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THE ATTENUATION OF ROD SIGNALS BY BLEACHINGS

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SUMMARY

1. Contrast flash technique allows the rod threshold to be measured even when it lies far above the cone threshold. In this way the rod dark adaptation curve after rhodopsin bleaching can be measured over 6 log units.

2. By retinal densitometry the regeneration of rhodopsin can be measured in the same subject. It is found that the log threshold is raised 1·2 units for each 10% of rhodopsin in the bleached state.

3. We have tried to discover whether bleaching raises the threshold by desensitizing the rods, or (like backgrounds) by attenuating their signals. Neither suggestion satisfies all conditions.

4. All are satisfied by

$$\frac{1}{N} = 1+\frac{\theta}{\theta_D}+\frac{\sigma}{\phi}\left(10^{12B}+\frac{\theta}{\theta_D}\right),$$

where N is the size of rod signal, constant for threshold; θ, θ_D are steady backgrounds of light and receptor noise; ϕ is the threshold flash with σ a constant of about 2·5 log td sec; B the fraction of pigment in the bleached state.

INTRODUCTION

It is well recognized that the bleaching of rhodopsin raises the threshold of the rod mechanism and that the dark adaptation curve, which plots the recovery of log threshold in the dark, in fact coincides closely with the regeneration of rhodopsin (Rushton, 1961). What is not clear is why or how bleaching raises thresholds. The most natural view is that somehow the rod sensitivity is depressed so that it needs a greater quantum catch to do the same thing. But this cannot be the whole explanation, for there

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are conditions where the effects of bleaching are not imitated by placing a suitable filter in front of the unbleached eye. For instance, in Lythgoe's (1938) brilliant little study of the Pulfrich pendulum, a filter placed in front of one eye makes the plane-swinging pendulum appear a conical pendulum circling in one direction. Bleaching that eye also makes it circle, but in the other direction. So bleaching obviously acts differently from filter interposition.

A more satisfactory view, initiated by Stiles & Crawford (1932) is that bleaching produces a condition of adaptation very similar to that of a luminous veil (or background) of light. And Barlow & Sparrock (1964) have made a case for supposing that the after-image *is* the luminous background against which the test flash has to be seen.

In two recent papers (Alpern, Rushton & Torii, 1970*a*, *b*, which we shall refer to as A.R.T. *a*, *b*), we have used Alpern's (1965) contrast flash inhibition to measure conditions for generating inhibitory signals N of various determined sizes. The results have come out surprisingly simple, and the size of N elicited by a flash ϕ falling upon a background θ is given by

$$\frac{1}{N} = \left(1+\frac{\sigma}{\phi}\right)\left(1+\frac{\theta}{\theta_D}\right), \tag{1}$$

where σ is the semi-saturation constant for flashes and θ_D is the receptor noise (or *eigengrau*) of the background; N is seen to be 1 when $\phi = \infty$ and $\theta = 0$.

We anticipated that the study of bleaching would turn out on the lines of equivalent backgrounds and would fit the pattern of eqn. (1). We knew that there were some difficulties but thought they would turn out to be mistakes or else realities easily understood. They have turned out to be realities not easily understood.

Since we cannot explain, we shall simply describe, and the most compact description is eqn. (2),

$$\frac{1}{N} = 1+\frac{\theta}{\theta_D}+\frac{\sigma}{\phi}\left(b+\frac{\theta}{\theta_D}\right), \tag{2}$$

where $\log b = 12B$ and B is the fraction of rhodopsin in the bleached state.

Equation (2) fits the three well known conditions.

(*a*) In the unbleached state, $B = 0$ therefore $b = 1$, hence eqn. (2) degenerates into eqn. (1), which in the former paper (A.R.T. *b*) we showed held over the full range of ϕ and θ.

(*b*) The ordinary dark adaptation curve is measured against a dark background ($\theta = 0$) with ϕ much less than σ. Hence, eqn. (2) becomes

$$\phi = N\sigma b.$$

In full regeneration $b = 1$, thus the absolute threshold, $\phi_0 = N\sigma$.

Hence, $$\log(\phi/\phi_0) = \log b = 12B. \quad (3)$$

This is the relation between log threshold and bleaching.

In Fig. 4 we demonstrate its validity in normal man over a threshold range of 6 log units.

(*c*) In the usual conditions where bleachings and backgrounds interact, ϕ is much less than σ and eqn. (2) becomes

$$\phi = \frac{N\sigma}{\theta_D}(b\theta_D + \theta). \quad (4)$$

In this form of eqn. (2), b enters with θ_D as a luminous background, a large multiple of θ_D, the receptor noise or 'dark light' as Barlow (1964) has described it. In eqn. (4) the dark light simply adds to θ, the real background light. Blakemore & Rushton (1965) have shown that this is what actually happens.

METHODS

The apparatus and procedures are those described in the previous papers (A.R.T. *a*, *b*). The spatial arrangements are shown in Fig. 1 inset. The 2° blue test flash λ (and, when used, its red background μ) were seen by rods in the temporal retina on the horizontal meridian 6° from the fovea. The surround flash ϕ (and its red steady background θ) with 8° outside diameter was concentric with λ but blacked out in the central region just slightly larger than the test flash area. In some experiments a 4-vane windmill (Fig. 2*b* of A.R.T. *a*), each vane a sector of 11¼°, replaced the full 360° annular surround flash. ϕ was flashed for 100 msec, beginning 100 msec after the onset of λ which lasted for 10 msec. Successive exposures were initiated with subject's control from a microswitch.

As before, ϕ, θ and μ beams entered the pupil through its centre, but λ entered through the bottom edge taking full advantage of the absence of a Stiles–Crawford effect for rods in order to keep the test flash exciting rods at as high an intensity as possible.

Rhodopsin was bleached in the surround area by presenting the ϕ light for 45 sec with sufficient filters interposed to give a total energy of 7·3 log td.sec.

RESULTS

1. *Dark backgrounds*

As we have noted, the effect of rhodopsin bleaching may be regarded either as a desensitization of the rods or the generation of 'after-image light' which raises the threshold just as a real background does. Our contrast flash threshold technique allows us to settle this in a simple situation, namely when no luminous backgrounds are present to assist in threshold raising. The technique (A.R.T. *a*, *b*) consists in finding how the threshold for flash λ (inset Fig. 1) is raised by a surround flash ϕ. In A.R.T. *a*, we measured the size of the inhibitory signal N as a function of ϕ and showed it to be given by

$$N = \phi/(\phi + \sigma)$$

and when a 'windmill stop' was introduced which reduced the surround area to $\frac{1}{8}$ (with radial symmetry)

$$N = (\tfrac{1}{8})\,[\phi/(\phi+\sigma)].$$

Fig. 1 shows how these results may be applied to solve the nature of bleaching desensitization. Curve A represents curve A of Fig. 4 (A.R.T. *b*) which plots log N against log ϕ. In that Figure the effect of steady background θ was to displace A vertically downwards, e.g. to B, the displacement being proportional to log θ. Consequently if that experiment is

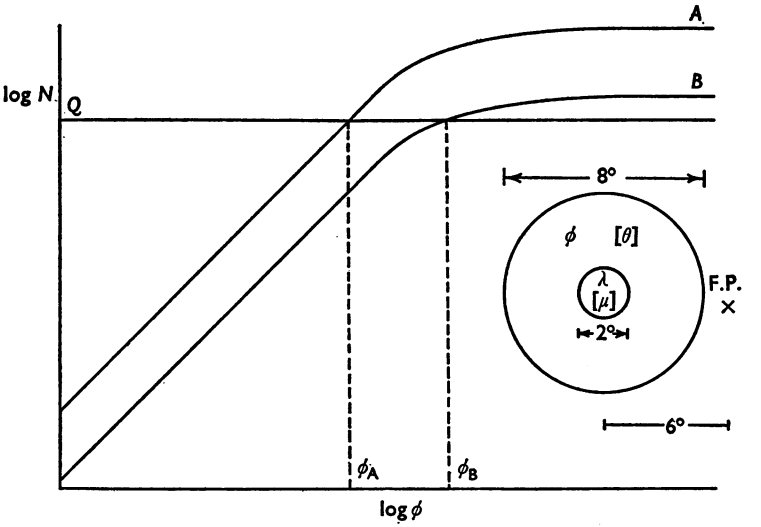

Fig. 1. Inset: spatial arrangement of target display. Fixation point (F.P.) shown for experiments on right eye. Test flash λ was blue (Ilford filter 622) lasted 10 msec and sometimes fell upon a steady red background μ. Contrast flash ϕ was white, started 100 msec later than λ, lasted 100 msec and sometimes fell on red background θ (Schott Jena RG-2 filter). Curves A and B to illustrate the experimental plan.

repeated with bleaching instead of background applied to the surround, then curve A will again be displaced vertically downward, provided that bleaching does act like a background. If, however, bleachings act by desensitizing the rods so that it needs an n-fold increase in flash to produce the same effect, then curve A will be displaced, not downwards but to the right, by a distance log n. Our experiment is therefore to bleach the ϕ area and see whether this displaces the curve downwards or to the right.

In order to make the experiment clearer in its significance, we performed two sets of measurements, one with, the other without, interposition of the windmill stop that reduces N to N/8. The background θ was zero throughout. Consider now that B, Fig. 1, is the log N curve reduced not by

θ but by the windmill that displaces it down a distance 0·9 (= log 8). If the test flash is brought to threshold when log N has the value Q (Fig. 1), it will just be inhibited by flash ϕ_B when the windmill is interposed and by ϕ_A when it is not. If bleaching acts like the backgrounds of (A.R.T. *b*) Fig. 4, both A and B will be displaced downwards and ϕ_A will have to be increased to mark the new intersection of A with the fixed Q criterion; but a small depression will stop B from intersecting Q at all and thus infinite ϕ_B will still not produce the required threshold inhibition. If, on the other hand, curves A and B slide to the right, the dotted verticals through ϕ_A and ϕ_B will remain the same distance apart. This in fact is what is found to occur.

The experiment was conducted as follows. The subject with dilated pupil was aligned in the apparatus with the windmill stop interposed. Using a very strong ϕ flash, the λ flash was brought just to threshold. Now λ was made 0·15 log units weaker than this and kept at that value throughout the experiment (the Q level of Fig. 1). Now ϕ was adjusted so that this λ was just at threshold, giving ϕ_B when the windmill was in, ϕ_A when out. The bleaching was a 45 sec exposure to white light that bleached 90 % of rhodopsin. Naturally, some of this light spread to the test area and raised the λ_0 threshold there in the absence of ϕ. After 7 min, however, the λ_0 threshold had returned to the dark value and so the effect of the ϕ flash upon λ could be seen uncontaminated. At this stage ϕ flashes were adjusted just to suppress the fixed λ flash, with the windmill stop alternately out and in; the ϕ_A, ϕ_B so measured is plotted against recovery time by white and black circles of Fig. 2. The same curve (vertically displaced) is drawn through both sets of points.

As argued above, if the curves of Fig. 1 were displaced to the right by bleaching, $\log \phi_B - \log \phi_A$ would remain constant. Thus the black circles of Fig. 2 should lie a fixed distance above the white at all stages of recovery. The curves A and B so drawn fit the points reasonably well. If, on the other hand, bleachings (like backgrounds) displaced the curves of Fig. 1 downwards, a very little bleaching would depress B below the criterion level (Q) so that no flash ϕ_B however strong could inhibit. In this case the black circles of Fig. 2 should lie above the top of the figure until the white circles had returned to within 0·15 of their resting value, after more than 20 min. The facts of Fig. 2 sharply contradict this but they accord perfectly with eqn. (2) when $\theta = 0$.

For curve A, Fig. 1 the relation is

$$\frac{1}{N} - 1 = \frac{\sigma b}{\phi_A}, \tag{5}$$

for B,

$$\frac{1}{8N} - 1 = \frac{\sigma b}{\phi_B}.$$

Dividing one equation by the other gives ϕ_B/ϕ_A as an expression independent of b, consequently $\log \phi_B - \log \phi_A$ is a fixed distance throughout dark adaptation. But each curve of Fig. 2 follows the curve obtained by dividing eqn. (5) by the expression it assumes in the unbleached state when $b = 1$ and ϕ_A becomes ϕ_0.

$$\log (\phi_A/\phi_0) = \log b = 12B.$$

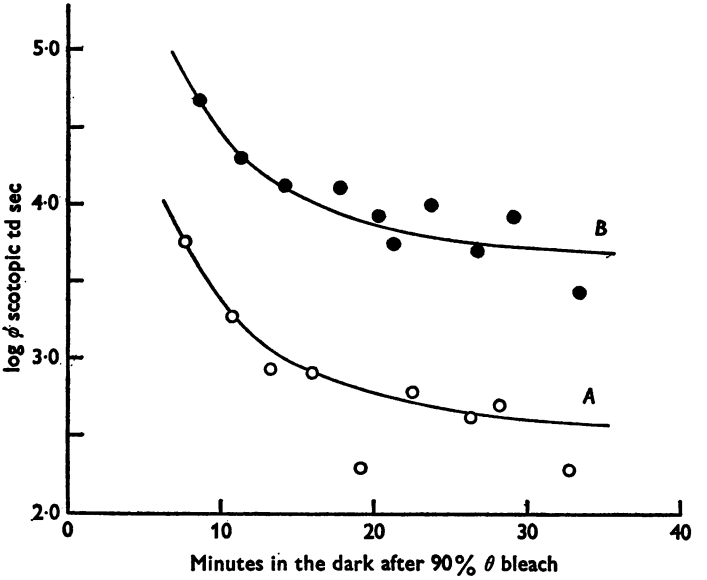

Fig. 2. Dark adaptation of ϕ measured by the criterion of the production of a fixed signal N that just inhibits the fixed test λ. A when ϕ falls on full annular surround; B when windmill is interposed in ϕ flash, but not in bleaching beam. Curve A is curve B vertically displaced.

Thus, curves A and B of Fig. 2 should coincide with ordinary dark adaptation curves. This correspondence is examined in detail in the next section where we confirm the present conclusion, namely when backgrounds are zero, the effect of bleaching is as though receptors are desensitized in proportion to 10^{-12B}, where B is the fraction of rhodopsin bleached.

2. *Bleachings and backgrounds*

There is difficulty in measuring the rod threshold when it lies above the cone threshold, for cone sensation is so dominant that many have even thought that rods are 'inhibited' by the cones. Our contrast flash technique is a powerful tool for isolating rod thresholds, and Fig. 3*A* shows rod dark-adaptation curves over a 6 log unit range, and Fig. 3*B* shows increment threshold curves running up to full saturation without a cone

break though both are far above the cone threshold. The principle was described and applied in the former paper (A.R.T. *b*, Fig. 8), but we briefly mention it again.

Alpern (1965) and Alpern & Rushton (1965) showed that contrast flash inhibition is receptor-specific, thus if rods are the receptors excited at threshold by λ (the test flash at centre, Fig. 1 inset) it is only the rods excited by ϕ (the surround flash) which inhibit them. The cones in the surround are also excited by ϕ and are often excited more strongly than

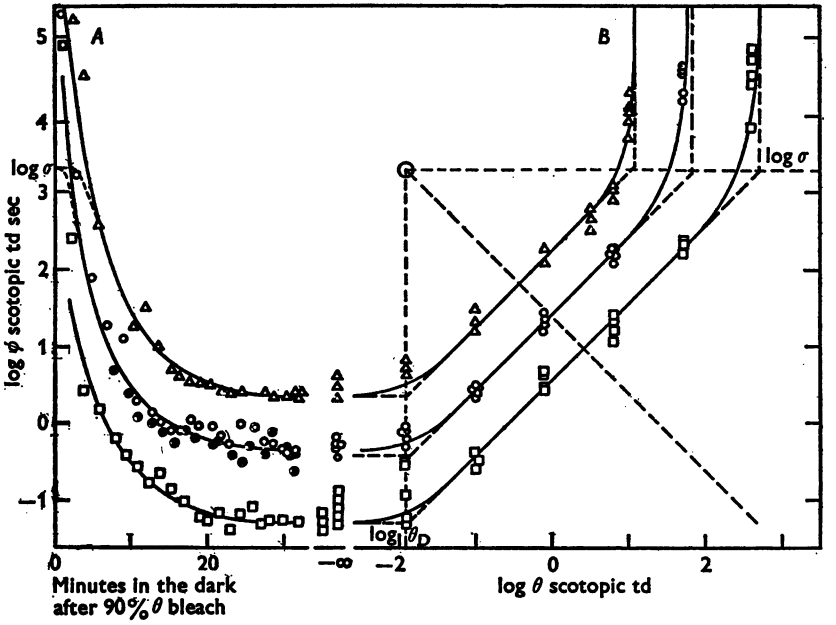

Fig. 3. *A*. Dark adaptation curves for ϕ with the same criterion as in Fig. 2, namely, that ϕ just inhibits λ whose value is fixed at 0·3 (squares), 0·6 (circles) or 0·9 (triangles) log units above threshold.

rods, but their action is only to raise the *cone* threshold at centre; the rods are unaffected by them. Thus, by keeping the test threshold λ on rods we ensure that the inhibitory signal measured is a rod signal and by adjusting the contrast flash ϕ in all conditions to produce a constant log threshold rise (log λ_1) in the test threshold, we ensure that ϕ is always generating a fixed rod-inhibitory signal. In Fig. 3*A* we have made the surround insensitive by bleaching it, in 3*B* by illuminating it with steady background lights. These are conditions where the threshold for seeing the flash ϕ itself is raised and has often been investigated. But conventional measurements break down when the cone threshold is reached. By using as criterion for ϕ threshold, not the constant signal necessary to see ϕ, but the constant

inhibitory signal N generated by ϕ, we may obtain the full range of rod thresholds shown in Fig. 3.

The inhibitory signal N is measured by the rise of threshold test λ at centre, and if nothing else raised the λ threshold the observed increase log λ would be the inhibition, due to the ϕ signal. But log λ is raised to log λ_0 in the absence of ϕ flash by the bleaching or the bright background of the surround region which cannot be confined exactly to the annulus but scatters somewhat into the centre. Fortunately, the observations of Alpern & Rushton (1967) allow us to compensate for this. They found that when bleaching or background was applied to the central area itself and raised the threshold by log λ_0, then it also raised the contrast flash threshold by log λ_0 so that

$$\log \lambda = \log \lambda_0 + \log \lambda_1. \tag{6}$$

In the present experiment we measure in rapid succession (*a*) the threshold λ_0 where ϕ is zero, and there is a fixed filter (say 0·6) also in the beam, (*b*) now the filter is removed so the test appears much brighter and it is reduced to threshold by adjusting the intensity of ϕ. Clearly, for each pair of measurements (*a*, *b*) log λ in (*b*) is 0·6 greater than log λ_0 in (*a*), hence from eqn. (6) log λ_1 is always 0·6 and hence the inhibitory signal N is always at a fixed level. By using different filters the N criterion level may be selected at will. In Fig. 3 squares correspond to 0·3, circles to 0·6, and triangles to 0·9 filter in the λ beam when λ_0 was measured and then removed to obtain λ_1.

The subject with dilated pupil was aligned in the apparatus and his annular region ϕ (inset, Fig. 1) was exposed for 45 sec to a strong white bleaching light. During this time he fixated as steadily as possible since it was important that the central region should not be much bleached. The after-image was later seen to encroach a little upon the 2° centre, which should have been spared, but most of the centre appeared free.

Bleaching of rhodopsin obeys the Bunsen–Roscoe law, $I.t = k$, up to 45 sec (Campbell & Rushton, 1955), and within this time the fraction p of pigment left unbleached is given (Rushton, 1956, 1961) by

$$\log \log 1/p = \log I.t - 7{\cdot}3 \quad \text{(in td sec)}.$$

We use a bleaching energy $I.t$ of 7·3 log td sec. Consequently, log $1/p$ = antilog 0 = 1, and hence the pigment is 90 % bleached.

Immediately after bleaching, threshold measurements were made as rapidly as was consistent with accuracy, first λ_0 (where ϕ is zero), then immediately with the interposed filter removed so that log ϕ could be measured with steady N criterion level. Fig. 3*A* plots the dark adaptation curves in conventional manner. After 40 min, curve *B* was determined by

projecting onto the annular surround steady lights of increasing strengths and measuring the increment threshold by the same criterion as in A, namely by finding λ_0 with ϕ zero, removing the same filter used in A, and adjusting ϕ so that this λ flash was reduced just to threshold. This second part is identical with that of Fig. 8 of the former paper (A.R.T. *b*) whose curves are quite similar to Fig. 3B here.

Note. The value of σ in these curves is 3·2 log td sec as compared with 2·6 in Fig. 8 (of A.R.T. *b*), obtained from the same subject. In all our experiments of many kinds, we have found a variation in σ value over about 1 log unit. We have not been able to satisfy ourselves as to the cause.

Our technique ensures that cones do not enter, thus no cone branches are seen in any curve, though the rod threshold is plotted over 6 log units. The same exponential curve is drawn through all the dark adaptation results. The points lie slightly above this curve during the first few minutes after bleaching. The relation between the dark adaptation curve so determined and the regeneration of rhodopsin is shown in Fig. 4, where black and white triangles plot the fraction of rhodopsin still bleached and the circles show the log contrast flash threshold. The pigment of the same subject (S.T.) was measured for us on two successive days by Dr Anne Fulton using our new Florida densitometer (W. A. H. Rushton & C. Hood, to be published) which in principle is similar to the old Cambridge instrument (Rushton, 1956). The pigment was fully bleached using a light three times as strong as in Fig. 3. Fig. 4 shows for the first time on a normal human eye that log threshold is raised after bleaching in proportion to the amount of pigment unregenerated and that this applies over the whole millionfold range of thresholds that can be covered by both measurements. It is seen that 50 % bleaching raises the threshold 6 log units. A similar comparison on the dark adaptation curve of a rod monochromat (Rushton, 1961) gave 8 log units for the visual threshold rise at 50 % bleach (slightly extrapolated).

In Fig. 3 the equivalent background may be found by comparing curves A and B. So long as B lies on the 45° Fechner line, the threshold is proportional to the background and both equally represent the relation to bleaching. But as curve B rises above the Fechner line, backgrounds no longer increase as fast as threshold does, and as log ϕ approaches saturation log θ comes to rest. Consequently when we plot curves A in 'equivalent θ values', they also come to rest as time in the dark is reduced to zero, as shown by the dotted curves that level out at log σ. Clearly the 'equivalent background' is a serious misrepresentation of dark adaptation at the highest ϕ values; the saturation bend of the B curves introduces a distortion in the log threshold curve, which in the simple undistorted A plot fits so well the rhodopsin measurements of Fig. 4.

Though the two sides of Fig. 3 do not correspond throughout to the equivalent background concept, they correspond perfectly with our formula

$$\frac{1}{N} = 1+\frac{\theta}{\theta_D}+\frac{\sigma}{\phi}\left(b+\frac{\theta}{\theta_D}\right). \tag{2}$$

In curves A, $\theta = 0$ and $1/N = 10^4$ or more so that 1 is negligible.

Thus $$\phi = \sigma N b,$$

or $$\log(\phi/\phi_0) = \log b = 12B,$$

as we saw in eqn. (3).

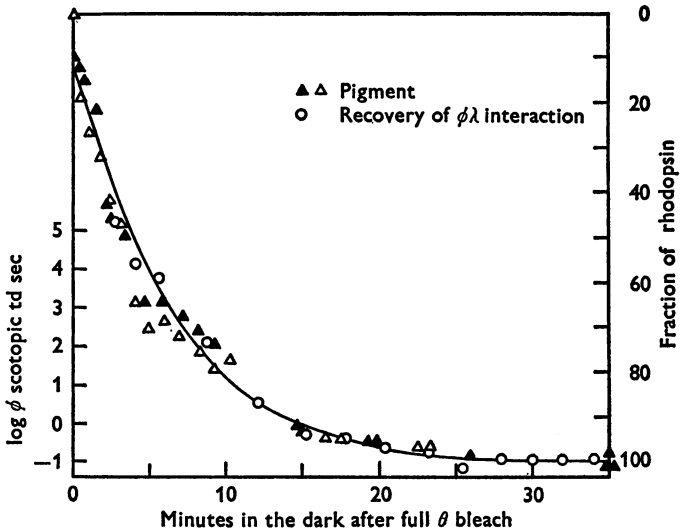

Fig. 4. Circles, ϕ dark adaptation curve similar to squares of Fig. 3 but with 3 times the bleaching intensity. Triangles, regeneration of rhodopsin after identical bleaching exposure measured by retinal densitometry (rhodopsin scale at right). The curve is an exponential with half-time of 4·5 min.

Figure 3A shows the vertical shift in log ϕ curves expected with change in N, and Fig. 4 demonstrates the linear relation of log ϕ to B. In Fig. 3B, $b = 1$; thus eqn. (2) becomes

$$\frac{1}{N} = \left(1+\frac{\theta}{\theta_D}\right)\left(1+\frac{\sigma}{\phi}\right)$$

which describes the symmetrical curves reflected in the $-45°$ line as discussed in our former paper (A.R.T. b).

DISCUSSION

The experiments of this paper do not combine bleaching and backgrounds simultaneously. Bleachings without background behave as though the rods were desensitized by the factor $b = 10^{12B}$. Unfortunately, this simple idea is not easy to reconcile with the results where backgrounds are also present or where test flashes of various areas are involved. In this whole range of conditions (the test flash being well below saturation) the concept of equivalent background or after-image light is valid and meaningful.

We have referred to Lythgoe's (1938) Pulfrich pendulum analysis; Crawford's (1947) comparison of dark adaptation with increment threshold using test areas of different sizes is well known. Blakemore & Rushton (1965) showed that the after-image light simply added to real light in its threshold-raising effect in the condition most sensitive to measure this (i.e. when the two are equal); and Barlow & Sparrock (1964) both measured the after-image brightness in cd/m^2 by comparing it with a stabilized real light and showed that when those two lights looked equally bright they raised equally the threshold of a superimposed test flash. Thus the idea that bleaching raises the threshold by generating a luminous background (the after-image) has a great body of evidence in its support. That is why we were somewhat dismayed to find in experiment I of this paper that bleaching certainly did *not* act as a luminous background. We had already shown (A.R.T. *b*, Fig. 4) that the log N curve, Fig. 1, is displaced downwards by a luminous background; bleaching moves it to the right. It seems certain that in this experiment bleaching acts like rod desensitization and not like an equivalent background.

Our eqn. (2) describes all our observations as exactly as we have been able to make them, but the formula is not easy to interpret, and can only be regarded as a compact parcel of trouble.

Figs. 3 and 4 accord better with conventional views and show how effectively the contrast flash technique may be used to study rod function far above the cone threshold. The view (still advanced) that rods are 'inhibited by cones' as soon as the rod threshold exceeds that of cones, becomes as hard to sustain in face of our bleaching results (Fig. 3) as it has been for the past 15 years in face of Aguilar & Stiles' (1954) increment threshold curves.

We cannot insist, however, that the dark-adaptation results of Fig. 3 correspond precisely to those of a 90 % bleach. There is little doubt that the annular ϕ area was 90 % bleached but the inhibitory signal N is not generated equally from all parts of that area; the ring contiguous to the 2° λ area certainly has a stronger contribution than rings more distant

from the centre. Now as Rushton & Westheimer (1962) showed by bleaching in stripes by means of a grating, the log threshold at any point is raised by the *average bleach* over the $\frac{1}{2}$–1° area surrounding that point. Thus, in considering the rise in inhibitory flash threshold of Fig. 3, we must give greatest weight to the inner ring of the ϕ area, and the *average bleach* of that ring will be diluted by the outmost ring of the λ area where the bleaching was intended to be zero. Consequently, the dark adaptation curves of Fig. 3 probably correspond to those taken in the centre of a large area bleached not 90, but 60 %.

In Fig. 4, on the other hand, the bleaching light was 3 times as intense and probably scattered so far towards the centre that this diluting outer λ ring was also bleached.

Thus in Fig. 4 the recovery following full bleaching measured by densitometry is matched against a very similar condition measured by contrast flashes. The log threshold seems raised throughout by a factor equal to 12 times the fraction of rhodopsin in the bleached state.

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