ROD-CONE INTERACTION IN LIGHT ADAPTATION

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SUMMARY

1. The increment-threshold for a small test spot in the peripheral visual field was measured against backgrounds that were red or blue.

2. When the background was a large uniform field, threshold over most of the scotopic range depended exactly upon the background's effect upon rods. This confirms Flamant & Stiles (1948). But when the background was small, threshold was elevated more by a long wave-length than a short wave-length background equated for its effect on rods.

3. The influence of cones was explored in a further experiment. The scotopic increment-threshold was established for a short wave-length test spot on a large, short wave-length background. Then a steady red circular patch, conspicuous to cones, but below the increment-threshold for rod vision, was added to the background. When it was small, but not when it was large, this patch substantially raised the threshold for the test.

4. When a similar experiment was made using, instead of a red patch, a short wave-length one that was conspicuous in rod vision, threshold varied similarly with patch size. These results support the notion that the influence of small backgrounds arises in some size-selective mechanism that is indifferent to the receptor system in which visual signals originate. Two corollaries of this hypothesis were tested in further experiments.

5. A small patch was chosen so as to lift scotopic threshold substantially above its level on a uniform field. This threshold elevation persisted for minutes after extinction of the patch, but only when the patch was small. A large patch made bright enough to elevate threshold by as much as the small one gave rise to no corresponding after-effect.

6. Increment-thresholds for a small red test spot, detected through cones, followed the same course whether a large uniform background was long- or short wave-length. When the background was small, threshold upon the short wave-length one began to rise for much lower levels of

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background illumination, suggesting the influence of rods. This was confirmed by repeating the experiment after a strong bleach when the cones, but not rods, had fully recovered their sensitivity. Increment-thresholds upon small backgrounds of long or short wave-lengths then followed the same course.

INTRODUCTION

Recent reports (Lennie & Macleod, 1973; Makous & Boothe, 1974) have described conditions under which steady background lights, equal in their effects upon rods but unequal in their effects upon cones, may not equally affect the threshold for a small, short wave-length test flash detected using rods. These findings are perplexing because they conflict with powerful psychophysical evidence that the sensitivities of rod and cone systems are independently regulated by steady background lights (Stiles, 1939; Flamant & Stiles, 1948; Hallett, 1969; Westheimer, 1970).

A simple hypothesis to reconcile the discrepant results is that independence is found if experimental manipulations affect rod and cone signals in the retina before they enter a common pathway to the brain, while interactions are found when the experiment touches upon more central mechanisms that are indifferent to the source of the visual signal. From this point of view, the interesting interactions are those that pinpoint where in the visual pathway (before or after the combination of rod and cone signals) a particular mechanism acts.

This paper explores further the mechanism whereby the threshold for rod vision in the peripheral retina can be raised by steady backgrounds that act through cones. It is shown that this happens principally when the background is small: when it is large the threshold over most of the scotopic range depends exactly upon the background's effect upon rods, as was shown first by Stiles (1939) and Flamant & Stiles (1948). The interactions involving cones, found when backgrounds are small, cause characteristic changes in the shape of curves relating increment-thresholds to background level, but similar changes are seen also when the effect of the small background can only be mediated by rods, or when a long wave-length test flash, affecting only cones, is presented against a small short wave-length background that only stimulates rods. Thus the mechanisms responsible seem to be indifferent to the source of the visual signal.

Our findings can be explained by the hypothesis, discussed by Lennie & Macleod (1973) and D. W. Blick & D. I. A. Macleod (in preparation), that central mechanisms selectively sensitive to backgrounds of small size have an important influence upon the detectability of small stimuli.

METHODS

Test spots and backgrounds were presented in Maxwellian view, using an optical system slightly modified from that described by Alpern, Rushton & Torii (1970). A test spot usually 6' in diameter was flashed on for 10 msec through one channel. Two other channels provided backgrounds when these were needed; one background was always 8° in diameter, the other of variable size. Both were defined by metal masks mounted on traverses that permitted them to be aligned exactly concentrically with the test spot. In all the experiments to be described, narrow band interference filters (Ealing TFP, 10 nm half width) were used to produce 486 nm (blue) or 656 nm (red) test spots and 480 nm (blue) or 656 nm (red) backgrounds. Neutral filters and wedges in each channel allowed independent control of the illumination from it. Light from all three beams converged to form a compound filament image 1 mm in diameter that fell in the centre of the observer's pupil.

Great care was taken over the calibration of luminosity. The densities of neutral filters were measured in a Carey recording spectrophotometer and, for each wavelength used, wedge densities were measured in the apparatus using a Tektronix J4502 radiometer placed in the position of the eye. The same radiometer, which had been calibrated against a thermopile, was used to find the irradiance of the light transmitted by each interference filter. Scotopic and photopic luminosities were calculated from these measurements (Wyszecki & Stiles, 1967). As a check on the relative accuracy of the calibrations, relative luminosities were also measured psychophysically; for rods by comparing thresholds for detection of a flashed 8° disk in the fully dark-adapted eye; for cones by comparing thresholds for small test spots measured during the cone plateau phase of recovery from a strong bleach. These stimuli fell on the temporal retina 8° from the fovea, as did the stimuli in all experiments. The greatest discrepancy between any psychophysical measurement and the corresponding estimate derived from radiometric measurements was 0·06 log units.

The observer (always one or other author) bit upon a dental impression and fixated with his right eye a dim orange spot while he brought the test flash to threshold by adjustment of the wedge in the test channel. Flashes were delivered every 1·5 sec until usually three or four determinations of threshold had been made. Both observers were myopic, M. L. severely enough to need a correcting lens. M. L. was deuteranomalous.

Every experiment (except that of Fig. 5, where only M.L. served) was made using both observers. Since results from both observers were quantitatively very similar, figures show results from only one.

RESULTS

The influence of cones depends upon background size

In the experiments of Lennie & Macleod (1973) and Blick & Macleod (1977), the test spot was presented against a small background disk that could be fully enclosed by an annular surround. Together, the disk and annulus could make a large field uniformly effective for rods, but not for cones, either by using disks and annuli of different colours (Lennie & Macleod, 1973) or by having light from the disk and annulus enter the pupil at different points (D. W. Blick & D. I. A. Macleod, in preparation). When this was done the

threshold for the test spot was substantially higher than when the background field was also uniform for cones.

These observations may be reconciled with those of Stiles (1939) and Flamant & Stiles (1948), who found a very exact dependence of the increment-threshold for rod-mediated vision upon the scotopic luminosity of a large background, if it is supposed that the effects of large backgrounds are confined to the distal retina where rod and cone signals are segregated, while the special effects of small backgrounds originate in more proximal mechanisms and may therefore include a contribution from cones (Lennie & Macleod, 1973). The following experiments show that under most conditions where the use of a small background exposes the influence of cones on the threshold for rod-mediated vision, there is no measurable action of cones when the background is large.

A 486 nm test stimulus lasting 10 msec and 6' in diameter fell upon the observer's temporal retina 8° from the fovea. By adjusting a wedge the observer brought this to threshold, first when the eye was fully dark-adapted, then when light-adapted to varying degrees by a uniform background 8° in diameter whose wave-length was either 480 or 656 nm. Fig. 1A shows the increment-threshold curves obtained in this way, together with a portion of a dark-adaptation curve measured during recovery from a strong bleach, to show the absolute photopic threshold for the flash. When scotopically equal, the backgrounds differed in their photopic luminosity by 2·83 log units; the arrows on the graphs mark (from other measurements) where the two backgrounds reached the threshold for cone vision, and the long wave-length one appeared red. The thresholds measured under the two conditions followed substantially the same course until within 0·5 log units of the cone plateau, when they began to diverge.

Where the threshold upon the 656 nm background reached the plateau, threshold upon the 480 nm background was a factor of 2 lower, the amount that might be expected were the rod and cone systems then contributing equally to detection of the test spot. This result agrees with the work of Stiles, but does not fit so well the more recent observations of Makous & Boothe (1974) and Sternheim & Glass (1975). Makous & Boothe measured thresholds for short wave-length stimuli presented against short or long wave-length backgrounds and found that threshold rose less steeply with background illumination when the wave-length of the background light was short. In that experiment flashes were delivered 2° from the fovea, on a part of the retina quite richly endowed with cones and this, the only substantial difference between the experiments, seems to be important for the results.

The pair of curves drawn in Fig. 1B describe measurements of threshold made as in the upper part of the Figure but with the background diameter
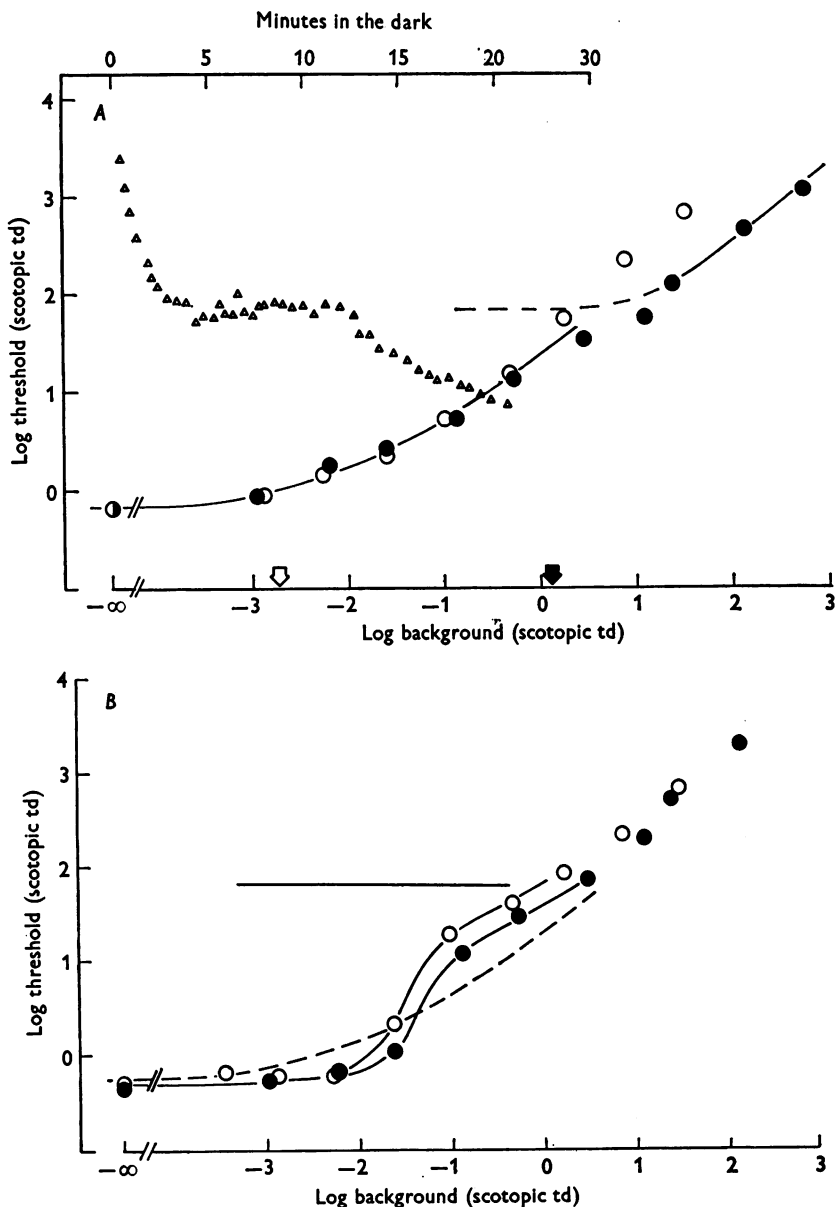
Fig. 1. *A*, increment-threshold for a 486 nm spot (6′ diameter, 10 msec duration) delivered on a 480 nm background (filled circles) or a 656 nm one (open circles) 8 deg in diameter. A dark-adaptation curve for the same test flash (triangles, upper abscissa) defines the cone plateau. *B*, increment-thresholds as in *A*, except backgrounds now 34′ diameter. The horizontal line marks the cone plateau, and the dashed curve is the continuous line of *A*, reproduced without translation or rotation. Within-session standard errors of threshold settings are less than the heights of the circles. Observer P.L.

reduced from 8° to 34'. Between the lowest background levels and the cone plateau (horizontal bar), the two graphs follow separate, but similar, paths and both are quite different from the dashed curve (reproduced from Fig. 1 A) that describes threshold on a large background field. This shape difference has two especially interesting features. First, when a small background of either wave-length was used, threshold began to rise only when background illumination was ten times that needed if the background was large. The simplest interpretation is that the adaptation 'pool' (Rushton, 1965) for scotopic vision is rather large, background area and illumination being to an extent interchangeable in controlling threshold (Westheimer, 1965). Second, on increasing the background illumination, the small backgrounds very soon overtook the larger ones in their influence upon threshold. The threshold curves made with the former have a pronounced 'knee' where threshold rose more than 1 log unit for a change in background illumination of only 0·6 log units. This has been observed before (Crawford, 1940; Westheimer, 1965; Lennie & Macleod, 1973) and appears to be associated with the emergence of a visible edge to the small background. The 656 nm background looked red as soon as it was clearly visible. Above the illuminance at which small backgrounds first had any influence, threshold on the 656 nm background was regularly higher by about 0·3 log units than on the 480 nm one. With the 8° background this difference appeared only when threshold came within 0·5 log units of the cone plateau, so over most of the scotopic range signals from cones influenced the rod threshold only when the background was small.

Lennie & Macleod (1973) suggested that the detectability of the test spot was dependent upon some size-selective mechanism the sensitivity of which was depressed by the steady signal from the small background patch, and the results of Fig. 1 may be understood within this framework. Threshold upon a small background rises steeply when the features of the background become clearly defined, because two mechanisms act co-operatively: a gain-controlling mechanism that is similarly affected by large and small backgrounds, and a size-selective mechanism that is activated only when the background is small. Once a small background is clearly defined the latter mechanism exerts a relatively constant effect upon the (log) threshold, hence the second inflexion in the increment-threshold curve for a small background. We suppose that the size-selective mechanism is more affected by a long wave-length than by a short wave-length background because cones as well as rods are much excited by it.

The influence of cone signals upon the threshold for rod vision was not remarkable in the results of Fig. 1, but was pronounced in the following experiment. The principle of this experiment was to find a uniform blue background that raised the threshold for rod vision, but not that for cone
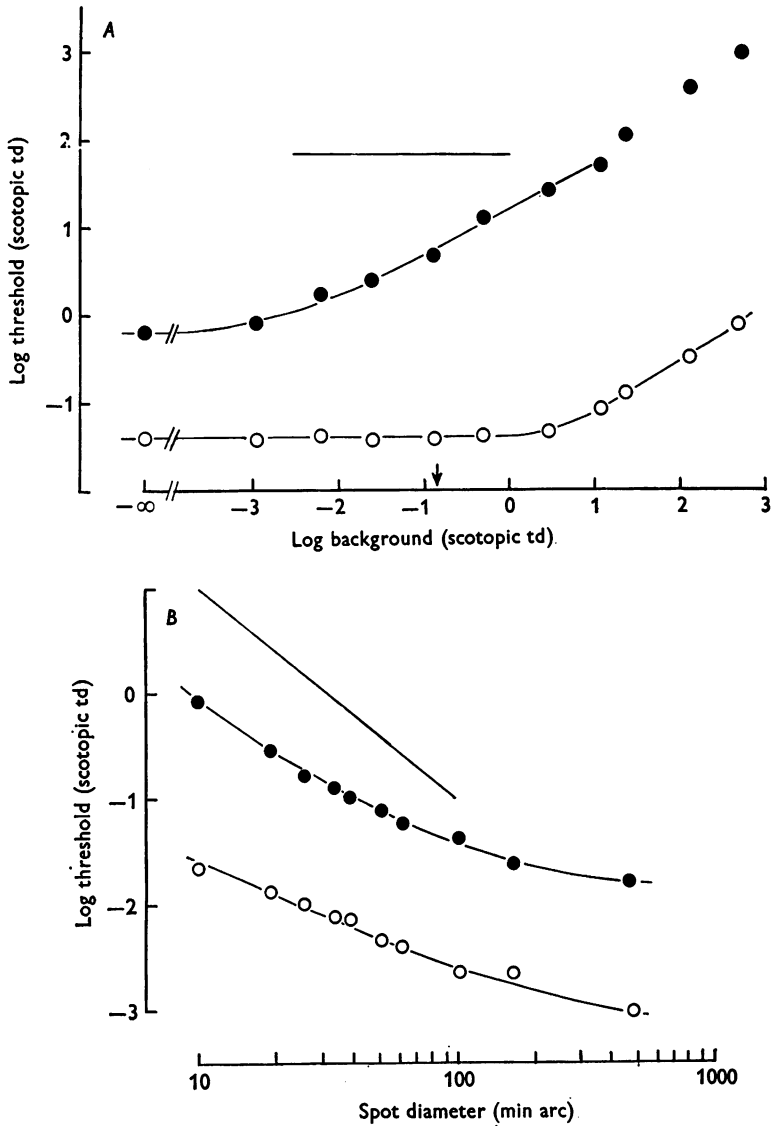
Fig. 2. *A*, increment-thresholds for 486 nm spots (filled circles) or 656 nm ones (open circles) delivered on 8° 480 nm background. The horizontal line marks the cone plateau for the test spot (from Fig. 1*A*) and the arrow marks the background illumination used in making the measurements of Figs. 2*B* and 3. *B*, threshold for detection of a 480 nm spot (filled circles) or a 656 nm one (open circles) as a function of spot diameter. Ricco's law of perfect spatial summation is shown by the straight line. Background − 0·85 log scotopic td. Observer P.L.

vision, substantially above its level in darkness. A relatively bright red patch, invisible as an increment using rods but clearly visible through cones, could then be superimposed upon it. We were interested to know how variations in the size of this red patch influenced threshold for the short wave-length test.

Fig. 2A shows, for one observer (although identical procedures were used for both), how the conditions were chosen so as to ensure both that the red patch was undetectable through rods, and also that the test spot was undetectable through cones. Thresholds determined using a 486 nm test spot on a uniform 480 nm background (filled circles) are shown together with determinations made using a 656 nm test spot (open circles) on the same short wave-length background. In this Figure the photopic absolute threshold for the 486 nm spot is defined by the horizontal line, which is the cone plateau of the dark-adaptation curve, reproduced from Fig. 1. The rod system's theshold for the long wavelength test spots would be the same as for the short wave-length ones, since scotopic units are used in the graph.

By choosing a 480 nm background of − 0·85 log scotopic td (arrowed) we ensured that the short wave-length test spot at threshold, and for about 0·7 log unit above, would be detected only through rods, while a 656 nm test at threshold and for about 2 log units above would be seen only with cones. The latter margin is reduced if the test is very large or of long duration, for there is greater spatial summation for rod-mediated vision (Arden & Weale, 1954). This may be seen also in Fig. 2B which compares two threshold *vs.* area curves made using the same large background (− 0·85 log scotopic td) that had raised the scotopic threshold 1 log unit from its level in darkness but had left cone sensitivity unimpaired. The upper curve is for a 480 nm test spot, the lower for a 656 nm one. In this experiment flashes lasted 100 msec. Although the curves converge for larger spot sizes, even when the spots were large the scotopic threshold always exceeded that of the cone system by more than 1 log unit.

Some results from the main experiment are shown in Fig. 3, in which the threshold for detection of the 486 nm spot is plotted against the size of the steady patch, 656 or 480 nm, upon which it fell. Each patch was fixed at 0·6 log units above its own threshold when presented as 100 msec flash (Fig. 2B) so the long wave-length one was always clearly seen through cones, but was always at least 0·6 log units below the level required for rod vision. Tests and patches appeared against the large 480 nm background of − 0·85 log scotopic td. Both patches influenced threshold substantially when small but not when large, and that influence was exercised similarly through rods and cones, for through rods the red patch was not detectable as an increment. The higher thresholds obtained with the short wave-

length patches are to be expected from their much greater scotopic luminance.

By re-plotting these results not against patch diameter, as in Fig. 3, but against the scotopic luminance of patch plus background (Fig. 4), it is easy to show that the mechanism whereby threshold is raised cannot be like those usually involved in the adjustment of gain. When 656 nm
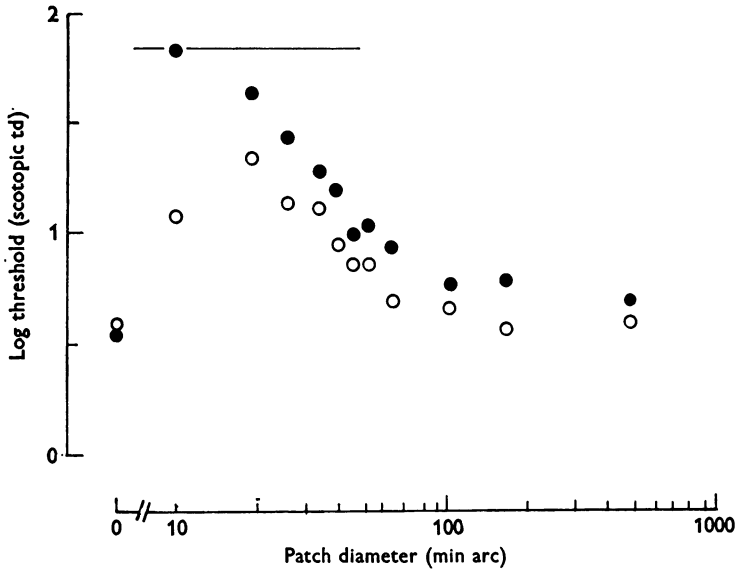

Fig. 3. Threshold for detection of a 486 nm test spot plotted against the diameter of the steady patch, of 480 nm (filled circles) or 656 nm (open circles), upon which it fell. Patch luminance was set to four times threshold, determined from the experiment of Fig. 2B. Both test and patch appeared on a 480 nm background field of −0·85 log scotopic td and diameter 8 deg. Observer P.L.

patches were used (open circles) the tiny additions to the over-all scotopic luminance of the background brought about a precipitous rise in threshold, and even 480 nm patches (filled circles) caused threshold to rise much more steeply than upon large background fields of equal luminance (triangles). The smaller patches were the most effective in raising threshold despite the fact that any pooling of adaptive signals would tend to make them relatively less effective than large ones

Both this and the previous experiment show that the influence of small patches is expressed similarly through rods or cones, thus implicating some mechanism to which rods and cones have equal access. It is likely that, in the central visual pathway, any size-selective mechanism serving the peripheral visual field will have connexions with both rods and cones. From
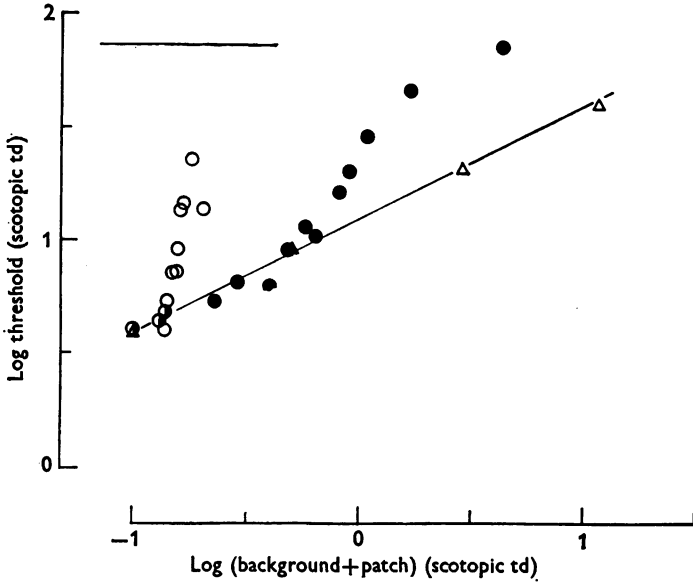
Fig. 4. Results of Fig. 3 plotted to show threshold for the 486 nm spot against the overall scotopic illumination of the patch plus background field. Open circles, 656 nm patches, filled circles, 480 nm patches. Triangles and line show the increment-threshold for the flash on the large 480 nm background alone.
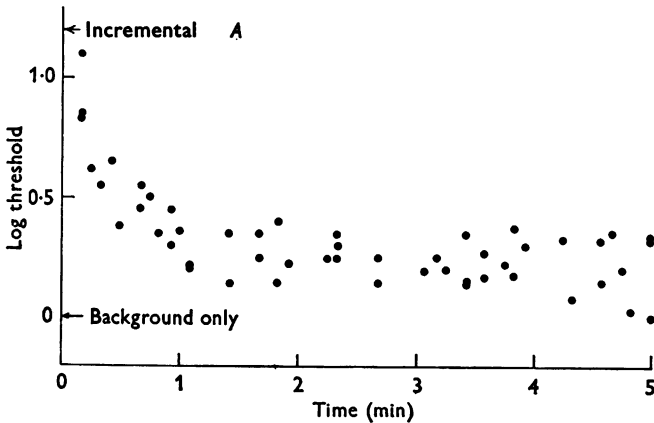

Fig. 5. Recovery of increment-threshold for a 486 nm test spot following extinction of a patch that had been added to a 480 nm background field (diameter 8 deg 0·14 scotopic td). *A*, 656 nm patch, 26′ diameter. *B*, 480 nm patch, 26′ diameter. *C*, 656 nm patch, 8 deg diameter. *D*, 480 nm patch, 8 deg diameter. The lower arrow on each ordinate marks threshold on the large background field before addition of the patch; the upper arrow marks threshold before its extinction. Observer M.L.
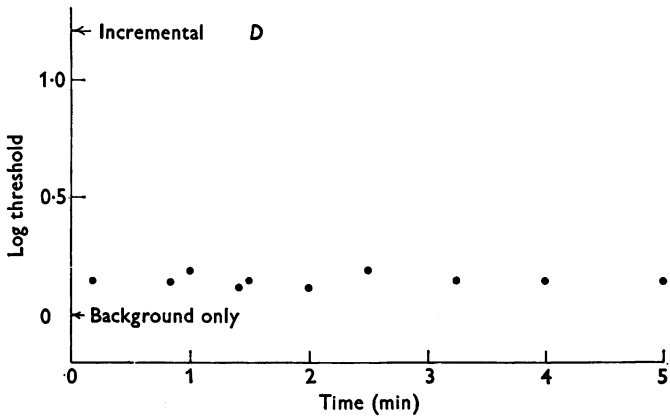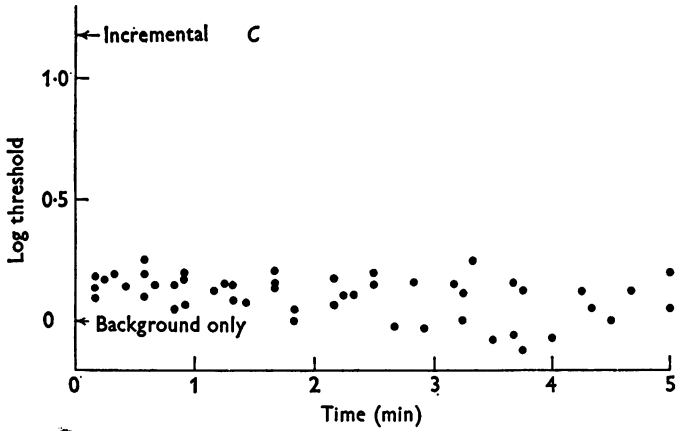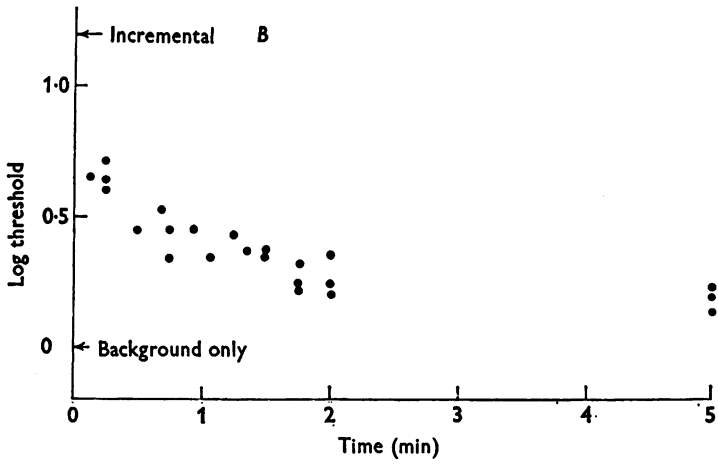
Fig. 5*B*, *C* and *D*. For legend see facing page.

what is already known about such mechanisms (Blakemore & Campbell, 1969) we expect that any depression of sensitivity to the test flash caused by prolonged viewing of a steady patch persists for some time after removal of the patch, and during our experiments we noticed just that; if a small, but not large, patch was switched off leaving only the 8°, 480 nm background, threshold did not immediately drop to the level previously found on that background field. The following experiments provide further information about this.

Recovery of sensitivity following removal of a patch. This was measured using a configuration like that of the previous experiment. The 486 nm test spot, and also the patch, fell upon the middle of the large 480 nm background, which was fixed at the level used in the earlier experiment (-0.85 log scotopic td). A 656 nm or 480 nm patch, 26' in diameter, was chosen so that it lifted threshold a little over one log unit above its level on the background field alone.

The patch was presented for 3 min, while the test spot was several times set to threshold, and then was extinguished. Threshold was measured repeatedly during the next 5 min and the results of these observations are shown in Figs. 5A and B. Following extinction of that patch, 480 or 656 nm, threshold took about 2 min to reach a stable level that remained slightly above that measured previously on the large background field. This might have been expected had some photopigment been bleached, but as an explanation of the slow recovery of sensitivity it is convincingly refuted by the results plotted in Fig. 5C and D. These graphs show recovery of sensitivity after extinction of an 8° patch of illuminance chosen so as to elevate threshold by the same amount as its smaller counterpart in the upper part of the Figure. Despite the fact that the illuminances of large patches were each nearly 2 log units greater than those of the small ones, within the time taken to make the first measurement threshold had recovered to a steady level just above that previously established on the background. Since larger fractions of rhodospin were bleached by the large than the small patches, the slow recovery of sensitivity observed only when the patch was small must have been of neural origin. This result may be understood in terms of the fatiguing, by the patch, of central size-selective mechanisms sensitive to it and to the test spot.

If central mechanisms do mediate the effects of small patches we might expect the threshold for detection of a test spot that excites cones to be susceptible to patches that excite rods, the complement of what was found in the experiments of Fig. 2.

The elevation of cone threshold by signals from rods

Fig. 2*A* shows that, when of long wave-length, the test spot was always detected through cones, not rods (and this was readily confirmed by the absence of a second (rod) branch in the dark-adaptation curve made following a strong bleach). Conversely, a short wave-length patch presented
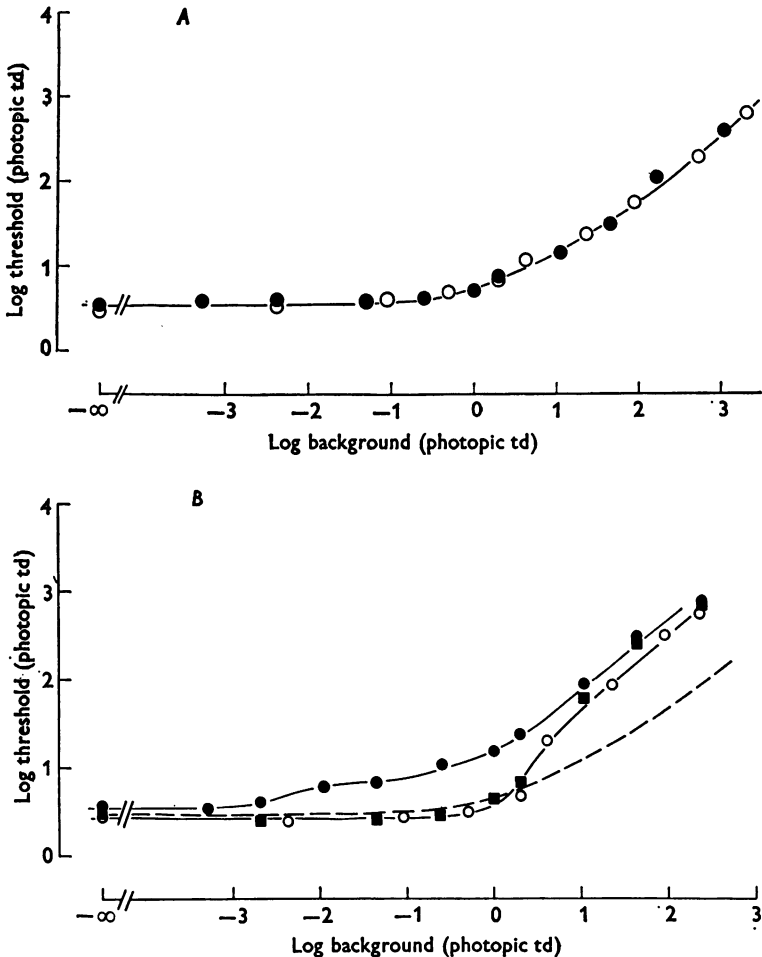

Fig. 6. *A*, photopic increment-threshold for a 656 nm test flash (10′ diameter, 10 msec duration) delivered on a 656 nm background field 8 deg diameter (open circles) or a 480 nm one (filled circles). *B*, circles show thresholds measured as in *A*, but with backgrounds now 34′ diameter. Squares plot the threshold on the 480 nm background, measured during the cone plateau phase of recovery from a strong bleach. The dashed line is the curve of *A*, reproduced without rotation or translation. Observer P.L.

in darkness was never detected through cones until more than 2 log units above threshold. So the simplest experiment is to compare thresholds for the long wave-length test upon short wave-length patches of low luminance that are large, or small. Were rod signals normally able to influence the threshold for cone-mediated vision this influence should be abolished if the experiment is repeated between 7 and 11 min after a strong bleach when the cones, but not the rods, have fully recovered their sensitivity.

The curves in Fig. 6A show thresholds for a 10' red spot as a function of the illuminance of both long and short wave-length backgrounds 8° in diameter. The continuous line that fits both sets of points is redrawn dashed in Fig. 6B, together with three threshold curves obtained with the spot presented upon a background 34' in diameter. One curve (open circles) was obtained with a long wave-length background and the other two with short wave-length ones, but in one case measurements were made before (filled circles) and in the other case long enough after (squares) a strong bleach for the cones, but not rods, to have fully recovered their sensitivity.

The measurements made using a small short wave-length patch are unlike those obtained with a large background: threshold upon the patch began to rise for lower illuminations and always stayed higher. Rods are already implicated by the fact that threshold began to rise when the photopic illuminance of the patch reached about $-2 \log$ td ($-0.89 \log$ scotopic td), just the illumination that rendered the patch clearly visible to rods, and too low for it to be detected with cones, but their involvement is demonstrated more securely by the following two comparisons. Consider first the threshold measurements made during the cone plateau phase of recovery from a bleach (squares). Until the patch illuminance reached $0.3 \log$ td the measurements fall on the line for large background fields, but above this value the threshold rises abruptly to the level expected in the absence of a bleach. The difference between the curves made before and after bleaching must be due to rods. This interpretation may be corroborated another way. If only cone signals were involved in regulating the threshold for cone vision the threshold measurements made upon short- and long wave-length patches would be expected to be the same, as they are with uniform backgrounds (Fig. 6A). Figure 6B shows they are not, unless the retina has first been bleached to abolish the influence of rods.

To explain these results we might suppose that rod signals affect the photopic gain control mechanism in the retina only when they arise from a restricted region around the test, but no anatomical or electrophysiological evidence renders this plausible.

DISCUSSION

The graphs of Fig. 1 show what we know already from the work of Stiles (1939) and Flamant & Stiles (1948), namely over most of the scotopic range threshold depends only upon the scotopic luminosity of a large background. The influence of cones found at higher background levels might result from the intrusion of cone signals into the scotopic gain control when the background was of long wave-length (so lifting threshold higher than if the background acted only through rods) or it might reflect the addition of rod and cone signals evoked by the test spot when the background was short wave-length (so pushing threshold lower than if the test excited only rods). The issue cannot be resolved by our results, although the experiments of Makous & Boothe (1974) support the first interpretation.

When backgrounds were small the influence of cones was observed at very low (scotopic) illuminations although over most of the scotopic range there was no question of the test spot being detected through cones rather than through rods. Likewise, when threshold for the long wave-length test spot was raised by a small background visible only through rods (Fig. 6*B*) there was no possibility that this reflected the suppression by the background of rod signals evoked by the test. Rod and cone signals are brought together at several points in the retina and the interactions we observed might be expected were there a mixing of messages in the gain control mechanisms.

Horizontal cells in the primate contact cones through their dendritic tree and rods through the axon terminal system (Kolb, 1970) and thus might appear to be well placed to mix signals from the two receptor types. But it is not known whether the long, thin, axon could support any communication between the two ends of the cell and, as D. W. Blick & D. I. A. Macleod (in preparation) point out, it is particularly hard to see why only signals from small backgrounds should be mixed. This is a difficulty for any explanation in terms of retinal mechanisms, but one possibility is discussed below.

If the rod system has a large adaptation pool and adapting signals from cones are accumulated from only a small region we might expect the penetration of cone signals into the scotopic gain control to be relatively much weaker when the background is large. We cannot directly exclude that possibility, but if we allow it we are left unable to explain why a steady background, acting through rods, was effective in raising the cone threshold only when the background was small (Fig. 6*B*).

Anatomical evidence (Boycott & Dowling, 1969) suggests that, in the near periphery of the primate retina, rod and cone signals are substantially segregated until they reach ganglion cells, and although the in-

fluence of background size could arise there, the bulk of the electrophysiological evidence is against it. Observations made upon retinal ganglion cells of the cat (Cleland & Enroth-Cugell, 1968; Sakmann, Creutzfeldt & Scheich, 1969) show no influence of background size like that found in the present experiments. Sensitivity to a test spot falling on the centre of the receptive field falls monotonically with background size, both when the ganglion cell is excited through rods and through cones (Enroth-Cugell, Hertz & Lennie. 1977).

The striking feature of all our experiments is not the effect of cone signals upon the threshold for rod vision, or vice-versa, but that when small backgrounds are used there is a break-down of the simple rules that describe threshold upon large background fields: the thresholds are no longer related to background illumination by the simple equations that serve so well when backgrounds are large. The more complicated relations found with small backgrounds are quite similar whether these backgrounds act mainly through rods or cones, and this similarity is the principal evidence that leads us to suppose that small backgrounds exert their peculiar effects in central paths, where signals from rods and cones in the peripheral retina are no longer segregated.

Much psychophysical evidence (Blakemore & Campbell, 1969; Sachs, Nachmias & Robson, 1971) suggests the existence in the visual pathway of mechanisms selectively sensitive to visual objects of a restricted range of sizes. Prolonged exposure to a target leads to a reduced sensitivity for that target and others of similar size, and this loss of sensitivity persists for some time after removal of the stimulus. Lennie & Macleod (1973) suggested, in the context of experiments like those described here, that the sensitivity of mechanisms selective for the test flash is reduced by the steady signal arising from the background when that is small. All the observations described here are consistent with that hypothesis: the increment-threshold curve made with a small background begins to diverge from that made with a large one just when the small background becomes clearly defined; the small background influences threshold similarly whether it acts through rods or cones; a small background, but not a large one, causes a prolonged elevation of threshold after it is turned off.

The use of discrete, steady, background fields made it easy to separate the contribution of rod and cone signals to the thresholds measured here, but in the context of the hypothesis discussed above it has the disadvantage of making it harder to separate the role of the background in regulating the state of light adaptation (where its principal effect is probably in the retina) from its presumed additional role of reducing the sensitivities of particular size-selective mechanisms (which may happen at a later stage in the visual pathway).

These roles may be separated by the use of stimuli, such as grating patterns, that permit the contrast of contours to be varied independently of the space-average luminance. One might then be in a position to identify, by electrophysiological techniques, the possible site of the contour-sensitive mechanism that seems to mediate the peculiar influence of small backgrounds on the thresholds for small spots.

REFERENCES

ALPERN, M., RUSHTON, W. A. H. & TORII, S. (1970). The size of rod signals. *J. Physiol.* **206**, 193–208.

ARDEN, G. B. & WEALE, R. A. (1954). Nervous mechanism and dark-adaptation. *J. Physiol.* **125**, 417–426.

BLAKEMORE, C. & CAMPBELL, F. W. (1969). On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* **203**, 237–260.

BOYCOTT, B. B. & DOWLING, J. E. (1969). Organization of the primate retina: light microscopy. *Phil. Trans. R. Soc.* B **255**, 109–176.

CLELAND, B. G. & ENROTH-CUGELL, C. (1968). Quantitative aspects of sensitivity and summation in the cat retina. *J. Physiol.* **198**, 17–38.

CRAWFORD, B. H. (1940). The effect of field size and pattern on the change of visual sensitivity with time. *Proc. R. Soc.* B, **129**, 94–106.

ENROTH-CUGELL, C., HERTZ, B. G. & LENNIE, P. (1977). Convergence of rod and cone signals in the cat's retina. *J. Physiol.* **269**, 297–318.

FLAMANT, F. & STILES, W. S. (1948). The directional and spectral sensitivities of the rods to adapting fields of different wave-lengths. *J. Physiol.* **107**, 187–202.

HALLETT, P. E. (1969). Rod increment thresholds on steady and flashed backgrounds. *J. Physiol.* **202**, 355–377.

KOLB, H. (1970). Organisation of the outer plexiform layer of the primate retina: electron microscopy of Golgi-impregnated cells. *Phil. Trans. R. Soc.* B, **258**, 261–283.

LENNIE, P. & MACLEOD, D. I. A. (1973). Background configuration and rod threshold, *J. Physiol.* **233**, 143–156.

MAKOUS, W. & BOOTHE, R. (1974). Cones block signals from rods. *Vision Res.* **14**, 285–294.

RUSHTON, W. A. H. (1965). The Ferrier Lecture, 1962. Visual adaptation. *Proc. R. Soc.* B **162**, 20–46.

SACHS, M. B., NACHMIAS, J. & ROBSON, J. G. (1971). Spatial-frequency channels in human vision. *J. opt. Soc. Am.* **61**, 1176–1186.

SAKMANN, B., CREUTZFELDT, O. D. & SCHEICH, H. (1969). An experimental comparison between the ganglion cell receptive field and the receptive field of the adaptation pool in the cat retina. *Pflügers Arch. ges. Physiol.* **307**, 133–137.

STERNHEIM, C. E. & GLASS, R. A. (1975). Evidence for cone and rod contributions to common 'adaptation pools'. *Vision Res.* **15**, 277–281.

STILES, W. S. (1939). The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc. R. Soc.* B. **127**, 64–105.

WESTHEIMER, G. (1965). Spatial interaction in the human retina during scotopic vision. *J. Physiol.* **181**, 881–894.

WESTHEIMER, G. (1970). Rod cone independence for sensitizing interaction in the human retina. *J. Physiol.* **206**, 109–116.

WYSZECKI, G. W. & STILES, W. S. (1967). *Color Science.* New York: Wiley.