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ROD THRESHOLD: INFLUENCE OF NEIGHBORING CONES[1]

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Abstract—Changes in rod increment threshold at the center of a desensitizing background disc were measured. Sensitization by an annular surround was shown to depend more upon the surround's effects on cones than on rods. This demonstrates a rod–cone interaction in which the activation of *cones* in the vicinity of a test flash influences the detection of that flash *by rods*.

INTRODUCTION

Experiments on light adaptation in human vision (Rushton. 1965) have shown that the regulation of sensitivity in the scotopic system does not proceed independently at neighboring points in the visual field: rod threshold for a small test flash presented at any point may be affected by a steady adapting stimulus that stimulates neighboring receptors. Nevertheless. Stiles (1939) and Flamant and Stiles (1948). using large uniform steady backgrounds. demonstrated a functional independence between rods and cones in light adaptation: rod threshold was not affected by altering the effect of the background upon cones. How can rods and cones adapt independently in this way. when rods and cones have to share the same ganglion cell (Gouras and Link. 1966; Daw and Pearlman. 1969) and also the same brain?

We suspect that Stiles' choice of a large uniform background is important. Electrophysiological records (e.g. Rodieck. 1967; Werblin and Dowling. 1969; Marrocco. 1972) suggest that the effects of large steady stimuli are confined mainly to the earliest stages of the visual system. where rod and cone signals still travel along separate pathways (Boycott and Dowling. 1969; Kolb and Famiglietti. 1976). Consequently. even if cones affect rod threshold by acting on common central pathways. the effect might not appear in experiments using large uniform backgrounds because such backgrounds do not strongly excite the central pathways which carry both rod and cone signals. But a non-uniform and non-stabilized background may produce signals that penetrate much deeper in the visual pathway. Such a background might therefore activate central sensitivity-regulating mechanisms with consequent rod–cone interaction.

This paper asks whether rod sensitivity can be influenced by cones when the steady background to which the test flash is added is non-uniform in the vicinity of the test flash. The background we used consisted of a small red illuminated disc centered on the test spot. with a contiguous red annular surround of variable luminance. The advantage of the disc–surround display is that the illumination in the vicinity of the test flash may be held constant by leaving the disc unchanged. while lateral interactions are investigated by varying only the surround. In our experiments the red surround could be adjusted to appear subjectively equal to. dimmer than or brighter than the enclosed red disc. Rod threshold was determined against each of these background fields.

Westheimer (1965) showed that for background discs like ours. the rod increment threshold is highest when the disc diameter is about 45′. Increasing the disc diameter further (up to 3° or 4°) produces a substantial reduction in threshold—a sensitization. For a disc diameter of about 45′. adding an annular surround of equal intensity is equivalent to an increase in disc diameter. Therefore the annulus will produce a similar sensitization via some sort of lateral interaction. The question we address is whether this lateral interaction takes place completely within the rod system (which detects the test flash at threshold). or whether cone responses to the red surround have some influence on the rod increment threshold. This question has been asked previously. Using a two-color display. Westheimer (1970) concluded in favor of rod–cone independence. However. Lennie and MacLeod (1973) showed that the threshold for an incremental flash detected only by rods is influenced by variations in cone activity in the vicinity of the test flash. They used a two-color display in which different scotopically equated wavelengths illuminated the surround. Thus rod stimulation remained roughly constant while cone activation by the surround was varied. Other recent reports (Frumkes and Temme. 1977; Latch and Lennie. 1977) have also demonstrated rod–cone interaction in sensitization.

The present experiments exploit the pronounced difference in directional sensitivity (Stiles–Crawford effect) between rods and cones to manipulate independently the excitation of rods and cones in the sensitizing surround. If the Maxwellian focal point of the beam illuminating the surround is displaced from the center toward the margin of the pupil. changing the surround beam's direction of incidence at the retina. the excitation of rods will be little affected whereas the excitation of cones will change substantially (Flamant and Stiles. 1948). Our test for rod–cone interaction is to compare the rod threshold obtained when the surround enters at the center of the pupil with

[1] A preliminary report of these findings was presented to the Association for Research in Vision and Ophthalmology in Sarasota. Florida. April 29. 1974.

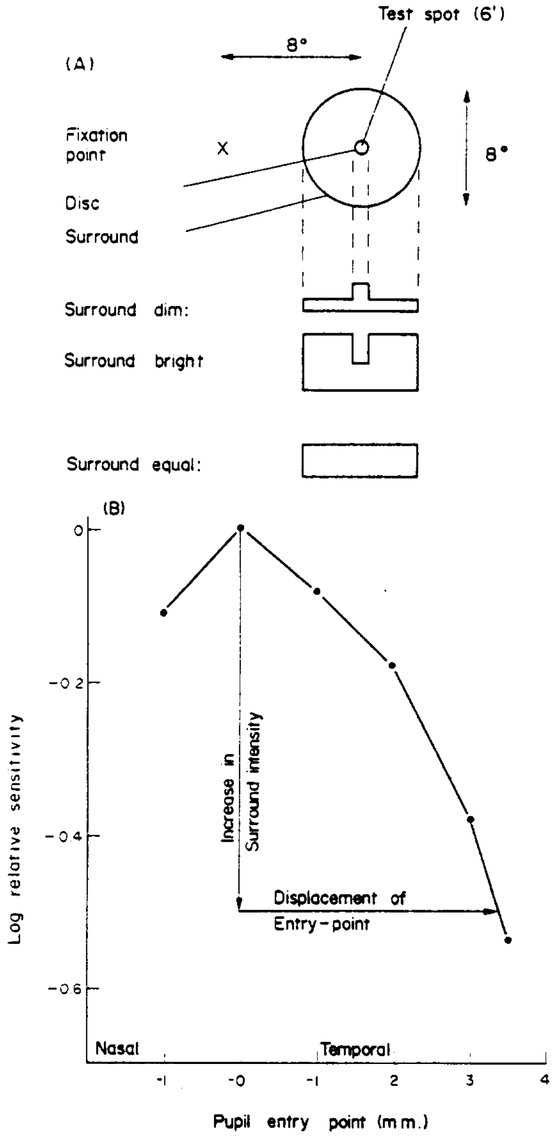

Fig. 1A. The display as seen by the observer. The central disc was less than 1° in diameter. The three diagrams below show the different background configurations available by manipulating the luminance of the surround; each diagram depicts the distribution of light in a cross-section of the display. Disc and surround were deep red (660 nm cutoff) and continually present. The test flash was blue (486 nm) and was presented for 100 msec every 1.5 sec.

Fig. 1B. Stiles–Crawford Effect for observer TW. The increase in intensity of the surround beam (0.5 log units) is shown by the vertical arrow. The compensatory displacement of the pupil entry point to reduce the visual effectiveness of this more intense light back to its initial level is shown by the horizontal arrow.

the threshold obtained when the surround enters near the margin. If any substantial difference is found, cones must be the cause of it.

METHODS

Apparatus

The Maxwellian view optical system was a modified version of the one used by Alpern, Rushton and Torii (1970). One of its channels supplied a tiny circular test flash, 6' in diameter (Fig. 1). A second channel continuously illuminated the area where the test flash fell. This circular area was adjustable in diameter but was always centered on the test flash: it will be termed the disc. The aperture defining the disc was a metal shim sheet perforated with a hole of suitable size. Either of the two remaining channels could be used to illuminate an annular surround encircling the disc and contiguous with it. The inner boundary of the surround was defined by a contact negative, made with high contrast film, of the metal sheet that defined the associated disc. The outer boundary of the surround was a circle 8° in diameter. At the start of each session, the observers themselves aligned the surround with the disc so as to minimize edge artifacts. To aid in this, the surround field stop was mounted on a holder equipped with fine horizontal and vertical adjustments. Figure 1A includes a diagram of the display as seen by the observer.

Luminances were varied by spectrophotometrically calibrated neutral filters and graded neutral wedges. For convenience in changing point of pupil entry, surrounds for central and eccentric entry were supplied from different channels. All beams were focused so that they formed circular (1 mm) images of part of the source near the plane of the pupil. For the test flash and disc beams, the focal point was at the pupil center, but the two beams for illuminating the surround had different points of entry—one at the pupil center and the other near the margin (except where noted).

The pupil entry point of the marginal surround beam could be changed by adjusting the tilt of a mirror placed just behind the field stop. Changes in intensity associated with this slight rotation of the beam were negligible, as the illumination falling on the stop was quite uniform over an area larger than the opening in the stop.

To allow the experimenter to view the plane of the pupil, the apparatus incorporated a removable magnifier which was used in setting up the beams and specifying their pupil entry points.

Calibration

Scotopic luminances are based on concordant estimates by two methods. In one, the beams were projected onto a magnesium oxide diffusing screen and the photopic luminance of the screen was measured using an SEI photometer; the photopic luminances were converted to scotopic luminances by referring to the standard photopic and scotopic luminosity curves. The second method was based on energy measurements taken with a Tektronix J6502 radiometer that had been calibrated against a thermopile. To apply the radiometric method to the short wavelength cutoff red filter, the filtered light was visually matched to a monochromatic light and the energy of the monochromatic light was measured.

Rod isolation

To isolate rods, the test flash passed through a 486 nm interference filter (Ealing-TFP interference filter, bandwidth 10 nm at half peak transmittance), and the background light for both disc and surround passed through deep red filters (660 nm cutoff). To ensure that the test flash was being detected by rods but was invisible to cones, thresholds were measured for detection of the test flash, viewed against the various backgrounds employed, during recovery from a strong bleaching exposure. The thresholds during the cone plateau phase of dark adaptation were always higher than the corresponding dark-adapted thresholds, usually by more than 0.6 log units. The lower thresholds obtained with the dark-adapted eye in the main experiment therefore represent detection by rods.

We obtained further confirmation of rod isolation, as well as verifying the rods' relative lack of directional sensitivity, by measuring the Stiles–Crawford effect, using the indirect method of Flamant and Stiles (1948). Test flash thresholds were measured against uniform backgrounds with either central or marginal pupil entry of the background. Threshold differences between these two conditions were negligible at low background luminances and never exceeded 0.15 log units under our conditions. Central background entry usually gave higher thresholds: this could reflect either the rod–cone interaction reported by Makous and Boothe (1974) for uniform backgrounds, or the slight directional sensitivity of rods (van Loo and Enoch, 1975).

Procedure

In the main experiment, rod thresholds were measured for different luminances and points of entry of the surround. These conditions were tested in random order. The approximate center of each observer's pupil was located at the beginning of the experiment by determining four points (nasal, temporal, high and low) at which the disc was almost totally occluded by the iris when the observer directed his gaze at the fixation point. The beam illuminating the disc always passed through the pupil center so determined, while the beam illuminating the surround entered either at the same point or at a point near the margin of the pupil. Observation was monocular (left eye). Appropriate correcting lenses were mounted in front of the eye, and chromatic differences of focus were compensated by moving the field stops.

For each observer, a suitable marginal entry point for the surround beam was chosen as follows. First the beam was adjusted to pass through the pupil center, and the observer gazed at the fixation spot and adjusted the intensity of the surround so that it matched the disc, creating an approximately uniform field centered 8° from the fovea in the temporal retina. Both observers were successful in making disc and surround merge, although this required quite careful adjustment of both the position of the surround field stop and the intensity of the surround. Next, the intensity of the surround beam was increased by 0.50 log units (observer TW) or 0.60 log units (observer ML) and the observer adjusted the point of entry toward the temporal margin of the pupil until disc and surround once again matched in brightness. The observer adjusted the position of the surround field stop to compensate slight displacements caused by optical aberrations. Because of its greater physical intensity, the marginally entering surround excited rods more strongly than the disc with which it was matched. Yet for oberver ML (who had deuteranomalous vision), disc and surround merged totally under steady fixation, and for observer TW (normal color vision) the border between disc and surround was barely detectable, being signalled mainly by a greater saturation of the marginally entering beam (presumably a Stiles–Crawford color shift rather than a rod intrusion effect, which would produce a desaturation). This subjective uniformity or near-uniformity is an indication that the images were of sufficient optical quality, even with the marginal entry point. There is evidence that even if a spatial transient were present at the center–surround border, it might have little effect on threshold in this situation (Westheimer, 1967). The displacement of the pupil entry point for the surround (to compensate its increased intensity) was quantitatively appropriate to the Stiles–Crawford effect of cones as measured for these observers in separate experiments, in which thresholds for a deep red test flash viewed against a dim blue background were measured as a function of the pupil entry point of the test flash (see Fig. 1B).

Occlusion of the marginally entering beam by the iris was easily recognized by the observers. Dilation with Cyclogyl or with hourly doses of Mydriacyl was found sufficient to prevent such occlusions. A dental impression kept the observer's head sufficiently steady.

The diameter of the disc was fixed for each observer, and was chosen to provide the largest possible sensitization effect when an appropriate surround was added. In the preliminary experiments to find the thresholds as a function of disc diameter, we followed Westheimer (1965) in employing a large dim auxiliary background field to hide light scattered from the test beam. The disc diameter giving highest threshold was determined for each observer at background luminance of 0.03 scotopic td: these discs were used throughout the main experiment, even though at higher background luminances slightly smaller discs would have produced slightly greater amounts of desensitization.

With the observer directing his gaze at the feeble orange fixation spot, the test flash was presented every 2 sec at 8° from the line of sight in the temporal retina. The observer adjusted a neutral density wedge in the beam to set threshold. The flash duration was 100 msec for the results presented here, but all the essential results have also been obtained using a 10 msec flash.

RESULTS

Figure 2 shows the test flash threshold as a function of surround intensity. Threshold is high with a dim surround and decreases with increasing surround intensity: this is the "sensitization" described by Crawford (1940) and Westheimer (1965). Although bright surrounds give lower thresholds than dim surrounds, threshold is lowest for intermediate surround intensities at which the perceived border between disc and surround is minimized. Like Lennie and MacLeod (1973), we find that use of a smaller disc makes the function relating threshold to log surround intensity more symmetric about its minimum, but the elevation of threshold induced by making the surround brighter than the central disc was generally slight. Our observations on this point are quantitatively intermediate between those of Westheimer (1965), who found a slight decrease, and those of Lennie and MacLeod (1973), who found larger increases.

The hypothesis of rod–cone independence may be examined by comparing thresholds for central and marginal entry of the surround. In Fig. 2, filled symbols show results for the normal condition with central pupil entry, and open symbols are with the surround entering near the margin. For rods these two conditions are practically the same, and so, if rod–cone independence holds, they should give the same rod threshold: filled and open symbols should coincide. This prediction is not fulfilled in Fig. 2: filled and open symbols fall along quite different loci. For instance, under the normal condition threshold is lowest on a physically uniform background (0 on the horizontal axis in Fig. 2), yet when the same surround enters at the pupil margin, threshold is much higher. This indicates that the surround affects rod threshold by its action on cones. But the results appear to support an even stronger conclusion: that rod threshold is affected almost exclusively by cones in the surround, the surround's effect upon rods being largely irrelevant. If this were true, then any two surrounds equivalent for cones (albeit different for rods) would produce the same rod threshold. Each marginally entering surround in Fig. 2 is equivalent, for cones, to a centrally entering surround of lower intensity. Thus if the measured thresholds are indeed exclusively cone-dependent, the open symbols could be brought into coincidence with the filled symbols by displacing them along the logarithmic horizontal axis

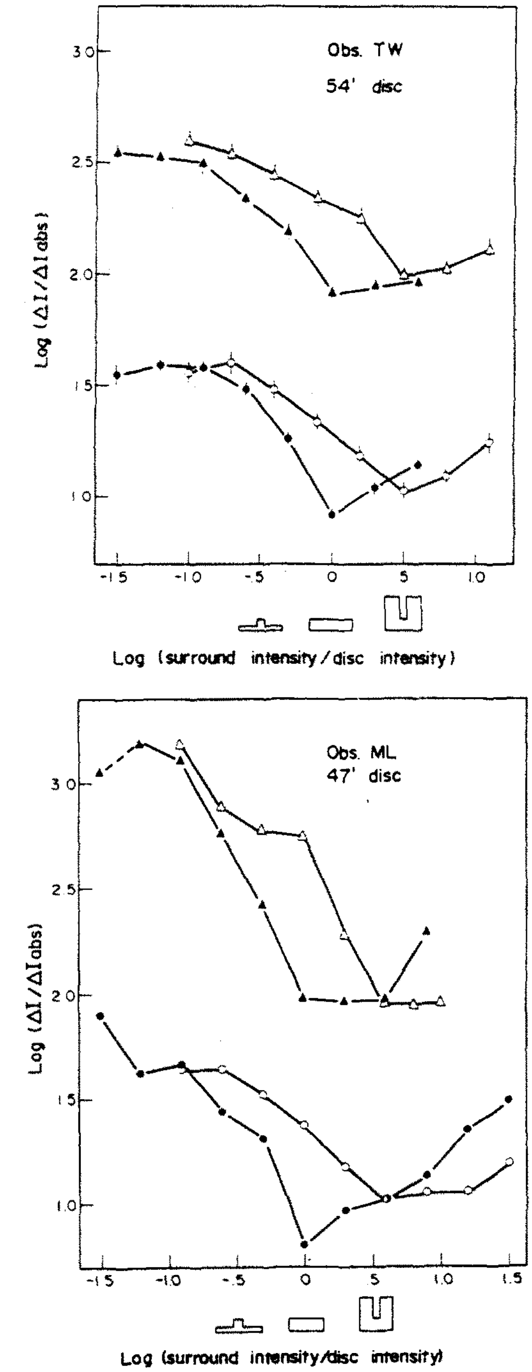

Fig. 2. Log of threshold (re absolute threshold) plotted against the log of surround intensity (re disc intensity). Filled symbols, central pupil entry for all beams. Open symbols, eccentric entry of the surround. Disc luminances: circles, 0.08 scotopic td; triangles, 1.3 scotopic td. Results are shown for two observers. Bars for observer TW subtend 2 × S.E. based on variation between sessions. For ML each point was typically measured in only one session and the standard errors based on variation within a session are usually less than the symbol heights.

by the amount appropriate to the Stiles–Crawford effect of the cones.

Figure 3 shows the result of applying this Stiles–Crawford compensation. The horizontal axis now represents the effect of the surround on cones. The approximate agreement between filled and open symbols in Fig. 3 means that marginal and central surrounds that are equal for cones always give roughly equal rod thresholds, even though these surrounds are quite different in physical intensity and thus quite different in their effects on the rods in the surround. Evidently the variation of surround intensity does little to modify threshold by processes operating solely within the rod system.

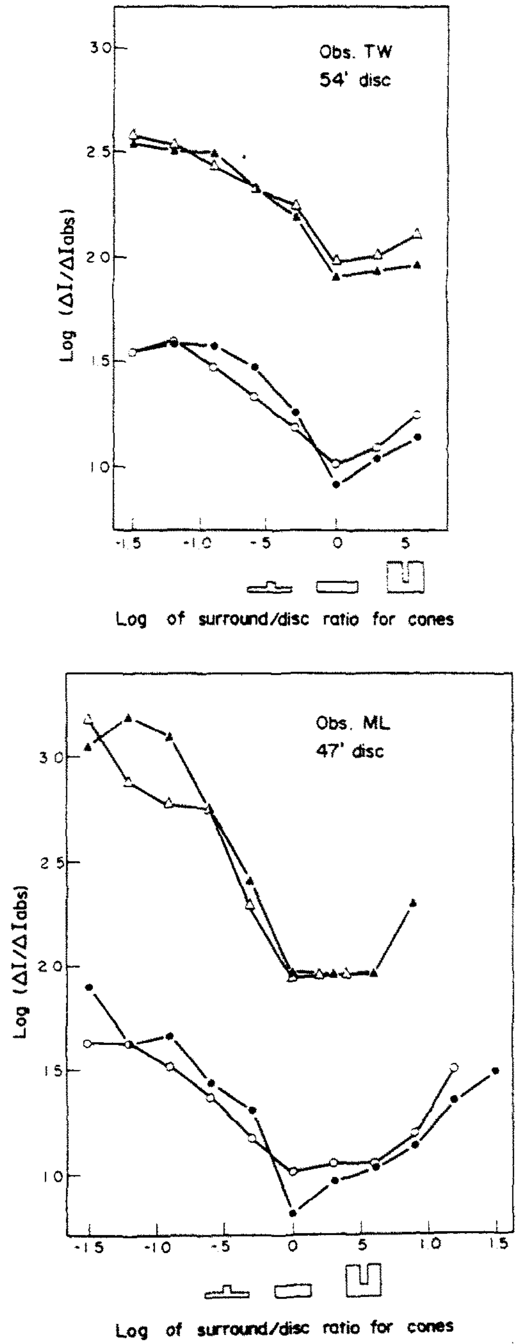

Fig. 3. Data of Fig. 2 with open symbols horizontally displaced to compensate for the Stiles–Crawford effect of cones. Observer TW, 0.5 displacement; observer ML, 0.6 displacement.

DISCUSSION

Our results clearly show that signals from cones in an annular zone concentric with the test flash may affect rod threshold. However, the mechanisms responsible for this result are not so clear. The simplest interpretation of sensitization by surrounds, following Westheimer (1965), has been that light falling in the receptive field surround of some critical cell decreases the cell's response to steady adapting stimulation of the center, and so increases its sensitivity to incremental flashes. On that view, many features of the present results are explained by supposing that the critical cells which determine rod sensitivity receive antagonistic surround inputs from cones as well as from rods. But this explanation implies departures from rod–cone independence even with uniform backgrounds. Makous and Boothe (1974) have convincingly demonstrated such departures from Stiles' concept of rod–cone independence with uniform backgrounds. However, the effect they reported would barely be measurable under our low-luminance condition. But Fig. 2 reveals that the disc–surround display produces a breakdown of independence so complete that rod threshold appears almost entirely cone-dependent. This rod–cone interaction may thus be specific to non-uniform backgrounds. Perhaps, unlike a uniform background, the small disc with dim surround activates more central threshold-raising mechanisms which receive inputs from both rods and cones. This is the interpretation offered by Latch and Lennie (1977) for their own observation of rod–cone interaction with small discs.

One possible central mechanism, proposed by Lennie and MacLeod (1973) and by Alexander (1974), is that size-tuned cortical channels are selectively desensitized by continued exposure to the background. The desensitization of these channels would vary with the intensity difference (for cones) between the disc and surround. Such a model could account for an interesting incidental observation in the present experiments. As surround intensity varied, the apparent size of the test flash changed, such that when thresholds were high, the test flash had a diffuse appearance. This association also occurred as the point of pupil entry of the surround was varied: with a marginally entering surround equal in intensity to the disc, threshold was higher and the test flash appeared more diffuse than with a centrally entering surround.

The dominant role of cones in determining rod threshold in this experiment may be associated with the fact that they are dominant in determining the appearance of the deep red background, particularly the appearance of the contour at the disc–surround boundary. The central mechanisms affecting the threshold may be influenced mainly by those receptors that determine the subjective appearance of the stimuli. Such mechanisms may interact as we have demonstrated only when the appearance of the background is largely determined by one class of receptors, while the test stimulus is detected by the other. This may be why rod–cone independence is reported by some investigators while rod–cone interaction is reported by others. When we compare the threshold-elevating effects of discs of different wavelengths superimposed on a steady deep red background, we find rod–cone interaction to be relatively inconspicuous, perhaps because these conditions favor a preponderance of rod signals in neural pathways shared by rods and cones. A similar argument may apply to Westheimer's (1965) results, also involving a fixed deep red background.

One means of separating the contributions of peripheral and central processes to sensitization is supplied by electrophysiological investigation of the retina. The evidence from this source also favors the view that central factors are involved (MacLeod, 1978). Cleland and Enroth-Cugell (1968) and Sakmann, Creutzfeldt and Scheich (1969), recording from cat retinal ganglion cells, found a monotonically decreasing relation between sensitivity and background size. Burkhardt (1974) and Copenhagen (1972) have observed sensitization by surrounds in the retina of the mudpuppy, as has Nakayama (1971) in the lateral geniculate nucleus of the cat, but in these studies sensitization could be demonstrated only at luminances high enough to induce incipient rod saturation; no counterpart of the psychophysical effect was observed at the appropriate luminance levels. More recently, Karwoski and Burkhardt (1976) have noted sensitization at scotopic levels in the mudpuppy retina; in this species, sensitization is present in off-center and on–off ganglion cells but absent in on-center cells. The absence of sensitization effects in the mammalian retina is a common finding (Enroth-Cugell, Lennie and Shapley, 1975; Barlow and Levick, 1976; see also review by MacLeod, 1978). In general, the physiological evidence does not support the hypothesis of a peripheral origin for the sensitization seen in psychophysical studies. Furthermore, the cone-dependence of rod threshold found in our experiments suggests that sensitization of rod threshold occurs at or central to the point at which rod and cone signals are mixed. However, some forms of rod–cone interaction can be seen even at the receptor level (Schwartz, 1975; Nelson, Kolb, Famiglietti and Gouras, 1976; Raviola, 1976; Nelson, 1977). Thus, interaction results like ours cannot rigorously exclude a peripheral mechanism for sensitization.

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