

## AFTER-EFFECTS OF SMALL ADAPTING FIELDS

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### SUMMARY

1. Sensitivity to a small test probe in the centre of a small, steady background is less than when the background is large (sensitization). When an equiluminous steady annulus is added to the region surrounding a small background, rod threshold takes several minutes to stabilize at its new, lower level. The after-effects of the small background follow a time course characteristic of cortical adaptation.

2. The sensitivity loss and time course of recovery after intense bleaching lights in the cone system depend markedly on the size of the retinal region bleached, although no such effect is observed in the rod system. If a steady annular surround is added to the region surrounding the bleached patch, threshold falls rapidly to the value it would have after a large-area bleach of the same intensity.

3. The interaction between bleaches and steady surrounds suggests that bleaches produce long-lasting signals in the cone receptors.

4. The different temporal properties of sensitization on rod backgrounds and sensitization after cone bleaches suggest that different mechanisms underlie the two phenomena.

5. In cone vision, if light is added to the area surrounding a small, steady background, the subsequent readjustment takes minutes to complete, as it does in rod vision. But in addition, for cones, a large proportion of the sensitivity loss caused by the small background can be rapidly restored, as it is with cone bleaches.

6. The above results, together with the known absence of sensitization in rod dark adaptation, are consistent with the hypothesis that sensitization occurs at least partly at the retinal level in the cone system, but not (or only weakly) in the rod system, and that there is an additional, probably cortical elevation, common to rod and cone systems, for small backgrounds, but not for small, brief bleaches.

### INTRODUCTION

The light-adapting effects of steady backgrounds are not solely dependent upon the amount of light falling on a given retinal region, but may reflect, in addition, the effects of stimulation of neighbouring regions. It is a well known feature of light adaptation that small, circular backgrounds raise threshold for a tiny, centred test flash more than large ones (the sensitization phenomenon; Crawford, 1940; Westheimer, 1965), and this is true for both rod and cone-mediated detection. This seemed a clear manifestation of the centre-surround antagonism of the receptive fields of

retinal neurones, since a large background (which falls on both centre and surround) would excite a cell less, and by inference adapt it less, than a small field confined to the centre (McKee & Westheimer, 1970; Teller, Matter, Phillips & Alexander, 1971; Barlow, 1972). By such a mechanism, then, the visual system might both make its adjustment to the ambient illumination and enhance (relatively) signals from contours, thereby serving the dual function of increasing the operating range of the retinal cells, and giving prominence to the critical information in the environment.

However, the role played in adaptation by the centre-surround organization of the receptive fields of retinal neurones is still not clear. Most of the support for this simple scheme in which sensitization is regarded as a manifestation of centre-surround antagonism comes from recordings from lower vertebrates (e.g. Burkhardt, 1974; Werblin, 1974), and also from studies of visual pathologies which demonstrate that sensitization is abolished by diseases of the retina, but not by more central pathologies (Enoch, 1978). However, the evidence in favour is not conclusive, and other evidence has been mounting against it (see review by MacLeod, 1978). In particular, sensitization is *not* observed in recordings from the retinal ganglion cells of the cat, the only mammal investigated (Cleland & Enroth-Cugell, 1968; Barlow & Levick, 1976; Enroth-Cugell, Hertz & Lennie, 1977), suggesting a locus more central than the retinal ganglion cells. Other evidence in favour of a central locus is threefold. (1) A small background, but not a large one, can raise rod threshold by its effect on cones (cone threshold may similarly be elevated by a small rod background). This suggests that small backgrounds, but not large ones, may have a site of sensitivity regulation beyond the convergence of rod and cone systems at the ganglion cell which transmits their combined signals to the brain (Lennie & MacLeod, 1973; Frumkes & Temme, 1977; Latch & Lennie, 1977). (2) In rod vision, when the background is stabilized with respect to the retina, threshold on a small background falls almost to the value it has on a large one (Barlow & Sakitt, 1973), implying that the site of action of small backgrounds follows the fading of stabilized images. (3) The sensitization effect is absent in rod dark adaptation; that is, sensitivity recovers as quickly from a small diameter bleach as from a large one (Westheimer, 1968; Teller & Gestrin, 1969). One possible explanation of this is that sensitization depends on a site of sensitivity regulation following the sensitivity loss imposed by bleaches. The implication of all these results is that (in rod vision at least) small backgrounds introduce an additional sensitivity loss by their action on some central mechanism, that is, a mechanism which follows rod-cone convergence, the fading of stabilized images, and the action of bleaches. If small backgrounds (and edges) excite the retinal neurones more than large diffuse fields, then neurones at later stages in the visual pathway will also be more excited by small backgrounds. This has been observed in the maintained discharge of monkey l.g.n. cells (Marocco, 1972). In this way, signals from small backgrounds have an opportunity to raise threshold at any point along their path from the retina.

However, although the course of dark adaptation in the rod system is independent of the size of the bleached area, the cone system behaves quite differently (Hayhoe, 1979). The loss of sensitivity, and the time course of recovery in the cone system after exposure to an intense bleaching light depend profoundly on the size of the bleached region. This sensitization in cone dark adaptation is not easily ascribed to

central processes. The effects of bleaches are generally thought to be confined to the early stages of the visual pathway. Amacrine cells and ganglion cells respond best to transients, so any persisting signals from the bleached receptors are unlikely to be propagated very effectively past the outer plexiform layer of the retina. In addition, since rods and cones converge on the same central pathways, it is not easy to see why sensitization should be observed in cones, but not in rods, if the central hypothesis is correct. Although the sensitization effect with rod backgrounds, and the sensitization effect with cone bleaches are superficially similar, it is possible that they are not the same phenomenon. Indeed, it is the purpose of this paper to demonstrate that small adapting fields might have their extra threshold-elevating effect at more than one locus. This has been done by making use of the observations of Latch & Lennie (1977) that small backgrounds, but not large ones, have long-lasting, only slowly reversible, after-effects on rod system sensitivity. It will be shown that this sluggish recovery is not observed in cone bleaching adaptation, but is characteristic of adaptation to small backgrounds in both rod and cone systems. (By bleaches, I mean lights which bleach a significant fraction of the visual pigment, and are extinguished prior to testing. In these experiments, the bleaching exposure is always of short duration. By backgrounds, I mean lights which bleach a trivial amount. Backgrounds are generally present during testing, but in these experiments, the after-effects of such fields are also referred to as 'background' adaptation.) Adaptation to small backgrounds therefore appears to involve an additional mechanism with sluggish temporal properties, which is not manifest in cone bleaching adaptation.

### EXPERIMENT I. STEADY BACKGROUNDS

This experiment demonstrates the existence of a sluggish readjustment of rod system sensitivity, following exposure to small backgrounds. A small adapting field is presented to the subject. This drives the threshold for a small, centred test flash higher than it would be on an equiluminous large field. After the subject adapts to the small field for a certain period, the small background is replaced by an equiluminous large field, an operation equivalent to adding light to an annular region surrounding the small background. The steady-state threshold on the large field will be lower than on the small field. How long does it take for threshold to fall back to the steady-state value on the large background?

The three experiments in this paper, on rod backgrounds, cone bleaches, and cone backgrounds are all of the above form. The rapidity with which the readjustment to the appropriate large-field threshold value is accomplished is used to distinguish between these three situations.

### METHODS

In the first part of the experiment, the subject adapted to a small (38 or 47' arc), red, circular background located 5° in the temporal retina for a period of either 45 sec, 1 min, or 3 min. (Thresholds were measured on small backgrounds of various diameters, and that which elevated threshold most was chosen for use in the experiment. The 38' background was mostly used, but the 48' background was used occasionally. Both raised threshold by about the same factor.) During this period the subject adjusted the intensity of a small (2' arc), brief (40 msec) text flash in the centre of the field to threshold by varying the position of a graded neutral filter. The

small background was then exchanged for an equiluminous  $7.3^\circ$  background which differed only in size from the small one. The subject continued to set thresholds after the exchange until threshold had stabilized at its new value.

During the experiment, a large ( $11.1^\circ$ ), blue (483 nm) background of 0.05 scotopic td retinal illuminance was continuously present. Its role was to mask stray light scattered from the test spot when the subject was setting threshold on the small background. The display as seen by the observer is shown in Fig. 1. The wavelength of the test light was 486 nm, and that of the

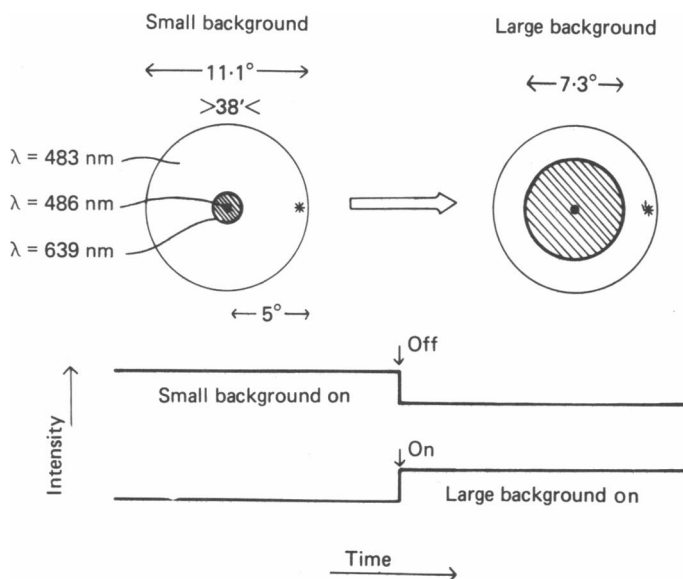


Fig. 1. The display as seen by the observer. Stimuli were centred on a retinal region  $5^\circ$  temporal from the fixation point. After a period of adaptation to the small red background (left hand side of Figure), it was replaced by the large one (seen on the right hand side of the Figure), and the subsequent recovery of sensitivity was measured. The blue auxiliary ( $11.1^\circ$ ) field was present throughout.

red background was 639 nm, which favoured detection of the test spot by the rod system. The retinal illuminance of the red background was 0.1 scotopic td (5 photopic td). Rod isolation was verified by measuring thresholds on the cone plateau during dark adaptation following a 10 sec exposure to a 560,000 td bleaching beam. The cone plateau was measured both in the dark, and under the conditions prevailing in the experiment. Cone threshold on the large background was found to be 0.6 (subject D.S.) or 0.8 (subject M.H.) higher than rod threshold; and 0.5 (subject D.S.) or over 0.4 (subject M.H.) log units higher on the small background.

Preliminaries at the start of each session included dark adapting for 30–45 min before the experiment, and then adapting to the large blue background for 3 min. The subject then made three threshold settings on the large blue background to establish baseline sensitivity. Following this, the large red background was turned on and the steady-state threshold measured after 3 min adaptation. The large red background was then extinguished, and the subject adapted to the large blue background alone for 3 min before the experiment proper began with the exposure of the small red background.

In the second part of the experiment similar manipulations were performed, but this time the cone system was isolated. To do this, the following conditions were used. (a) The intensity of the large ( $11.1^\circ$ ) blue background was increased to 1.0 scotopic td (0.08 photopic td; approximately 0.3 log units dimmer than was required to detect the colour of the background). This raised rod threshold without affecting cone system sensitivity. (b) Rod threshold was further elevated (relative to cones) by making the 38' and  $7.3^\circ$  backgrounds green (500 nm). The retinal

illuminance of the green background was 6.5 photopic td (50 scotopic td). (c) The colour of the test spot was changed to red (630 nm cut-off). Such a small, brief, longwave test favoured cone detection. This was verified by measuring dark adaptation following a 10 sec exposure to a 560,000 td bleach. No rod branch was observed after 47 min dark adaptation. The threshold level measured during cone plateau was the same as that measured in the presence of the large blue background, showing that it caused no loss of sensitivity in the cone system. The position of the test diaphragm was shifted further from the observer, for best focus.

*Precautions against habituation.* Repeated exposures to a small peripheral test flash can cause a decrement in sensitivity (Baker & Bargoot, 1977; Singer, Zehl & Poppel, 1973; F. Frome, D. MacLeod, S. Buck & D. R. Williams, in preparation). Several precautions were taken to guard against this. The subject presented the test flash herself, when she was ready, and was therefore able to make economical use of the test presentations in his judgements of threshold. The average rate of presentation was about one flash every 2 sec. The subject rested for about 5 min between runs (i.e., a sequence of adaptation to the small background, and recovery on the large) to allow recovery from any habituation during a run. At the beginning of a run the subject set a baseline threshold on the large blue background to check for long-term drifts in sensitivity. Thresholds were generally stable over a session, and no attempt was made to adjust for baseline variations. On some runs, the subject refrained from setting thresholds during the period of adaptation to the small background, to see whether these trials affected the subsequent settings in the recovery phase. No such influence was observed. On two occasions, one subject, (M.H.) continuously set thresholds on the large blue background for 10–15 min. Negligible threshold rise (about 0.1 log units) was observed in this period, which was much longer than that required during the experimental conditions. This was less than expected, in view of other reports, but variability in fixation position and the low presentation rate may account for the small size of the threshold elevation.

*Apparatus.* Stimuli were delivered by a four channel Maxwellian view optical system. The image of the source in the plane of the pupil measured 0.4 by 3 mm. Small and large red (or green) backgrounds were supplied by two different channels which were made equal in intensity by a side-by-side brightness match. The matching range was approximately 5%. The coloured filter was in the common path of the two beams. Field stops were at optical infinity. The position of the blue (or red) diaphragm was adjusted for best focus. Lights were measured with an E.G. & G. silicon photodiode placed in the pupil plane. All neutral filters and wedges were calibrated for the appropriate wavelengths.

*Subjects.* The author and one other observer served as subjects. Both had good acuity. The second observer had had some experience in experiments of this sort, but was kept uninformed about her results until the experiment was complete.

## RESULTS

### *Rod system*

Fig. 2 shows the time course of the sensitivity readjustment following the exchange between a small and an equiluminous large red background. Zero on the abscissa corresponds to the time when the backgrounds were exchanged. Data for two subjects are shown. In this case, the small red background was present for 3 min before the exchange. The dotted line shows threshold on the small background; the dashed line shows the steady-state (pre-adaptational) threshold on the large background. There is some immediate recovery of sensitivity during the first few seconds (0.15–0.23 log units) but thereafter sensitivity returns very slowly. Most of the recovery is accomplished in about 2.5 min, but threshold has still not quite returned to its pre-adaptation level after 400 sec. (This long tail may be due to habituation to the repeated test flashes. However, with longer periods of adaptation, e.g., 10 min, the threshold elevation may last for over 40 min, despite very infrequent exposure to the test flash, so it probably represents a real after-effect of the small background.)

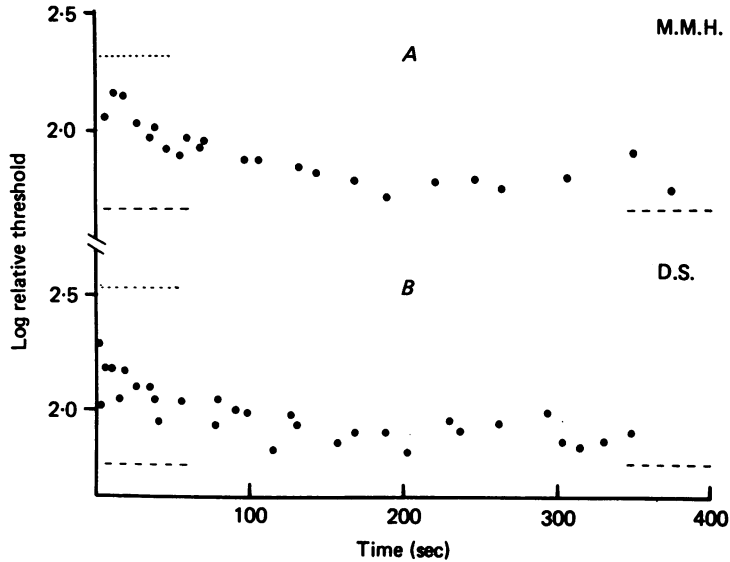


Fig. 2. Time course of threshold following the replacement of the small background by an equiluminous large one. Threshold is relative to dark adapted value. Dotted line indicates threshold on the small background; the dashed line, steady-state threshold on the large background. Small background pre-adaptation lasted 3 min before the exchange. *A*, subject M.M.H.; 47' small background; two runs are plotted. *B*, subject D.S.; 38' small background; three runs. M.M.H.

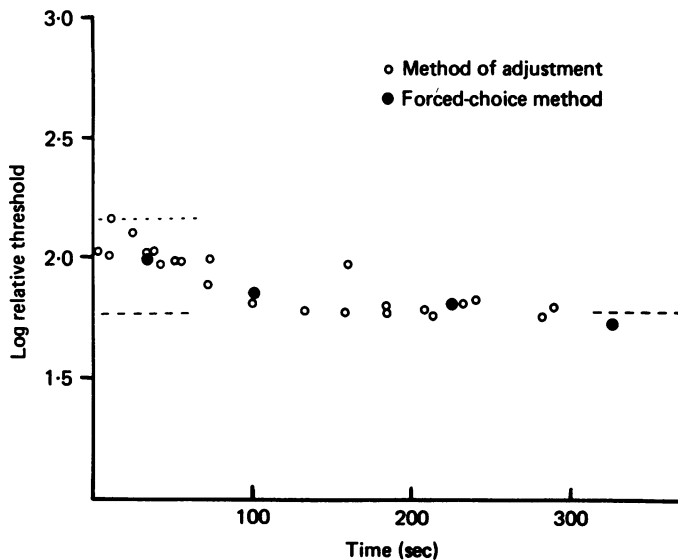


Fig. 3. Comparison of method of adjustment and forced-choice methods. Time course of rod threshold following exchange of 38' and 7.3° backgrounds. Small background pre-adaptation lasted 45 sec. Open circles, method of adjustment; filled circles, forced-choice. Dotted line, threshold on small background; dashed line, threshold on large background. Subject M.M.H.; three runs.

This pattern of results was obtained on many occasions, including trials on lower luminance backgrounds, and for one minute adaptation periods. The one minute adaptation periods gave similar recovery curves. Informal confirmation was also made on two other observers.

Fig. 3 shows data for a similar experiment for an adaptation period of only 45 sec. Here, too, the recovery is extremely sluggish, it takes at least 2 min for the readjustment of sensitivity to be accomplished. The 45 sec pre-adaptation period was used so that the results of this experiment and that on cone bleaching adaptation (Experiment II) could be directly compared. This Figure also gives a comparison between method of adjustment (open circles) and two-alternative temporal forced-choice thresholds (filled circles). There is a pleasing agreement between the two methods.

Latch & Lennie (1977) have also demonstrated sluggish recovery of rod sensitivity from the effects of small backgrounds, but not large ones. In their experiment, the small background was not replaced by a large one, but was simply turned off at the end of the adaptation period (3 min). Latch & Lennie's experiment was repeated, with similar results (although a slight loss of sensitivity of about 0.1 log units was also consistently observed for about a minute after the large background was turned off). The background exchange method used in the present study, however, has the advantage of holding constant the state of adaptation of the receptors in the region of the test spot, and isolating the effects peculiar to the small background, since retinal illuminance in the region of the test spot remains constant (except for light scattered from the outer region when the background is enlarged).

#### *Cone system*

Fig. 4 shows the readjustment of sensitivity following adaptation to the small green background, and subsequent exchange to the large green background. M. H.'s data are for a 1 min adaptation period, D.S.'s are for a 3 min adaptation period. The difference in threshold levels between large and small backgrounds is much larger for the cones, even though the large red background is much more effective in raising rod threshold than the green one is in raising cone threshold (a factor of 10 above the large blue background, as opposed to a factor of 2.5 or 5.0, depending on the subject). As with the rods, the readjustment of sensitivity takes an extremely long time to reach completion, but in this case a large, immediate reduction in threshold (0.5–0.8 log units, compared with about 0.2 log units for rods) precedes the cone phase of recovery. The size of the threshold elevation for the sluggish component is about the same, however. Fig. 5 shows the same experiment as Fig. 4, except that the small background was exposed for only 45 sec before the surround was light-adapted. The sluggish component is slightly diminished, but still clearly present.

### EXPERIMENT II. BLEACHING ADAPTATION: CONE SYSTEM

This experiment measures the recovery of cone system sensitivity after brief exposures to a light which bleaches a large fraction of the visual pigment. When compared with a large bleach, the threshold after a small bleach is greatly elevated, and recovery much delayed (see preceding paper). This effect is clearly analogous to the sensitization effect on steady backgrounds. The following experiment demon-

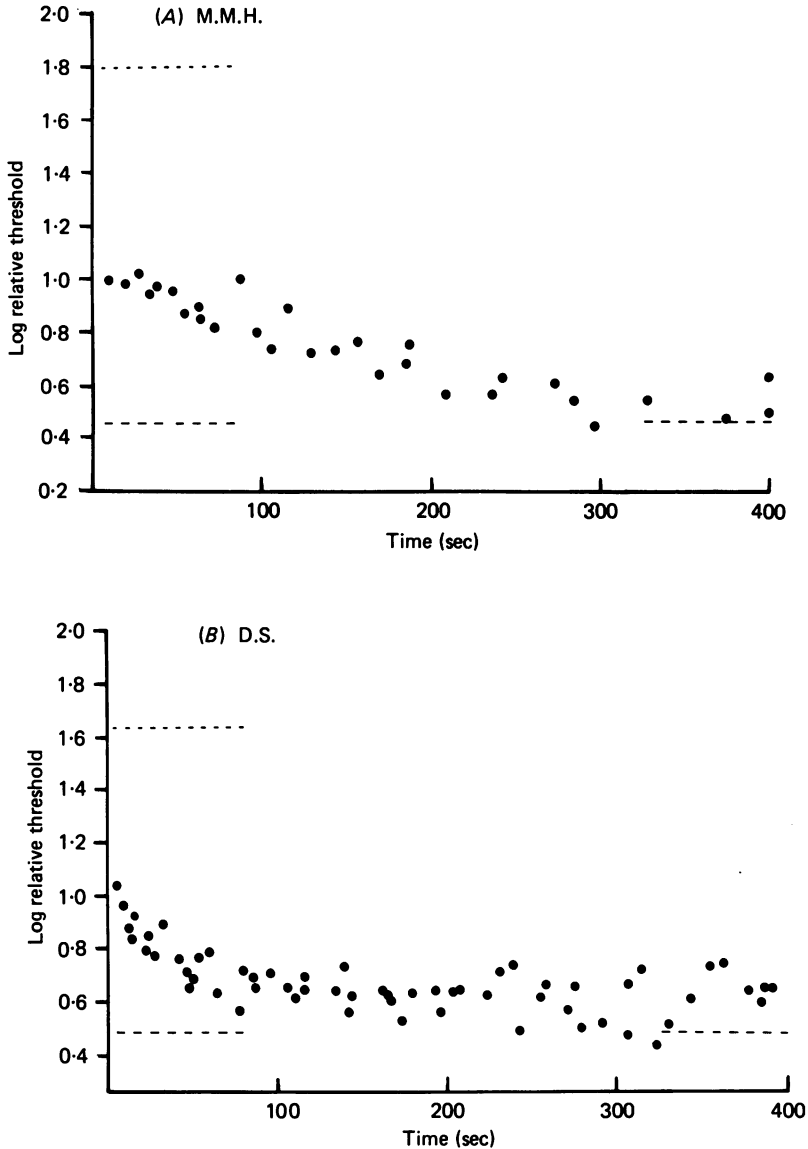


Fig. 4. Time course of cone threshold after the exchange of a 6.5 photopic td,  $7.3^\circ$  background for an equiluminous  $38'$  background. Threshold is measured relative to the cone dark adapted state. Dotted line, threshold on small background; dashed line, steady state threshold on large background. *A*, subject M.M.H., 1 min pre-adaptation to small background; three runs. *B*, subject D.S., 3 min pre-adaptation; five runs.

strates an interesting feature of the effect: if the region surrounding a small bleached patch is exposed to light at any time following the bleaching exposure, threshold in the centre of the bleached area falls greatly; that is, sensitivity is improved. This was demonstrated in the preceding paper, but the present experiment shows also that light adapting the surround can lower threshold all the way down to the level it would have after a large bleach, and moreover, that the recovery of sensitivity



from that appropriate to a small bleach to that appropriate to a large bleach is accomplished within a few seconds. This is quite distinct from the sensitivity re-adjustment observed using background adaptation in Experiment I, where the recovery of sensitivity following the addition of light to the surround (that is, following the exchange) took minutes to complete. This leads one to the conclusion that the sensitivity loss due to the small adapting field is caused by different mechanisms with different temporal properties, in the two cases.

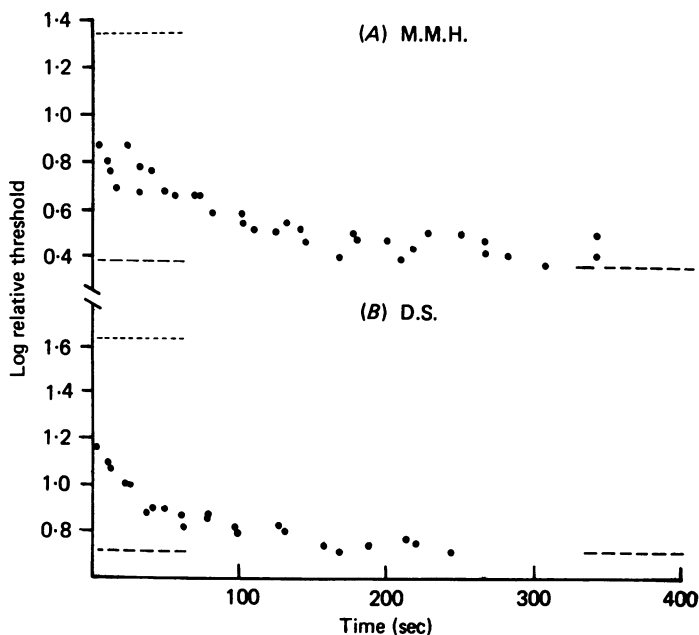


Fig. 5. As for Fig. 4, but for a 45 sec pre-adaptation to the small background. *A*, subject M.M.H., three runs. *B*, subject D.S., two runs.

#### METHODS

The procedure and apparatus were as described in the Methods section in the preceding paper. The bleach was always white, and the test red (Melles-Griot 630 nm cut-off filter). The bleaching flash lasted 200 msec. The test flash lasted 20 msec and subtended 3' arc. There were three conditions of interest: one, where the bleach subtended 115' arc (the 'large' bleach); the second, where the bleach subtended 27' arc (the 'small' bleach); and the third, where a small bleach was delivered first, and 45 sec later a 27-115' annular background surrounding the bleached patch was turned on. On some trials, a brief, 27-115' annular bleach was delivered 45 sec after the first bleach, in place of the background. This was done in order to see whether the results were affected by the method used to light adapt the surround.

The arrangement of polarizers and half-wave plate described in the preceding paper was used here. Either the 27' spot or the complementary annulus could be delivered by rotating a polarizer in the beam through 90°. When the experiment called for a steady annulus instead of a second bleach, the polarizer was rotated through 90° and neutral filters were added to the beam, which was then exposed continuously. Extinction in the central spot was 0.2%, and in the annular surround, 4%. The unextinguished light in the surround was shown to be insufficient to affect

the dark adaptation curve for the small bleach, and can presumably be neglected. To deliver a large uniform bleach of the same intensity as the central spot, the polarizer and half-wave plate were replaced by two parallel polarizers. The polarizers reduced the intensity of the bleaching beam from its maximum to  $10^7$  td, sufficient to bleach 47% of the cone pigment in a 200 msec exposure. The latency of any saccade triggered by the bleach would have been about 200 msec (Alpern, 1972) so smearing of the image by eye movements should not have been serious. Calibrations were described in Experiment I.

*Subjects.* Observations were made on three subjects; two with normal acuity (M.H. and D.M.) and the other (J.A.) 1.5 D myopic (a correction was considered unnecessary for the viewing distance used here - 72 cm). M.H. and J.A. were well practised at this task. J.A. was not informed about the nature of the experiment.

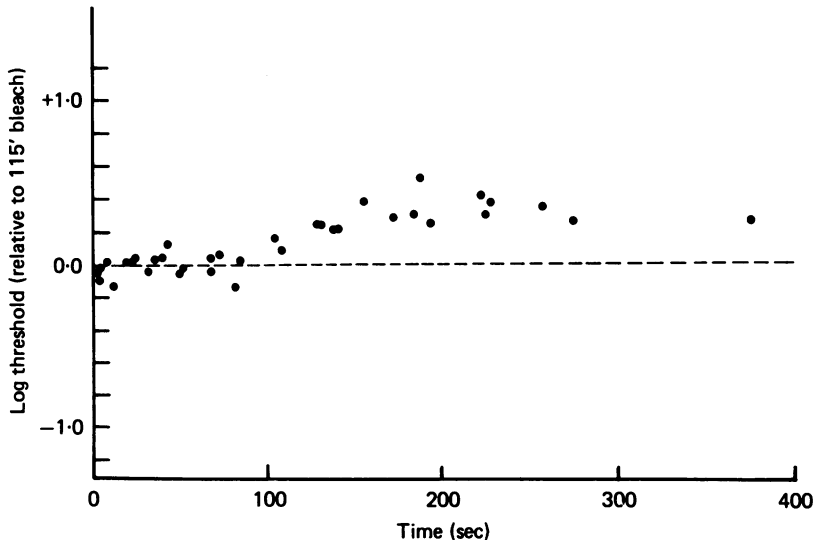


Fig. 6. Dark adaptation for a 27' bleach followed by onset of 180 td, 27-115' annulus plotted relative to dark adaptation curve after 115' uniform bleach (shown as the dashed zero-line). The bleaching flash lasted 200 msec, and was  $10^7$  td. Zero on the time axis corresponds to the onset of the annulus, 45 sec after the bleach. Subject M. M. H.; four runs.

## RESULTS

This experiment shows that threshold after the small bleach may be rapidly modified by the addition of an annular background to the surrounding retina. The polarizers and half-wave plate were placed in the bleaching beam. A small bleach was delivered to the subject, who then waited in the dark for 45 sec. The polarizer was rotated and the steady annulus was exposed to encircle the bleached area, and the observer then set thresholds as quickly as possible, continuing for several minutes until an asymptote was reached. (The intensity of the annulus was chosen so that a large uniform field of the same intensity raised threshold to the level on the large bleach dark adaptation curve reached after 45 sec dark adaptation). Ordinary dark adaptation curves following a 115' bleach and a 27' bleach (without an added annulus) were also recorded. The dark adaptation data for the small bleach with an added annulus are shown in Fig. 6, plotted relative to the dark adaptation curve following the 115' bleach. Zero on the abscissa is the time at which the annulus was

switched on. Threshold falls immediately to the large bleach base line (represented by the dotted line). If the background had not been turned on, threshold would have been too high to measure for another 20–30 sec. The annulus has the effect of lowering threshold, in a few seconds from its onset, from its small bleach level to that appropriate to the corresponding large bleach – an improvement in sensitivity of a factor of over 50, and probably much more (see discussion in preceding paper, Hayhoe, 1979. This value is obtained from the dark adaptation curve for the 27' bleach alone, which is not plotted.) The data points do not asymptote at the dark adapted threshold level. This difference on final level is probably caused by light scattered from the annulus into the central area and is of no interest in the present context. Since effects of backgrounds and bleaches are additive (Rushton, 1965), the stray light would have had a negligible effect during the period of interest here. The results of Fig. 6 were also found on observer D.M.

As discussed in the previous paper, these results may be explained if the extra insensitivity caused by the small bleach is the result of the action at some spatially opponent stage of persisting signals from the receptors in the bleached area. A persisting hyperpolarization has been observed in the receptors of the rat, gekko, and turtle after exposure to intense lights (Penn & Hagins, 1972; Baylor & Hodgkin, 1974; Kleinschmidt & Dowling, 1975). 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.

If the bleach produces a persisting signal, and therefore acts like a background, the similarity between the situation in Fig. 6, and that of Figs. 3 and 5 becomes much clearer. In both cases a small adapting field was present for 45 sec. Then light was added to the surrounding region. In both cases, threshold falls to the level appropriate to the corresponding large field. What is of particular interest here is that in Figs. 3 and 5 it takes about 2 min to fall 0.4 log units (a factor of 2 or 3). In Fig. 6 it takes less than 4 sec to fall more than 1.8 log units (a factor of more than 50).

It is interesting to note that in the case of the small bleach, an after-image is observed only for a fairly short period after the bleach. For much of the time that threshold remains high nothing in the field is visible except the dim red fixation points. But when the bright annulus suddenly illuminates the field, threshold falls precipitously. This effectively rules out 'perceptual interference' or high level masking hypotheses as a basis for this effect, since there should be more masking with the annulus than in the dark.

The rapid modulation of the small bleach threshold by the annulus acts reversibly – that is, if the annulus is turned on, and then off, threshold is first abruptly lowered to the level of the large bleach, and then abruptly raised back to the level on the small bleach. This is shown in Fig. 7. The continuous curves are for the large and small bleach dark adaptation. Crosses show threshold after a small bleach. After 17 sec, the annulus was added, and it was subsequently extinguished at 35 sec after the bleach. Threshold rose too rapidly to track above the highest intensity available in the test beam, and the run proceeded as it normally would after a small bleach. The open circles show the same effect, for an annulus that was turned on at 25 sec, and off again at 45 sec. Filled circles plot another condition, when the annulus was

turned on at 14 sec and kept on. This simply extends the generality of the result of Fig. 6.

*Double bleaches.* Another test for the rapid reversibility demonstrated above is to bleach the annular surround, rather than adding a steady field. As for the annular background, the annular bleach was delivered 45 sec after the first bleach.

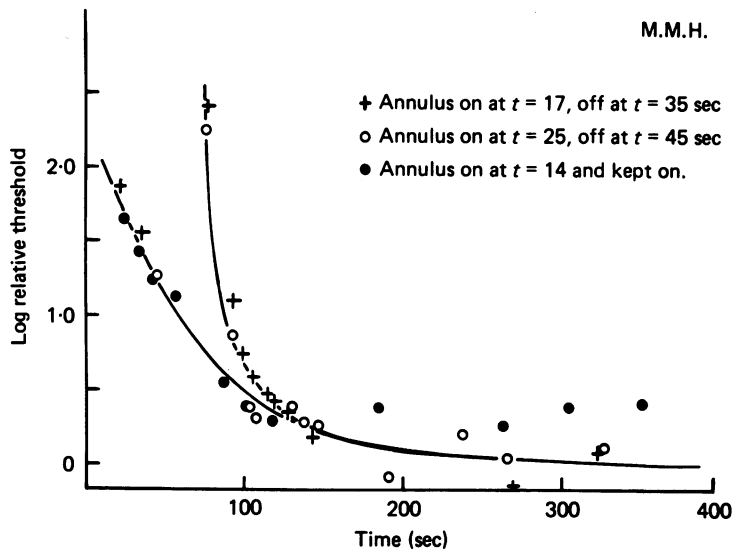


Fig. 7. Cone recovery from small 27' bleach for various times of annulus onset and offset. Curves show recovery in the dark after 115' and 27' bleaches. M. M. H.

Ideally, one would like to simulate a large uniform bleach 45 sec after the first bleach. That is, the first stronger bleach, and the second weaker bleach, delivered 45 sec later, should produce about the same threshold elevation. Therefore, the intensity of the second bleach was chosen so that a displacement of 45 sec to the right on the time axis aligned this dark adaptation curve with the large bleach curve. However, the alignment held only for the later part of the curves. Threshold for the first 30 sec after the weaker bleach was too high. However, this does not appear to be a critical factor in the results. This deviation from an exponential form is to be expected for such a weak bleach (22%; Hollins & Alpern, 1973).

The results for two observers are plotted in Fig. 8. These data are in the same form as Fig. 6. For M.H., the rapid restoration of sensitivity observed in Fig. 6 with surround illumination is also observed here with surround bleaching. It is not so clear in J.A.'s data, where threshold takes about 20–30 sec to fall to the large bleach value. Even in J.A.'s case, the time course of recovery is still clearly more rapid than the sluggish curves of Experiment I, however. It is possible that bleaching in the central region by scattered light causes a transient elevation of threshold (Hollins & Alpern (1973) and Rushton & Powell (1972) show that such weak recent bleaches cause a substantial elevation of threshold. See discussion above.) Scattered light may have been worse for J.A. because of his poorer optics. This interpretation is supported by an observation that the annulus used in the previous experiment (Fig. 6) raised J.A.'s dark adapted threshold by a log unit (compared with 0.33 log units for M. H.).

J.A.'s data are relative to the dark adaptation curve generated by equal-strength spot and annular bleaches delivered sequentially, within a few seconds of each other. This is the appropriate control condition, rather than a large uniform bleach, because of possible misalignment of the two bleaches. No differences between the two curves was observed, however. For M.H. the control condition was simply the large uniform bleach curve. This is a conservative comparison.

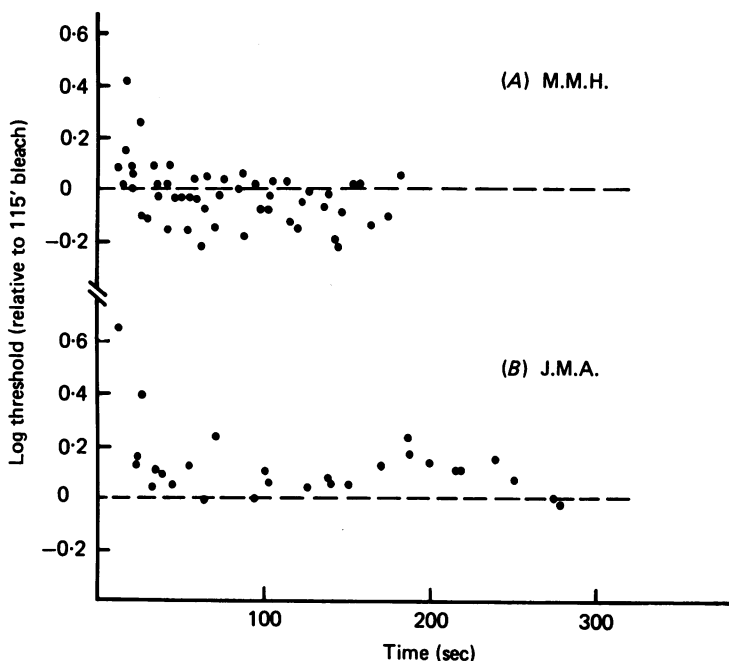


Fig. 8. Double bleach condition plotted relative to dark adaptation after 115' bleach (dashed zero-line). Zero on time axis corresponds to the time at which the annular bleach was delivered. *A.*, subject M.M.H.; five runs. *B.*, subject J.M.A.; four runs.

#### DISCUSSION

These experiments demonstrate that when light is added to the region surrounding a small, steady background, the subsequent improvement in the centre of the background is not completed until several minutes have elapsed. This is observed whether detection is mediated by rods or by cones. But if the cone receptors in the central area are made insensitive by a small bleach, rather than a small, steady background, then light-adapting the surround brings about a much more rapid increase in sensitivity. Another feature of these results is that, for cones, a large proportion of the threshold elevation caused by the small background recovers very quickly, so cone backgrounds resemble cone bleaches with respect to this property of 'rapid reversibility.' These results suggest that there is not just *one* underlying mechanism operating to produce the sensitization effect observed in all these settings. It may be possible to make a further inference, however. If the sluggish recovery observed in Experiment I signals the involvement of neurones in visual cortex, as suggested by Latch and Lennie, and discussed below then it may be that such neurones are responsible

for much (if not all) of the rod effect, at least some of the cone background effect, but are probably not involved in the cone bleach effect. The results, together with the fact that there is no sensitization by surrounds in rod dark adaptation, are consistent with the hypothesis that sensitization occurs mostly at the retinal level in the cone system, but not (or only weakly) in the rod system, and that there is an additional site of elevation common to rods and cones probably at the cortical level for small backgrounds, but not for small bleaches. The evidence for this position is examined in what follows.

*Evidence for cortical involvement.* There is only partial or no binocular transfer of the sensitization effect (Markoff & Sturr, 1971; Sturr & Teller, 1973; Johnson & Enoch, 1976), so if the effect is cortical, monocular neurones in the striate cortex (area 17), the last site of monocular neurones (Hubel & Wiesel, 1970), must be largely responsible.

Long-lasting after-effects which likely have a cortical origin have long been observed by psychophysicists (e.g. McCollough effect, figural after-effects (Hammer, 1949), spatial frequency-specific adaptation). Blakemore & Campbell (1969) and more recently Bodinger (1978) have observed the time-course of recovery from spatial frequency-specific adaptation, which is quite similar to that observed here. In general, the time-course is somewhat shorter than that observed here, but the very long time course observed by Bodinger after 10 min adaptation has been observed in these experiments also (although no systematic measurements have been made, and no data presented). There have been some physiological observations which confirm the psychophysics (Maffei, Fiorentini & Bisti, 1973; Vautin & Berkley, 1978). Vautin & Berkley, recording responses of cells in area 17 of the cat to drifting bars and gratings, found a response decrement in the cell during the exposure, and a subsequent depression in the maintained discharge after the stimulus was removed. The time course of recovery of the maintained discharge was very similar to that observed by Blakemore & Campbell, and they present evidence that the origin of the long-lasting decrement was cortical and not some earlier level. Maffei *et al.* also conclude in favour of a cortical origin, since their adaptation effect showed binocular transfer. Similar prolonged losses of sensitivity have been observed by Movshon & Lennie (1979) in cat area 17, but not at the l.g.n. level (P. Lennie, personal communication).

Apart from the evidence of Maffei *et al.* and Vautin & Berkley that the after-effects they observe originate in the cortex, there is a paucity of evidence as to whether such long-lasting insensitivity after low intensity stimulation can occur subcortically. Rapid modification of sensitivity of bipolar cells in the mudpuppy by addition of light to the receptive field surround may be observed in the recordings of Werblin (1974) and Burkhardt (1974). On the other hand, Barlow & Hill (1963) have observed long-lasting effects of stimulation in directionally selective units in the rabbit retina. More evidence on the rapidity of retinal processes is necessary before the sluggish mechanism can be located in the cortex with any confidence.

At first thought it may seem surprising that these relatively weak adapting fields should produce a sensitivity loss which lasts so long; but in normal circumstances the eyes are continually moving over the environment and rarely come to rest for the sorts of periods involved here.

*Evidence for a peripheral locus in cone background and bleaching sensitization.* The absence of a sluggishly recovering component in the effects of small cone bleaches suggests that the locus of the bleaching sensitization effect precedes the mechanism responsible for the prolonged after-effects observed here. The arguments mentioned in the Introduction, and other evidence discussed below provide a fairly strong case for a retinal locus for cone bleaching sensitization. If the bleach effect is retinal, then a retinal mechanism is also likely to be involved in the action of small cone backgrounds, particularly in view of the interactions between backgrounds and bleaches observed in Experiment I (bleaching the surround may also lower threshold on a small steady background in cone vision (Hayhoe, 1979)). Sensitization on cone backgrounds may therefore reflect the action of retinal, as well as cortical processes. 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.

Further evidence for retinal involvement comes from studies of retinal pathologies (Enoch, 1978) and experiments involving a black ring in the region of the test spot. J. Ambrose & M. M. Hayhoe (in preparation) show that the dark adaptation curve after a 115' bleach which spares a 5' wide annular region (with inner diameter 27') is the same as that after a uniform 115' bleach. A similar effect is observed with backgrounds (Westheimer, 1967). This presents a difficulty for the size-selective channel hypotheses, suggested by Lennie & MacLeod (1973), whereby the small background would desensitize those channels responsible for detection of the (small) test spot, since contours near the test region that should be desensitizing high spatial frequency channels are present in one case, but not in the other.

The ability of a small bleach to make the cone pathways completely insensitive (see preceding paper) is not consistent with the channel hypothesis either, although it does not rule out a central locus in general. The channel hypothesis predicts that less sensitive channels should be able to take over the task of detection when the small channels are made insensitive with only a moderate resulting loss of sensitivity. A total loss of sensitivity, however, is observed after small bleaches.

*Possible mechanisms for a retinal effect.* Mechanisms which might underlie a retinal effect have been described in the preceding paper. The rapid reversibility of the threshold elevation when light is added to the surround of a small field follows naturally from such a centre-surround model, since the sensitivity loss associated with the overloading of a cell would be redressed as rapidly as the balance of excitation and inhibition within the receptive field could be altered.

The choice of the outer plexiform layer as a likely site of sensitization in cones is suggested by the fact that ganglion cells and amacrine cells do not respond well to sustained input (Werblin & Dowling, 1969; Werblin & Copenhagen, 1974), which is what they would be receiving from the bleached region. Some amacrine cells give sustained responses, however (Chan & Naka, 1976), so this is not conclusive.

*Nature of the rod effect.* Although most of the rod effect recovers slowly, there is some immediate recovery, so it is a little difficult to say whether there is no sensitization at all in the rod system at the retinal level, or whether it is simply slight. Teller (1971) observed some modulation of sensitivity following the onset and offset of an annulus surrounding a small adapting field, recycling once every 2 sec. The sluggishly recovering process should not have been able to follow this rate of alternation, and in confirmation of this, the modulation was generally small (0.2–0.3 log units). Under some conditions for one subject, however, it was as large as 0.5 log units. There is no reason, of course, why part of a central component might not be rapid. The absence of sensitization in the rod-dominated retina of the cat (Cleland & Enroth-Cugell, 1968; Enroth-Cugell, Hertz & Lennie, 1977; Barlow & Levick, 1976) suggests that there is no retinal mechanism for sensitization in the rod system, but perhaps the best evidence is that of Blick & MacLeod (1978) who show, using the Stiles-Crawford effect, that background displays equivalent for cones but very different for rods give, under their conditions, practically the same rod threshold. This leaves little room for sensitization processes operating before rod-cone convergence within the retina.

*Conclusion.* These experiments suggest that small adapting fields raise threshold at more than one site in the visual pathway. The results are consistent with a retinal basis for sensitization in cone vision (but perhaps not in rods), mediated by the antagonistic action of centres and surrounds of retinal neurones (perhaps bipolar cells). Such a mechanism would increase the effective operating range of retinal cells by discounting the space-average luminance, reserving the full response range for signalling contrast, with presumable benefits for differential sensitivity. Since the sensitization effect with cone bleaches appears to be relatively uncontaminated by central processes, it may provide a useful paradigm for the psychophysical investigation of retinal mechanisms.

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