

THE NATURE OF RISE IN THRESHOLD PRODUCED BY CONTRAST-FLASHES

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(Received 3 November 1966)

SUMMARY

1. The rod threshold for seeing a flash on a $2\frac{1}{2}^\circ$ square is raised by a nearly simultaneous flash that falls on the surround. When this 'contrast-flash' is held fixed in intensity, it raises the log test threshold by a *fixed* amount no matter how far that threshold has already been raised by light adaptation owing to background or bleaching.

2. This is surprising since fixed backgrounds and bleachings raise the log test threshold much more when the eye is dark than when light adapted.

3. When the test flash is held at some fixed supra-threshold value, the contrast flash exhibits a 'critical level', above which the test will no longer be seen. If the surround region upon which the contrast-flash falls is adapted by background or bleaching, its efficacy is reduced so that the 'critical level' is raised.

4. Surround adaptation raises the log 'critical level' by the same amount that it raises the log threshold for seeing the contrast-flash itself.

5. The way that contrast flashes raise the test threshold is thus entirely different from the way that adaptations by bleachings or backgrounds do. Contrast-flash signals appear to inhibit test-flash signals by interaction at some point central to the site where adaptation occurs.

6. This permits the effect of adaptation on signals to be measured. A given state of adaptation attenuates all flash signals in the same proportion. And in any state of adaptation a single flash will reach threshold when the attenuated signal has a fixed size.

INTRODUCTION

In two recent papers, Alpern (1965) and Alpern & Rushton (1965), it was shown that the visual threshold for a 5 msec flash λ (see inset of Fig. 1) was substantially raised by a 5 msec 'after-flash' ϕ that was presented 50 msec later and fell upon the region surrounding (and not overlapping) the area of λ . Further experiments have shown that the effect does not depend at all critically upon the time relations of the two flashes, and

though the phenomenon is most surprising when the 'after-flash' raises the threshold for a test that has been presented 50 msec earlier, the effect is essentially the same when the 'after-flash' comes first. The name '*contrast-flash*' therefore seems more appropriate.

Now anyone who has experimented with visual thresholds knows that some distraction may cause a faint flash to be missed, and that any strong sensory stimulus (e.g. a kick on the shin bone) may raise the threshold in this way. It is therefore natural to suspect that a bright contrast-flash, separated from the test flash both in space and time, may act simply by distraction.

But this conclusion is not at all supported by the quantitative study of threshold-rise using one colour for test and another for contrast-flash. The results indicate that there is a specific organization in contrast-flash thresholds almost exactly like the organization which Stiles (1939, 1949) has found in increment thresholds. That is that rods and the three types of cone act nearly independently of each other, so that the threshold of any one type of receptor is raised to the extent that the background (or the contrast-flash) affects that type and is nearly independent of the excitation of all other types of receptor.

For instance, in Fig. 4 of Alpern (1965) the test flash excited the rods, and the colour of the contrast-flash was either red (black squares) or green (white squares). As plotted, the log energy of contrast-flash is shown upon a scale of photopic brightness units—that is the apparent brightness of the flash, since (for the most part) it was well above the cone threshold. This plot, therefore, should be upon a scale of equal *distraction*. But it clearly is not a plot of equal rise in test threshold, since the white squares are far from coinciding with the black. In fact the black squares lie on a curve which coincides with that through the (lowest set of) white squares after 1.5 log units of lateral displacement—precisely the displacement required to change the horizontal plot from photopic to scotopic units.

Thus we conclude that when the test flash excites the rods, and the contrast-flash is expressed in scotopic (= rod) units then no matter what is the wave-length, the effect on the rod threshold is the same, though the 'distraction' may appear very different. With cones the analogous relation holds (Alpern & Rushton, 1965). If at threshold the test flash excites (say) the green cones, it is the green cone stimulation by the contrast-flash that alone is significant in raising the threshold. The situation is quite analogous to what Stiles found with coloured backgrounds.

Figure 2 of Alpern (1965) suggests a rather obvious explanation of contrast action. There it was shown that by adding a fixed contrast-flash to a background that already raised the test threshold, it was raised further—by just the amount expected if the fixed contrast-flash added

a fixed quantity to that background field. Perhaps the effect of the strong contrast-flash is simply to scatter light on to the area of the test flash where in effect it adds to the background already there, for Stiles & Crawford (1937) showed that a *steady* glaring light source raised thresholds very much as though light was simply scattered across the retina. Experiments to confirm this trivial interpretation refuted it entirely; the contrast-flash organization is much more interesting.

In this paper we present the experimental analysis in 2 parts. In Part 1 the sensitivity of the retina where the test flash falls is depressed by applying exactly there, backgrounds or bleachings. A *fixed* contrast-flash is applied to the surround, and its effect upon the log threshold of the test observed. In Part 2 it is the sensitivity of the surround region that is depressed by backgrounds and bleachings, and we measure the increase in the contrast-flash intensity required for the test flash still to be raised by a fixed amount. This part concludes by extending conditions to the case where the background covers both test and surround.

METHODS

The apparatus and technique have already been described (Alpern, 1965; Alpern & Rushton, 1965), and so they need only brief summary here. A three-channel Maxwellian view optical system was used to provide to the observer's dark-adapted right eye a green (527 nm) test flash (λ), a background field (μ and/or θ), and a contrast flash (ϕ) of variable dominant wave-lengths. The other eye was occluded. The spatial arrangements are illustrated in the inset of Fig. 1 in which *F.P.* represents the point of fixation. The 5 msec flashes were obtained mechanically by rotating sectored disks adjusted to give any desired time relation between exposure of λ and ϕ . Usually, ϕ followed λ by 50 msec. The cycle was repeated every second, and the subject adjusted the intensity of λ for visibility. For measurements after full dark-adaptation or against a fixed background, three successive settings were made; but during the course of dark-adaptation, naturally, only individual settings could be obtained. Intensity was varied by neutral (Wratten no. 96) filters and by rotating crossed polaroids (confined to the middle range to avoid the colour changes evident at their extreme positions). Dominant wave-lengths of the various fields were varied by narrow band interference filters or occasionally by Wratten gelatin filters. Field stops confined the background to the limits of the ϕ field or to the test field, and in the last experiment to both.

In experiments in which the θ area was bleached and the recovery of λ in the dark was measured in the presence of a contrast flash, it was found that during an intermediate period in the dark a 'flash' frequently appeared in the test area even when no flash was exposed there. To avoid confusion from this source, a thin set of cross-hairs were stretched across the field stop in the test flash area and the observer adjusted target intensity for threshold visibility of these cross-hairs in these experiments. The settings were typically 0.2 log₁₀ units higher than the usual threshold settings of λ .

RESULTS

Part 1. Contrast-flashes of fixed intensity

1. *Test upon a background.* As shown in Fig. 1 (inset) the test flash λ fell upon a $2\frac{1}{2}^\circ$ square whose centre was situated 6° from the fixation

point. The steady background μ was in principle confined exactly to this square, but optical scatter and small eye movements made this imperfect. The contrast-flash ϕ filled the 9° circle except for the test square which was spared.

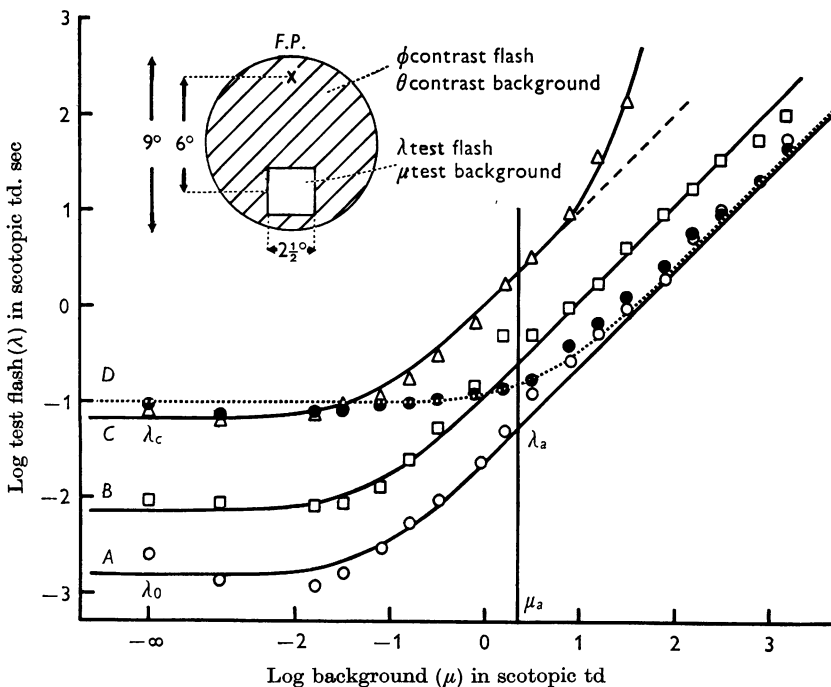


Fig. 1. Inset shows fixation point *F.P.*, $2\frac{1}{2}^\circ$ square where test flash λ fell upon a steady background μ ; and the 9° surround where the contrast-flash ϕ fell upon its steady background θ . These two areas do not overlap. Curve *A* plots log threshold of λ for various log backgrounds when ϕ and θ are zero. Curves *B* and *C* are when ϕ is 0.02 and 0.2 scotopic td. sec respectively and $\theta = 0$. Curve *D* is when $\phi = 0$ and $\theta = 5$ td. Wave-lengths are as follows: $\mu = 625 = \phi = \theta$, $\lambda = 525$ nm. λ and ϕ were both 5 msec flashes and ϕ was presented 50 msec after λ .

The experimental results in Fig. 1 are plotted as log λ against log μ . In the lowest curve the contrast-flash ϕ is zero hence curve *A* is simply an ordinary log increment threshold curve, with the 5 msec flash λ of wave-length 525 nm and the steady background μ of 625 nm to raise the cone threshold and make all the results refer to rods only. Curve *B* was obtained in conditions like *A* except that now the 5 msec contrast-flash of 625 nm wave-length and 0.02 scotopic td. sec energy was presented 50 msec after the test. The effect of the fixed contrast-flash was to raise log λ by a fixed amount, namely 0.6 if the curves drawn represent the true run of the points. Curve *C* shows the same relation when ϕ is 10 times as great,

namely 0.2 scotopic td.sec, the curve being raised a further 0.9 log units.

This is not at all the result that is obtained by adding a constant increment of energy to the background. *That* would change curve *A* not into *C* but into the dotted curve *D*, which is curve *A* slid up the 45° Fechner line. In fact the black circles are the experimental results where, instead of applying the fixed contrast-flash ϕ , we used a fixed steady background θ that fell on the same surround (and avoided the test square). The strength of θ was 5 scotopic td, chosen so that curves *C* and *D* nearly coincided on the left. Thus with the local background μ zero, the contrast-flash ϕ and the steady background θ falling on the same retinal area raised the test threshold equally. But the manner in which they did it was not the same since, as μ increases, curves *C* and *D* run quite different courses. *D*, as would be expected of light scattered from the surround on to the test square, coincides with *A* slid up the 45° line. *C* on the contrary coincides with *A* displaced vertically upward. None of the commonly studied types of adaptation does this.

The steep rise of curve *C* when the background μ lies between 1 and 2 log td might be due to rods becoming 'saturated' (Aguilar & Stiles, 1954).

1(b) *Bleaching of the test area.* The bleaching light was applied only to the retinal region occupied by the test square. The intensity was 360,000 td lasting 30 sec so about 70% of rhodopsin was bleached. Figure 2 shows three dark-adaptation curves following this bleaching procedure, measured with a 5 msec test flash of wave-length 525 nm. All curves show the usual cone and rod branches but the lower (rod) branch alone concerns us here.

Curve *A* is a simple dark-adaptation curve with no contrast flash. Curve *C* is when a fixed 5 msec contrast-flash of wave-length 500 nm and energy 0.02 scotopic log td.sec was applied 50 msec after the test flash. Curve *D* (analogous to *D* in Fig. 1) is when, instead of the fixed contrast flash ϕ , a fixed white steady background μ was added to the test square. Its intensity was adjusted so as to raise the fully dark-adapted threshold by as much as the contrast-flash did in curve *C*. These three curves, as in the previous section, show that the effect of the fixed contrast-flash is to raise the log threshold by a fixed amount—curve *C* is curve *A* vertically displaced. A fixed background does something quite different.

Stiles & Crawford (1932) pointed out that adaptation to bleaching as judged by various kinds of test flash could be simply described by the concept of 'equivalent background'. Blakemore & Rushton (1965) extended the experiments to cover the case of dark-adaptation curves where the threshold is measured as increment threshold against luminous backgrounds. Two real luminous backgrounds acting at once are naturally

identical to one background that has the sum of their luminances. It turns out to be the same when one of these backgrounds is not real but the 'equivalent background of bleaching'. The threshold is raised as though a single real background was present whose luminance was the sum of the real and the equivalent background luminances. Curve *D* (Fig. 1) shows the result of adding two real backgrounds. *D* (Fig. 2) shows the result when one is the equivalent background of bleaching, the dotted curve being that calculated from the addition of real and equivalent luminances.

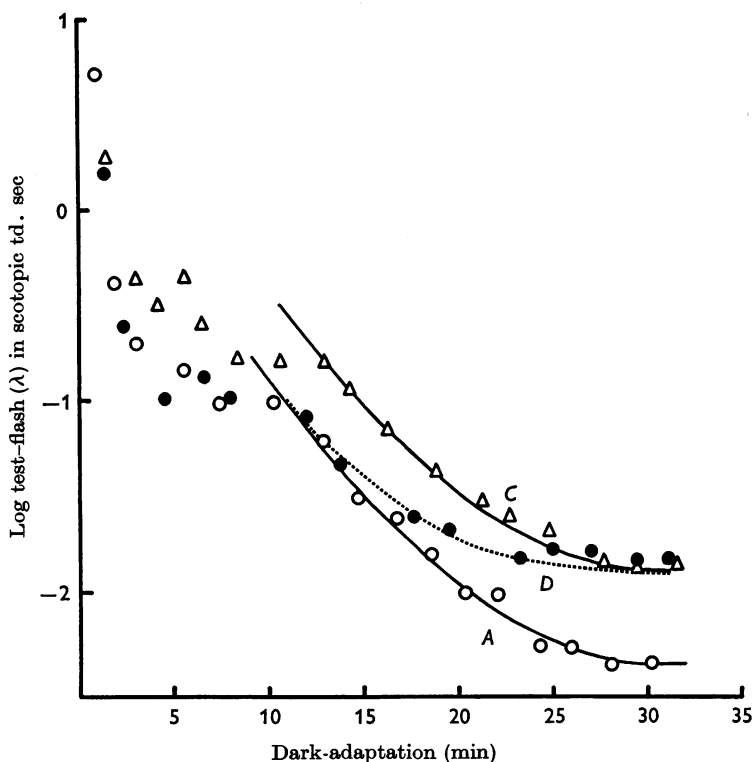


Fig. 2. Curve *A* plots an ordinary dark-adaptation curve, for test flash λ when the $2\frac{1}{2}^\circ$ square alone has been bleached. Curve *C* is when the log threshold is further raised by the contrast-flash ϕ with $\theta = 0 = \mu$. Curve *D* is when $\phi = 0 = \theta$ and μ is a steady background that in full dark-adaptation raises the threshold as much as ϕ did in *C*. Wave-lengths and timing as in Fig. 1.

Now we may extend the principle of 'equivalence' to a new domain, that of contrast flash. In Fig. 1 it is seen that ϕ which raises $\log \lambda$ at the left of the figure by an amount k above the level of *A* (absolute threshold), will raise it k above *A* for any other background. If we may apply the principle of equivalence now to Fig. 2 we predict that ϕ which raises

$\log \lambda$ at the right of the figure by an amount k above the level of A (also the absolute threshold), will raise it k above A at any other stage in dark-adaptation. This was found to be so.

Part 2. Contrast-flashes of fixed efficacy

2(a) *Contrast-flashes upon a background.* In Part 1 the eye was adapted by placing a steady background μ upon the test area only; now we place the steady background θ on the surround area only. However, though applied only to the area where the contrast flash ϕ falls it is not true to suppose that θ exerts its effect only upon ϕ . In Fig. 1 curve D shows that in the absence of ϕ , θ raises the test threshold λ just as though some light was scattered from the θ area to the λ area and added to the background μ there. And no doubt that was what occurred. Thus we should expect to find the result shown in Fig. 3 curve A_λ which plots the rise in $\log \lambda$ for various \log luminances of the steady surround θ in the absence of contrast flash ϕ or explicit test background μ . Curve A_λ is nearly the same shape as A_ϕ which is an ordinary log increment threshold, namely that for the visual detection of flash ϕ against its background θ . Naturally A_λ is displaced somewhat to the right since θ is somewhat attenuated by scatter.

From the results A_λ and A_ϕ it is plain that in the main experiment where the contrast-flash ϕ is presented upon its background θ , two causes will operate to raise the test threshold λ , (a) scatter from θ whose effect is shown in curve A_λ and (b) the contrast flash which acts in quite a different way as we saw in Part 1. About (b) all we know so far is that (in absence of θ) when ϕ remains at any fixed value its effect is to raise $\log \lambda$ by a corresponding fixed value.

The presence of the background θ reduces (of course) the efficacy of flash ϕ as judged by its visual appearance, and curve A_ϕ shows how much $\log \phi$ must be increased to remain at threshold with increasing $\log \theta$. It is natural to ask 'Does θ reduce in the same way the efficacy of flash ϕ as judged by its capacity to raise the λ threshold?' The answer comes out to be 'Yes. The ϕ signal is reduced equally whether judged by its visual threshold or by its inhibition of λ .' But we must remember that an increase in θ operates upon λ in two ways (a) through scatter and (b) through the effect on ϕ . To avoid confusion we performed the experiment as follows.

After obtaining curves A_λ and A_ϕ where only one or other flash was presented, we found the λ threshold against various backgrounds θ when the ϕ flash was just threshold for seeing ϕ , i.e. ϕ had the log energies recorded in curve A_ϕ . This flash rose to a value 10,000 times the absolute threshold but it was always only just visible and always had a negligible effect in raising the λ threshold. Curve B_0 (Fig. 3) plots the increase in

log threshold of λ above the values recorded in A_λ —the extra result of adding the ϕ flash to the steady θ background. It is seen that the increase is nearly zero throughout when ϕ had the threshold values of curve A_ϕ .

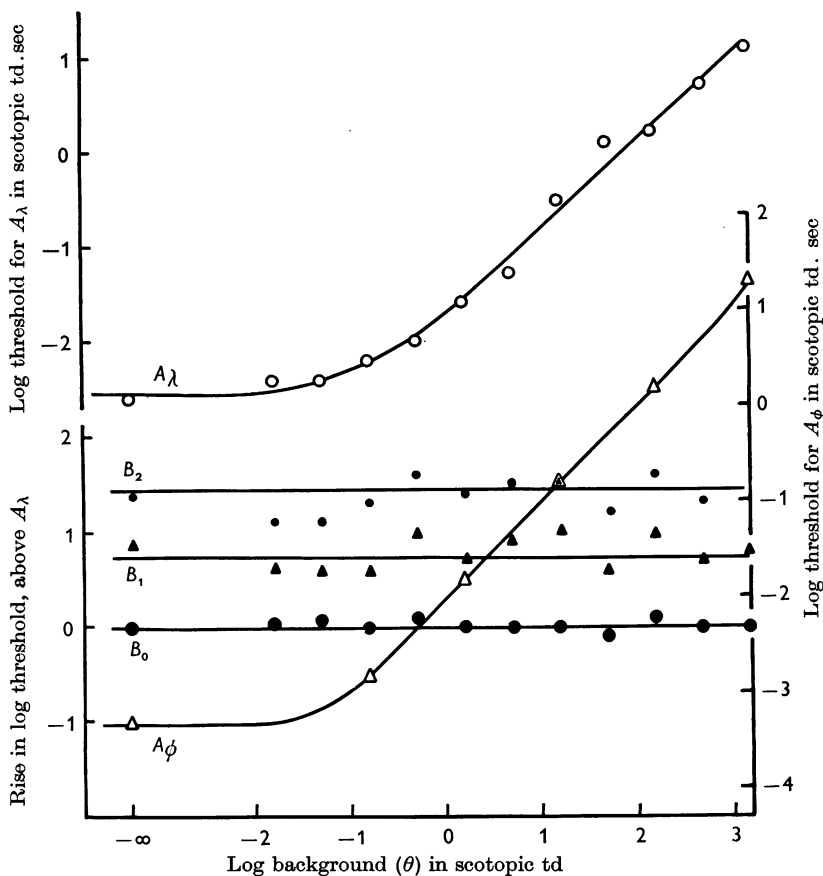


Fig. 3. Curve A_ϕ plots the log increment threshold for seeing ϕ against various strengths of θ (scale on right). Curve A_λ plots the log increment threshold for λ against the scatter from θ (upper scale on left). Curves B_0 , B_1 , B_2 show by how much this A_λ threshold is raised by ϕ of intensity 0, 1, 2 log units above the A_ϕ value. Wave-length of $\lambda = 527$ nm, $\phi = 500$ nm, $\theta = 625$ nm.

Curve B_1 shows the results similarly plotted when ϕ was 1 log unit above the corresponding point in B_0 , i.e. 10 times the threshold for seeing the ϕ flash, B_2 when ϕ was 2 log units above threshold. The points show more scatter than those of B_0 (as would be expected) but they still lie near the horizontal lines that signify a constant rise in log λ by a 10,000-fold change in ϕ , adjusted however to remain a fixed multiple of the visual threshold. This establishes that backgrounds reduce the efficacy of ϕ to

raise the λ threshold in about the same proportion by which they reduce visibility.

2(b) *Bleaching of contrast-flash area.* The ϕ area was bleached by an exposure that removed about 10% of the rhodopsin and curve A_ϕ of Fig. 4 (open triangles) shows the dark-adaptation curve measured by detecting the ϕ flash all other lights being absent. Curve A_λ (open circles)

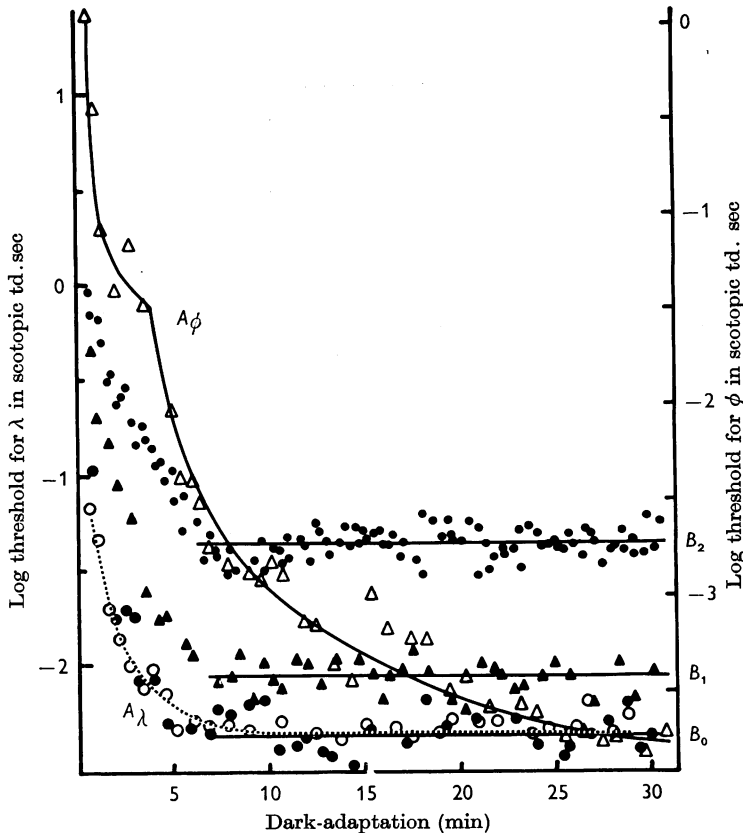


Fig. 4. Curve A_ϕ (open triangles), dark-adaptation curve for seeing ϕ flash after bleaching ϕ area. Curve A_λ (open circles) dark-adaptation curve for seeing λ flash after bleaching only ϕ area. Curves B_0 , B_1 , B_2 (filled symbols), repetition of curve A_λ with addition of contrast-flash 0, 1, 2 log units above the threshold shown in A_ϕ .

shows the dark-adaptation after a similar bleaching exposure but measured by the λ flash that falls upon the test square that had been spared direct bleaching. The λ threshold was, nevertheless, raised initially (no doubt owing to some light scattered from the bleached area); however, by 7 min of dark-adaptation A_λ has reached the fully dark-adapted state, and we shall not be concerned with earlier times.

Curves B_0 , B_1 , B_2 (black symbols) are dark-adaptions following the same strength of bleaching, but now the λ threshold is found when the contrast ϕ is added. In B_0 the value of ϕ is at each moment that shown in curve A_ϕ , thus ϕ is always just barely visible at that stage of dark-adaptation. This threshold ϕ has no effect upon λ and curve B_0 (black circles) coincides with A_λ (white circles).

Curve B_1 (black triangles) is when ϕ is 1.0 log unit stronger than the threshold value A_ϕ at each moment. Curve B_2 is when it is 2.0 log units stronger. It is plain that for times greater than 7 min when rods alone are involved and curve A_λ runs horizontal, curves B_0 , B_1 and B_2 run horizontally also. These results are precisely analogous to those with backgrounds (Fig. 3). When the ϕ flash is some fixed value above its visual threshold, it raises the log test threshold λ by a fixed amount.

A combined experiment

This paper opened with the observation of Alpern's (1965) Fig. 2 which suggested that a contrast-flash acted simply by scattered light. We have now seen that the effect of the contrast-flash (Fig. 1 curve C) does not act like scattered light (curve D) but that a flash of fixed efficacy raises $\log \lambda$ by a fixed amount. In Alpern's experiment the fixed contrast-flash did not do this, but it was not a flash of fixed efficacy since it fell upon a background that was continually being made brighter. From Fig. 3 of this paper we can find the ϕ efficacy for each background of Alpern's (1965) Fig. 2, and from his Fig. 4 we can predict the effect of such efficacy upon $\log \lambda$. The result corresponds well with the filled squares that Alpern actually found (1965, Fig. 2). But a more pleasing display of expectation and result from that uniform background which spreads over the whole $(\mu + \theta)$ region is presented here in Fig. 5.

In this experiment the log increment threshold for seeing flash ϕ against the background $(\mu + \theta)$ is plotted as black circles; that for seeing flash λ alone, white circles. Both lie on curve B_0 . Curves B_1 , B_2 , B_3 , give $\log \lambda$ when the contrast-flash ϕ is 1, 2 or 3 log units above the threshold value shown by the black circles. The curve drawn through B_0 , B_1 , B_2 and B_3 is the same curve displaced vertically.

Thus over a fairly wide range we find the former generalization confirmed. When ϕ is a fixed multiple of its visual threshold (black circles) its effect upon the test flash is also fixed. This effect is to raise by a fixed amount the log threshold that obtains when the contrast-flash is zero.

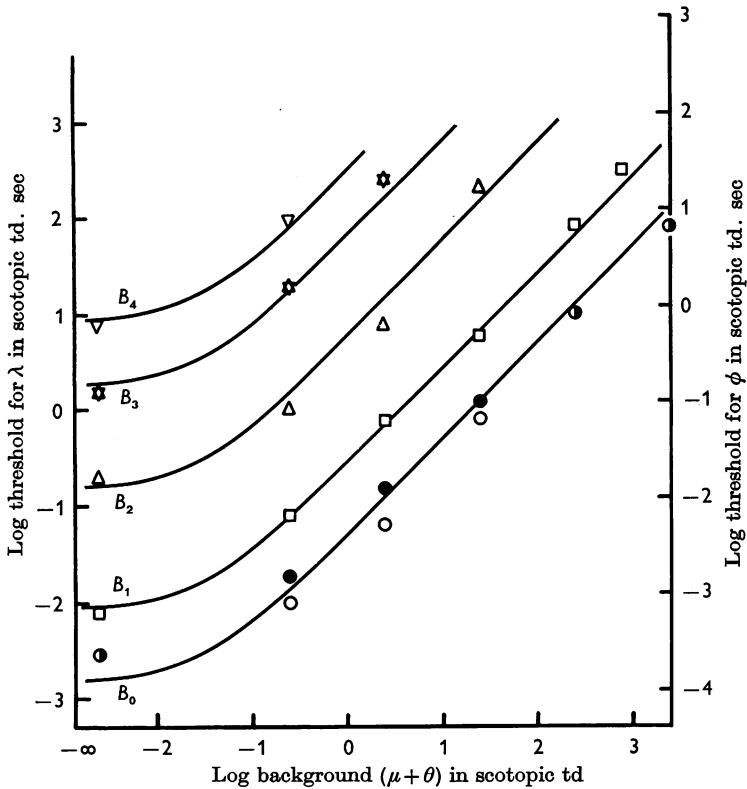


Fig. 5. Black circles (and half circles) log increment threshold for seeing flash ϕ against uniform background ($\mu + \theta$). White circles (and half circles) log increment threshold for seeing λ against the same background. Curves B_1, B_2, B_3, B_4 the log threshold for λ against ($\mu + \theta$) when ϕ has values 1, 2, 3, 4 log units above the threshold shown by black circles. All curves are B_0 displaced vertically upward. Wave-lengths of $\lambda = 527$ nm, $\mu = \theta = 621$ nm, ϕ was 'white'. All the curves drawn in Figs. 5 and 1 have the mathematical formula $\log \lambda = \log (aI + b)$ where λ is the test flash threshold, I the background luminance, and a, b are constants—the Fechner relation.

Analysis

We shall now derive a mathematical expression that describes all the relations of this paper.

- Let λ be the threshold for test flash in any condition;
- λ_0 be the value of λ at absolute threshold;
- ϕ_0 be the absolute threshold for seeing the contrast flash; and
- ϕ be the energy of contrast flash in any condition.

Let the magnitude of adaptation whether by background or bleaching

be defined as the factor by which the visual threshold is raised above absolute by this adaptation. Thus

u is the μ adaptation if the threshold is raised by it from λ_0 to $u\lambda_0$;
 v is the θ adaptation if the threshold for seeing ϕ is $v\phi_0$.

Now as was shown in Fig. 4 of Alpern (1965), in the absence of adaptation, contrast flashes raise the threshold for test flashes on a continuously rising curve that may be described as

$$\lambda/\lambda_0 = f(\phi/\phi_0). \quad (1)$$

In Fig. 1 of the present paper, curve A was obtained with zero contrast flash and thus it represents simply the adaptation to the background. Calling λ_a the threshold of any point on the curve corresponding to the background μ_a , we know from our definition what is the adaptation at that point, for

$$u = \lambda_a/\lambda_0. \quad (2)$$

Curve C on the other hand was obtained with some fixed contrast flash ϕ_c . At the left extremity of this curve the background was zero and hence the condition of eqn. (1) applies. Thus calling λ_c the ordinate of that point we have from (1)

$$\lambda_c/\lambda_0 = f(\phi_c/\phi_0). \quad (3)$$

But the experimental fact is that curve C is curve A displaced vertically upward. Thus the threshold λ of the point on curve C where the background is μ_a satisfies

$$\log \lambda - \log \lambda_a = \log \lambda_c - \log \lambda_0,$$

or

$$\lambda/\lambda_a = \lambda_c/\lambda_0 = f(\phi_c/\phi_0)$$

from (3), and substituting from (2)

$$\lambda/u \cdot \lambda_0 = f(\phi_c/\phi_0). \quad (4)$$

This obviously describes what was found in Fig. 1. For with constant ϕ_c , the right side of eqn. (5) is fixed and we get a defined curve relating λ and u . When ϕ_c changes to ϕ_b , for each u -value, λ changes in some fixed ratio, or $\log \lambda$ by some fixed amount—i.e. curve B is curve C shifted vertically. Since nothing has been said of the *kind* of adaptation to which eqn. (2) must apply, the argument holds equally for bleachings, and the formula may be used to describe also the vertical shifts of Fig. 2.

Turning now to Fig. 3 we may argue in a similar fashion about contrast-flash adaptation. Calling ϕ_a the threshold of any point on curve A_ϕ we have from the definition of adaptation

$$\phi_a = v\phi_0. \quad (5)$$

Now in all the contrast-flash measurements (B , Fig. 3) the flash ϕ was adjusted to be some fixed multiple n of the threshold ϕ_a , thus

$$\phi = nv\phi_0. \quad (6)$$

But the horizontal course of the curves B_0, B_1, B_2 means that a given change of n causes the same change in $\log \lambda$ whatever the background θ , and in particular the same as when $\theta = 0$. In that case we know from eqn. (1) in the absence of adaptation

$$\lambda/\lambda_0 = f(\phi/\phi_0) = f(n).$$

We may write the more general case when $\theta \neq 0$ by substituting for n from eqn. (6) giving

$$\lambda/\lambda_0 = f(\phi/v \cdot \phi_0). \quad (7)$$

If there is also adaptation u in the test area we must combine eqn. (7) with eqn. (4) and obtain the general expression for independent adaptations at test and contrast-flash areas

$$\frac{\lambda}{u \cdot \lambda_0} = f\left(\frac{\phi}{v \cdot \phi_0}\right). \quad (8)$$

This fits the pattern of all the experiments of this paper.

DISCUSSION

Retinal organization

The chief interest of these results is the fact that a fixed contrast-flash raises the log threshold, λ , by a fixed amount independent of the state of adaptation. Neither backgrounds nor bleachings, the two common ways of raising the visual threshold, behaves like this. A moderately strong background or bleach will gently raise the log threshold in the rather dark-adapted state, but will hardly change it in the light adapted condition. Obviously contrast-flashes do not act upon the visual organization like backgrounds or bleachings, and we shall now consider one way in which they might act.

In a recent paper (Rushton, 1965*a*) a somewhat crude model was proposed to describe quantitatively adaptation to backgrounds and bleachings. This '*G-box*' is reproduced here in Fig. 6(*a*). It is seen that backgrounds, I , enter at input, and bleaching signals, B , enter at feed-back. If the contrast-flash entered in the manner either of I or B it would not differ from I or B in the nature of its effect, and so could not cause the observed fixed rise in log threshold.

But if the contrast-flash cannot enter at input or at feed-back it cannot enter the *G-box* at all and must impinge upon the output V somewhere on its course towards the brain, as represented in Fig. 6(*b*).

As was developed qualitatively in Rushton (1965*a*) and more analytically in Rushton (1965*b*), light signals I Fig. 6(*a*) enter the *G-box* at input and suffer a controlled attenuation to emerge as V , which is more or less proportional to $\log I$. This has two destinations, one towards the brain where it may give rise to the sensation of vision, the other is fed

back to the G -box and controls the gain. Thus the greater the I the greater the feed-back signal V , and the greater the attenuation. Hence the greater must be the increment threshold ΔI to produce some fixed increment of output ΔV_0 .

Bleaching adaptation acts in a different way. The bleaching signal was proved to enter the feed-back directly without first going through the box and suffering a logarithmic transformation. This difference in the place of entry fits nicely the experimental facts. For log threshold is raised by bleaching in proportion to B , the fraction bleached, whose signal enters the feed-back directly. But it is raised by backgrounds, not in proportion to the incoming signal I , but to $\log I$ (or V) which is the signal from input that actually passes to the feed-back.

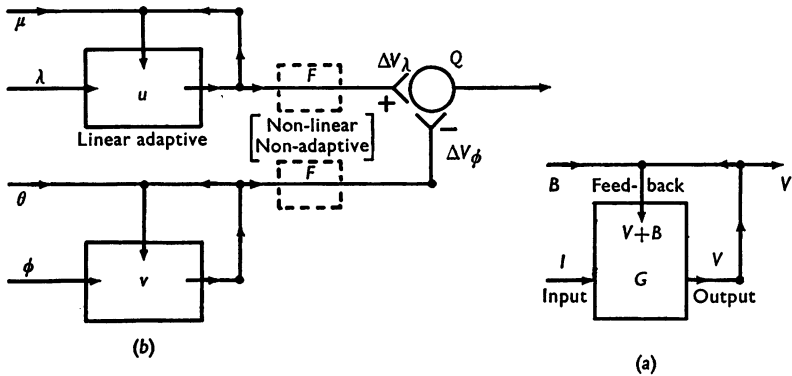


Fig. 6(a) 'G-box' model of visual adaptation. I , light signal input; V , signal output going right towards brain and left to feed-back. B , bleaching signal direct to feed-back. (b) Two 'G-boxes' for λ and ϕ flashes whose outputs transformed by 'F-boxes' interact at Q . ΔV_ϕ signal inhibits ΔV_λ signal.

Model of Fig. 6(b). If the contrast-flash ϕ raises the threshold of λ by impinging upon the λ output at Q , as indicated in Fig. 6(b), then from the experiment of Alpern's (1965) Fig. 4 we know that (a) the stronger the flashes λ , ϕ , the stronger are the output increments ΔV_λ , ΔV_ϕ , and (b) the stronger ΔV_ϕ , the stronger must be ΔV_λ to overcome it and be seen as a visual threshold.

Now in curves B of Fig. 4 of the present paper when ϕ was some constant multiple n of the ϕ threshold during dark-adaptation, the threshold λ (after 7 min) was some constant value; hence ΔV_λ was constant; hence ΔV_ϕ was constant. Thus we conclude that when ϕ is a constant multiple of the visual threshold the output ΔV_ϕ is a signal of fixed size. As a particular case, we may conclude that the visual threshold itself is a signal of fixed size. This has often been assumed; Fig. 4 gives experimental proof.

Now turn to Fig. 2. Curve A (where ϕ is zero) is an ordinary dark-adaptation curve where, as we have just proved, ΔV_λ is constant. Curve C is where ϕ is constant and hence ΔV_ϕ is constant and hence the new ΔV_λ is also constant. Thus throughout A the value of ΔV_λ is one value, throughout C it is another value, and consequently at each moment of dark adaptation, to go from A to C is to change the outputs ΔV_λ in a fixed ratio. But, since between A and C there is fixed vertical displacement of the log thresholds, to go from A to C is to change the inputs λ in a fixed ratio. Consequently for every state of adaptation u a fixed ratio of inputs produces a fixed ratio of outputs. In full dark adaptation when $u = 1$ let the input-output relation be

$$\lambda/\lambda_0 = F(\Delta V_\lambda), \quad (9)$$

where F is any non-linear transformation imposed on the λ -output (see below)

Then Fig. 2 shows that in any other state of adaptation u

$$\lambda/u \cdot \lambda_0 = F(\Delta V_\lambda). \quad (10)$$

This signifies that the G -box in some fixed state u attenuates all inputs λ in the same proportion. This could not easily happen unless the λ signal got through the G -box before a significant feed-back operated.

The adaptation to backgrounds though affecting the G -box by a different entry operates upon the same gain mechanism—there is only one control knob in the box and everything that changes gain has to turn that knob. Thus, equation (10) applies equally whether u is adaptation by bleaching or by background. And, as expected, Figs. 1 and 3 show the same contrast-flash relations as Figs. 2 and 4.

We have seen that for any setting u of the G -box knob there is some fixed attenuation of all the λ signals in passing through the box so we may say that the λ -output is proportional to λ . But it does not follow that the signal ΔV_λ that reaches Q , the point of interaction with ΔV_ϕ , is proportional to λ . The only property of ΔV_λ and ΔV_ϕ that we have used in this paper is that over a certain range of conditions each remained constant. It was argued that when ΔV_λ remained constant the λ -output from the G -box must have remained constant, and this will follow if, interposed between Q and the G -box, there is an F -box shown dotted in Fig. 6(b) that is non-adaptive and imposes upon the λ -output any (monotonic) non-linear transformation F . This has in fact already been incorporated in the mathematical treatment in eqn. (9).

Two awkward questions we leave unanswered, not because they are unimportant, but because we do not know the answers.

(a) Where is the place in the retina (or in the brain) represented by Q where inhibition occurs? And how well does the interaction correspond to the centre-surround inhibition of receptive fields studied by retinal electrophysiology?

(b) What are these signals that pass through the *G*-box so swiftly that they escape the feed-back change in gain that they generate? And how are they so oblivious of time at *Q* that the contrast-flash can exert its inhibition with equal effect when it presented 50 msec *after* the test flash which it inhibits?

Despite these and other unsettled questions, the experiments of this paper have enlarged our views on adaptation by presenting a new and coherent set of relations. The equivalence of bleaching and background has been established in a new situation, and the method of thresholds can now be applied in conditions that have hitherto been considered supra-threshold. If the results may be treated in terms of the model of Fig. 6 (*b*), we may conclude that the condition for a visual threshold is that the output from the adaptive mechanism should be a signal of fixed size, and that in any fixed state of adaptation, all signals are attenuated in a fixed proportion.

The structure of the experimental results is given in equation (8). This is independent of the particular model of adaptation favoured. But to the extent that it is true it must be embraced by all theories of adaptation which aim to explain the facts.

We are grateful to Mr Clive Hood for continued assistance in the work, and to the National Science Foundation (NSFG 10045), the National Institutes of Health (NB 01578) and to the Wellcome Foundation for grants.

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