EFFECTS OF BLEACHING AND BACKGROUNDS ON THE FLASH RESPONSE OF THE CONE SYSTEM

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SUMMARY

1. Increment-threshold functions for flashed backgrounds were measured in the human fovea under several conditions: (1) during dark adaptation following full bleaches, (2) in the presence of steady adapting backgrounds and (3) 500 msec following extinction of adapting backgrounds.

2. To prevent the intense flashed backgrounds from interfering with the course of dark adaptation the inter-trial interval was continuously increased during dark adaptation. This technique may prove generally useful for presenting suprathreshold stimuli during dark adaptation.

3. All the increment-threshold functions measured during dark adaptation were found to be roughly shape invariant and continuously accelerating when plotted in log–log co-ordinates. Furthermore, in order to translate a function obtained at any given time into coincidence with a function obtained at any other time, it had to be translated vertically and horizontally the same number of log units. This is equivalent to adding or removing neutral density filters from in front of the eye.

4. The increment-threshold functions obtained with steady adapting backgrounds were also continuously accelerating, but could not be brought into coincidence by equal vertical and horizontal translation. However, this became possible again if the adapting background was extinguished during presentation of the flashed background.

5. These results contradict the equivalent-background hypothesis. None the less, they suggest that under present conditions the effects of bleaches and backgrounds may be similar except that steady backgrounds provide additional quanta which drive the visual system part of the way up its intensity–response function.

6. The conclusions above were supported by applying a simple model based on the equation $R = R_{max} \cdot I^n/(I^n + I_1^n)$, which has frequently been used to describe the peak responses of retinal neurones to flashed stimuli. Virtually all of the data reported here were fitted by this simple model with R_{max} held constant.

7. The parameters estimated from the model imply that the flash responses measured in the present experiments differ in at least one fundamental way from receptor responses. Even after taking into account changes in the half saturation constant I_1, steady backgrounds were found to be much less effective than flashed backgrounds in driving the visual system up its intensity–response function. A subtractive inhibitory network prior to the non-linear stages responsible for threshold saturation could explain this result.

INTRODUCTION

Many electrophysiological studies of visual adaptation have examined the effects of bleaching and steady backgrounds on the intensity–response functions of retinal neurones (Naka & Rushton, 1966; Boynton & Whitten, 1970; Dowling & Ripps, 1971, 1972; Grabowski, Pinto & Pak, 1972; Baylor & Hodgkin, 1974; Norman & Werblin, 1974; Werblin, 1974; Kleinschmidt & Dowling, 1975; Green, Dowling, Siegel & Ripps, 1975; Fain, 1976; Norman & Perlman, 1979). Although in psychophysics there has traditionally been an interest in measuring the flash response of the human visual system (Craik, 1938; Crawford, 1947; Boynton, 1961), most recent work on adaptation has focussed either on the classical technique of measuring absolute thresholds during dark adaptation (see Barlow, 1972; MacLeod, 1978) or on the newer techniques involving the measurement of thresholds for detection of small perturbations about steady background levels (Kelly, 1961, 1971; Rashbass, 1970; Roufs, 1972a, 1974). However, for theoretical reasons that will be made clear below and because of the many recent electrophysiological studies there has been renewed interest in measuring the effects of backgrounds and bleaches on the flash response of the human visual system.

The psychophysicist cannot, of course, measure directly the flash response of the visual system but must resort to indirect methods. Alpern, Rushton & Torii (1970a, b) employed what at first appeared to be a very powerful metacontrast paradigm to study the effects of bleaches and backgrounds on the response of the rod system, but Wandell (1976) has shown that some of their theoretical analyses will at least need to be modified.

A more recent approach has involved measuring the effects of adapting backgrounds on increment-threshold functions for flashed backgrounds (Geisler, 1978b; Hood, Ilves, Maurer, Wandell, & Buckingham, 1978; Hood, Finkelstein & Buckingham, 1979). Using rather simple theoretical analyses, these studies have provided evidence that in the cone system the effects of adapting backgrounds are roughly consistent with the measurements obtained in many of the electrophysiological studies listed above.

The present paper describes further experimental and theoretical work with the increment-threshold technique. The first part describes experiments in which foveal increment-threshold functions for flashed backgrounds were measured during dark adaptation following full bleaches. In real life, these experiments would correspond to measuring how well observers can detect objects upon entering environments of various intensities as a function of how long they have been in the dark. Although such experiments would seem to measure some very basic capabilities of the human visual system, it appears that similar experiments have not been reported previously. This may be due in part to the technical difficulties of obtaining the measurements without the flashed backgrounds interfering with the course of dark adaptation. In addition to the measurements obtained during dark adaptation, increment-threshold functions for flashed backgrounds were also measured against steady backgrounds and with backgrounds that were momentarily extinguished during presentation of the flashed background. The next part of the paper describes and develops more fully the theoretical framework and analysis applied previously by Geisler (1978b, 1979), Hood (1978), Hood et al. (1978), and Hood et al. (1979).

METHODS

Apparatus and stimuli

All stimuli were generated in a three-channel Maxwellian-view system that was under control of a PDP-11 computer. All three channels were derived from a single tungsten source. The images of the tungsten filament were 2 mm in diameter, and were superimposed at the centre of the pupil which was always dilated with 1 % Mydriacyl (Alcon Lab., Fort Worth, Tx).
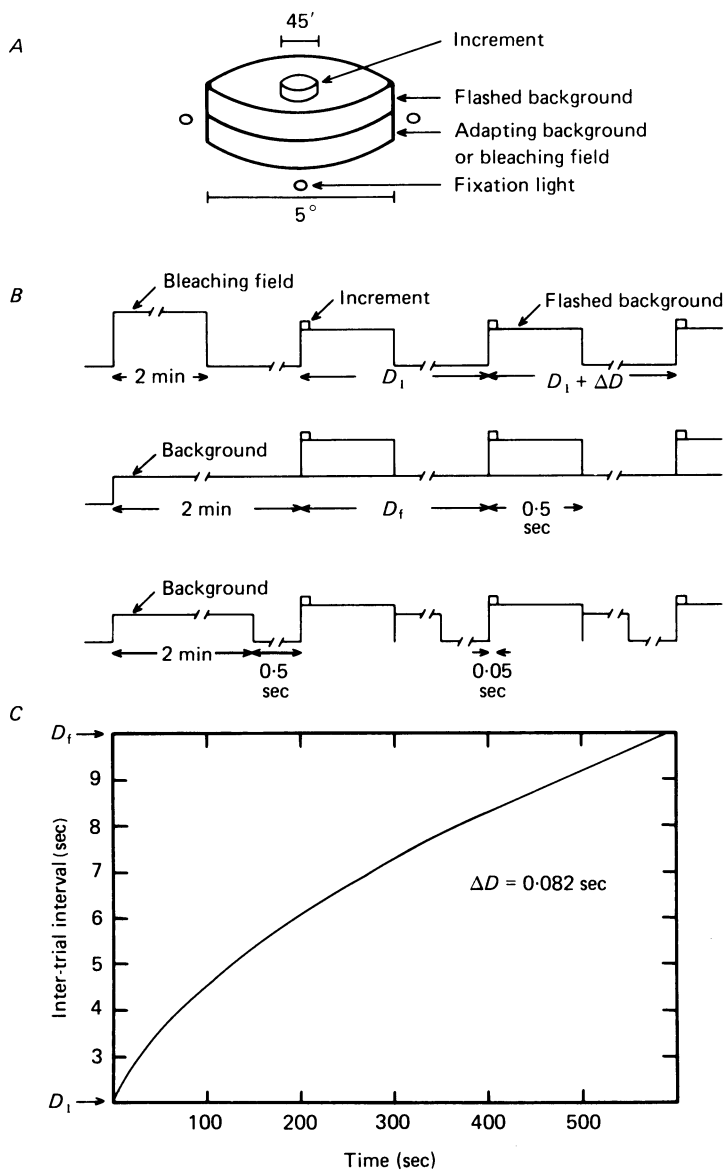

Fig. 1. *A*, stimulus display. All stimuli were tungsten white (3000 K) except for the four red fixation lights. *B*, stimulus presentation sequences used for measuring increment thresholds for flashed backgrounds during dark adaptation (upper line), against steady backgrounds (middle line) and shortly after the offset of adapting backgrounds (lower line). *C*, the inter-trial intervals used in the dark-adaptation experiment as a function of time after the bleach.

The stimulus display (see Fig. 1 A) comprised a 45′ increment field that fell in the centre of the flashed-background, adapting-background and bleaching fields which were all 5° in visual angle. Subjects were instructed to fixate the centre of the imaginary cross formed by four fixation lights that surrounded the 5° fields.

For the measurements reported here the stimuli consisted of the white light from the tungsten source (colour temp. 3000 K). Another study (Geisler, 1980) has shown that for a wide range of flashed-background intensities, the threshold spectral sensitivity of the increment field agrees fairly well with the C.I.E. photopic luminosity curve. Thus, although the present experiments were not measuring the response of a single receptor system, the set of receptors transmitting the threshold signals was probably not changing significantly across conditions. Another reason for starting, at least initially, with achromatic stimuli was to avoid some of the complicated interactions possibly due to the opponent channels (Pugh & Mollon, 1979; Finkelstein & Hood, 1979).

All wedges and filters were calibrated by placing an RCA phototube in the position normally occupied by the subject's pupil. The phototube was also used to set the maximum intensities of the channels prior to each experimental session and to check the intensities after each session. Absolute calibrations were obtained with the method recommended by Westheimer (1966).

The stimulus presentation sequence used for measuring increment thresholds during dark adaptation is shown in the upper line of Fig. 1 B. All timing was done by the computer and the fields were switched on and off with electromagnetic shutters that yielded rise and decay times of less than 1 msec. The bleaching field, whose intensity was 5·85 log td, was presented for 2 min. The reflexion densitometry measurements of Rushton & Henry (1968) imply that this stimulus should have bleached 95–98 % of the red and green cone photopigments. Densitometry measurements were obtained on one of the present subjects and confirmed this estimate.

Following the bleach, the background and increment fields were flashed repeatedly throughout the course of dark adaptation (for about 11 min). The background field was held at a fixed intensity throughout a given dark-adaptation run and was always flashed for 500 msec. The onset of the 50-msec increment field was always simultaneous with that of the background. The duration of the background flash was extended past the offset of the increment field to prevent the increment from being detected in the short-term after-image (Geisler, 1978 b, 1979, 1980). However, at the highest flashed-background intensity used in the present experiment (4·56 log td) it was possible late in the dark-adaptation run to detect the increment field in the short-term after-image. The subjects were instructed always to adjust the increment field so that it was just detectable at the onset of the 500 msec background.

The primary difficulty that had to be overcome in order to measure increment thresholds during dark adaptation was to present the background flashes with a large enough separation to prevent them from interfering with the course of adaptation, yet have them presented frequently enough to obtain reliable thresholds. This was accomplished by continuously increasing the inter-trial interval during dark adaptation. The technique was to start with an initial interval, D_1, and then add a fixed increment, ΔD, to this interval after each trial. Thus, the inter-trial interval on the Kth trial of the experiment was $D_1 + (K-1)\Delta D$. A control experiment described below showed that an adequate sequence of intervals was obtained by letting $D_1 = 2$ sec and $\Delta D = 82$ msec. Fig. 1 C shows how the inter-trial interval increased as a function of time after the bleach.

The stimulus-presentation sequence used for measuring increment-threshold functions against steady adapting backgrounds is shown in the second line of Fig. 1 B. Prior to measuring any threshold the subject adapted to the steady background field alone for at least 2·0 min. The inter-trial interval remained fixed at 10 sec, the final interval reached in the dark-adaptation experiments.

The presentation sequence for the interrupted-background condition is shown in the third line of Fig. 1 B. This condition was the same as for the steady background except that the adapting background was extinguished for 1·0 sec while the flashed background was presented.

Procedure

In each experimental session the intensity of the flashed background remained fixed at one of the seven levels tested, and there were at least two sessions at each flashed-background intensity. In each session the neutral density wedge was initially set so that the increment field would become visible shortly after the 2 min bleach. After the increment became visible the subject decreased its intensity until it just disappeared. He then pressed a button causing the computer to record the time and threshold. For the next 11 min the subject repeated the cycle of increasing the intensity

of the increment until it was clearly visible, decreasing the intensity until it just disappeared and then pressing the button to record the threshold. Rather surprisingly, the task seemed no more difficult than the usual one in which short inter-trial intervals are used throughout. Following the dark-adaptation run the intensity of the flashed background remained fixed and thresholds were obtained for a series of steady background intensities. The thresholds were obtained by starting at the lowest background intensity and working upward to the highest. The subjects used the same adjustment procedure as in the dark-adaptation conditions. Finally, about 10 min after obtaining the last measurement with the steady background, another entire dark-adaptation run was completed.
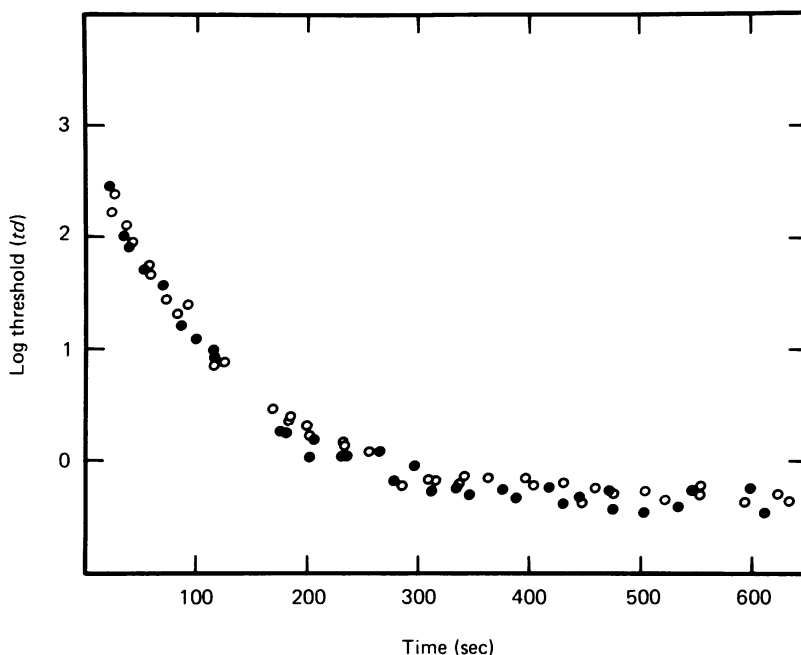

Fig. 2. Results of a control experiment for validating the dark-adaptation procedure Absolute thresholds were measured without a flashed background (●) and with the increment field presented 500 msec prior to a flashed background of 4·5 log *td* (○). Each symbol is an individual threshold setting.

The increment thresholds for interrupted backgrounds were obtained in a separate experiment. The procedure was the same as for the steady backgrounds, except that (1) within a session the intensity of the interrupted background was held constant while the intensity of the flashed background was varied and (2) the measurements were not prefaced by a dark-adaptation run, although the subject first underwent at least 10 min of dark adaptation.

Validation of the dark-adaptation procedure

An experiment was carried out to determine whether the sequence of inter-trial intervals used in the dark-adaptation experiment was sufficient to prevent the flashed backgrounds from interfering with the course of dark adaptation. The experiment consisted of two conditions. In the first, the flashed background was turned off, thus yielding a standard dark-adaptation experiment. In the second, the flashed background was set at 4·5 log *td* (the highest intensity level used in the main experiment), and the increment was flashed 500 msec prior to onset of the flashed background. If the flashed background has no effect on the course of dark adaptation, the dark-adaptation curves obtained under these two conditions should be identical. The results are shown in Fig. 2. As can be seen, the dark-adaptation curves are very nearly identical.
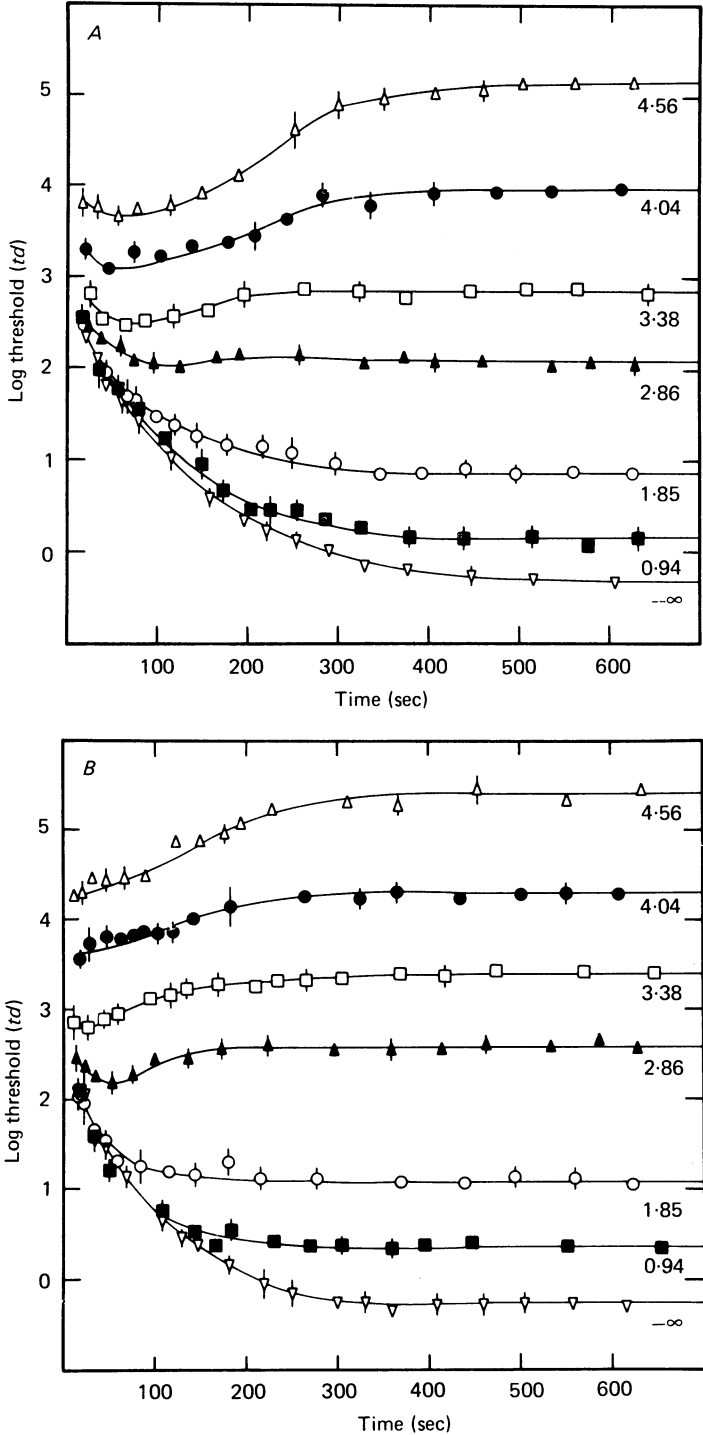
Fig. 3. Increment thresholds for flashed backgrounds measured during dark adaptation following full bleaches. Each curve shows the results for a fixed flashed-background intensity. Flashed-background retinal illuminance (log td): ▽ without a flashed background; ■, 0·94; ○, 1·85; ▲, 2·86; □, 3·38; ●, 4·04; △, 4·56. *A*, subject WG. *B*, subject JLI.

Bleaches

The increment thresholds obtained during dark adaptation for the two subjects are shown in Fig. 3. Each curve shows the thresholds for the flashed-background intensity indicated in the legend. Each point represents the mean of three to six observations and the vertical bars indicate ± 1 s.d. of an observation. (Where the error bars are not visible they fall inside the symbol.)

The lowermost curves in Fig. 3 A and B were obtained without a flashed background, thus they show the result of a standard dark-adaptation experiment. Comparison of these curves in Fig. 3 A and B reveals that subject WG has a slower rate of recovery than subject JLI. Although the time course of recovery turns out not to be critical for either the analyses or conclusions presented here, it is probably worth noting that subject WG's rate of recovery is more representative of other subjects reported in the vision literature.

For flashed backgrounds of up to 2–3 log *td* the dark-adaptation curves decrease monotonically, but above this level they show an initial decrease followed by a slower monotonic increase. Intuitively, this is not surprising. When one goes from a very bright environment into darkness and then returns some time later into a bright
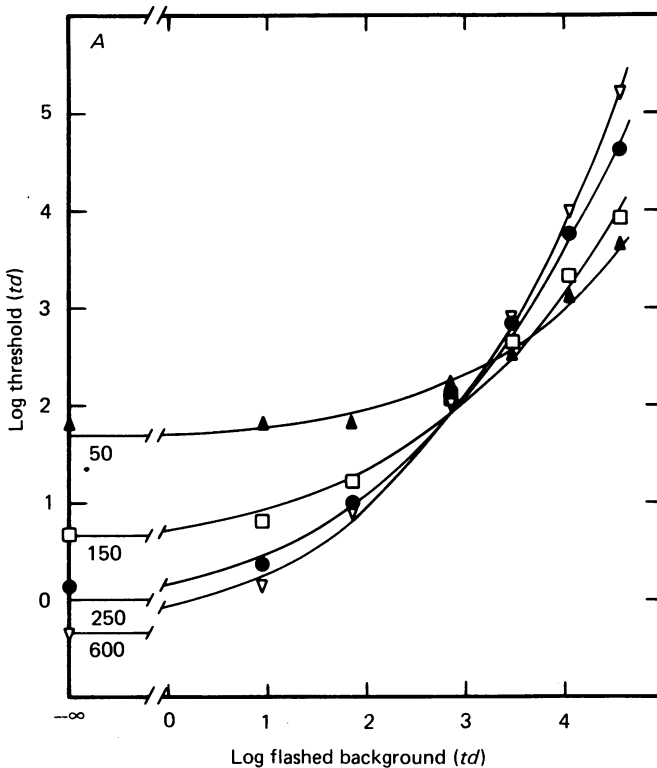

Fig. 4 *A*. Increment-threshold functions for flashed backgrounds obtained at 50 sec (▲), 150 sec (□), 250 sec (●) and 600 sec (△) after a full bleach. Continuous curves are prediction of eqns. (2) and (3). Parameter values: $n = 0.7$, $\delta = 0.015$. (*Continues on p. 420.*)
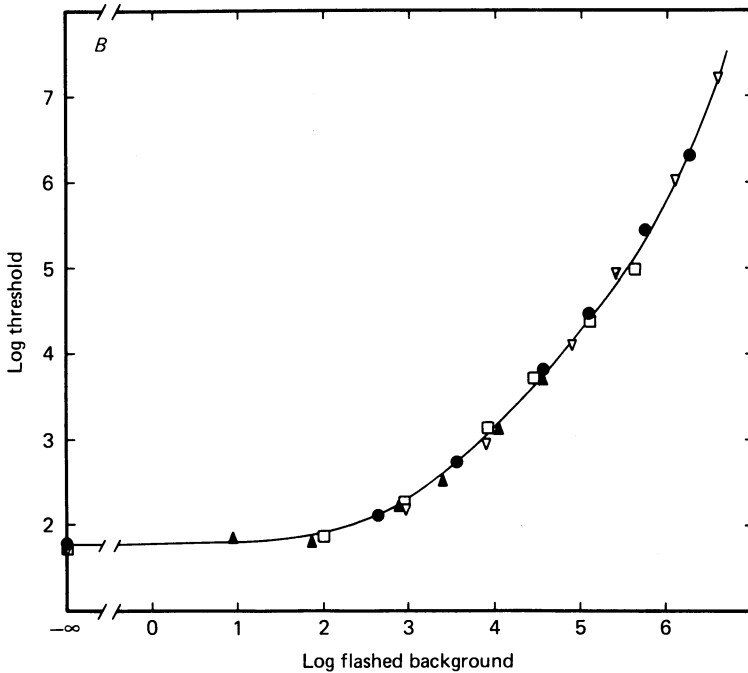
Fig. 4B. The same functions as in A but each has been translated along a 45° line until
all lower asymptotes are superimposed.

environment it is reasonable to expect intensity discrimination to be better after a
short while than in a state of total dark adaptation.

A more revealing way to display the data in Fig. 3 is to construct flashed-background
increment-threshold functions for a number of different fixed times after the bleach.
These increment-threshold functions were constructed from the smooth curves drawn
through the data. Fig. 4A shows the functions obtained for subject WG at 50, 150,
250 and 600 sec. Functions were also obtained at 100, 200 and 300 sec. They follow
exactly the same pattern, but are omitted from Fig. 4A for clarity. Note that the
open triangles show the increment-threshold function for the dark-adapted cone
system, and it is essentially the same as those reported previously for the same subject
(Geisler, 1978b, 1980).

There are two important aspects of these functions (and the others not shown).
First the curves are roughly shape invariant. The smooth curves in the Figure are all
identical except for vertical and horizontal translations. Secondly, and more
surprisingly, all the translations of these smooth curves are along a 45° line. In other
words, to translate any one curve in Fig. 4A into coincidence with any other, it must
be translated the same number of log units vertically and horizontally. This is
demonstrated in Fig. 4B. The above properties also hold accurately for JLI's data.
As mentioned in Geisler (1978b) adding or removing a neutral density filter from in
front of the subject's eye would have exactly this same effect. All the dark-adaptation
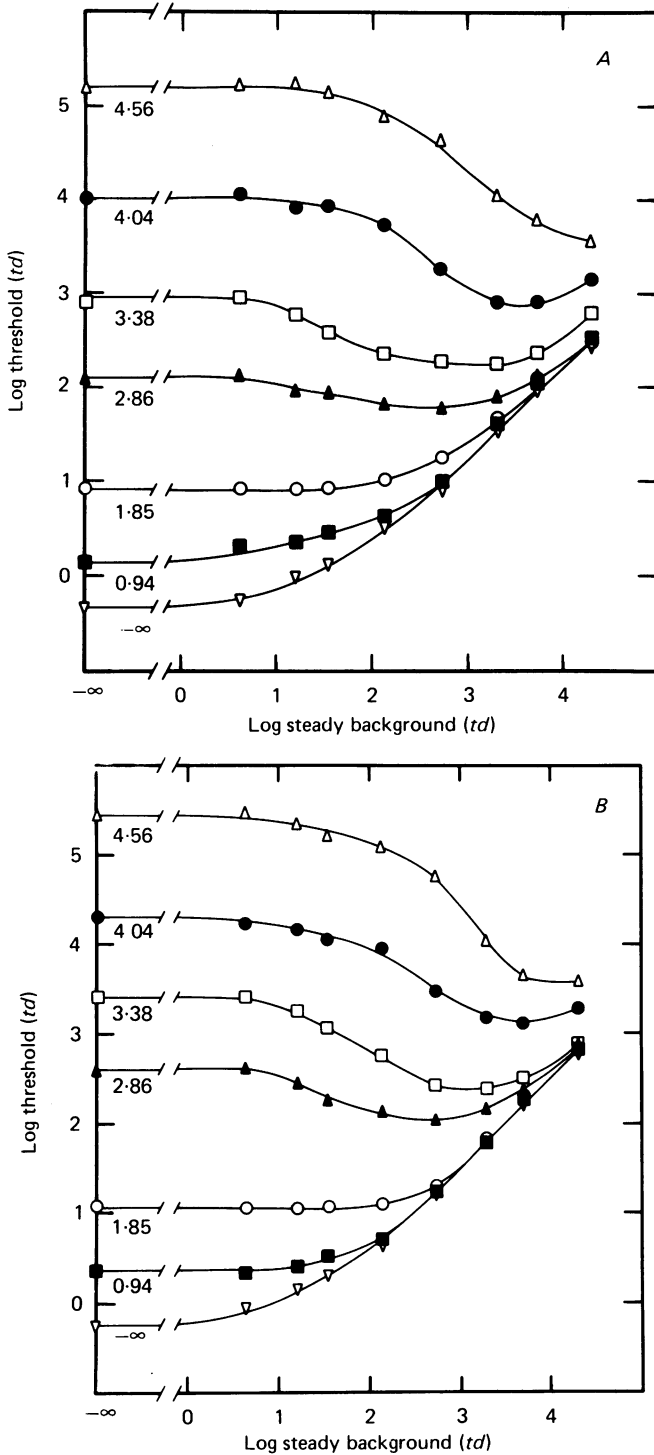data reported here are adequately described by this simple law.

Fig. 5. Increment thresholds for flashed backgrounds measured against steady adapting backgrounds. Each curve shows the results for a fixed flashed-background intensity. Flashed-background retinal illuminance ($\log td$): $\triangledown$, without a flashed background; $\blacksquare$, 0·94; $\bigcirc$, 1·85; $\blacktriangle$, 2·86; $\square$, 3·38; $\bullet$, 4·04; $\triangle$, 4·56. *A*, subject WG. *B*, subject JLI.
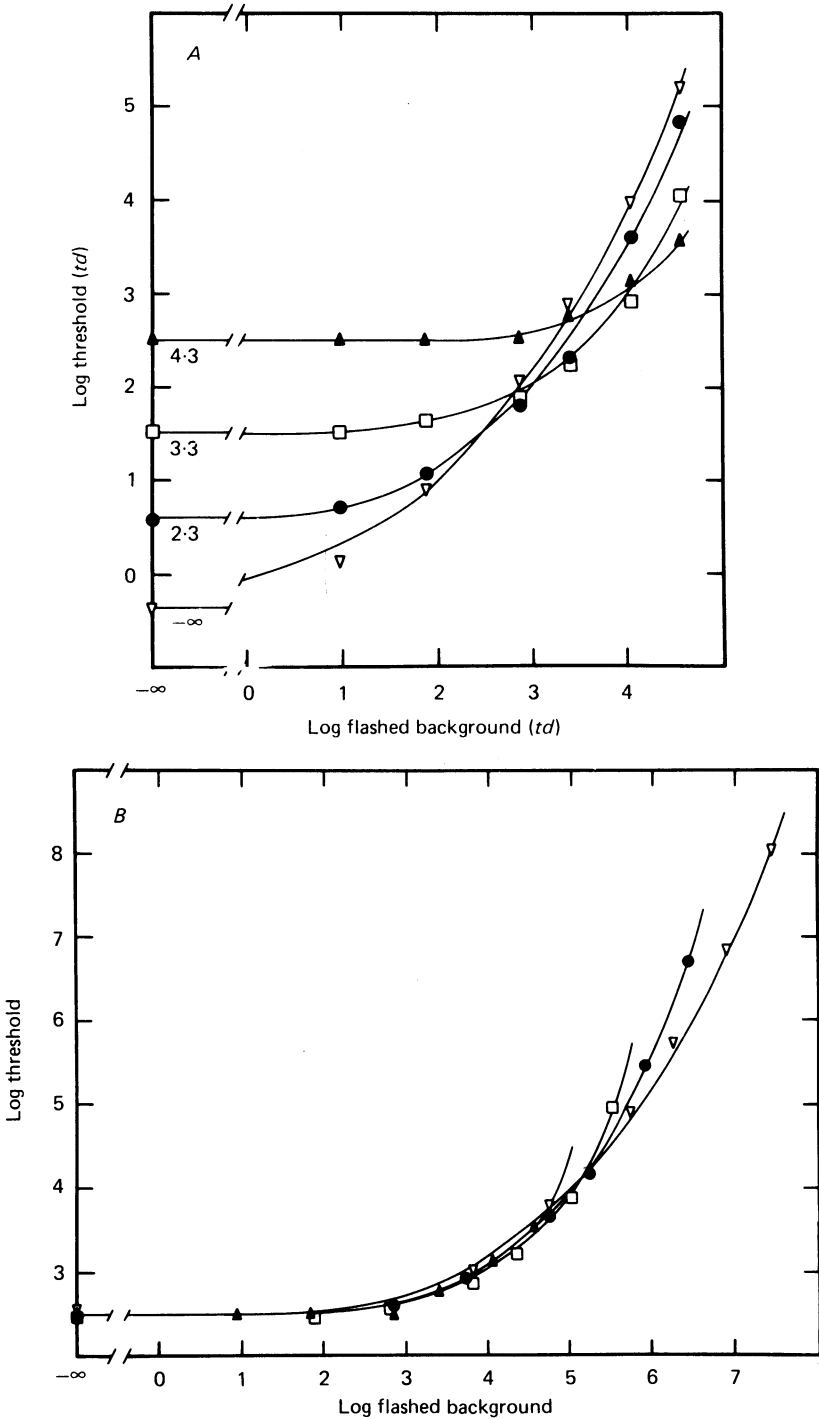
Fig. 6. *A*, increment-threshold functions for flashed backgrounds in the dark-adapted eye
(∇) and against steady backgrounds of 2·3 log *td* (●), 3·3 log *td* (□), and 4·3 log *td* (▲).
Continuous curves are the predictions of eqns. (2) and (3). Parameter values: $n = 0·7$,
$\delta = 0·015$, $\gamma = 0·1$. Subject WG. *B*, the same functions as in *A* but each has been translated
along a 45° line until all the lower asymptotes are superimposed.

Steady backgrounds

The increment-threshold data obtained with the steady backgrounds are shown in Fig. 5 for the same two subjects. As in Fig. 3, each curve shows the results for a fixed flashed-background intensity.

The lowermost curves in Fig. 5A and B were obtained without a flashed background and so give the results of a standard increment-threshold experiment. The straight line drawn through the data points above 2·5 log *td* has a slope of 1·0. The pattern of results in Fig. 5 appears to parallel that of the dark-adaptation experiment. For low flashed-background intensities, the increment thresholds increase monotonically with steady background intensity, but for high flashed-background intensities they are bowed.

Increment-threshold functions at fixed steady-background intensities were obtained from the smooth curves drawn through the data in Fig. 5. Fig. 6A shows the functions obtained for subject WG for the dark-adapted eye and for steady backgrounds of 2·3, 3·3 and 4·3 log *td*. Functions were also obtained at backgrounds of 1·3, 1·8, 2·8 and 3·8 log *td*. They were all perfectly consistent with the pattern of results in Fig. 6A, but again were left out for clarity. The open triangles in Fig. 6A show the increment-threshold function for the dark-adapted eye and it is exactly the same function shown in Fig. 4A.

Superficially, the increment-threshold functions in Fig. 6A appear to be similar to those in Fig. 4A, suggesting that the adaptation effects of steady backgrounds and bleaches are the same. However, closer inspection reveals some important differences. Most importantly, the functions in Fig. 6A (and those obtained for subject JLI) are not identical in shape and cannot be superimposed by translation along a 45° line. This is demonstrated in Fig. 6B.

Interrupted backgrounds

The increment-threshold functions obtained with the interrupted backgrounds are shown in Fig. 1A. The smooth curves in the Figure are all identically the same curve except for translation along a 45° line (see Fig. 7B). Thus, if the adapting background is briefly extinguished during presentation of the flashed background, the pattern of results becomes more like that obtained for bleaches.

DISCUSSION

The increment-threshold functions that were obtained in the dark-adapted eye (open triangles in Figs. 4A and 6A) are similar to most of those obtained previously under similar conditions (King-Smith & Webb, 1974; Shevell, 1977; Geisler, 1978*b*, 1980; Hood *et al.* 1978; Hood *et al.* 1979). An exception is the study by Alpern, Rushton & Torii (1970*c*). Their function increases rapidly (saturates) at a much higher background intensity. Earlier studies that measured increment-threshold functions in the dark-adapted eye used equal-duration background and increment fields, and did not observe threshold saturation (Bartlett, 1942; Brindley, 1959; Sperling, 1965). However, this is undoubtedly due to the intrusion of after-images at high background intensities (Geisler, 1978*b*, 1979).
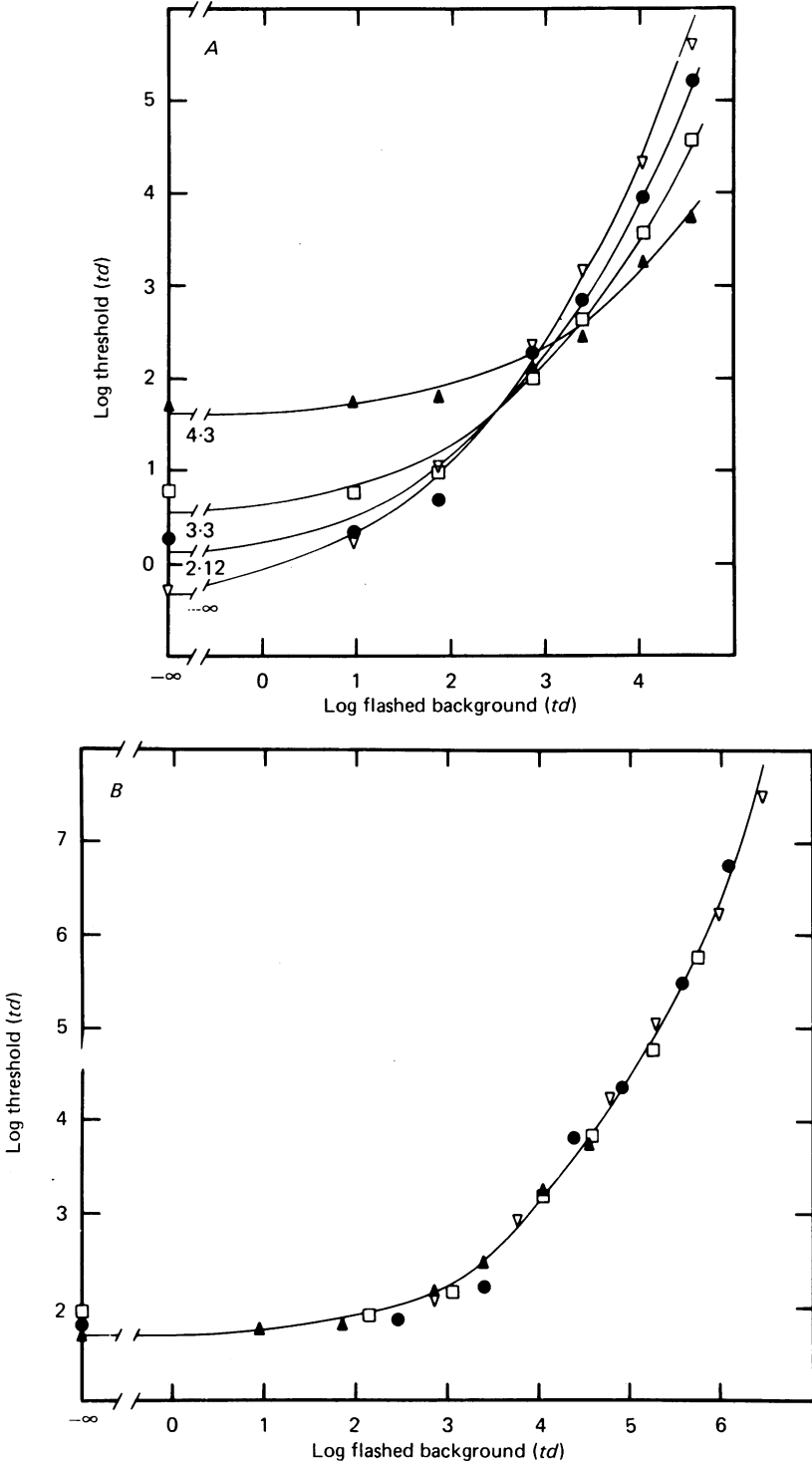
Fig. 7. Increment-threshold functions for flashed backgrounds obtained in the dark-adapted eye (∇) and in the presence of interrupted backgrounds of 2·12 log *td* (●), 3·3 log *td* ($\square$) and 4·3 log *td* (▲). Continuous curves are the predictions of eqns. (2) and (3). Parameter values: $n = 0.7$, $\delta = 0.021$. *B*, the same functions as in *A* but each has been translated along a 45° line until all the lower asymptotes are superimposed.

The first major attempt to measure the effects of adapting backgrounds on flashed-background thresholds was carried out by Craik (1938). Craik used interrupted backgrounds and obtained qualitatively similar results to those reported here; however, his conditions and degree of stimulus control were such that a quantitative comparison with the modern studies is not possible.

The effects of steady backgrounds on increment threshold shown in Fig. 6 are similar to those reported by Hood *et al.* (1978). As in Fig. 6, the functions obtained by Hood *et al.* cannot be superimposed by translation along a 45° line.

Since steady backgrounds do not behave like bleaches, the equivalent-background hypothesis does not hold under present conditions. On the other hand, Fig. 6 in Geisler (1978b) and the present Fig. 7 show that if the background is momentarily extinguished before the flashed background is presented then the increment-threshold functions can be approximately superimposed by translation along a 45° line. This suggests that the adaptation effects due to bleaching and backgrounds might differ (under the present conditions) only because the additional absorbed quanta from the background are driving the visual system part of the way up its intensity–response function. The theoretical analyses described below support this hypothesis.

Electrophysiological studies, including those listed in the Introduction, have often found that the intensity–response functions of neurones in the vertebrate retina that are obtained with brief flashes can be described by the equation:

$$R = \frac{I^n \cdot R_{max}}{I^n + I_1^n} \tag{1}$$

where I is the intensity of the flash, R_{max} is the maximum electrical response of the neurone, I_1 is the half-saturation constant, and n is an exponent whose value often lies between 0·7 and 1·0 (at least for receptors). Furthermore, changes in the intensity–response function due to bleaching and backgrounds can often be described by changes in the parameters R_{max} and I_1. Usually, most of the changes due to bleaching and backgrounds appear as changes in I_1, which is equivalent to adding or removing filters from in front of the eye. This, of course, suggests a possible connexion between the electrophysiology and the present psychophysical results. However, great care must be exercised in comparing neural intensity–response functions with the results of intensity-discrimination experiments.

An important consideration is that equation (1) only describes how the peak response of a neurone, or perhaps response at a fixed delay (Baylor *et al.* 1974), changes with flash intensity. But, this may *not* be the aspect of the response carrying the information used for discrimination (Geisler, 1978b, 1979, 1980). Nevertheless, it may be reasonable here to test the simple models that are suggested by the peak-response characteristics of retinal neurones. The primary reason for using a 500 msec background field and a 50 msec increment field in the present experiment was to force detection to occur when or almost when one would expect the peak response of the retina to occur. There are two pieces of evidence suggesting that this is at least approximately correct. First, by varying the duration of the background from 50 to 500 msec, Geisler (1978b) showed that detection of the increment field under the present conditions depends only on the background quanta absorbed during the first 50 msec or less and not on those absorbed afterwards. Secondly, under the present

conditions reaction time for detection of the increment field at just above threshold is constant (or very slightly decreasing) as a function of flashed-background intensity (Hood *et al.* 1979; Geisler, 1980).

Peak response (or fixed-delay) model

This section describes and tests a simple model based on eqn. (1). Only the analysis for subject WG is shown here. Essentially the same conclusions are reached from the analysis of JLI's data.

Steady backgrounds. The model proposed here for the steady-background conditions is slightly different from that proposed by Hood (1978) and Hood *et al.* (1978). In Hood's model, and in the present one, it is assumed that threshold is reached when the neural response R_+ to the background plus increment exceeds the response R to the background alone by some fixed criterion amount, δ. That is, threshold is reached when

$$R_+ - R = \delta. \tag{2}$$

Hood assumes that R_+ and R represent the increase in response above any ongoing activity produced by the steady background, and that R is given by eqn. (1). The equation for R_+ is simply eqn. (1) with $I + \Delta I$ substituted for I.

A weakness of eqn. (1) is that it does not take into account the excitatory effect of quanta absorbed from the steady background. Thus, a more complete and apparently more parsimonious model is given by the equation:

$$R = \frac{(I + \gamma I_A)^n \cdot R_{max}}{(I + \gamma I_A)^n + I_1^n} \tag{3}$$

In this case R represents the total response including that to the steady background of intensity I_A. The parameter γ takes into account temporal integration (or, more generally, the temporal-weighting function) and is included to adjust for the fact the I_A is continuous and I is a flash (Williams & Gale, 1977). Another parameter, ζ, multiplying I should also be included to represent the relative effectiveness of the flashed background to that of the increment. However, it can reasonably be set to 1·0 since the increment is fairly large (45′) and Geisler (1978*b*) has already shown that threshold only depends on the background quanta absorbed during presentation of the 50 msec increment.

When $n \neq 1\cdot0$, eqns. (1) and (3) make different predictions, but as Naka & Rushton (1966) showed they are equivalent when $n = 1\cdot0$. However, even when $n = 1\cdot0$ the estimated parameters for the equations are different and may lead one to a different interpretation. For example, the fit of eqn. (3) to Kleinschmidt & Dowling's (1975) data leads to the conclusion that essentially all of the adaptation effects are represented by changes in I_1. On the other hand, the parameters values estimated by Kleinschmidt & Dowling using eqn. (1) lead to the conclusion that both R_{max} and I_1 change significantly with adaptation level. (Their fit actually involved an additional parameter, the DC level at each background intensity.)

An efficient minimization routine, STEPIT (Chandler, 1969), was used to determine the least-squares fit of eqns. (2) and (3) to the flashed-background increment-threshold functions obtained against the steady backgrounds. It was decided to first test the model with R_{max} held constant. When it is held constant, it can be set to 1·0 without

loss of generality. The estimated values of n, δ, and γ were found to be the same across all conditions. Thus, the only parameter that varied across the conditions was the half-saturation constant, I_1. The theoretical predictions for the conditions shown in Fig. 6A are given by the continuous curves. The fits to the other increment-threshold functions not shown are equally good. The estimated value of I_1 as a function of steady-background intensity is shown in Fig. 8A.
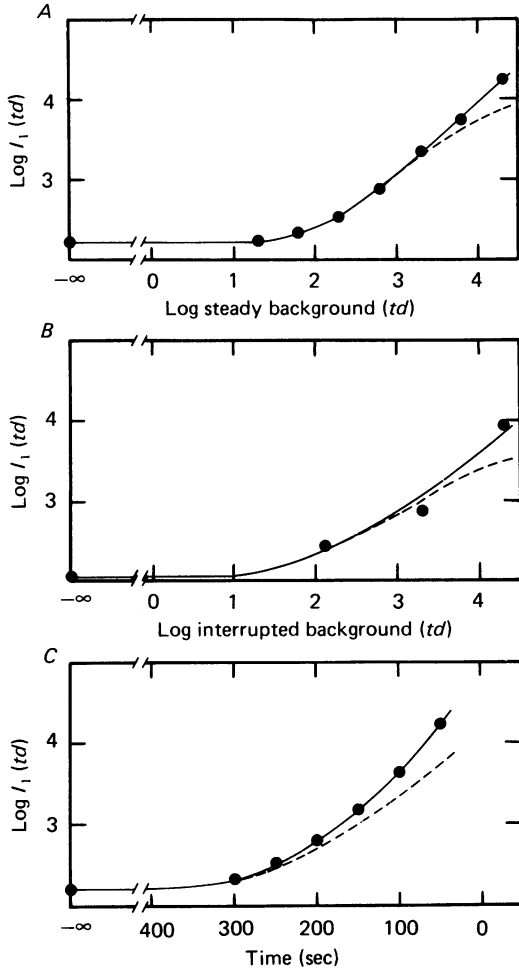

Fig. 8. The values of the half-saturation constant estimated by fitting eqns. (2) and (3) to flashed increment-threshold functions obtained for steady backgrounds (A), for interrupted backgrounds (B) and during dark adaptation (C). The dashed curves show the values of I_1 that would be obtained if there were no photopigment depletion.

In fitting receptor response data, such as those of Kleinschmidt & Dowling (1975), we typically find γ to be greater than or equal to $1\cdot0$. However, the estimated value of γ for the present results is much less than $1\cdot0$. This is an important result that is discussed in more detail later.

Interrupted backgrounds. Eqns. (2) and (3) were also used to generate predictions for the conditions in which the adapting background was extinguished during

presentation of the flashed background. Under the reasonable assumption that most of the excitatory effects of the steady backgrounds would dissipate in less than 500 msec, I_A was set to 0·0. The predicted functions are shown in Fig. 7A, and were obtained by varying only the parameter I_1 across conditions. The estimated values of I_1 are shown in Fig. 8B. The adequate fit of the model provides support for the hypothesis that the extra elevation of the lower asymptote obtained with continuous backgrounds is simply due to the background quanta (I_A) driving the visual system part way up its intensity–response function.

  Bleaches. The predictions of eqns. (2) and (3) for the increment-threshold functions obtained during dark adaptation are shown in Fig. 4A. The estimated values of n and δ were the same as for the steady backgrounds and only I_1 was varied across conditions. The predictions for the other functions not shown are equally accurate. In Fig. 8C the estimated values of I_1 are plotted as a function of time after the bleach.

  The rather surprising conclusion of the above analyses is that all of the increment-threshold data in this paper can be fairly accurately predicted by such a simple model. Furthermore, the only parameter that changes across the very wide range of stimulus conditions is the half-saturation constant, I_1.

Photopigment depletion

  One obvious adaptation mechanism that would cause changes in the half-saturation constant is simple photopigment depletion. It cannot account for all the changes in I_1, but undoubtedly must be a component. To determine the magnitude of the depletion effect, densitometry measurements were obtained on subject WG, with H. D. Baker's densitometer at Florida State University.

  One common difficulty with reflexion densitometry deserves mention. Owing to the unknown level of stray light, one must know or guess the dark-adapted optical density of the photopigment at the wave-length of the measuring beam, D_m, in order to estimate the proportion of unbleached photopigment. If D_m is underestimated the time constant of regeneration, t_0, is underestimated and the half-bleaching constant, I_0, is over-estimated (Geisler, 1978a; Padmos, 1979). Under the assumption that $D_m = 0·3$ (measuring beam wave-length = 589 nm) it was found that $t_0 = 133$ sec and $I_0 = 4·2 \log td$. For $D_m = 0·3$, WG accurately satisfies the Dowling–Rushton relation (Dowling, 1960; Rushton, 1961), but for the other assumptions tried ($D_m = 0·5$ and D_m negligible) the relation was found to hold with much less accuracy. Thus, the analysis described below must be viewed as only approximate.

  Using the above constants and the appropriate solutions to Rushton & Henry's (1968) differential equation, the contributions of photopigment depletion in the present experiment were calculated for WG. If we let I_1' be the value of I_1 in the dark-adapted eye, then the contributions of depletion and the other adaptation mechanisms can be represented by the equation:

$$I_1 = I_1'/(p \cdot \mu) \tag{4}$$

where p is the proportion of pigment present and μ is the adaptation factor due to the other mechanisms. The dashed curves in Fig. 8, which are plots of $\log (I_1'/\mu)$, show the values of I_1 that would be observed if there were no photopigment depletion. Thus, photopigment depletion is a relatively minor factor. Note that eqn. (4) is based on

the assumption that self-screening effects are negligible. Calculations show that if $D_{\lambda\mathrm{max}} < 0.5$ this assumption is very nearly correct for white tungsten light.

Dynamic models

Geisler (1979) proposed a simple model of intensity discrimination in the dark-adapted eye that is based on the models of receptor responses proposed by Penn & Hagins (1972), Baylor, Hodgkin & Lamb (1974) and others. The model (see Fig. 9 *A*) consists primarily of an initial linear stage *L*, with a slow time constant, representing the transduction of light into internal transmitter followed by a static (zero-memory) non-linear transform *N* representing the non-linearities that arise at the receptor level and beyond.
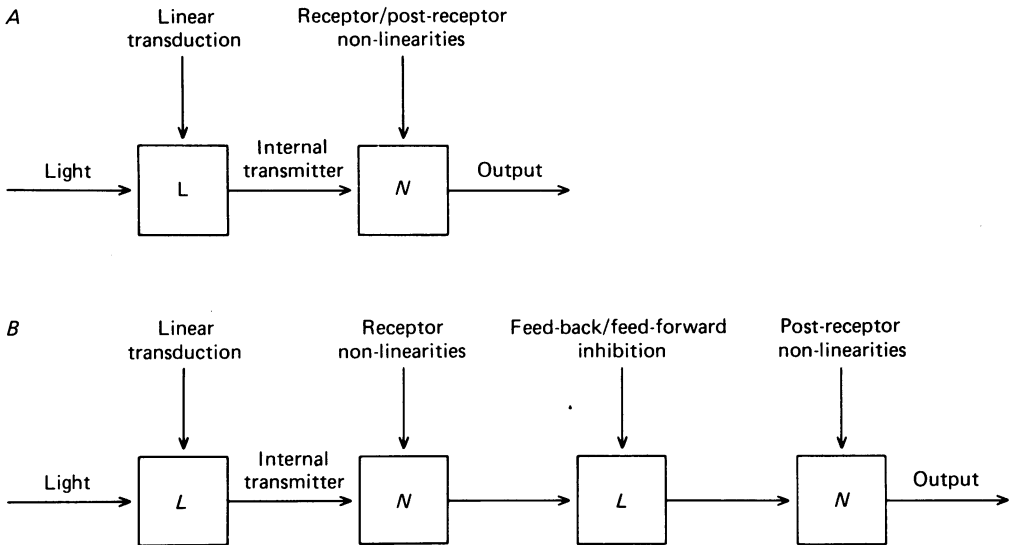

Fig. 9. Dynamic models of intensity discrimination. L represents a linear transform, N represents a static non-linear transform.

. With the static non-linearity in the form of eqn. (1) the model is able to predict many of the unusual properties of increment thresholds in the dark-adapted rod and cone systems. Many of these unusual properties are predicted independent of the particular form of the initial linear stage or the non-linear stage (for details see Geisler, 1979, 1980).

Unlike the peak-response models described above, the *L–N* model assumes (more realistically) that detection of a difference in the responses from the background and increment regions can occur at any point in time, whenever the difference exceeds the criterion δ. However, with nearly the same parameter values as used in the peak-response model, the *L–N* model predicts that for the 500 msec background, detection of the increment occurs near the peak response. As a consequence both models predict about the same increment-threshold function for the dark-adapted eye.

If we suppose that adaptation acts like placing a filter over the eye, which is equivalent to vertically scaling down the impulse–response function of the initial

linear stage, then the *L–N* model will predict all the data it previously could, plus the increment-threshold functions obtained during dark adaptation and with the interrupted backgrounds. In addition to vertically scaling down the impulse–response function, adaptation may change the half-saturation constant I_1 also by, for example, reducing time constants in the initial linear stage (Baylor *et al.* 1974; MacLeod, 1978). These changes are, of course, not strictly equivalent to placing a filter over the eye, but still lead to essentially the same predictions for the present increment-threshold experiments.

As formulated above the *L–N* model will *not* predict the increment-threshold functions obtained with steady backgrounds. The model predicts that aside from changes in I_1 the steady backgrounds should be at least as effective as the flashed backgrounds in driving the non-linear stage. But the data show that they are much less effective. This is revealed by the fact that γ in eqn. (3) was estimated to be around 0·1. If the initial linear stage were simply integrating quanta, the value of γ would have to be greater than or equal to 1·0. In order for the *L–N* model to have, in effect, a value of γ less than 1·0, the temporal impulse–response function of the initial linear stage must have at least one negative (inhibitory) lobe following the positive lobe.
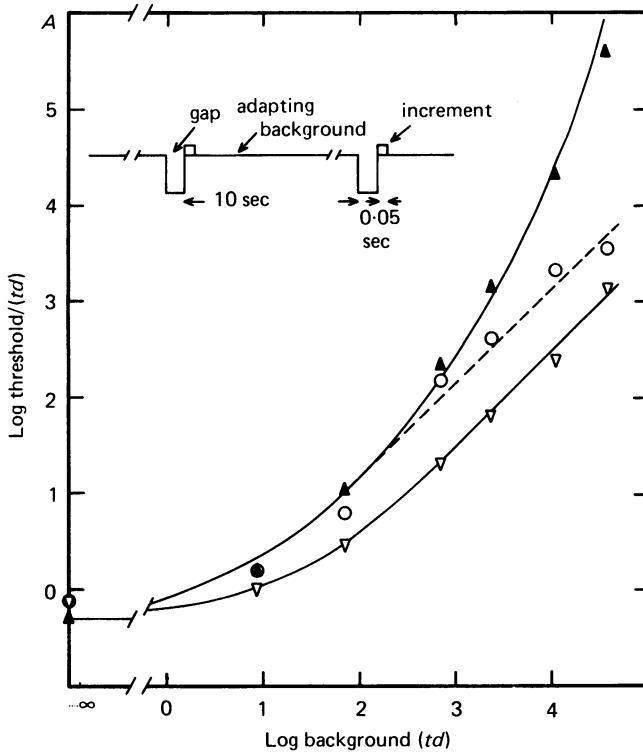

Fig. 10*A*. Increment-threshold functions obtained for 500 msec flashed backgrounds in the dark-adapted eye (▲), for steady adapting backgrounds (▽), and for adapting backgrounds with a 100 msec gap just prior to presentation of the increment field (○). The dashed line is the best performance that can be obtained for steady adapting backgrounds, if light adaptation only causes increases (or decreases) in I_1 and/or decreases in R_{max}. *(Continues on p. 431).*
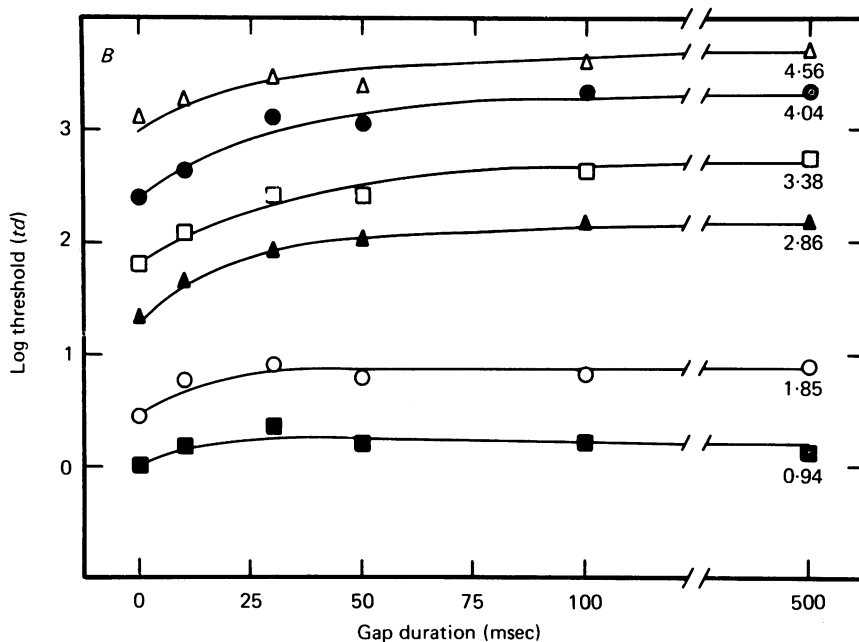
Fig. 10*B*. Increment thresholds on adapting backgrounds as a function of the duration of a gap just prior to presentation of the increment field. Adapting background intensity (log *td*): ■, 0·94; ○, 1·85; ▲, 2·86; □, 3·38; ●, 4·04; △, 4·56.

The need for this modification is illustrated more clearly in Fig. 10*A*. The filled triangles are from Fig. 7*A* and are the increment-thresholds obtained in the dark-adapted eye. The open triangles are the increment-thresholds obtained with steady backgrounds (i.e. without flashed backgrounds). The continuous curves are the predictions of the peak-response model that can be obtained if we allow γ to be less than 1·0. Increasing γ causes the predicted curve for the steady backgrounds to slide to the left; yielding, for example, the dashed curve. In fact, if $\gamma \geqslant 1\cdot 0$ then increases (or decreases) in I_1 and/or decreases in R_{max} in eqns. (2) and (3) can never yield predicted thresholds below the dashed curve. Similarly, if the impulse–response function of the initial linear stage were strictly positive and if (as in receptors) light adaptation only causes increases in I_1 and/or decreases in R_{max} then the best possible performance with steady backgrounds is given by the dashed curve. A negative lobe on the impulse–response function would result in the steady background signal partially cancelling itself ($\gamma < 1\cdot 0$) before reaching the non-linear stage. However, owing to the temporal lag of inhibition, the neural signal produced at the onset of a background or an increment field would not partially cancel itself. The supersensitivity observed with steady backgrounds could also be accounted for if light adaptation causes increases in R_{max}, but this seems unlikely on the basis of electrophysiological evidence.

It is unlikely that receptor adaptation can account for the supersensitivity with steady backgrounds since there is no physiological evidence that the impulse–response functions characterizing the release of internal transmitter have substantial negative

lobes. This suggests that the increased sensitivity may be due to a subtractive inhibitory network beyond the receptors, and that the non-linearities responsible for threshold saturation may be located even deeper in the system. The hypothesis that the primary non-linearities are located beyond the receptors is supported by the evidence that bipolar and ganglion cells saturate at lower flash intensity levels than receptors (Werblin, 1974; Green *et al.* 1975).

If the open triangles in Fig. 10 *A* are well below the dashed line owing to the slightly delayed action of an inhibitory network, then briefly turning off the steady background just prior to presenting the increment field (see the inset in Fig. 10 *A*) should allow the inhibitory effect of the steady background on itself to dissipate. Thus, the thresholds should jump back up to or above the dashed line. The open circles in Fig. 10 *A* show the increment-threshold function obtained for adapting backgrounds with a 100 msec gap just prior to presentation of the increment. The hypothesis is clearly confirmed. Increment-threshold functions were also obtained for gaps of 10, 30, 50 and 500 msec, in order to determine the time course of the threshold changes. Fig. 10 *B* shows the changes in threshold as a function of gap duration for several adapting-background intensities. The time course of these threshold changes is roughly consistent with the time course of the inhibitory mechanisms inferred from flicker studies (Kelly, 1971; Roufs, 1972 *b*, 1974). (Of course, there may be some contribution of receptor dark adaptation during the first 50–100 msec after the adapting background is extinguished, but it is probably secondary since we have already seen that the known effects of adaptation on receptors cannot predict the present effects.)

The simplest scheme consistent with the above conclusions is illustrated in Fig. 9 *B*. The first stage is, as before, a linear transform with a strictly positive impulse–response function which, at least when the eye is dark-adapted, has a relatively slow time constant. The second stage is a static non-linear transform which represents the receptor non-linearities. It has a relatively large half-saturation constant. Next is a linear transform with relatively fast time constant representing the subtractive inhibitory network. The last stage is another static non-linear transform with a small half-saturation constant representing the post-receptor non-linearities. Bleaches and backgrounds may affect the half saturation constants at either or both non-linear stages.

If most of the non-linearities are due to the second non-linear stage, the model in Fig. 9 *B* will approximately reduce to the L–N model except that the impulse response of the combined linear stages will have a negative lobe. Thus, with appropriate choices for the stages, the model must make predictions similar to those of eqns. (2) and (3) for all the increment-threshold results reported here. Indeed, specific versions can be constructed which are able to account reasonably well for the results reported here, plus those results (Geisler, 1979, 1980) already handled by the L–N model.

Current electrophysiological knowledge of vertebrate receptors plus the psychophysical findings described here appear strong enough to rule out any other possible ordering of the four stages in Fig. 9 *B*. Unfortunately, with four stages there are more degrees of freedom available for constructing specific models. The data that have been considered here are not sufficient to exclude all but one specific version.

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