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THE EFFECT UPON THE ROD THRESHOLD OF BLEACHING NEIGHBOURING RODS

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Ever since Kohlrausch (1922) plotted upon a logarithmic scale the visual threshold during dark adaptation it has been plain that the curve consists in general of two branches, the earlier due to cones, the later to rods. In the present paper we shall be concerned with the rod branch. Following strong light-adaptation this branch starts at the kink after 10–15 min of dark-adaptation, and in the course of the next half hour the threshold drops about 2·5 log. units (Fig. 2). In this paper we enquire what change has occurred in the mechanism of visual excitation as a result of exposure to strong light, such that during the next half hour a flash near the absolute threshold will not excite vision, but a much stronger light will.

Adaptation to strong light certainly bleaches away the rhodopsin and hence diminishes the quantum-catching power of the rods, but this turns out to be a small factor in the rise of threshold observed. For in experiments where rod threshold and rhodopsin were both measured together during dark adaptation (Rushton, 1961*a*) it was found that, when the threshold was still 2 log. units above the final dark value, the rhodopsin was already 90% regenerated. Decline in quantum-catching would raise the threshold to 1·1 times absolute, but the threshold rose a hundred-fold. Clearly the quanta which are caught are for some reason far less effective to elicit vision after light-adaptation.

We know from the pioneer work of Hecht, Shlaer & Pirenne (1942) that a *rod* may be excited by the absorption of a single quantum, but that at least five rods must be simultaneously excited for vision. This means that at least five rods must synchronously send their signals to some integrating centre which may be called '*the summation pool*'.

It thus appears that in early dark-adaptation quanta which have been caught are ineffective for vision either (*a*) because it now needs (on average) more than one caught quantum to set up a rod signal, or (*b*) because many more than five signals must combine at the pool to elicit vision. Obviously

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(*a*) and (*b*) are not mutually exclusive. We shall refer to (*a*) as 'the change in threshold for a rod signal', to (*b*) as 'change in threshold of the pool', and we shall use the common expression 'rod threshold' in the ordinary way to signify the intensity of flash necessary to elicit vision without discriminating between (*a*) and (*b*).

Explanation (*a*) is commonly held, and Wald's (1954) compartment hypothesis is one form of it, but the attempt of this paper to decide between the two seems to favour (*b*).

LIGHT ADAPTATION

The experiment in principle

We might discover whether the rise in rod threshold is due to a change in the rod or in the pool if we could bleach some rods of the pool and then find the threshold change for a flash of light applied to the other rods of the pool which had not been bleached. According to (*a*) in its extreme form, if these rods had received no bleaching light at all, their threshold would not have changed at all; thus they would exhibit the full dark-adapted threshold from the outset. According to (*b*) in its extreme form, the threshold would be raised equally, whether measured upon rods that had been bleached or those that had been spared, for both measure equally the threshold of the pool, and the threshold for rod signals never changes.

Naturally there are considerable difficulties in performing this experiment in practice. It is impossible to bleach some rods and entirely to spare their neighbours, because of diffraction, scatter and other imperfections of the retinal image; and eye movements make it hard to localize satisfactorily the bleached and spared regions. However, the differences to be expected upon mechanism (*a*) and (*b*) are very great, and in fact they transcend the imperfections of our method, which schematically is as follows:

Experimental schema

The bleaching light was an electronic flash which lasted less than 1 msec and was applied to the eye in Maxwellian view at such intensity that it probably bleached more than half the rhodopsin. Interposed, and in sharp focus upon the retina, was a grating of black and transparent equal stripes, so that the retina was 'bleached' and 'spared' in parallel strips each of 0·5° subtense. The dark-adaptation curve was then obtained by means of brief test flashes subtending a circular area of 3° diameter. It is plain that according to mechanism (*a*), the 'bleached' rods will have their threshold so much higher than the 'spared' rods that the latter alone will contribute to the dark-adaptation curve until the absolute threshold is nearly reached.

For comparison, a second and similar region of the retina was bleached

with a similar flash except that, instead of the grating, a neutral 0·4 density filter was interposed, this being found to transmit the same total light as the grating. Dark-adaptation in the two regions was measured with test flashes which resembled the bleaching flashes but the other way round, i.e. the uniformly bleached area was tested with the grating interposed, and the stripe-bleached area with 0·4 density filter interposed. These two tests are equivalent as to spatial distribution both on mechanism (*b*), where only the light total is significant, and on (*a*) where both tests stimulate the retina in similar strips. Thus any difference found in the dark-adaptation curves from the two regions lies not in the test but in the state of adaptation of the regions tested.

It turns out that there is no detectable difference in the two dark-adaptation curves—a result not easy to reconcile with mechanism (*a*) but which is more or less what (*b*) requires.

METHODS

The subject sat biting upon a dental impression with his head further immobilized by a forehead rest, and his pupil and accommodation paralysed by a drop of Cyclogil in the conjunctival sac.

Bleaching and test flashes were delivered by electronic flash discharges from S_1, S_2 respectively (Fig. 1), focused on to the pupil by the lens L. S_1 was covered with a thin diffusing sheet, so that the image at the pupil was uniform and filled it. The mirror M was removed when the bleaching flash S_1 was delivered. S_2 flashed repeatedly every 1 sec; both flashes lasted less than 1 msec.

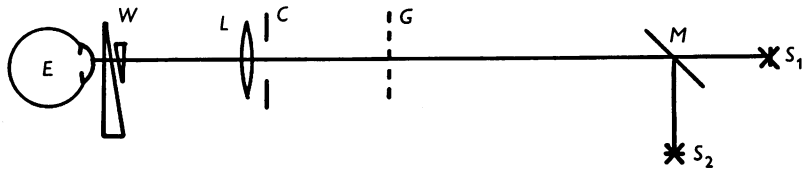

Fig. 1. Arrangement for sending flashes into the eye. M mirror, S_1 bleaching flash (with M removed), S_2 test flash, L Maxwellian lens, C stop, G grating or 0·4 neutral filter, W photometric wedge, E subject's eye.

The grating G was placed at such a distance behind L that it was in sharp focus for the subject. The iris stop C was opened for S_1 to give a bleached circle of 3·7° radius. For test flashes S_2 the stop was closed down to a radius of 1·5°. There were usually two fixation points, one above and one below L, at a displacement 4·5° from the centre of the lens. A calibrated photometric wedge W, operated by the subject, controlled the intensity of the test flash. The subject was properly aligned and given preliminary dark-adaptation. Bleaching was then applied to the upper and lower retinal regions by firing the flash S_1 three times at 15 sec intervals. The first was a blank, fired with the object of securing that both subsequent bleaching flashes should be similar by being fired at the end of exactly 15 sec of charging.

The second and third flashes differed, as shown in the inset to Fig. 2. With (say) the upper fixation point, the grating was interposed in the bleaching flash. With the lower point the 0·4 density was interposed instead. Dark-adaptation was measured by means of test flashes, as shown in the insets by smaller circles; the lower had the grating interposed in

the test flash, the upper had the 0·4 density. The subject was told to fixate upon one or other of the points (usually the two in alternation) and he adjusted the wedge *W* until he could not or could only just see something flashing. He grunted when he was satisfied and the operator noted the time and wedge setting and then gave instruction for the next fixation.

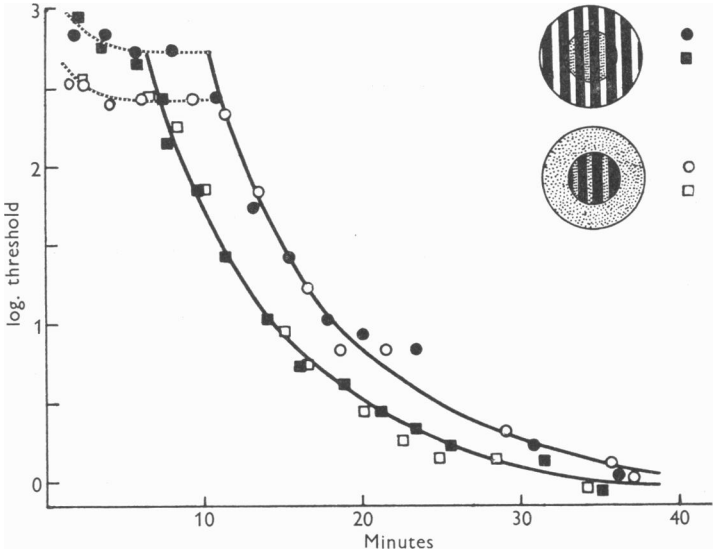

Fig. 2. Dark-adaptation curves showing cone and rod branches. Circles after mean bleaching flash of about 7 log. td sec; squares after bleaching with additional 0·5 density filter interposed. Insets: Large circle shows bleaching field with grating or uniform light distribution: small circle shows test flash with light distribution reversed. Bright and dark bars of grating each subtend 0·5°.

RESULTS

Figure 2 shows one set of curves with our best subject, R.L.G., best not only because he was very reliable but because he had a very large summation area for rods, which makes this experiment clearer in its conclusions. The curves are plotted in the usual way, log. threshold against time.

Consider first the black and white squares. As indicated in the explanatory inset, the black squares show dark-adaptation after a full bleaching flash with 0·5 neutral filter, together with the grating, interposed, the test flash having 0·4 neutral filter interposed. The white squares show adaptation after bleaching with 0·5 + 0·4 neutral filter in the full flash and the grating in the test. The two curves coincide about as well as the accuracy of the work permits, and all the measurements we have made, including those with three other subjects, confirm this general conclusion.

It is not what would be expected if the mechanism of light desensitization was (*a*) above, namely a change in the threshold for the rod signal. For the strip of retina which lay under the dark bar of the grating image

must have received a bleaching illumination less than the average over the whole illuminated patch, and hence less than that in the comparison patch. The rhodopsin in this strip must therefore have been less bleached than in the uniform region, except for one possibility. If the bleaching light was so strong that even the shaded strip was fully bleached, obviously all parts of both patches would be totally bleached and no difference in dark-adaptation could be expected. This interpretation is excluded by the circles of Fig. 2.

White and black circles represent results exactly similar to white and black squares, except that the 0·5 neutral density filter was removed from the bleaching flash so that the bleaching was about three times as strong as in the former experiment. Obviously, if the weaker light had already produced complete bleaching everywhere, the stronger light could have done nothing more; but that is not the result of Fig. 2. The circles lie upon a curve which is shifted 4 min to the right of the squares, and this corresponds roughly to twice the amount of average bleaching. And the black and white points still lie upon the same curve. The shaded strip must have been less bleached than average, yet its threshold is not detectably lower.

Though it is clear that the shaded strip must be illuminated less strongly than average, it is not clear by how much less. If light spread, due to diffraction, scatter, etc., introduced so much blurring into the optical image that the light–dark modulation was very poor, the bleaching of the shaded strips might hardly differ from average bleaching, and hence the black and white points of Fig. 2 could show very little separation. In order to appreciate the significance of our experiment the modulation of the retinal image must be measured. This we have done by a slight modification of the method of Westheimer & Campbell (1961, 1962).

PHYSICAL ANALYSIS OF THE RETINAL IMAGE

METHODS

The principle is to form upon the retina of the subject a sharp image of the brilliantly illuminated grating *G*, Fig. 3. The ophthalmoscopic image is reflected in the beam-splitting pellicle *P* and brought to a focus in the plane of the slit *S*, the distances *PS* and *PG* being equal. Behind the slit, which is very narrow and accurately parallel to the bars of the grating, is a photomultiplier tube *P.C.*, whose d.c. output is recorded as vertical deflexion of an oscilloscope. The grating *G* is mounted so that it may move across the beam in the plane of the paper; thus bright bars shift into positions formerly occupied by dark bars. The movement is driven mechanically with an amplitude of about 6 cycles of the grating, and the movement is linked by a potentiometer to the horizontal deflexion of the oscilloscope, so that a tracing such as Fig. 4 (*B*) is obtained. Obviously, as the grating moves its image on the retina moves, and the aerial image in the plane of the slit moves across it, giving the phases of bright and dark bands shown in Fig. 4.

It is important to know the point upon the vertical deflexion which corresponds to zero

light reflected from the retina. This is not obtained by blocking the slit or extinguishing the ribbon source F, Fig. 3, for some light gets to the slit that has never been in the eye, and would still deflect the oscilloscope if a retinal image of zero luminance were projected upon the slit.

We obtained an estimate for the zero point by removing the subject and replacing the lens L_2, which brought the grating G into focus upon his retina, by another lens which formed an image of G about 100 cm behind the instrument, where it was received upon a white card. Since the card and G are conjugate foci, the card and the slit S are also conjugate foci after reflexion in P. The record of Fig. 4A shows the oscilloscope deflexion with card substituted for eye as described. Though the card reflects far better than the fundus oculi very little of the diffuse reflexion reaches the pellicle; thus the amplitude of the upper record is small. The luminance ratio of bright and dark bars upon the card was certainly greater than 10:1; thus the horizontal line passing through the troughs of the record lies above the level of zero luminance by less than 1/10 the amplitude of the record. The same zero line is reproduced in Fig. 4B and shows the level to which the output would have fallen if the dark bars of the grating had screened the retina completely.

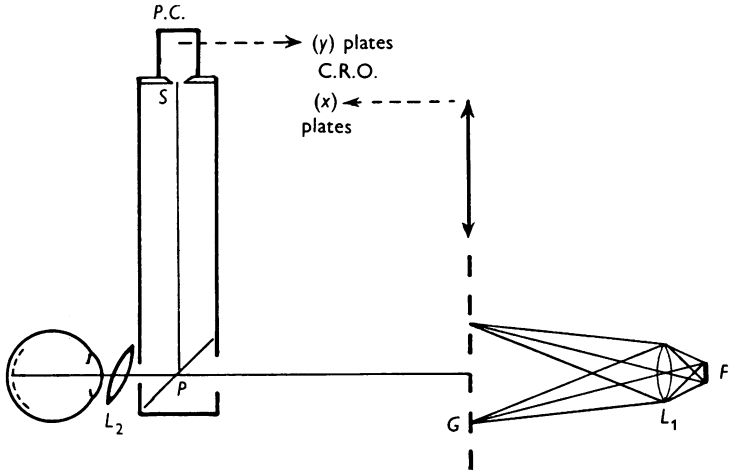

Fig. 3. Arrangement for measuring modulation grating image on retina. F, ribbon filament imaged by L_1 on to the vertical bars of G, the grating, which are brought to focus upon the retina by oblique lens L_2. P, half-reflecting pellicle forming an aerial image of retina at S a fine vertical slit, behind which is photocell $P.C.$, with output to y plates of C.R.O., the oscilloscope.

RESULTS

The record of Fig. 4 is taken from the subject R.L.G., who gave the results of Fig. 2, and the conditions of image formation were the same in both cases, e.g. dilated pupil filled with a uniform light, grating with same angular subtense, etc.

Calling the amplitude from the base line to *mean* height unity, it is clear that a geometrically perfect image would have amplitude 1 ± 1; the image recorded has $1 \pm 0{\cdot}75$. This is the image at the slit S, and it has been blurred both on entering the eye and on leaving it. Since these two paths

are equivalent, each will contribute equally to blurring. Thus, if on the inward path the modulation was $1 \pm 0{\cdot}87$, the modulation at S would be $1 \pm (0{\cdot}87)^2 = 1 \pm 0{\cdot}75$. Since this is the modulation recorded at S, we infer that $1 \pm 0{\cdot}87$ represents the light actually upon the centres of the retinal

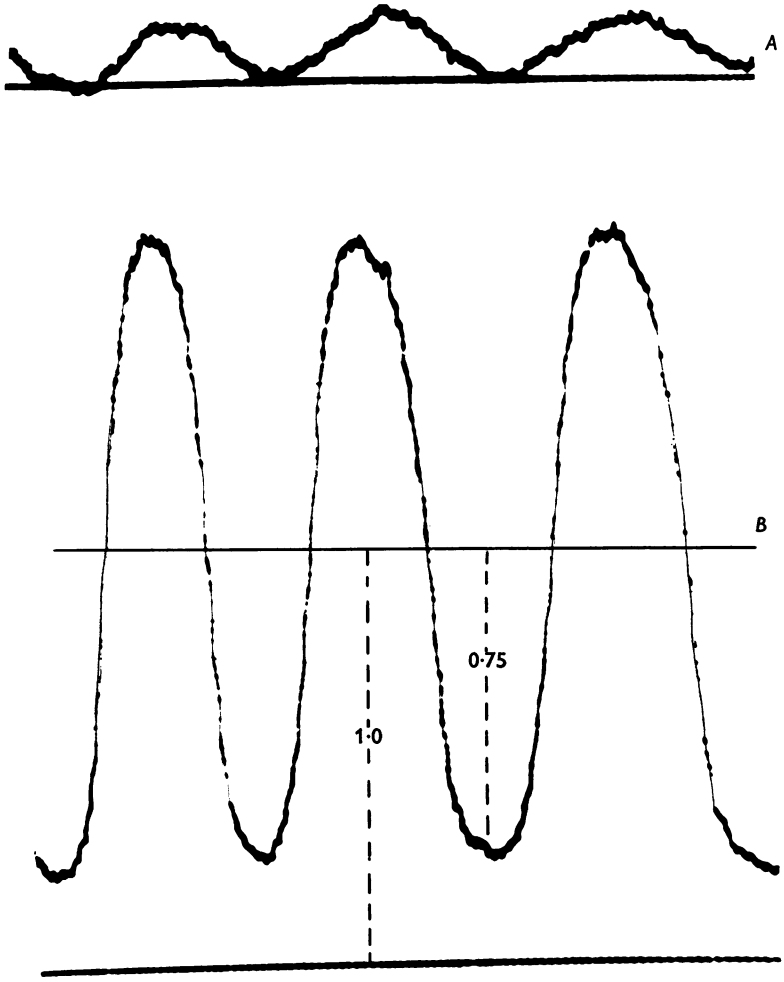

Fig. 4. Record of output of photocell (Fig. 3) as function of lateral displacement of grating. Record *A*, comparison record with white card in place of eye to give zero of retinal reflectance. *B*, record from eye with horizontal line at same level as in *A*.

strips, and that the shaded strip receives only 0·13 of the mean light—which corresponds to the interposition of a density filter of 0·9.

We are now in a position to assess properly the results of Fig. 2. In comparing the white and black circles we note that in 'black' conditons

the shaded rods were bleached by a light 0·9 log. unit less than the rods in 'white' conditions. But the interposition of only 0·5 density filter into the bleaching light changes the curves of Fig. 2 from circles to squares—a shift of 4 min. The interposition of 0·9 ought certainly to cause a shift greater than that. But the fact is that no detectable difference is seen.

This proves that the threshold of a rod may be raised by bleaching the rhodopsin in its neighbours.

DISCUSSION

The results of Fig. 2 show that as far as threshold during dark-adaptation is concerned the grating bleach was completely smudged; for the result was identical with a uniform distribution of the same light. The smudging certainly did not occur in the optical image upon the retina, for that must have been sharper than the record of Fig. 4*B*. Two possibilities of smudging remain, chemical and nervous. No significant points in Fig. 2 lie earlier than 8 min after the bleaching flash; if it is supposed that chemicals can diffuse from the regions that are bleached, and affect the threshold of rods 0·1mm distant, there is certainly plenty of time for this to occur.

We may suppose two classes of this chemical interaction:

(i) Some product of bleaching might have the property of raising the threshold for rod signals. If it were diffusible, it would desensitize unbleached rods and improve the sensitivity of the rods it quitted. For smudging to be as complete as it is, this imaginary photoproduct would have to be the principal cause of threshold change in dark adaptation.

(ii) Retinene is certainly diffusible in the retina and according to von Jancsó & von Jancsó (1936) in the rat it normally diffuses between the bleached rods and the pigment epithelium. Is it possible that the balanced reaction

$$11\text{-}cis \text{ retinene} + \text{protein} \rightleftharpoons \text{rhodopsin}$$

might lead bleached rods to rob their rosy neighbours till all reached equality of destitution? We can only say that the equality is not so extreme but that a flash somewhat above rod threshold but below that of the cones shows a sharp negative after image of the grating 20 min or more after the bleaching flash.

Smudging by nerve interaction seems more likely, and we had it in mind in designing this experiment. The great convergence of thousands of rods upon those summation pools with the lowest thresholds is an arrangement expressly designed to pool, and hence to smudge, certain aspects of the retinal signal. But a grating will not be perfectly smudged if its image on the retina has a period much larger than the diameter of the low-threshold pools. For most of our subjects (including W.A.H.R.) a grating of period 30′ was the largest which would result in identical dark-adaptation curves

after striped and uniform bleachings. A period of 40′ showed slightly earlier recovery after striped bleaching, as would be expected if now the black stripes are wide enough to allow some pools to be substantially more than half obscured. Our subject R.L.G., whose results are shown in Figs. 2 and 4, was abnormal in that his curves coincided up to a grating period of 60′ and broke down only at 80′, a peculiarity which is very favourable to this experiment since optical smudging, though not serious in the others, is quite out of the question in his case, as we have seen.

If this interpretation is correct, 30′ ought to correspond to the size of the summation pool determined by other methods. Some accurate measurements have recently been made by Hallett (1962) in two ways. In one the absolute dark threshold was found for various areas of test flash. This experiment has been done by many investigators, and, as is well known, there is an area below which the threshold depends upon the total light flux independent of its distribution (Ricco's Law). It has often been claimed that the Ricco area represents the size of the summation pool, and the well known statistical treatment of van der Velden (1946) and the extensive work which has been based upon it give this a quantitative interpretation. Hallett's other method was to detect a black disk against a dim background (Pirenne, 1946). It is plain that a black disk cannot entirely screen a summation pool from receiving quanta if it is much smaller than the size of the pool. Thus we might expect that the smallest disk that can be detected should have an area equal to the Ricco area. This is approximately what Hallett has found. Both methods give a diameter of about 1° at a point on the retina 20° from the fovea, and about 30′ at 7° eccentricity (confirming earlier workers, e.g. Barlow, 1958). Thus the limiting 30′ for the period of grating which we found with most of our subjects at 5° eccentricity is of the right order if the smudging is due to the pooling of receptor signals.

Another detail of Fig. 2 confirms this interpretation. In the cone branch of the curves the symbols have changed partners. This is what would be expected if the summation pools for cones were so small that dark and bright bars fell on quite different pools. The threshold with the grating in the test would then be determined by the bright bars, without being influenced by the dark bars and would be the same as a uniform test, not with the 0·4 neutral filter interposed, but with a neutral filter of density equal to that of the transparent bars of the grating, namely 0·1. The fact that the measurement was made with 0·4 instead of 0·1 means that the black symbols should be situated 0·3 log. unit above the white, as is seen to be the case.

The electrophysiological experiments of Lipetz (1961) upon the excised frog's retina give powerful support to the belief that the threshold for some rods may be raised by the bleaching of their neighbours and that the interaction is at the retinal level. Lipetz recorded the threshold for single ganglion-cell activity when a tiny point of light was flashed on to one or

other of two spots in its receptive field. Spot *A* was much more sensitive than spot *B*—presumably because it contained a greater density of receptors connected to the ganglion. Thus a bleaching light applied to *A* would be expected to cause greater light-adaptation of the pool than the same light applied to *B*. It was, in fact, found that the threshold at *B* was raised far more by a bleaching light applied to *A* than by the same light applied to *B* directly. Since this could not be due to stray light, it proves that rods at *B* had their threshold raised by the bleaching of the rods at *A*, and this in the way to be expected if the factor that changes in light-adaptation is the threshold of the pool for rod signals.

In the human eye at absolute threshold the pool needs five or more rod signals to elicit vision (Hecht *et al.* 1942). If the flash is superposed upon a background of 0·01 td, it must be raised ten-fold to be seen (Aguilar & Stiles, 1954). But this background corresponds to about 1 quantum absorbed per second among 100 rods. It therefore appears likely that the threshold has gone up ten-fold, not because 90 % of the quanta (so sparsely absorbed) fell upon 'refractory' rods, but because fifty rather than five rod signals were required at the pool in order to detect reliably the flash against an irregular flow of some 50/sec signals from the background (Barlow, 1957). There is a good deal of evidence suggesting that the threshold of the pool varies: there is little to suggest that a quantum absorbed in a rod ever fails to elicit a rod signal. An extreme formulation of this situation is as follows:

α. Each quantum absorbed by rhodopsin elicits a signal to the pool.

β. A flash attains threshold when the number of signals to the pool exceeds some critical value.

γ. This value depends upon the past and present inflow of signals to the pool.

δ. All signals to the pool are equivalent.

There are many ways in which this stark formulation will need modification in the light of experiment, but the experiments for the most part have yet to be done. It is easy to see that it accords reasonably well with the results of this paper.

From α the test flashes we used are equivalent, since they transmit the same total light and fall upon rhodopsin which is more than 90 % re-generated; thus the same number of quanta are absorbed in each flash and the same number of rod signals produced.

The bleaching flashes also transmit the same total light, and for small bleaches will send the same adapting stimulus to the pool so the course of dark-adaptation should be identical (as found). But in fact the bleaches

are not small. The average bleach (white circles Fig. 2) probably amounts to 60%, which means that the strips after the corresponding grating exposure would be 82 and 12% bleached, an average of 47%, and the black circles should lie on a curve 1½ min to the left of the white circles. The black squares similarly should lie ¾ min to the left of the white. The latter lay within experimental limits, but 1½ min should have been detectable.

When it was established (Rushton, 1961*a*, *b*) that during dark-adaptation the log. visual threshold was proportional to the amount of rhodopsin still remaining bleached, it seemed that the rise in threshold must be located where the rhodopsin was situated, namely in the rod. But the present investigation shows that the threshold depends also upon the rhodopsin level of neighbouring rods, thus localization is not so simple upon any viewing.

If we accept the summation pool postulates formulated above, we must suppose that every bleached molecule of rhodopsin sends to the pool a steady signal which only ceases when that molecule is regenerated. The steady signal from all the molecules determines the state of adaptation of the pool, not only the critical number of rod signals for threshold detection but also the summation time and degree of lateral inhibition.

It has long been known that the condition of light- and dark-adaptation affects time and space resolution (i.e. flicker-fusion and acuity) as well as threshold. There has been a tendency to regard threshold changes as photochemical, space–time resolution as synaptic, and to leave open the question of how the synaptic changes were coupled to dark-adaptation which was essentially a chemical process elsewhere. If the present suggestion that unregenerated rhodopsin signals its condition to the pool seems rather fanciful, we may reflect that something of the sort is inevitable if we are to explain the long accepted fact that space–time resolution does depend upon the state of adaptation.

SUMMARY

1. The object of this investigation was to find out whether the rod threshold rises after bleaching rhodopsin (*a*) because the rods need more light to generate their signals, or (*b*) because the summation pool needs more signals to activate the optic nerve.

2. Rods were bleached by an intense electronic flash in two ways. In one a grating (30′ bright bars, 30′ dark bars) was interposed to produce a striped bleach upon the retina. In the other a 0·4 density filter was substituted for the grating so that the same total light was spread evenly upon the retina.

3. Dark-adaptation curves were taken following each type of bleach and compared.

4. The modulation of the retinal image of the grating was measured physically and found to be $1 \pm 0{\cdot}87$ at the bright or dark bars.

5. If 1 (*a*) were true the dark-adaptation curve following the striped bleach should correspond to the threshold of the relatively unbleached rods at the dark bars. This curve should lie about 8 min earlier than the comparison curve of uniform bleaching.

6. If 1 (*b*) were true the dark-adaptation should depend upon the total bleach of the rod cluster, but not much upon the distribution of bleaching within the cluster.

7. In fact, the two curves are not separated by 8 min; they coincide.

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