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# LATERAL INTERACTIONS IN HUMAN CONE DARK ADAPTATION

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## SUMMARY

1. The course of cone dark adaptation after exposure to a strong bleaching light depends on the size of the bleached region. Threshold for brief, tiny test flash centred in the bleached region is elevated more, and recovery is retarded by a small bleach. This effect has its parallel in the sensitization effect observed with steady backgrounds.

2. Previous results, that a similar sensitization effect is *not* observed in rod dark adaptation, are confirmed.

3. This sensitization effect in cone dark adaptation does not transfer binocularly, and is unaffected by pressure blinding during the bleaching exposure.

4. Threshold following a small bleach may be lowered by adding a steady annular background to the region surrounding the bleached patch. Conversely, bleaching the area surrounding a small, steady background can lower threshold for a test flash centred on the background.

5. These interactions between backgrounds and bleaches may be explained if bleaches produce long-lasting signals from neurones in the bleached area, which then lead into a spatially opponent stage of processing.

6. It is likely that the persisting signals come from the cone receptors, since the Bunsen-Roscoe Law (intensity-time reciprocity) holds for small bleaches as well as large, for durations up to about 3 sec.

## INTRODUCTION

The mechanisms of light and dark adaptation in human vision are not yet well understood. Both receptoral and post-receptoral processes appear to be involved. Receptor adaptation has been demonstrated by recording from the retinae of various vertebrates (for example, Boynton & Whitten, 1970; Baylor & Hodgkin, 1974; Kleinschmidt & Dowling, 1975; Fain, 1976). The first indication of the involvement of post-receptoral sites came from psychophysical experiments which showed that the sensitivity loss induced by steady backgrounds is not applied point-by-point across the retina, but involves both summative (pooling) and antagonistic spatial interactions (see review by Barlow, 1972) and similar effects have been observed physiologically (Cleland & Enroth-Cugell, 1968; Werblin, 1974; Green, Dowling, Siegel & Ripps, 1975).

Teasing out the separate actions of the various sites of adaptation poses a problem for the psychophysicist, for example, whether it is the receptors whose sensitivity has been most affected by the adapting light, or whether it is some more proximal neurones may depend on the particular stimulating conditions. For this reason, it may be important to distinguish between 'bleaching' adaptation – the after-effects of strong bleaching exposures – and 'background' adaptation, where 'background' adaptation refers to the adjustment of sensitivity in the presence of a steady field which bleaches only a negligible fraction of pigment (Rushton, 1965).

A striking example of the different action of backgrounds and bleaches is the absence of lateral antagonistic interactions (sensitization) in rod dark adaptation (Westheimer, 1968; Teller & Gestrin, 1969; Tachibana, 1977) although it is a well known feature of light adaptation (Westheimer, 1965, and many subsequently) that a small backgrounds elevate threshold more than large ones. Teller & Gestrin argue that the failure of backgrounds and bleaches to act equivalently in this respect shows more proximal sites are involved in field adaptation than in bleaching adaptation. The sensitization effect has generally been taken as a manifestation of the antagonistic centre-surround organization of the receptive fields of retinal neurones, revealing centre-surround antagonism as a mechanism by which the visual system makes its adjustment to the ambient illumination, but there are difficulties with this interpretation (MacLeod, 1978). The possibility remains open that small backgrounds have an extra threshold-elevating effect at some central locus and that the sensitization effect is not fundamentally involved in the adaptation process. If this were the case, bleaches and backgrounds could still, as far as the essential aspects of adaptation are concerned, be considered equivalent.

The evidence for the lack of equivalence of backgrounds and bleaches with respect to sensitization has come from experiments with rods. Whether this is also the case for cones is not clear. There is not much reason to suspect that rod and cone systems employ fundamentally different mechanisms of adaptation (although there are some indications that they may: for example, Norman & Werblin (1974) show quite different behaviour of rods and cones at the receptor level).

It was therefore surprising to observe that cone dark adaptation, unlike rods, exhibits sensitization. Contrary to expectation, the experiments reported here uphold the equivalence of backgrounds and bleaches in the cone system with respect to sensitization. Unlike the rod system, both bleaches and backgrounds in the cone system appear to involve the same post-receptoral adaptation processes. In addition, the experiments favour a retinal locus, rather than a central one, for the cone sensitization effect.

## METHODS

*Procedure.* Nearly all the measurements were of dark adaptation curves, and the matter of interest was the effect of varying the size of the bleached region. The observations were made in the retinal region 5° temporal from the fovea. The subject looked at one of an array of small red fixation lights in an otherwise dark field (an array of 5 min squares was used, instead of just one dot, in an attempt to aid accommodation (Owens & Liebowitz, 1975)). The observer delivered the bleaching flash when he felt he was fixating accurately. The bleaching flash lasted 50 or 100 msec, except where noted otherwise. The observer then delivered himself repeated exposures of a brief, tiny spot initially set, for the start of each run, at a fixed intensity high above the dark adapted threshold. The test flash lasted 10 msec and subtended $0 \cdot 5'$ arc, unless otherwise indicated. It fell in the centre of the bleached patch when the observer was fixating accurately, and was self-presented so that he would not be distracted by flashes arriving during an eye movement and falling on unbleached retina. With this procedure the observer could keep the number of presentations as small as possible, thereby minimizing any possible habituation to the test flash. The observer signalled the experimenter when the test flash first became visible, and thereafter adjusted the intensity of the test himself, using a neutral density wedge, making threshold settings until the recovery of the cone system was complete. The bleach was always unfiltered white light, as was the test, except where noted otherwise. The bleaches ranged in size from 27 to 115′. With the smaller bleaches, stray light from the test flash may fall on surrounding unbleached retina. Stray light from the test flash was detected most readily by rods. It was possible to mitigate the problem by alternating large and small bleaches at 10 min intervals. Stray test light after the small bleach therefore fell on retina whose rods were insensitive, since the slowly recovering rods in the 115′ area were kept continously insensitive by the recurring bleaches.

*Apparatus*. A two channel Maxwellian view stimulator was used for the experiments. One coil of a 400 W quartz iodine source was imaged at high magnification so as to fill an artificial pupil of 3·2 mm diameter. Fixation point and display were located at a distance of 72 cm from the observer. Bleach and test were delivered through Uniblitz shutters. This simple system provided $5{\cdot}0 \times 10^7$ td of retinal illumination so that a considerable fraction of pigment could be bleached in a brief flash, without undue smearing of the retinal image, an important factor in these experiments because of the small dimensions of the bleaches. Heat absorbing glass was interposed in the beam to protect the retina from heat damage. The stimuli were measured using an E.G. & G. silicon photodiode placed at the pupil.

*Subjects*. Observations were made on two subjects; one with normal acuity (M.H.) and the other (J.A.) 1·5 D myopic. (No correction was necessary for this viewing distance.)

## RESULTS

### *The effect of bleach diameter on dark adaptation*

The first experiment demonstrates the basic phenomenon with which this paper is concerned: the profound dependence of cone dark adaptation on the size of the region bleached. Fig. 1 shows dark adaptation curves following two bleaches which differed only in diameter, the one subtending 115′ arc (filled circles), and the other 27′ arc (open circles). Both bleaching flashes delivered 6·7 log td sec to the region containing the test spot. The test spot was red (630 nm cut-off), 20 msec duration, and subtended 3′ arc. Recovery after the larger bleach follows the usual (approximately exponential) time course, but recovery following the smaller bleach is initially much delayed. The test flash is initially quite invisible at the highest intensity shown on the graph. After 70 sec it abruptly becomes visible, after which threshold falls precipitously, accomplishing most of its descent in about 40 sec. The extra elevation caused by the small bleach is considerable; when threshold after a large bleach has recovered to within a factor of 9 of its dark adapted value, threshold after the small bleach remains elevated by a factor of more than 3,000. It has not been possible to measure threshold during the first 70 sec, because at the highest test intensity used (4·5 log units above absolute threshold), stray light from the test flash becomes so intense that it could well mask a weak sensation from the bleached area. As far as one can tell, the subject is effectively blind in the bleached area for at least 70 sec after the 6·7 log td sec small bleach. For the small area bleaches, variability between different runs is best expressed in terms of the shift on the time axis required to align the dark adaptation curves. The within session standard

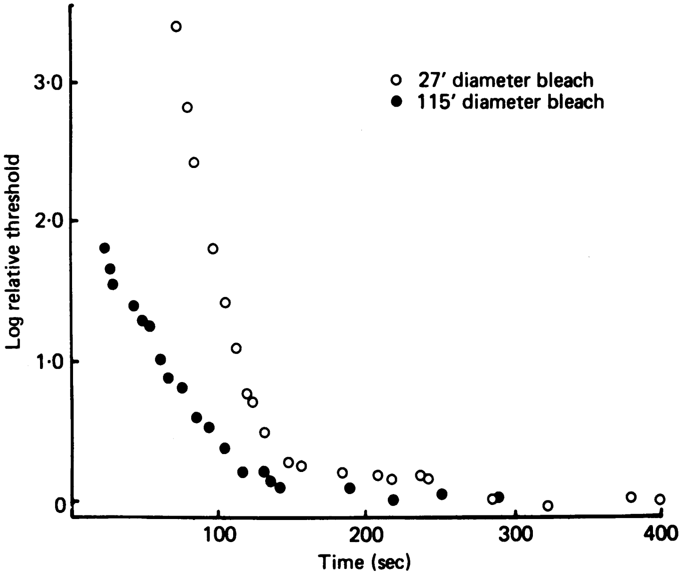

Fig. 1. Cone dark adaptation curves following 100 msec exposure to a $5{\cdot}0 \times 10^7$ td bleaching flash.

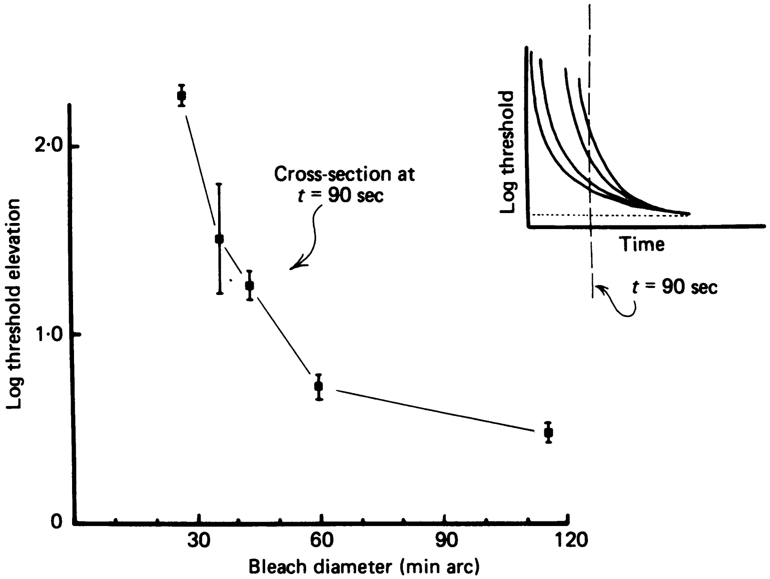

Fig. 2. Log threshold elevation (relative to dark adapted value) 90 sec after bleaches of various sizes. Error bars are ± 1 S.E. of the mean.

deviation of the time to recover a criterion threshold elevation following the bleach was estimated to be about 2·7 sec.

To show how the effect depends on the bleach diameter, dark adaptation curves were recorded after a number of different-sized bleaches. A cross-section through the different dark adaptation curves was taken at 90 sec after the bleach, and these values are plotted as a function of bleach diameter in Fig. 2. The data in the Figure are for a white test spot (0·5′ arc, 10 msec). Even after 90 sec the extra elevation caused by bleaches less than 1° in diameter is considerable – as much as 1·8 log units for the smallest one used here. When functions such as this are plotted for steady backgrounds instead of bleaches (see e.g. Westheimer, 1965, 1967) the curve is u-shaped, the threshold being lowest for very small and very large backgrounds, and highest for intermediate values. It was not possible to investigate very small bleaches in this experiment because of the difficulty of fixating well enough to keep the test on the bleached area, and because it exacerbated the problem of stray light detection by the sensitive retina surrounding the bleach.

The results of Figs. 1 and 2 are quite different from those of previous investigations, which dealt with rod dark adaptation. The absence of a sensitization effect in rod dark adaptation (Westheimer, 1968; Teller & Gestrin, 1969; Tachibana, 1977) was confirmed in this investigation. A 486 nm test flash was used to favour rod detection and expose as much of the rod branch as possible. Dark adaptation curves following 36 and 115′ bleaches were found to follow a similar time course.

### *Binocular transfer*

The dependence of the course of cone dark adaptation on the size of the bleached area strongly suggests that some mechanism proximal to the receptors can influence cone dark adaptation. But just how proximal is it? It is possible to rule out a retinal locus if it is found that the effect transfers binocularly, so the next experiment tests for such transfer.

Since a binocular apparatus was not available, the subject viewed the same display through the artificial pupil successively with the two eyes. An extra dental bite was clamped to the apparatus, which the subject aligned for his other eye (the left). Binocular transfer was tested in two ways. The first was to see if a small bleach in one eye raised the threshold in the other eye. The subject bit on the original 'right-eye' bite and adjusted the test to threshold in his right eye. The test was then set 0·2 log units above this value, a level at which it was reliably and unmistakeably visible. The subject moved to the other bite and delivered a 27′ bleach to his left eye. He then quickly moved back to the first bite and presented several flashes of the test stimulus. The test was clearly visible at its first presentation (usually about 10–30 sec after the bleach). An afterimage of the bleaching stimulus was clearly visible, and the subject was able to see the test stimulus (in the right eye) well centred in the after-image (in the left eye), but the visibility of the near-threshold test light was unimpaired. (M.H. also repeated the experiment with the bleach in the right eye, and the test in the left eye.)

In a second test for binocular transfer, dark adaptation was measured after a 27′ bleach in the right eye, and the test was to see whether a 27–115′ annular bleach in the left eye could lower threshold in the right eye. Binocularly, the small, circular bleach and the annular bleach together made up a large 115′ uniform bleach. If small bleaches have their extra threshold-elevating effect in binocular pathways, threshold might be lowered by enlarging the bleach binocularly, just as it is when enlarged monocularly.

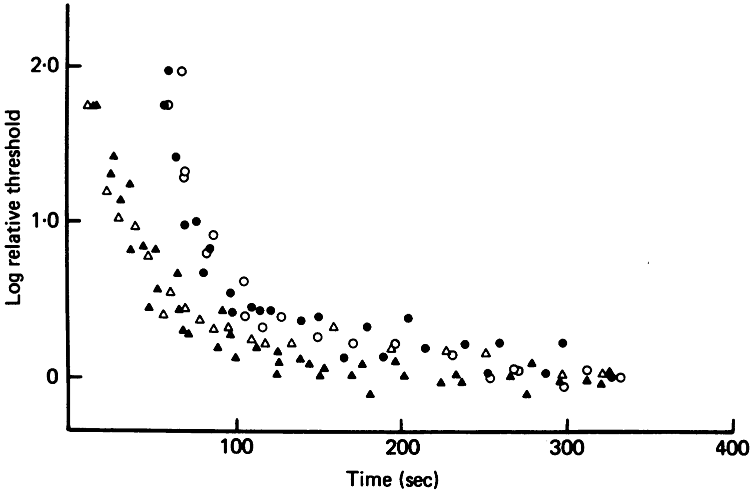

Fig. 3. Dark adaptation curves showing failure of binocular transfer. Open triangles, 115′ uniform bleach in the right eye; open circles, 27′ bleach in the right eye; filled circles, 27′ bleach in the right eye, followed by 27–115′ annulus in the left eye; filled triangles, control condition, 27′ bleach in the right eye, followed by 27–115′ annulus in the same eye. M.M.H.

A slight modification was made to the apparatus for this experiment a piece of linear polarizing material was placed in the beam, attached to the diaphragm defining the 115′ field. Attached to the polarizer on the subject's side was a piece of half wave plate at 45° to the polarizer. The half wave plate had a 27′ hole punched out of the centre. Following the polarizer and half wave plate in the beam came another polarizer. When this polarizer was parallel to the first piece, polarized light was transmitted through the 27′ hole, but blocked in the surrounding 27–115′ annulus. When the second polarizer was orthogonal to the first, the central spot was blocked, and the annulus transmitted. Either the spot or the complementary annulus could then be bleached by rotating the polarizer through 90°. Extinction in the central spot was 0·2 %, and in the annular surround, 4 %. The unextinguished light in the surround was found to be insufficient to affect the dark adaptation curve for the small bleach, and can presumably be neglected. The polarizers reduced the intensity of the bleaching beam from its maximum to $10^7$ td. The duration of the bleach was 100 msec.

First, a dark adaptation curve in the right eye was measured after a small (27′) bleach in that eye. The subject then repeated the 27′ bleach, but immediately after bleaching, moved to the other bite, delivered the annular bleach to the left eye, moved back to the original bite, and measured the subsequent dark adaptation in that eye. The results are shown in Fig. 3. Dark adaptation after the small bleach with, and without, the annular bleach in the other eye is shown by filled and open circles respectively. The curves lie close together; the bleach in the other eye has no obvious effect. The filled triangles are for the control condition, where bleach and annulus were delivered to the same eye. The open triangles plot dark adaptation after a uniform 115′ bleach in the right eye. Open and filled triangles appear to trace out similar recovery curves, as they should if the sequential presentation of central spot and annulus is a suitable close approximation to simultaneous presentation. It usually took the observer 5–6 sec to move from one bite to the other and deliver the second bleach, and about the same time elapsed between bleaches when they were delivered to the same eye. In the binocular condition the observer typically saw a large uniform afterimage (although at some times during a run the uniform afterimage would give way to the afterimage of either small bleach alone, or annulus alone, presumably due to binocular rivalry) so it seemed likely that conditions necessary for binocular transfer to become apparent had been achieved. The data shown in the Figure represent 2–3 runs in each condition, except for the open triangles, which represent only one run. The experiment was also run with annular bleach preceding the central bleach, with similar results, and similar data were also collected on another subject. On occasional runs the curve for the control condition (filled triangles) deviated from the large uniform bleach curve in the direction of the circles. This was correlated with an obvious misalignment of the two bleaches in the afterimage. Despite possible difficulties in ensuring perfect alignment between the bleaches in the two eyes, the two experiments taken together provide reasonable evidence that there is little, if any, binocular transfer of this sensitization effect. The retina is still, therefore, a contender for the site of the effect, as are the central monocular pathways.

### *Pressure blinding*

Pressure on the eyeball blocks the blood supply to the retina from the ophthalmic artery causing anoxia and temporary blindness. This allows a test of the hypothesis that small bleaches induce their added sensitivity loss at some central (post-retinal) locus during the adapting exposure. Pressure blinding the eye during bleaching prevents any central record of the bleaching exposure, so the small bleach should produce more rapid recovery after pressure blinding, if its effect is central. This technique was used by Craik & Vernon in 1941 to show that the sensitivity loss after (large diameter) bleaches has a retinal origin, since dark adaptation was unaltered by pressure blinding.

Dark adaptation curves were measured for large (115′) and small (27′) bleaches with, and without, pressure blinding during the bleaching exposure. For the pressure blinded runs, the subject pressed the temporal side of the globe with a finger and maintained pressure for approximately 10 sec after the fixation point had become invisible. (The fixation point was turned up to 500 times the foveal dark adapted threshold.) The subject then released the pressure and delivered the bleaching flash the moment he was able to see the fixation point and return his gaze to it. Vision fades later and returns faster in the fovea than in the temporal retina (Howarth, 1956). It was therefore possible to deliver the bleach while the 5° temporal retina was still blind. (On some trials a dim flash was seen, and these trials were not included.) This procedure was adopted because pressure on the globe leads to its dislocation and subsequent misalignment with the artificial pupil. Note that the minimum amount and duration of pressure were used to ensure blindness to the bleaching flash. Although all the retinal cells except the receptors are likely to be affected by pressure anoxia (see Pugh, 1975) (the receptors are supplied with oxygen via the choroidal circulation) the moderate pressure used here may not have eliminated retinal activity (Arden & Kolb, 1964; Pickersgill, 1964). Since the observer did not see the bleaches, it can be concluded that transmission along the optic nerve was blocked. The experiment therefore discriminates between retinal and post-retinal loci, but not between receptoral and post-receptoral.

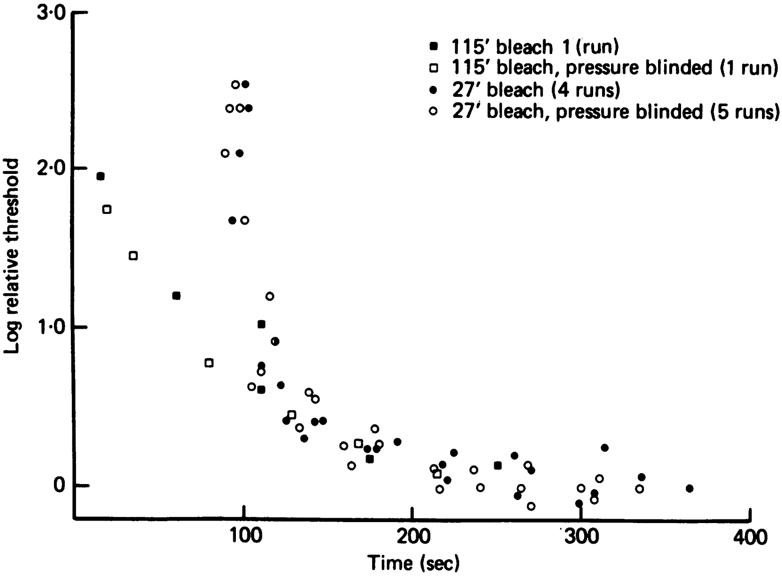

Fig. 4. Cone dark adaptation curves with and without pressure blinding during the bleaching exposure. M.M.H.

The results are plotted in Fig. 4. Open symbols are for the pressure blinded condition, filled symbols for the standard, unblinded condition. Circles are for the small bleach, squares for the large. Data from two sessions are included. Open and filled symbols lie close together for either bleach size. Neither could any effect of pressure blinding be discerned for the other subject. Pressure blinding during the bleaching exposure has no apparent effect on subsequent dark adaptation, for either large or small bleaches. Since the bleaching flash was quite invisible to the subject during pressure binding, it cannot be true that either sized bleach causes a sensitivity loss in the central (lateral geniculate nucleus or later) visual pathways during the bleaching exposure.

### *Interactions between backgrounds and bleaches*

The next two experiments were designed to show whether bleaches can do the work of backgrounds, and backgrounds the work of bleaches in controlling sensitivity in this situation. Can surrounding a bleach with a steady annulus of light lower threshold, just as enlarging the bleach does? Can bleaching the region around a small background lower threshold, just as enlarging the background does? The two experiments that follow are similar to those performed by Westheimer (1968) on the rod system, but with different results.

The arrangement previously described on p. 130, with a half wave plate sandwiched between two polarizers, was used again in these experiments. First, with the polarizers parallel, a 27′ spot was bleached, then the polarizer was rotated through 90°, producing a 27–115′ annulus, and neutral density filters were added to the beam to reduce it to 2·6 log td. The subject then measured recovery of sensitivity in the presence of the steady annulus surrounding the bleached area, and this is plotted as open circles in Fig. 5. Filled circles plot recovery after the same bleach, but this time measured in the dark. Note first that the asymptotic values of the curve differ by about 0·4 log units. An elevation of this amount from the dark adapted would be expected from the light scattered by the annulus into the central area (1·4–4 %, Gubisch, 1967). The most important feature of the Figure, however, is that the annulus lowers threshold in the early part of dark adaptation. Filled circles drop far below the open circles until dark adaptation is almost complete. (Further data under similar conditions are shown in the following paper.)

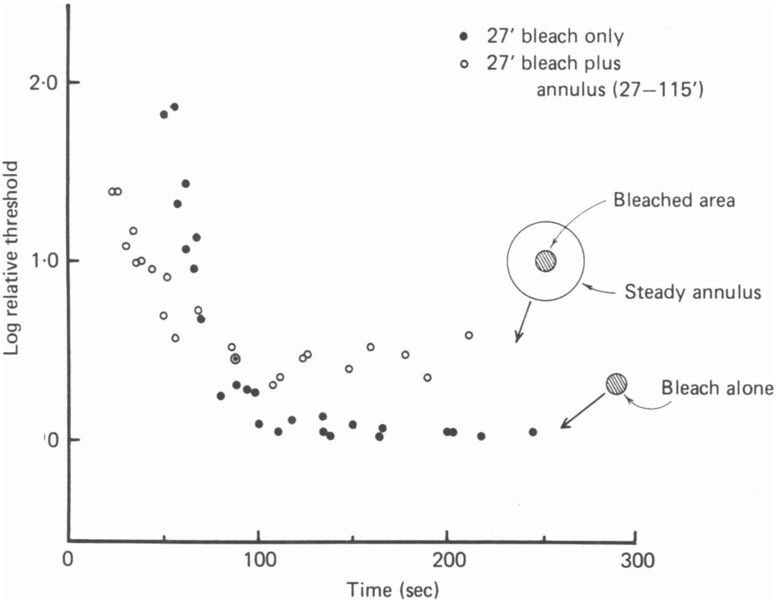

Fig. 5. Cone dark adaptation curves after a 27′ bleach, either in the dark (filled circles) or in the presence of a 27–115′ steady annular background (open circles). Two runs for each condition are plotted. M.M.H.

To explain the results, the signals produced by the annular background must somehow modify sensitivity in the region where the test spot falls. This could be achieved if the extra insensitivity caused by the small bleach is the result of the continued action at some spatially opponent stage of persisting signals from the bleached receptors, rather than the result of some fixed, irremediable lack of responsiveness caused during the bleaching exposure. It is difficult to see how such a lack of responsiveness could be mitigated by adding light around the bleached area. However, if the bleach produces long-lasting signals from the receptors like those produced by backgrounds, then the effects of a large bleach might be mimicked by exciting the central patch of retina by bleaching, and the surrounding retina by a background, as observed here.

The converse experiment gave similar results. Bleaching the area surrounding a small background can lower threshold for a test centred on the background. The same annular region as before was bleached with a light of 6·3 log td sec. The subject then set thresholds on a 27′ background of 1·0 log td, which fell inside the annular bleach. The subject contined setting threshold for 6 min or more, by which time the cones had completely recovered from the effects of the bleach. The thresholds are plotted as a function of time in Fig. 6. Thresholds are lowest, and sensitivity greatest in the first minute or two following the bleach. Threshold on an equiluminous 115′ background is 0·92 log units (a factor of about 8) lower than on the small one. A noticeable feature of these data is their variability. It was particularly difficult to set thresholds on the small background. Thresholds were less well defined subjectively, and were unstable over time. However, the data from many (10) runs have been plotted, and on each run, thresholds were lowest shortly after the bleach, and a test spot set just below threshold in the presence of the small background alone, invariably became clearly visible after bleaching the surround. Another subject gave similar results, in this experiment, and in the previous one.

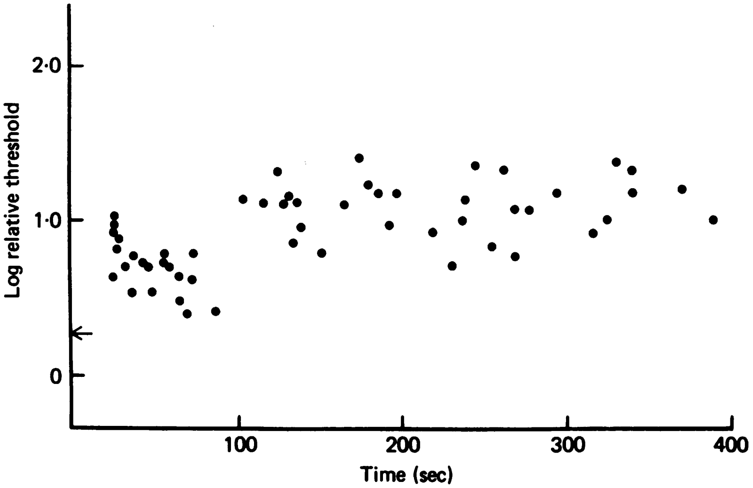

Fig. 6. Effect of bleaching the region (27–115′) surrounding a small, steady 27′ background. Threshold on the small background is plotted as a function of time after the bleach. The arrow shows threshold in the presence of an equiluminous 115′ background. The data points after about 100 sec show the steady state threshold in the presence of the small background. Zero is the dark adapted cone threshold. M.M.H.

The above interactions between backgrounds and bleaches suggest that bleaches act like continuously present backgrounds in producing a persisting signal in the receptors which lasts for much of the duration of dark adaptation, and which can be laterally transmitted to a spatially opponent site.

### *Bunsen–Roscoe Law*

Within limits, the course of human cone dark adaptation depends only on the total bleaching energy, and is unaffected by the way the energy is distributed over time (Bunsen–Roscoe Law) (Crawford, 1946). It cannot be assumed that this is also true in the case of the small diameter bleaches used in this experiment. If the extra threshold elevation after the small area bleach is initiated by the effects of the bleach on some post-receptoral stage, then one would not expect it to depend simply on the total bleaching energy. The intense bleaching exposures used here would presumably saturate the receptor response, so that information about the different strengths of the various bleaching lights would not be passed on to proximal neurones (during the bleaching exposure), and the initial equation of time – integrated energy would be upset. If the Bunsen–Roscoe Law holds, however, and total energy is what matters, then recovery after small bleaches, as well as large, must be governed, at least indirectly, by the amount of pigment initially bleached.

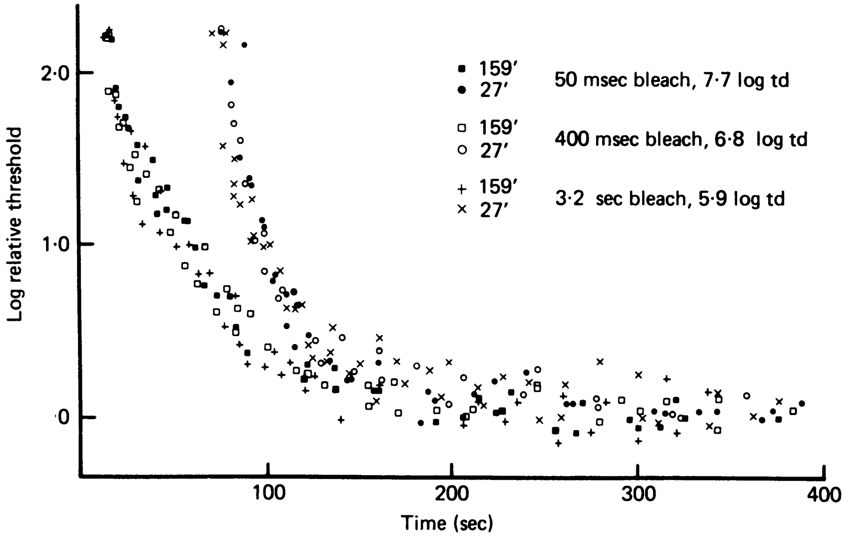

Fig. 7. Cone dark adaptation curves following equal energy bleaches of various durations and intensities. See inset for details. Time is measured from the offset of the bleach. Crosses, three runs; two runs for each other condition. M.M.H.

Fig. 7 shows dark adaptation curves after various bleaches of the same total energy, but different durations from 50 msec to 3·2 sec. The bleaching energy was 6·4 log td sec. The curves for the different bleaching durations coincide (within experimental error), for both small and large diameter bleaches. Similar results were obtained on another subject, and on three other occasions for M.H. Over three directly comparable sessions for M.H., the average difference in time for threshold after 3·2 sec and 50 msec bleaches to fall to 1·7 log units above the dark adapted threshold was 2·7 sec ± 3·4 (between session S.E. of mean). For 400 msec and 50 msec bleaches, the difference was 1·7 ± 5·2 sec. (The time for the 50 msec condition was subtracted from that for the other condition.) (A consistent deviation from the Bunsen–Roscoe Law was observed for both subjects for a 6·4 sec bleach, which gave more rapid recovery than the equal-energy 100 msec one, but the deviation is not peculiar to the small bleach. Both sizes deviate by about the same amount. Shifting the two bleaches relatve to each other by about 10 sec re-aligns both large and small bleaches.) To summarize: the Bunsen–Roscoe Law holds for durations between 50 msec and 3·2 sec (a 64 to 1 range in illuminances) for small diameter bleaches, as well as large ones. This suggests that (within these limits) the peculiar dark adaptation curves after small bleaches depend on the amount of pigment initially bleached, and supports the conclusion of the previous section that the origin of the persisting signals is receptoral.

## DISCUSSION

The results in this paper indicate that post-receptoral neurones are involved in human cone dark adaptation. Sensitivity in a given region is affected by light falling on surrounding regions. The lateral interactions observed here are implicit in the results of Crawford (1940) who showed that different-sized adapting fields which gave equal threshold elevations, also produced equal dark adaptation curves. Excitatory signals from the receptors persisting after the bleach may saturate proximal neurones in the case of small bleaches as a result of reduced surround antagonism (e.g. from horizontal cells; such a process is elaborated below). In the case of a large bleach, however, there may in fact be no further loss of sensitivity after the receptors if the persisting excitatory signals are cancelled out by surround antagonism, so that the dark adaptation curve after a large bleach might reflect only the receptoral sensitivity loss, despite the involvement of post-receptoral neurones in cancelling out the steady signal. (This applies only to areas remote from the edge of the large bleach, since there is also reduced surround antagonism near the edge.) The small bleach, however, may reflect both a receptoral loss plus an added attenuation by response compression at a later stage.

It is possible that inter-receptor coupling could lead to effects similar to those observed here, but since the connections between receptors are sign-conserving, it is not easy to account for the result in terms of receptor crosstalk alone, and it seems more likely that opponent signals from other neurones are involved. If post-receptoral neurones are indeed involved in cone dark adaptation, at least for small diameter bleaching exposures, how far past the receptors is it necessary to go to explain the sensitization effect? From MacLeod's (1978) review of the evidence concerning the sensitization effect for steady backgrounds, it is not at all clear whether the underlying mechanism is retinal or central. Lennie & MacLeod (1973) and Latch & Lennie (1977) have proposed that the sensitization effect is due to adaptation of size-selective channels in the central visual pathways. (The small background desensitizes just those units which would normally do the task of detecting the small test spot.) The pressure blinding experiment with small bleaches rules out a central loss of sensitivity established during the bleaching exposure. However, a positive afterimage is visible in the dark for some time after the bleach, so some persisting after-effect of the exposure might well penetrate far into the visual system to a central stage where large and small bleaches exert their differential effects. Some observations on afterimages suggest that if this is the case, the locus must be before the fading of afterimages is accomplished. The afterimage of the small bleach is never very conspicuous and fades about 30 sec after an 80 % bleach. Threshold, however, remains unmeasurable for another 40–50 sec. The afterimage gives no hint of the devastating effect of the small bleach.

Although a central locus of the sort described cannot be excluded, the fact that a parallel effect is not observed in the rod system, which shares its central pathway with the cone system, makes a retinal locus more plausible than a central one. Lennie & MacLeod's experiments and Latch & Lennie's were mainly under scotopic conditions. It is not necessary that the effects they deal with have the same underlying mechanism as that here. In addition, the physiological evidence for a sensitization effect in retinal cells is much stronger under photopic conditions than at low light levels (MacLeod, 1978). Indeed, some further experiments on the interaction between bleaches and backgrounds suggest the mechanisms are different (see following paper). Fig. 5 showed that a steady annulus present during dark adaptation lowers threshold after a small bleach. Further experiments show that the effects of the annulus are immediate; threshold may be raised or lowered at will during the slow progress of recovery by switching the annular background on or off. On the other hand, Latch & Lennie show that it takes one or two min to recover from the effects of their small backgrounds. In the present situation it takes only a few seconds. This difference in time course of recovery from the effects of small backgrounds in one case, and small bleaches in the other, suggests that different mechanisms are involved in the two situations. This is the subject of the following paper.

Tulunay-Keesey & Vassilev (1974) have also proposed that more than one mechanism may underlie the effects of small cone backgrounds. They found that stabilizing the background with respect to the retina reduced the amount of sensitization observed, but did not abolish it. Tulunay-Keesey & Jones (1977) have subsequently shown that stabilization abolishes sensitization at low luminances, but not at the highest luminance they used (9 ml.). Together, these results suggest that at least with intense lights sensitization may be produced by a relatively peripheral mechanism which does not require transient signals produced by eye movements for its operation.

If the sensitization effect in bleaching is initiated by persisting signals from neurones in the bleached area, then it is likely that these signals come from the receptors. Such persistence is observed physiologically in turtle cones (Baylor & Hodgkin, 1974), in rat rods (Penn & Hagins, 1972), and in gekko rods (Kleinschmidt & Dowling, 1975), and a receptoral origin is suggested by the Bunsen–Roscoe experiment, supposing that the duration of the persistence depends on the amount of bleached pigment. Receptoral persistence is likely (MacLeod, 1978) to be the basis for the psychophysically observed afterimage, and a physiological realization of Barlow's hypothetical 'dark light' (Barlow, 1964).

A plausible hypothesis to explain the course of dark adaptation after small bleaches is one previously suggested to explain sensitization with steady backgrounds (McKee & Westheimer, 1970; Teller, Matter, Phillips & Alexander, 1971; Werblin, 1974) whereby horizontal cells reduce the input to bipolars and prevent overloading there. Horizontal cells sum over large areas relative to the bipolars, making small adapting fields a poor stimulus for them. With lateral antagonism from the horizontal cells correspondingly reduced, the bipolars might be saturated or overloaded by the persisting signals from the receptors, whereas after large bleaches, horizontal cell antagonism may be sufficient to bring the bipolar back onto its normal operating range. The bipolar is then responsive to the test after a large bleach, but not after a small one. An alternative to this hypothesis would be one where the receptor signals themselves are kept near the resting level by feed-back from the horizontal cells. In that case the saturating stage for small background would be at the receptors. There is evidence for both feedback (Burkhardt, 1974; Werblin, 1977; Trifonov & Byzov, 1977) and feedforward (Werblin, 1974; Richter & Simon, 1975) even within the one species, so it is not clear which is more likely to be involved here. The main discouragement for putting forward such retinal models is the failure to find sensitization on photopic backgrounds in cat retinal ganglion cells (Enroth-Cugell, Hertz & Lennie, 1977). However, the ratio of cone to rod populations in the cat is relatively much smaller than in the human, so the cat may not be a very good model in this case.

These experiments show up an unexpected difference between rod and cone dark adaptation. The absence of sensitization in rod dark adaptation is well documented. Even if a sensitization effect were present early in rod dark adaptation where it has not been possible to follow its course, there would still be a difference between rod and cone dark adaptation to be explained, since the sensitization effect in cones lasts throughout their recovery. Equivalence of backgrounds and bleaches in this respect holds for cones but not for rods. This difference between rods and cones in dark adaptation suggests that the cone effect has an origin prior to the convergence of the rod and cone systems at the ganglion cell. The horizontal cells differ in their anatomical relation to rods and cones, the dendrites connecting only to cones, and the axons only to rods (Kolb, 1970), and might well differ functionally with respect to surround regulation of bipolar cells.

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