ scotopic trolands (□), impulse of 0·6 log scotopic troland sec added to steady background of 0·6 scotopic trolands (○). The five curves have been displaced vertically by zero (▲), 0·5 (■), 1 (●), 3 □ and 3 (○) log units respectively for clarity. The lines correspond to the exponential time constant $\tau_2 = 0{\cdot}08$ sec.

*Bottom.* Threshold $q_{B,X}(t)$ for step backgrounds of various intensities $B$. At $t = 0$ the long duration (500 msec) square wave illuminates the hitherto dark-adapted eye. Thresholds for steady illumination (steady-state or *s.s.* thresholds) are also shown. Steps of $-2{\cdot}3$ (▲), $-1{\cdot}2$ (■), and 1·6 (●) log scotopic trolands.

The corresponding step functions calculated from the dark-adapted impulse response functions (▲, ■, ●) at top, via equation (4) with the upper limit changed to $t$ (see text), are shown as curves. The step function (●) cannot be reproduced by the present theory and better fits to the other step functions (▲, ■) could probably be obtained from somewhat smaller impulse functions than those actually used.

Rod isolation technique. Small brief testing signal viewed against large background. Conversions: to log quanta (507 nm) cornea sec$^{-1}$ deg$^{-2}$, add 5·65 to values in log scotopic trolands; to log quanta absorbed per rod, add 0·55 to values in log scotopic troland sec.

rising portion for testing signals delivered prior to the background, the slope of which increases with the height of the response; (ii) a fairly tight peak at $t = 0$, and (iii) a declining portion of more or less constant slope.

The open symbols at the top of Fig. 1 indicate how the threshold of the hitherto *light-adapted* eye is disturbed by an impulse background of

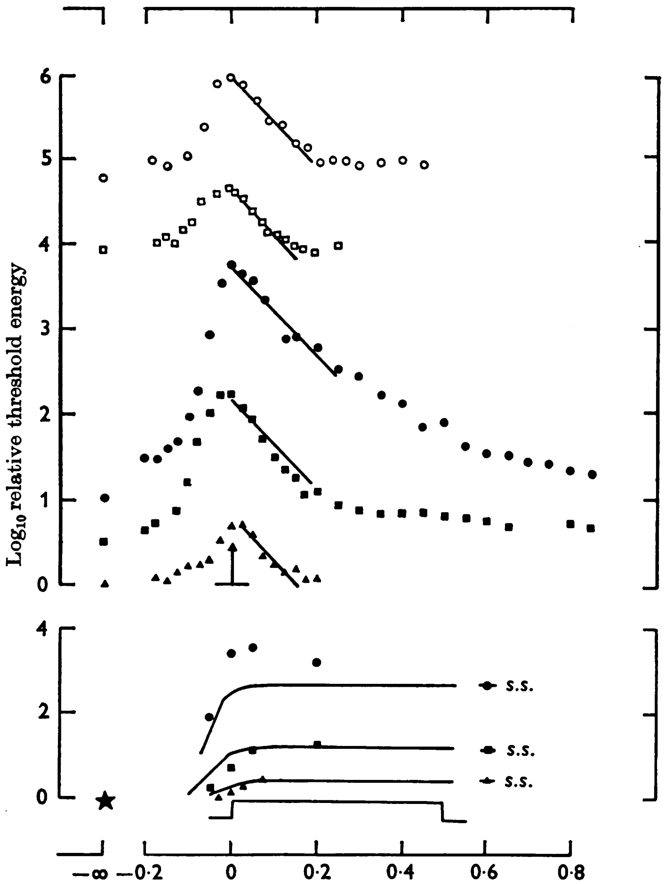


Fig. 1. For legend see opposite page.

energy $Q$ delivered at $t = 0$. These experiments (○, □) were for exactly the same impulse background intensities as used in the corresponding dark-adapted experiments (●, ■), with the important difference that the shutter was partially transparent (density 2·8). The peak thresholds, relative to the absolute threshold, are much the same as in the corresponding dark-adapted experiments, as is the slope of the recovery phase at $t > 0$, but the slope of the ascending phase at $t < 0$ is less than in the dark-adapted case (●, ■). The experimental conditions have been chosen so that the peak thresholds of the light-adapted responses (○, □), relative to the light-adapted base line, are much the same as the small amplitude dark-adapted response (▲). It is easy to see that the shapes of all three responses (○, □, ▲) are nearly the same.

The lower part of Fig. 2 shows a few well-measured points on the response to a 500 msec square wave background which is exposed to the dark-adapted eye at $t = 0$. In agreement with the findings of the previous paper the log response to an on-step is not complete at $t = 0$ but approaches the steady-state (*s.s.*) value quickly in a damped fashion for weak or moderate inputs. The slope of the log response increases with input, and a marked overshoot with a peak close to $t = 0$ to $+50$ msec is observed for large inputs. In this latter case the threshold does not settle to the steady-state value until later than $t = 0{\cdot}2$ sec.

## *Theory*

Suppose that the impulse function $y(t)$ of the visual pathways is both measurable and deterministic (it might be analogous to the response of the automatic gain control of Fuortes & Hodgkin, 1964) and that the response to a recent background at time zero is being examined at some time $t_{\text{out}}$ (Fig. 2*a*). There is no way of knowing whether the observed magnitude of the response is the consequence of quanta absorbed from the background alone or whether it is due to the combined action of quanta from both the background and a testing signal. All that can be done is to set limits on the response due to a background alone and to declare with limited confidence that the testing signal is present when these limits are

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Legend to fig. 2.

Fig. 2. Flow diagram of the real system.

The first block shows a threshold testing impulse of mean energy $q_Q(t)$ and a background impulse of mean energy $Q$. The second block shows the response to $Q$. The response to the testing signal is not shown but can be considered to be dissipated about the time $t_{\text{out}}$. The third block is the signal recognition process which may take various forms according to what aspect of performance is being optimized, e.g. a statistician might consider the confidence limits to the integral of the whole response if it were important to detect the signal at the expense of knowing its time of occurrence, but might attach confidence limits to each point on the response if he wished to know the timing of the signal. The fourth block is the only accessible output, the observer's decision.

(*b*) Flow diagram of the analogue used in this paper.

The most important simplification is that the threshold of a signal at time $t$ is assumed to be dependent upon the filter response at the *same* time $t$. As a result the filter impulse function $h_Q(t)$ has necessarily the same characteristics as the observed signal/background relation $q_Q(t)$, e.g. a section at $t < 0$, etc.

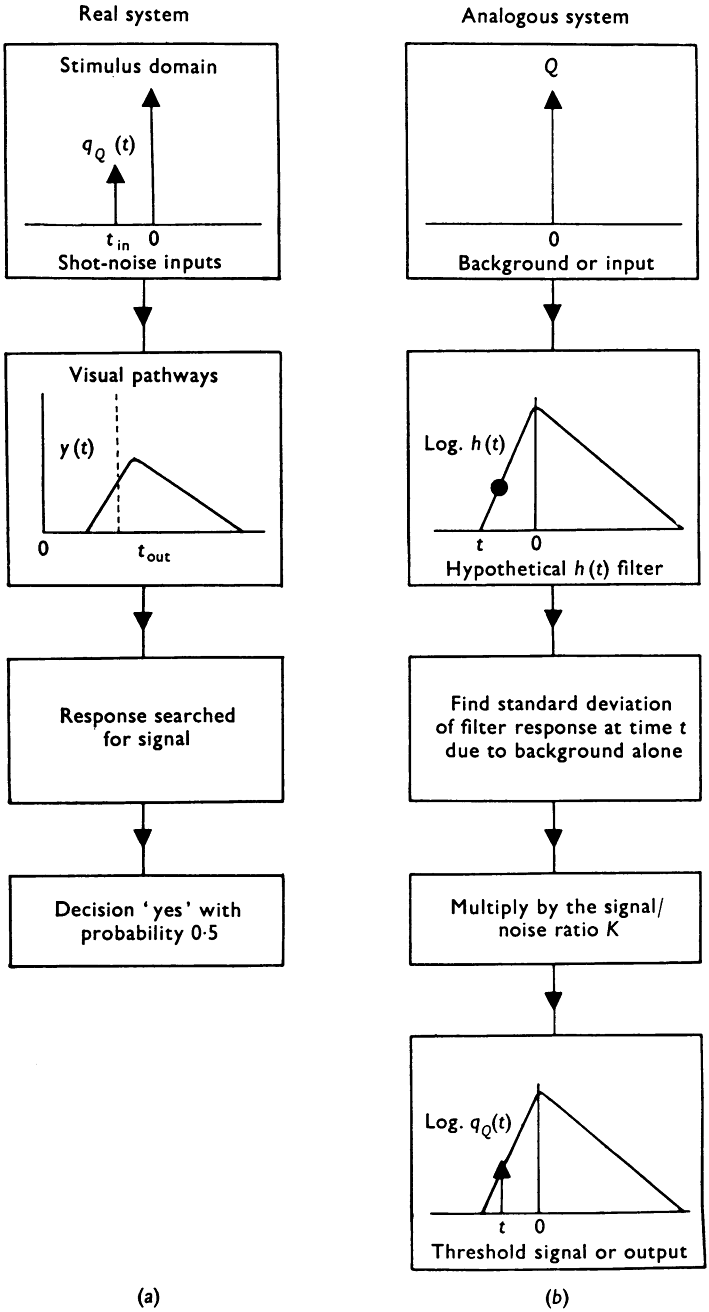


Fig. 2. For legend see opposite page.

exceeded. Clearly the standard deviation at $t_{out}$ of the response to the back ground (or some similar statistic) determines the threshold strength of the testing signal. Now the testing signal will be most obvious when its peak effect occurs at $t_{out}$, which will only be the case if the test occurs at some appropriate time $t_{in}$; this may be either before or after the background impulse according to how long the peak effect of the test is delayed. In principle, then, it is possible, given *both* the impulse function $y(t)$ of the visual pathways *and* the rules of the process by which the testing signal is detected, to find the signal/background relation for the filter—the relation between the strength of the background impulse and the timing and threshold strength of the impulse testing signal—and so on for other background wave forms.

The data of Fig. 1, however, present the reverse problem and unfortunately it is scarcely possible to find $y(t)$ from the relationship between the test and background stimuli without knowing something about the visual pathways in the first place, viz. the details of the process by which the effects of the signal are distinguished from the effects of the background. The easiest thing is to set up an analogous system, as in Fig. 2*b*, and to test the usefulness of this analogy. One imagines a linear filter which produces a response to the various shot-noise inputs (real backgrounds and dark light of the eye). The variance of this response at time $t$ is determined by the impulse function $h(t)$ of the filter. This variance, together with the observer's signal/noise criterion, $K$, determines the strength of a just threshold signal delivered at time $t$. As will be apparent later the impulse function $h(t)$ proves very useful because one is able to obtain from real impulse functions, such as those of Fig. 1, independent measures of quantities which hitherto have been used to describe the threshold for a small brief test on a *steady* background.

Let

$t$ sec denote the time of arrival of the small brief duration testing signal relative to the beginning of the large background flash at time zero, then $t < 0$ means that the signal precedes the beginning of the background and $t > 0$ that it follows,

*threshold energy* be the mean energy of a signal which can be detected in a single presentation with probability 0·5,

$X$ be the dark light of the eye in quanta (507 nm) at the cornea per deg$^2$ per sec,

$B$ be the intensity of a steady or step background in the same units as $X$,

$Q$ be the energy of an impulse background in quanta (507 nm) at the cornea per deg$^2$,

$q_X(s.s.)$ be the absolute threshold energy of the signal when the eye is fully dark-adapted and no real backgrounds are present in quanta (507 nm) at the cornea,

$q_{B+X}(s.s.)$ be the threshold energy of the signal determined by the additive effects of a real steady background and the dark light in the same units as $q_X(s.s.)$

$q_{B,X}(t)$ be the threshold energy necessary at time $t$ due to the additive effects of an on-step background and the dark light in the same units as $q_X(s.s.)$,

$q_{Q,X}(t)$ be the time course of the threshold energy disturbance produced by illumination of the fully dark-adapted eye by an impulse background of value $Q$, in the same units as $q_X(s.s.)$,

$q_{Q,B+X}(t)$ be the threshold energy required when an impulse background of energy $Q$ is added to a steady background of intensity $B$,

$h(t)$ be the unit impulse function in the time scale $t$ of the filter in Fig. 2*b*,

$K$ be the observer's signal/noise criterion,

$g_B\ g_Q$ be the gains of the signal/background system (*v.i.*),

$\tau$ be the classical integration time of the eye,

$\tau_1, \tau_2$ be time constants,

then, if linear signal/noise theory is true, and since the variance of the filter response is given by the convolution of the time course of the Poisson parameter ($X$, $B$ or $Q$) with $h^2(t)$, we have

$$q_X(s.s.) = K\left(X\int_{-\infty}^{+\infty} h^2(t)\,\mathrm{d}t\right)^{0\cdot5}, \tag{1}$$

$$q_{B+X}(s.s.) = K\left(X\int_{-\infty}^{+\infty} h^2(t)\,\mathrm{d}t + B\int_{-\infty}^{+\infty} h^2(t)\,\mathrm{d}t\right)^{0\cdot5}, \tag{2}$$

$$q_{Q,X}(t) = K\left(X\int_{-\infty}^{+\infty} h^2(t)\,\mathrm{d}t + Qh^2(t)\right)^{0\cdot5}, \tag{3}$$

where all these statements express the mean strength of the signal which significantly exceeds the standard deviation of the response of the filter to the total input.

*Practical methods for evaluating thresholds.* Clearly if the above linear system signal/noise theory works then, using equations (1)–(3), it is easy to obtain $Kh(t)$ or to set up equations in which the threshold for a small brief test on a steady background (the steady-state threshold $q_{B+X}(s.s.)$) is predicted from measured impulse function data $q_{Q,X}(t)$. Equations (4) and (8) *of the previous paper* were obtained in this way. From (1) to (3) above,

$$\frac{q_{B+X}(s.s.)}{q_X(s.s.)} = \left\{\frac{B}{Q}\int_{-\infty}^{+\infty}\left(\frac{q^2{}_{Q,X}(t)}{q^2{}_Q(t)}-1\right)\,dt+1\right\}^{0\cdot5}$$

$$= \left\{\int_{-0\cdot2}^{+0\cdot8}\frac{q^2_{Q,X}(t)}{q^2_X(s.s\,)}\,dt\right\}^{0\cdot5} \text{evaluated at } Q \text{ numerically equal to } B. \quad (4)$$

The middle term of (4) shows how the threshold elevating effects of the dark light are eliminated from the observed impulse function $q_Q(t)$ and then re-incorporated after calculating the variance due to the real background $B$ alone. The final statement of (4) follows because the unit of time is the second, and the limits are then broad enough to incorporate the complete threshold disturbance. Similarly, it is possible to calculate the threshold disturbance caused by an on-step, $q_{B,\,X}(t)$—the latter is given by the same form as (2) but the integral in (2), expressing the contribution of the step $B$ to the variance, extends only to the upper limit $t$, and after rearrangement one obtains the same form as the middle term of (4) but with the upper limit set at $t$.

*Comparison with Barlow's* (1957) *formulation.* It should be noted that equations (1)–(3) are consistent with the spirit of Barlow's analysis and differ only in the use of functions of the unit impulse function $h(t)$ to replace $\tau$, the classical integration time of the eye, and two other constants ($F$, $\alpha$) used by Barlow. It will prove convenient to define the absolute steady state gain $g_B$ and the absolute peak gain for an impulse $g_Q$ by

$$g_B = \left(\frac{q^2_{B+X}(s.s.)-q^2_X(s.s.)}{B}\right)^{0\cdot5} = K\left(\int_{-\infty}^{+\infty} h^2(t)\,dt\right)^{0\cdot5}$$

$$= \left\{Q^{-1}\int_{-\infty}^{+\infty}(q^2_{Q,X}(t)-q^2_X(s.s.))\,dt\right\}^{0\cdot5}, \quad (5)$$

$$g_Q = \left(\frac{q^2_{Q,X}(t=0)-q^2_X(s.s.)}{Q}\right)^{0\cdot5} = Kh(0) \quad (6)$$

where the first and second terms in (5) and (6) define the absolute gains and the other terms follow from (1) to (3) above and are only true if the system is unaffected by illumination. The terms $q^2_X(s.s.)$ in (5) and (6) are used to eliminate the (usually trivial) threshold elevation due to the dark light. If these definitions of absolute gain are applied to Barlow's model it is easy to show that the steady-state gain $g_B = K(\alpha\tau/F)^{0\cdot5}$, which is Barlow's 'lumped constant', and that, by a small extension of the argument, the peak gain is $g_Q = g_B\tau^{-0\cdot5}$. The relations between the gains $g_B$ and $g_Q$ can be summarized for both the present theory and that of Barlow by

$$\frac{g_B}{g_Q} = \frac{\left(\int_{-\infty}^{+\infty} h^2(t)\,dt\right)^{0\cdot5}}{h(0)} = \tau^{0\cdot5}. \quad (7)$$

Now the limitation of Barlow's approach is that although the steady-state gain, $g_B = K(\alpha\tau/F)^{0\cdot5}$, can be fitted to the increment threshold data it cannot be independently evaluated with any accuracy from the individual constants: in principle $K$, the signal/noise ratio, can be evaluated from the false positive rate but this is low and hard to measure and not compatible with the dark light of the eye $X$ (Hallett, 1969*d*); $\alpha$, the integration area, is not easy to measure exactly by varying the size of the test flash (Barlow, 1958; Hallett, Marriott & Rodger, 1962), although its magnitude is confirmed by very difficult measurements on rod visual acuity (Hallett, 1962) and by experiments on rod dark-adaptation (Rushton & Westheimer, 1962); $\tau$, the integration time, is perhaps the most accurately known of all the constants, *ca.* 0·1 sec; $F$, the fraction of corneal quanta (507 nm) which are effective for vision, is on a simple view given nicely by Rushton's (1956) ophthalmoscopic measurements of the density of rhodopsin in the living rods ($F$ = 0·1–0·15) but on more complicated views might range from 0·05 to 0·15 (Barlow, 1962; Hallett, 1969*d*). These various uncertainties accumulate so that the uncertainty in Barlow's lumped constant is of the order of $\pm$ 0·4 log.

The advantage of the present approach is that, *provided* the signal/noise criterion is the same when the observer views steady or transient backgrounds, the steady-state gain $g_B$ can be evaluated from impulse function data, using the third or fourth terms of (5), and this prediction checked against $g_B$ from steady-state experiments, evaluated from the second term of (5). In fact $g_B$ calculated in this way is not constant (the value obtained from $q_{Q,X}(t)$ varies with $Q$ in much the same way that the value obtained from $q_{B+X}(s.s.)$ varies with $B$), a fact which can be exploited in such a way that high steady-state rod thresholds can be predicted from impulse functions of the *dark-adapted* eye. Furthermore, the dark light of the eye $X$ can be evaluated from impulse functions, since $q_X(s.s.) = g_B X^{0\cdot5}$, and so can $\tau$ via equation (7).

## *Analysis and predictions*

*Impulse functions for the dark-adapted eye.* The exact shape of the threshold disturbance $q_{Q,X}(t)$ caused by an impulse background $Q$ is hard to measure. Experiments are conducted on logarithmic scales and there are considerable variations in the log measurements which cannot always be eliminated even when the results of 50 hr of observation at one value of $Q$ are pooled. Generally speaking for $t < 0$ the responses $q_{Q,X}(t)$ in Fig. 1 are satisfactorily approximated by simple exponential growth and for $t > 0$ by simple exponential recovery. There is no single impulse function $h(t)$ but rather a separate $h_Q(t)$ for each $Q$ of the *approximate* form,

$$Kh_Q(t) = \left(\frac{q^2_{Q,X}(t) - q^2_X(s.s.)}{Q}\right)^{0\cdot5} = g_Q \exp\{-\text{mod}\, t/\tau_t\}, \qquad (8),$$

where

$\tau_t(t < 0) = \tau_1$, which varies from 0·02 to 0·05 sec in Fig. 1 according to the input $Q$ and the initial conditions $q_X(s.s.)$ or $q_{B+X}(s.s.)$,

$\tau_t(t > 0) = \tau_2$ is about 0·08 sec (Fig. 1),

and $g_Q$ varies rather slowly with $Q$ as shown in Fig. 3.

From this it is clear that the speed of growth increases with the input but that the speed of recovery is independent of the input. The constants for the time course can be estimated either from the slopes of $\log q_Q(t)$ or from integrals of $q_Q(t)$.

Expression (8) is the simplest approximation which is satisfactory for the present purposes. Particularly artificial is the dissociation of the function into two parts with an abrupt transition at $t = 0$. It is simply convenient to represent $\log q_Q(t)$ by a straight line rising from the base line at $t = ca.\ -0·12$ sec to the peak at $t = 0$ and thereafter by a descending straight line, small corrections being made for the joint effects of the dark light and the impulse background when the threshold is within 0·3 log of the base line. In actual fact the impulse functions of Fig. 1 are only sampled in 0·025 sec steps and for this reason it is not impossible that the ascending section of $\log q_Q(t)$ is slightly sigmoid and that the peak region

$$-0{\cdot}025 < t < +0{\cdot}025$$

is rounded or even fairly flat.

Expression (8) conveys the important information that the response peaks at $t = 0$, i.e. for testing signals synchronous with the impulse background, and that a significant threshold raising effect stretches in both directions along the time scale $t$ for about the classical integration time, $\tau = 0·1$ sec, of the dark-adapted eye, which should cause no surprise in view of the proven value of the integration time concept and the frequency with which variations on the experiments of Crawford (1947) on the pseudo-retroactive effects of light have been repeated over the years (Baker, 1963; Sperling, 1965). Some of these points have been discussed in the previous paper. The explanation for the apparent defiance of causality at $t < 0$ is, of course, that the responses of the nervous system are delayed so that the effects of signal and background actually interact at $t > 0$ even though the signal may precede the background impulse by *ca.* $\tau$ sec. Similar effects can be produced in *Limulus* etc. (Ratliff, Hartline & Miller, 1963).

*Steady-state responses from* $q_{Q,X}(t)$. It is not possible to predict the system steady-state gain $g_B$ with complete rigour because, as Fig. 3 shows, the value of $g_B$, whether obtained directly from steady-state backgrounds $B$ or from impulse functions due to backgrounds of energy $Q$, increases very slowly with $B$ or $Q$. The rate of change of $g_B$ with input magnitude is slow because the use of a small brief duration signal ensures that this is the case, and provided one uses data for a reasonably weak impulse background $Q$ to evaluate $g_B$ for a reasonably weak steady background $B$ and so on for stronger inputs, there is no problem in making accurate predictions (e.g.

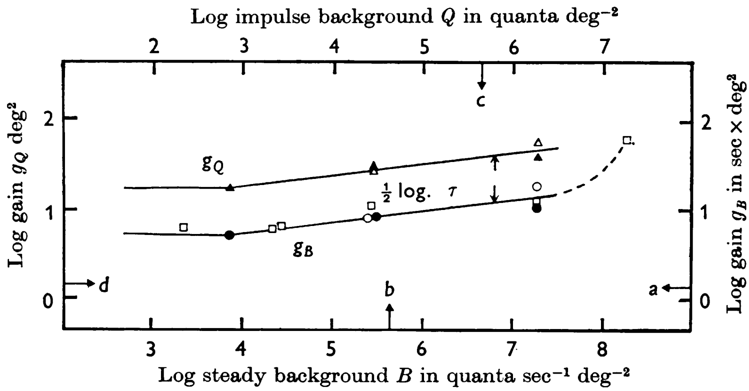


Fig. 3. Log gains versus log input.

Top and left scales. The peak gain due to an impulse background relates the peak of $q_Q(t)$ to $Q^{0\cdot5}$: calculated from the impulse functions of the dark-adapted eye (▲; equation (6)) and of the light-adapted eye (△; equation (6) with $q_{B+X}(s.s.)$ substituted for $q_X(s.s.)$). The smallest measured value of $g_Q$ is *ca.* 16 deg$^2$ but otherwise $g_Q$ is nearly $16 \times (Q/700)^{0\cdot1}$ deg$^2$ over a considerable range of $Q$.

Top and right scales. The steady gain $g_B$ may be calculated from impulse functions due to backgrounds of energy $Q$: from dark-adapted (●; equation (5)) and from light-adapted impulse functions (○); equation (5) with $q_{B+X}(s.s.)$ substituted for $q_X(s.s.)$). The curves $g_B$ and $g_Q$ are separated by about 0·55 log, which is consistent with an integration time of *ca.* 0·08 sec. The smallest calculated value of $g_B$ is about 4·5 sec deg$^2$.

Bottom and right scales. The observed steady-state gain $g_B$, (□; equation (5)). The values match quite well those calculated from impulse functions (●, ○), particularly if the top and bottom scales are related as shown. The dark light of the eye and the absolute threshold yield a $g_B$ of about 4·5 sec deg$^2$.

Conversions: the arrows $b$ and $c$ indicate 1 scotopic troland and 1 scotopic troland sec respectively. The arrows $a$ and $d$ show relative gains of 10 absolute threshold units per scotopic troland (or per scotopic troland sec) respectively.

TABLE 1. Steady-state thresholds predicted from dark-adapted impulse functions

| Steady background $B$ (log scotopic trolands) | Impulse background $Q$ (log scotopic troland sec) | | Observer D.B. | Observer B.S. | Observer M.G. |
|---|---|---|---|---|---|
| 1·6 | 0·6 | Observed | 2·76 | 2·76 | 2·65 |
| | | Expected | 2·73 | 2·64 | 2·86 |
| −0·2 | −1·2 | Observed | 1·77 | 1·74 | 1·95 |
| | | Expected | 1·64 | 1·62 | 1·82 |
| −1·2 | −1·2 | Observed | 1·14 | 1·12 | 1·38 |
| | | Expected | 1·14 | 0·98 | 1·33 |
| −1·3 | −2·8 | Observed | 0·93 | 0·92 | 1·18 |
| | | Expected | 0·91 | 0·95 | 1·15 |
| −2·3 | −2·8 | Observed | 0·41 | 0·43 | 0·62 |
| | | Expected | 0·39 | 0·43 | 0·63 |

The thresholds are log elevations above the absolute threshold. Calculated from the data of Fig. 1 using equation (4). The average error (observed − expected) over the fifteen pairs of entries in this table is +0·03 log.

Table 1), at least for steady backgrounds of up to $B$ equivalent to 40 scotopic trolands ($10^{2.15}$ quanta absorbed per rod per second). If predictions at such high intensities present no very great problems, despite the variation of $g_B$, then it should be easy to determine the dark light of the eye, $X$, since $q_X(s.s.) = g_B(\min) X^{0.5}$. It is assumed that $g_B$ is constant and minimal for the weakest inputs, and the value estimated from the smallest amplitude impulse function in Fig. 1 (▲; 4·5 sec deg²) gives a dark light of $10^{-3}$ scotopic trolands ($10^{-2.5}$ quanta absorbed per rod per second) which is exactly that measured in the steady-state experiments on the present observers, using the technique of Barlow (1957).

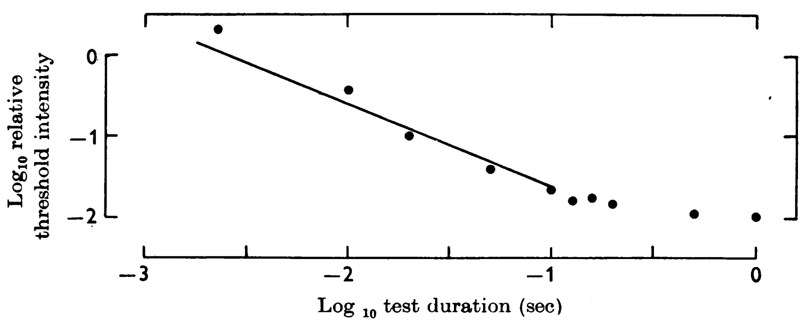


Fig 4. Threshold intensity as a function of the duration of the small test signal. Fully dark-adapted eye. Complete temporal integration extends to about 0·1 sec, as shown by the line of slope −1.

Figure 3 is drawn in such a way as to suggest that the steady-state threshold due to a steady background of intensity $B$ is best calculated from an impulse function of energy $Q$ numerically equal to $0{\cdot}1B$, if the unit of time is the second. This is a very small point in practice, as Table 1 shows, but this, and the separation of the gain curves $g_B$ and $g_Q$ in Fig. 3, is in keeping with an overall integration time of *ca.* 0·1 sec.

*Integration time* $\tau$ *from* $q_{Q,X}(t)$. Figure 4 shows a classical integration time experiment for the three observers of this paper. $\tau$ is given by the longest duration test flash for which the absolute threshold energy is still minimal. The data are typical of what is available elsewhere (Barlow, 1958; Baumgardt, 1961) but do show that $\tau$ is undoubtedly about 0·1 sec for the *present* observers.

Now an alternative method of obtaining $\tau$ is from the evaluation of equation (7), using only impulse function data for the same three observers. Figure 3 shows log plots of the gain $g_Q$ and $g_B$, the latter obtained by numerical integration of impulse functions. The separation of the gain plots is consistent with a value for $\tau$ of about 0·08 sec. It does seem, then, that the estimates of $\tau$ obtained from impulse function data, using the present linear approach, are about the same as those obtained from the classical integration time experiment at the absolute threshold of vision.

Neither the classical nor the impulse function method of determining $\tau$ is very precise because each depends upon the measurement of small threshold changes, which is very difficult. The above estimate was derived from numerical integration of the observed impulse function data. Alternatively, one may try exact integration of the approximation (8). The integral of the square of $\exp\{-\mathrm{mod}\, t/\tau_i\}$ over the limits $-\infty \leqslant t \leqslant +\infty$ is $\frac{1}{2}(\tau_1+\tau_2)$ sec and it is this function of the exponential time constants which should correspond to the classical integration time $\tau$. Now, as stated earlier, $\tau_1$ varies in Fig. 1 from 0·02 to 0·04 sec and $\tau_2$ is 0·08 sec, so the integral is 0·05–0·065 sec. This is a little low for $\tau$ but it must be remembered that the form of the impulse function between $t = \pm 0{\cdot}025$ sec is not established; if the peak of the function were flatter than indicated by (8) the integral would be increased by as much as 0·05 sec. In brief, however one approaches the data it does seem that impulse functions are closely related to the classical concept of the integration time of the eye.

*Step responses.* The responses to on-steps of moderate intensity are not complete by $t = 0$, as is appropriate if the response is given by some sort of convolution of the input with an impulse function similar to expression (8). Only a few responses to off-steps have been measured (Hallett, 1969*a*), but if linear threshold scales were used some of these would look like the opposite to the on-step. Large on-steps lead to marked overshoot of the threshold disturbance at $t = 0$ but the threshold eventually settles to predictable values. This suggests that the gain can be excessively high at 'on'. The other possibility, that the impulse function $h(t)$ at high inputs develops a late undershoot, is impossible according to the present approach since both $+h(t)$ and $-h(t)$ increase the threshold by increasing the variance of the filter response according to $h^2(t) = [-h(t)]^2$. In addition large impulse responses (e.g. Fig. 1, ●) of the dark-adapted eye do not display undershoot, nor is this possible on the present model for the reason just given.

So far as the linear threshold disturbance $q_{B,\,X}(t)$ due to moderate on-steps is concerned the response should be given by (2) with the upper limit of the second integral changed to $t$ as mentioned earlier. On inserting (8) into (2) it will be noted for moderately large threshold elevations, when the effects of the dark light of the eye $X$ can be omitted from the calculations, that $\log q_B$ $(t < 0)$ is proportional to $t/\tau_1$. This immediately raises the problem as to what is $\tau_1$ for an on-step of $B$. No answer is offered but so far as the available data go it seems likely that the slope of the log on-response increases with the height of the response in much the same way as the slope of the rising part of the log impulse function increases with the height of the response. Figure 1 shows step responses calculated from the numerical integration of $q_Q(t)$ data (middle term of equation (4) with the upper limit changed to $t$). The calculated responses are slightly high because the step-width $\Delta t$ of numerical integration is quite large, being that used to sample the impulse function ($\Delta t$ = 25 msec). These responses are also somewhat spurious because no change in $\tau_1$ is permitted but they are a great deal better than the results of more arbitrary approaches than the present theory.

In summary it looks as if step responses should be calculable from $Kh(t)$ of (8) but the problems presented by the non-linear part of (8) (the $\tau_1$ section for $t < 0$) are such that it is difficult to show that this is so.

*Successive impulses.* In principle one of the easiest ways of finding a method of linearizing the signal/background system and allowing for the changes in $\tau_1$ would be to study the way in which two successive equally bright impulse backgrounds combine their threshold raising effects. If the threshold $t_1$ sec *after* the first impulse alone is $q$ absolute threshold units and if it is also $q$ at $t_2$ sec *before* the second impulse alone then if the two impulse backgrounds occur at $t = 0$ and $t = t_1 + t_2$ respectively, the threshold due to combined effects at $t_1$ should be $(2q^2 - 1)^{0 \cdot 5}$ absolute threshold units if linear signal/noise theory applies and $\tau_1$ does not change. Unfortunately the log threshold change is very small and hard to measure and preliminary experiments are not exact enough to reveal anything about the changes in $\tau_1$.

*Successive subthreshold impulses.* Similarly, it should be possible to obtain a linear impulse function by studying the effect of a subthreshold test flash of fixed energy and timing on the threshold of a second test flash. Unfortunately the maximum threshold change is only about 0·2 log and the experimental labour necessarily very large.

In summary linear treatment of the impulse functions of the dark-adapted eye yields independent measures of quantities that have been previously used to describe steady-state signal/background data. Since the observer's sensations are more complicated when the background illumination is transient, and his observations more difficult to make, it is really rather remarkable that impulse and steady-state data should be so clearly related in terms of the dark light of the eye, the effective integration time and the gain changes (or deviations from a constant signal/noise ratio) that occur on progressive light adaptation. Whether or not further information can be extracted from impulse functions which will allow the dynamics of threshold disturbances to all input wave forms to be specified is not at all clear.

*Analysis of light-adapted responses.* If the impulse function of the fully dark-adapted eye $q_{Q,X}(t)$ supplies *all* the information needed for the calculation of steady-state thresholds of the light-adapted eye it should scarcely matter if the impulse response functions $q_{Q,\,B+X}(t)$ are measured when the eye is light-adapted by a steady background $B$. This is probably true, at least for adapting backgrounds of up to 2 scotopic trolands.

Comparison of the light-adapted impulse functions of Fig. 1 (○, □) with the dark-adapted responses (●, ■) suggests that for a given $Q$ light

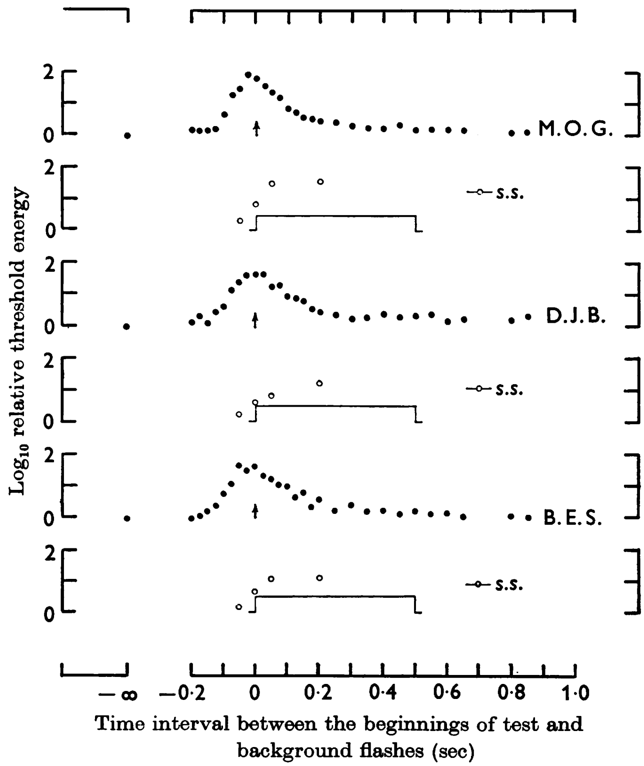


Fig. 5. Responses of the dark-adapted eye to impulse and square wave background illumination. Individual results for the three observers. The average result is given in Fig. 1 (■). 1·5 msec 12 min subtense testing signal. Impulse background: 1·5 msec and −1·2 log scotopic troland sec. Square wave: 500 msec at −1·2 log scotopic trolands. *s.s.* is steady background at −1·2 log scotopic trolands. The threshold disturbances are remarkably similar, although fine comparison reveals plausible differences. Rod isolation technique.

adaptation yields a progressively larger exponential time constant $\tau_1$. As expected integration of the squared impulse function yields a slightly larger estimate of $\tau$ in the light-adapted case but the observed increase is only of the order of 0·01 sec which is of no consequence compared to the possible (but unmeasured) changes in the relatively unexplored peak region of the impulse function ($-0{\cdot}025 < t < +0{\cdot}025$ sec). These small changes

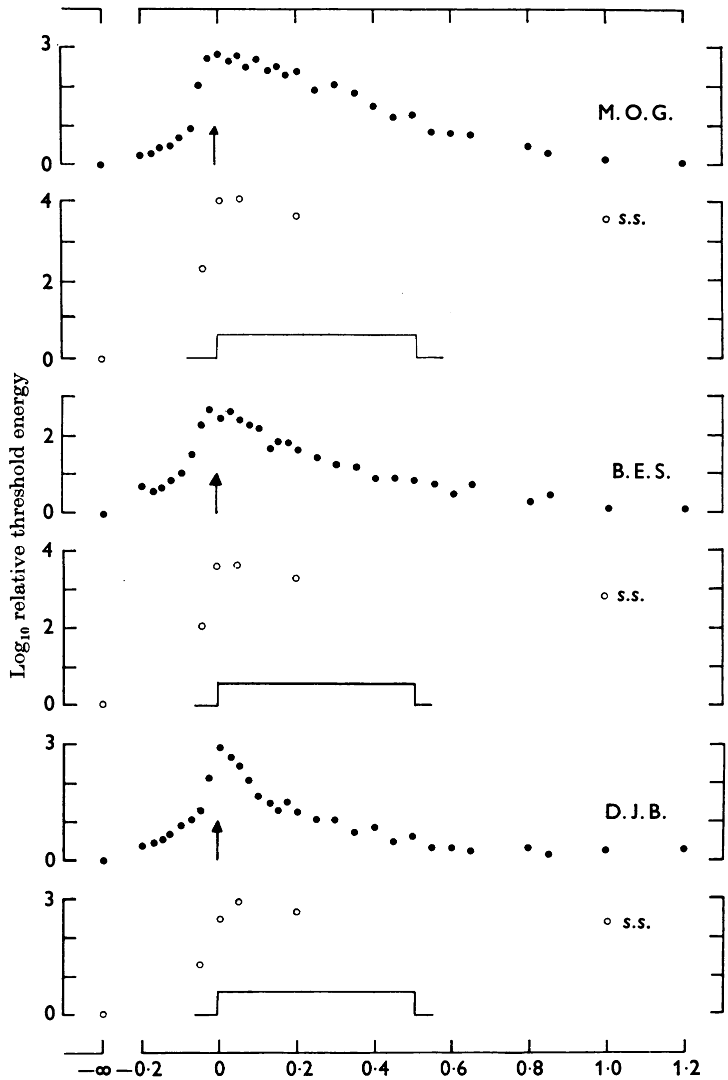


Fig. 6. Responses of the dark-adapted eye to impulse and square wave background illumination. Individual results for the three observers. The average result is given in Fig. 1 (●). Impulse background: 1·5 msec and 0·6 log scotopic troland sec. Square wave: 500 msec at 1·6 log scotopic trolands; *s.s.* steady background of 1·6 log scotopic trolands. Impulse experiments, testing signal of duration 1·5, 15 and 1·5 msec respectively from top to bottom. Step experiments, testing signal of 15, 60 and 15 msec duration, respectively, from top to bottom. These changes in the test are not thought to make much difference to the shape of the log. test energy disturbance. Clearly there are very real individual differences between the impulse and step functions of the observers for large inputs. Rod isolation technique.

are best ignored and it does seem not unfair to say that $\tau$, whether from dark *or* light-adapted impulse functions, is sensibly close to 0·08 sec ($\pm$ 0·1 log). There is probably no serious disagreement with what Barlow (1958) found when measuring the integration time of a testing signal for various degrees of light-adaptation. The integration time was *reduced* by light-adaptation but this was a small change in terms of the usual log. scale of the experiments and one which was difficult to measure precisely.

Figure 3 shows $g_B$ estimated from the two light-adapted impulse functions of Fig. 1, via equation (5) with the substitution of $q^2_{B+X}(s.s.)$ for $q^2_X(s.s.)$ in order to eliminate the threshold raising effects of both $B$ and $X$. The results are probably consistent with the dark-adapted estimates of $g_B$; this is because the absolute peak height of the impulse function $q_Q(t)$ (in quanta at the cornea) is more or less unaffected by the presence or absence of the background, so $g_B = g_Q(\frac{1}{2}\tau_1 + \frac{1}{2}\tau_2)^{0\cdot5}$ is necessarily much the same as in the dark-adapted experiments, since the right hand terms are much the same.

In summary, although light-adaptation has some effect on the exponential growth of $Kh(t)$, it makes little difference to the estimation of $g_B$, $\tau$ and $X$ from the impulse functions $q_Q(t)$.

*Variations between observers.* Figure 5 and 6 show that even if the form (8) is adequate for the averaged data of the three observers then at least the constants vary with the observer.

## DISCUSSION

### *Gain*

The introduction of the gains $g_B$ and $g_Q$ scarcely needs apology, since the aim of research subsequent to the work of Hecht, Shlaer & Pirenne (1942) is to discover the ways in which a human observer differs from an ideal noise limited detector of constant fallibility, and the present paper does this to the extent of specifying something about the observer's inertial characteristics. The present data on impulse and steady backgrounds can be summarized by four parameters and a describing function similar to (8): one parameter specifies the system gain ($g_Q$), another ($q_X(s.s.)$ or $X$, etc.), which is needed to specify the initial conditions, and the third and fourth (e.g. $\tau_1$ and $\tau_2$) are time constants of dynamic response which are closely related to the classical integration time $\tau$ of the eye. Unfortunately these parameters are not quite constant, despite having chosen the experimental conditions with this in mind, but the variations are sufficiently small for a satisfactory analysis to be possible.

The units of $g_B$ and $g_Q$ are given in seconds and square degrees since this seems simplest, bearing in mind that the units of standard deviations and means are the same. The appearance of the spatial dimension in these units reminds one that the effects of quantum absorptions are dissipated in both time and *space* but the present experimental design is intended to avoid the spatial aspects as much as possible since their proper study represents a considerable increase in the labour of the experiments and the analysis.

*Dark- and light-adaptation*

These terms are used in this paper to denote the condition of the eye before the arrival of an impulse background. In the one case the eye is fully dark-adapted, or can be assumed to be (since the total log threshold disturbance only lasts 1 sec at most and the backgrounds occur only every 5–6 sec) and in the other case the eye continually views a steady adapting background. Now, sufficiently bright backgrounds will bleach an appreciable amount of the rhodopsin. As is well known, largely as a result of extensive investigations by Rushton (e.g. Rushton, 1965*a*, *b*) on rhodopsin and the dark light, bleached rhodopsin has a potent effect on the log threshold, it is as if the dark light of the eye is added to the feed-back of the Fuortes–Hodgkin filter, and both log threshold and rhodopsin recover with an exponential time constant of 6 min. Two impulse functions in Fig. 1 (●, ■) do show evidence of slow processes at $t > 0{\cdot}2$–$0{\cdot}4$ sec but otherwise the impulse functions $q_Q(t)$ and the form (8) for $Kk_Q(t)$ are processes very much faster than the regeneration of rhodopsin. In any case the brightest impulse backgrounds (*ca.* 10 quanta absorbed per rod) bleach only about $10^{-7}$ of the rhodopsin.

So far as the dark light is concerned Rushton's work suggests that the present corrections, which follow Barlow (1957) and are traceable to Fechner, are not the best but are good enough. The dark light is treated here as if it is at the input rather than at the output of a filter.

*How useful is the $h(t)$ filter?*

The present linear analysis has been applied to the results of ninety-one experimental sessions on ten observers. In all of the sessions it has been possible to demonstrate that integrals of the squares of the impulse functions $q_Q(t)$, relative to the peak $q_Q(0)$, give a value which is approximately $\tau$, the classical integration time of the dark-adapted eye. It must be noted, however, that the present approach lumps together $K$, the signal/noise criterion, and $h(t)$, the filter impulse function. There is no particular reason why $K$ should be the same in different types of experiments and if it is consistently different this will affect the values of $g_Q$, $g_B$ and $X$ obtained from impulse functions, $q_Q(t)$. Proper prediction of $g_B$ (and thus $X$) has proved possible in seventy-one of the ninety-one sessions (six observers). Seventeen of the twenty failures (four observers) have been considered in the previous paper. It does seem quite likely that some observers on some occasions find the observations extremely difficult. They behave as if $K$ is much greater in the impulse experiments than for steady backgrounds. $K$, or something like it, varies for the data in the present paper (Hallett, 1969*c*) but fortunately no consistent effect remains after averaging. On a very simple view $K$ is related to the false positive rate but this does not seem to be the case for the present three observers (Hallett, 1969*d*).

In brief signal/noise theory applied to the quasi-linear filter of impulse function $h_Q(t)$ *usually* gives a good description of the available data, but there are no strong grounds for believing that this approach will deal easily with the dynamics of the threshold changes due to various background wave forms.

*How arbitrary is the $h(t)$ filter?*

The present approach deals entirely in terms of the linear input and quantities $B$, $Q$, $X$, $q_Q(t)$, $q_B(t)$, etc., and the non-linear aspects of the simple model, the appearance of the powers 0·5 and 2, are a consequence of applying signal/noise theory to the output of the $h(t)$ filter. It turns out that treated in this simple way the system is very nearly linear, except that the quantities $\tau_1$ and $g_Q$, which should be constants, do change rather slowly with the size of the input (e.g. Fig. 3). Perhaps other, better approaches could be developed, e.g. by working with log backgrounds and log thresholds, etc.? This may be so but the approaches that have been tried (defining an impulse function for the log background, log signal relation or replacing the integrals in equation (1) to (3) by $\int h(t)\mathrm{d}t$) seem very arbitrary and are probably worse than the present scheme. The log–log case leads to considerable difficulties, as can be seen by examining Fig. 1. The ascending phase of $\log q_Q(t < 0)$ is linear with the log input but the descending phase $(t > 0)$ is not, and the whole $\log q_Q(t)$ function is of considerable duration in comparison with the rapidity of the step response (which lasts about 3–4 times $\tau$ and is for this reason more closely related to the function $q_Q(t)$ of similar spread, although the actual calculation presents a problem, as was seen earlier). The present linear approach is arbitrary only to a very small extent and is essentially compatible with the approaches of other workers (e.g. Barlow, 1957; De Lange, 1961).

*What the $h(t)$ filter represents*

It is important to remember that $Kh_Q(t)$ represents the quasi-linear impulse function of the filter in Fig. 2*b*. It is fairly certain $Kh_Q(t)$ differs from the response of the visual pathways by a great deal more than mere lateral shifting on the time scale, for the photo-electric transduction process is quasi-logarithmic (e.g. Tomita, 1968) and on a finer view displays considerable changes in gain and a lesser change in time scale on altering the input magnitude (Fuortes & Hodgkin, 1964). If this is remembered then certain inferences about the response of the visual pathways can immediately be recognized as fallacious, e.g. 'the input-dependent exponential birth process represented by (8) suggests that this phase of the threshold disturbance is determined by the number of pores opened in a membrane by quantum absorptions but the dependence of $\tau_1$ on the output term $q_X(s.s.)$ or $q_{B+X}(s.s.)$ demonstrates parameter modifying feedback', etc. The fact is that form (8), together with $g_Q$ from Fig. 3, is no more than a fair description of the filter or 'black box' in Fig. 2*b* which summarizes the present experiments on impulse and steady background illumination.

A more promising approach to the data of Fig. 1 is to replace the 'visual pathways' in Fig. 2*a* with a plausibly analogous filter and then by using two shot-noise impulse inputs, one of fixed mean and timing (the background), the other of adjustable mean and timing (the test), to discover the filter which has signal/background characteristics similar to those measured in this paper. Before performing the present experiments it seemed possible that $h(t)$ for small impulses could be approximated by the signal/background relation of a simple high order, low pass, linear filter (all $n$ stages isolated and of equal time constant $\tau_0$) with an impulse function

$$p(t) = \text{const.}\ \frac{e^{-t/\tau_0}(t/\tau_0)^{n-1}}{(n-1)!}.$$

This function, the Poisson impulse function, can be chosen on various grounds: its properties are simple and something like it has been used by De Lange (1961) to describe flicker fusion and by Fuortes & Hodgkin (1964) to describe the *small* amplitude depolarizations of the retinular and eccentric cells of *Limulus* eye by light. The Poisson impulse function is, however, of limited usefulness: in the case of the present data the errors in the log. threshold measurements are such that one prefers to measure *large* threshold disturbances; at higher levels of adaptation De Lange's data show pseudo-resonance for sinusoidal inputs of period about 0·1 sec; the impulse functions of *Limulus* eye show large changes in gain and lesser changes in time scale as the input increases, and the step functions display overshoots. Fuortes & Hodgkin (1964) have therefore radically altered their linear filter by using the output to change the time constants and thus the gain and time scaling of the response. This non-linear Fuortes–Hodgkin filter would seem to be of basic importance to problems in human vision (e.g. Rushton, 1965*a*) and it would be of interest to know its De Lange characteristics and the parameters, or modifications, which are required to generate the signal/background relations, $q_Q(t)$ or $h_Q(t)$, of

Fig. 1. Such an approach is not without its difficulties. The data of Fig. 1 do conceal certain variations between the observers (Figs. 5 and 6) and the number of possible varieties of these non-linear models is rather large (Marimont, 1965; Sperling & Sondhi, 1968).

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