

## SHARED PATHWAYS FOR ROD AND CONE VISION

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**Abstract**—We have used heterochromatic gratings falling on 10 deg temporal retina to measure the spatial contrast sensitivities of the isolated rod and cone systems in the mesopic range. As the level of illumination was raised within this range, the contrast sensitivity of the rod system increased, reaching a peak of about 50 (and providing an acuity of 6 c/deg) at 20 scot. td, whereupon the rod system began to saturate. Over most of the mesopic range the sensitivity of the cone system was lower than that of the rod system, although it provided better acuity (up to 15 c/deg). Within the range of spatial frequencies capable of exciting both rod and cone systems, a grating that excited only rods was indistinguishable from a grating of the same spatial frequency that excited only cones. Moreover, contrast adaptation to gratings that excited either rods or cones raised threshold for gratings that excited rods or cones. From these results we conclude that signals from rods and cones travel together in pathways subserving the detection of low spatial frequencies, while only signals from cones travel in pathways subserving the detection of high spatial frequencies.

Contrast sensitivity    Rods    Cones    Spatial vision

### INTRODUCTION

Psychophysical observations show that spatial summation increases and visual acuity declines as the level of light-adaptation is reduced. This change has often been attributed to the transition from cone to rod vision, and interpreted as evidence that mechanisms excited by rods have larger receptive fields than those excited by cones. Physiological evidence is equivocal on this point: in both cat (Enroth-Cugell *et al.*, 1977) and monkey (Gouras, 1967) signals from rods always travel in ganglion cells that also receive input from cones (the converse may not be true of monkey), and there is no clear evidence that the rod and cone receptive fields have different sizes.

The question therefore arises as to how the spatial properties of rod vision come to differ from those of cone vision, and how the nervous system manages to distinguish, in the output of a single ganglion cell, signals that arise in rods from those that arise in cones. A comprehensive description of the spatial sensitivity of the visual system is obtained from the spatial contrast sensitivity curve, and it should be possible to answer these questions by comparing contrast sensitivities obtained when one or the other receptor system alone determines threshold.

This paper introduces a new technique for the measurement of the spatial contrast sensitivities

of isolated rod and cone systems when the retina is adapted to a uniform white background. Our results provide evidence that rod signals travel in pathways used by cones, and that the rod and cone signals in these pathways cannot be distinguished.

### METHODS

#### *Principle of the technique*

The aim is to produce a spatial modulation of a uniform field so that either rods alone or cones alone can detect the grating. To make a grating invisible to rods we need to modulate between two lights that are scotopic metamers; similarly, to make a grating invisible to cones (but detectable to rods) we need to modulate between lights that are photopic (but not scotopic) metamers. In both cases the lights must be metameric with the uniform field upon which the modulation is imposed. Because we are dealing with mechanisms that may be driven by four classes of photoreceptors, we need, in principle, four dimensions along which stimuli can be varied. In practice, a three-dimensional stimulus space was used (which permits us to silence two classes of mechanism at once), and experimental conditions were chosen so as to ensure that the third class did not intrude upon the measurements.

The lights used may be represented in a three-dimensional space introduced by Der-

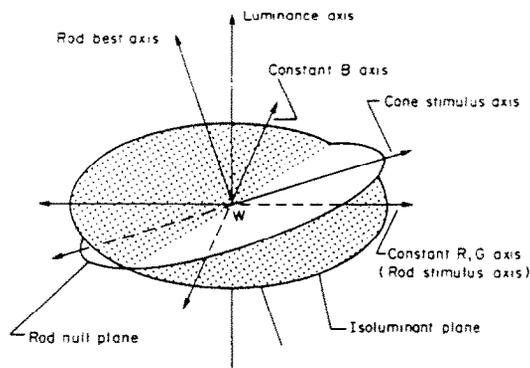


Fig. 1. Diagram showing the positions of the "rod-isolating" and "cone-isolating" axes in the three-dimensional color space. To isolate the rods one may modulate about the white point (W) along the constant R,G (tritanopic) axis, below B-cone threshold. The cone achromatic mechanism is isolated by modulation within the rod null plane along an axis that lies in the null plane for the R-G chromatic mechanism, while keeping the overall level of illumination below B-cone threshold. The chosen axis lies directly above the constant R,G axis of the color space. The *azimuth* of the rod null plane is the angle between its axis of intersection with the isoluminant plane and the constant B axis; its *elevation* is the angle between the isoluminant plane and the rod null plane in a direction perpendicular to its azimuth.

rington *et al.* (1984) and described fully in that paper. The space is defined by three orthogonal axes that intersect at a white point (see Fig. 1). Along one axis (the "constant B" axis), excitations of red-sensitive (R) cones and green-sensitive (G) cones vary inversely so as to keep the sum constant without changing the excitation of blue-sensitive (B) cones. Along the second axis (the "constant R,G" axis—the tritanopic confusion line through the chosen white point) only the excitation of B cones changes. If one accepts that luminosity depends only upon the sum of excitations of R and G cones (Smith and Pokorny, 1975), then the intersection of the constant B and constant R,G axes defines a plane that is isoluminant. Along the third axis of the space the excitations of cones of all three classes (and also of rods) change proportionally, and movement parallel to this axis alters luminance without changing chromaticity.

For any class of photoreceptor (or indeed any mechanism that combines linearly the signals from different classes of photoreceptor), there is in this space a plane (the "null" plane) that passes through the white point and within which all lights are equally effective (i.e. metamers). For example, the null plane for an "achromatic" mechanism with  $V_L$  spectral sensitivity would be the isoluminant plane of Fig. 1; move-

ment within this plane will produce no change in the excitation of the achromatic mechanism. Similarly, the null plane for a mechanism that receives opposed inputs from only R and G cones will pass vertically through the constant R,G axis. Thus, in the mesopic range we can isolate cones if we confine modulation to any axis that lies within the null plane for rods. We are interested only in the spatial properties of the cone achromatic mechanism, and not the properties of putative R-G and B-Y chromatic channels. We avoid the possible intrusion of the R-G mechanism by using an axis defined by the intersection of the null plane for rods and the null plane for the R-G opponent mechanism, and we avoid intrusion of the B-Y mechanism by operating below the threshold for B cones.

In this three-dimensional space one cannot modulate the rod signal without also modulating the signals from at least one class of cone, but with appropriately chosen axes of modulation one can silence two classes of cone and by other means avoid intrusion of the third. Modulation along the constant R,G axis varies the excitation of only rods and B cones, so by using this axis and operating at levels of illumination below the threshold for B cones, modulations can be made detectable only to rods. The two axes along which stimuli were modulated to isolate rods and cones are marked on Fig. 1. Directions in the color space are specified by their *azimuths* and *elevations*. Both terms are explained in the caption to Fig. 1.

#### Apparatus and procedure

Stimuli were drawn on the face of a Tektronix 690SR television monitor, set to provide an interlaced display of 512 lines at 120 Hz. Sinusoidal gratings whose chromaticity and luminance could be modulated in time about a white point were produced by a PDP 11/60 computer via an interface designed by W. J. Kropfl of AT&T Bell Laboratories. The unattenuated mean luminance of the display was  $120 \text{ cd/m}^{-2}$  (photopic) and this was reduced when necessary by interposing neutral density filters between the screen and the observer. Unless otherwise indicated, all references to illuminations use photopic units. Mean illuminations may be converted to scotopic units by multiplying by 2.3.

At levels of illumination below those that excited B cones (see "Controls", below), gratings whose chromaticity was modulated along the constant R,G (tritanopic) axis were used to excite the rod system. The cone system was

isolated by modulating the chromaticity and luminance of gratings along a line defined by the intersection of the null plane for the R-G chromatic mechanism and the null plane for rods. The null plane for the R-G mechanism is the plane spanning the constant R,G axis and the luminance axis; the position of the null plane for rods was calculated using the emission curves of the television phosphors and the  $V'_\lambda$  spectral sensitivity function, and was confirmed by experimental observation, as follows.

After 20 min dark-adaptation a circular patch of screen, 4 deg in diameter, was viewed with 10 deg temporal retina of the preferred eye. Mean luminance was  $5.9 \times 10^{-2}$  td. The observer viewed a horizontal high-contrast grating that was photopically isoluminant and moving at 4 Hz and adjusted the azimuth of modulation until the pattern became invisible. Then, with a grating of azimuth orthogonal to this, the observer adjusted the elevation of the grating until the pattern became invisible. The null plane for rods is the plane spanning these two axes of invisibility. The position of this null plane was sharply defined and practically identical for the three observers for both low and moderate spatial frequencies, and frequent checks throughout the five-month period of the experiments showed no shift of its position.

For the main experiments a circular patch of grating, 4 deg in diameter, was centered 10 deg in the temporal retina of the preferred eye. Except for a small fixation light, the room was in darkness. The observer's head was held steady by a bite bar, and the pattern was viewed through a 2.5 mm artificial pupil and spectacle lens. The two principal observers (M.D. and P.L.) required lenses of  $-0.75$  and  $-1.25$ D respectively. C.P. required  $+2.0$ D.

A two-alternative forced-choice staircase procedure was used to measure contrast sensitivity. A single trial lasting 2.6 sec contained two intervals of 1 sec that were marked by distinctive tones. During one of these intervals, randomly selected from trial to trial, a grating appeared moving at 4 Hz. The contrast of the grating was modulated in time by a raised cosine of period 1 sec. By pressing one of two response keys the observer indicated which interval contained the grating. If a particular grating was detected on three successive presentations its contrast was reduced for the next appearance; an error always caused the contrast to be raised for the next presentation. Contrast steps were reduced progressively until they reached 25%, and after

five reversals at the smallest step the staircase stopped automatically. This procedure converges on stimuli that are detected on 75% of trials.

Whenever experimental conditions allowed gratings of a particular spatial frequency to be detected by both rods and cones, presentations of "rod-isolating" and "cone-isolating" gratings were randomly interleaved in a single experimental session.

#### *Calculation of contrast*

The present experiments use gratings that contain chromatic contrast. We therefore needed to establish their "equivalent luminance contrast" for both rods and cones. For the "cone-isolating" grating this can be obtained directly by resolving the modulation into a component along the luminance axis of the color space. For the "rod-isolating" grating the equivalent contrast can be obtained by resolving the (chromatic) modulation into a component along the axis orthogonal to the rod null plane (i.e. along the axis that best excites rods). In this case the values obtained were checked by experiment, as follows. At a low mean luminance ( $5.9 \times 10^{-2}$  td) the observers made concurrent threshold settings for an achromatic grating and a "rod-isolating" grating of the same low spatial and temporal frequency. Because both gratings are detected by rods, one can establish directly what modulation of the chromatic grating is equivalent to a known modulation of the achromatic one. The values obtained agreed very closely with calculation.

#### *Controls*

The value of our results depends upon our being able to isolate receptor systems reliably. Rods can be isolated by modulation along the constant R,G axis only as long as B cones are inactive. For levels of illumination at or below 2.9 td (P.L.) and 9.3 td (M.D.) no grating appeared colored at threshold. Gratings of the lowest spatial frequencies were occasionally tinged with color at threshold for P.L. at 9.3 td and for M.D. at 29 td, suggesting the intrusion of the B-Y mechanism.

At the highest levels of illumination at which sensitivity measurements were routinely made (9.3 td, M.D.; 4.7 td, P.L.) all gratings appeared colorless, and thresholds for rod-isolating gratings were always substantially elevated when measured during the cone plateau of recovery from a strong bleaching exposure. This is illus-

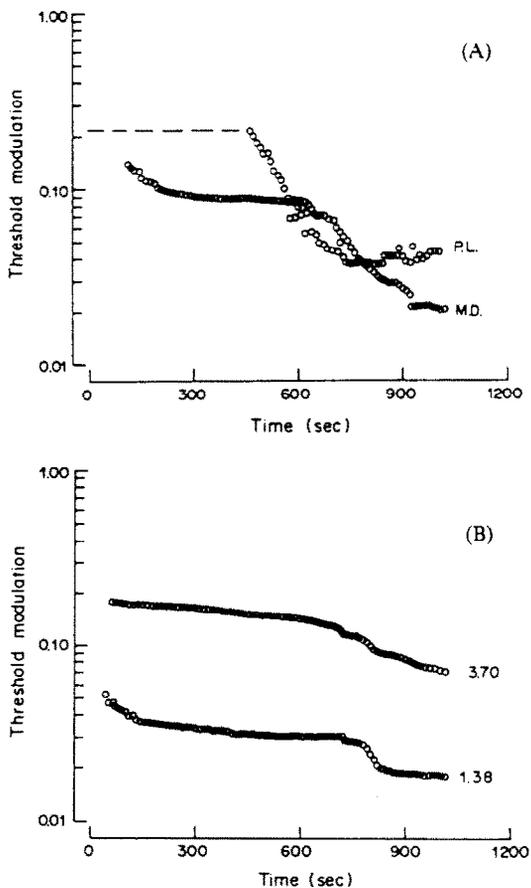


Fig. 2. Recovery of threshold for a "rod-isolating" grating at 4 Hz after a 60-sec bleach by a light of 6.7 log td at 554 nm. The bleached area subtended 7 deg and was centered on 10 deg temporal retina. The test field subtended 4 deg and was concentric with the bleached region. (A) Recovery of threshold for a 1.38 c/deg grating at a mean illumination of 9.3 td (M.D.) or 4.7 td (P.L.). Cone thresholds are substantially elevated above rod thresholds for M.D., and more so for P.L., who was unable to set cone thresholds at the maximum attainable contrast of 0.2 (marked by dashed line in the figure). (B) Threshold recovery at 29 td at spatial frequencies of 1.38 and 3.7 c/deg for observer M.D. At this level of illumination, modulation of a uniform field appeared colored at threshold.

trated in Fig. 2(a) for the two principal observers. The curves show the recovery of threshold for a 1.38 c/deg grating of mean illumination 9.3 td (M.D.) or 4.7 td (P.L.) following exposure for 60 sec to a light of 6.7 log td at 554 nm that substantially spared B cones. The 7 deg bleaching field completely covered the test region. The technique used to isolate the rod system restricts the maximum equivalent contrast to 0.2, and while thresholds on the cone plateau were obtained by M.D., no cone thresholds could be found for P.L. At higher levels of mean illumination it was still often possible to isolate rods at medium (*ca* 1 c/deg) and high (*ca*

4 c/deg) spatial frequencies. This is shown in Fig. 2(b) for observer M.D. at 29 td.

## RESULTS

### *Spatial contrast sensitivity curves*

Figure 3 shows, for the two principal observers (M.D., left column; P.L., right column), contrast sensitivity functions obtained with "rod-isolating" (solid circles) and "cone-isolating" (open circles) gratings at a series of illuminations spanning the range where both mechanisms could be isolated. Since the technique used to isolate the rod and cone systems restricts the maximum equivalent contrast to 0.2, no graph shows contrast sensitivities of less than 5. The smooth curves drawn through the

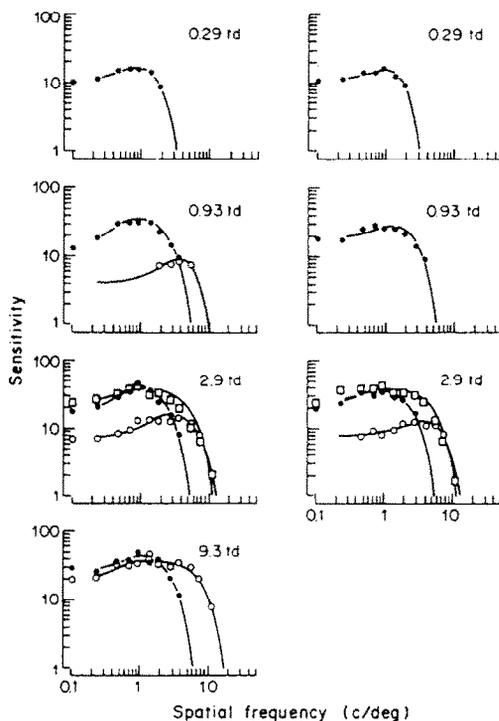


Fig. 3. Rod (●) and cone (○) spatial contrast sensitivity functions for observers M.D. (left column) and P.L. (right column) at mean illuminations of 0.29, 0.93, 2.9 and 9.3 td. Gratings were modulated at 4 Hz. Intrusion of B-cones at low spatial frequencies precluded the measurement of complete rod contrast sensitivity curves at 29 td (M.D.) and 9.3 td (P.L.). Spatial contrast sensitivity functions obtained with achromatic gratings at 2.9 td (□) envelop the isolated rod and cone functions of the two observers. Sensitivities less than five could not be measured with "rod-isolating" and "cone-isolating" gratings. At 0.93 td, P.L. reliably saw "cone-isolating" gratings of only a single spatial frequency (2.77 c/deg, sensitivity 8.8); point not shown. Points positioned at 0.1 c/deg show sensitivity to modulation of a spatially uniform field. Smooth curves are best-fitting solutions to equation (1).

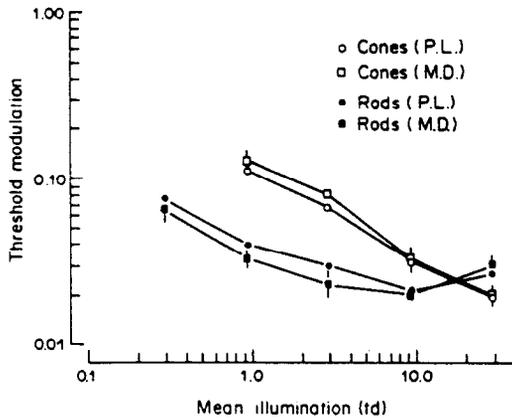


Fig. 4. Effect of level of illumination on threshold for gratings of optimal spatial frequency. Thresholds were determined by M.D. (squares) and P.L. (circles) using 0.92 c/deg "rod-isolating" gratings (solid symbols) and 2.77 c/deg "cone-isolating" gratings (open symbols). Gratings moved at 4 Hz. Points shown in this and the previous figure are the averages obtained from four threshold determinations; error bars (SEM) are shown here for M.D. Rod threshold is lowest (2%, Rayleigh sensitivity of 50) at about 9.3 td (22 scot. td) and thereafter rises with the onset of saturation, while cone sensitivity increases steadily over the range of illuminations covered.

points are best-fitting solutions to the function

$$G(f) = K_c e^{-(\pi f r_c)^2} - K_s e^{-(\pi f r_s)^2} \quad (1)$$

where  $f$  is spatial frequency,  $K_c$  and  $K_s$  are sensitivity constants governing curve height and  $r_c$  and  $r_s$  are frequency constants governing curve shape. This function has little theoretical significance in the present context, but since it describes the observations well its parameters can be used to characterize the curves.

At the lowest level of illumination (0.29 td) only rod sensitivities can be measured, but as illumination is raised to 0.93 td one sees the emergence of the contrast sensitivity function for cones. Initially, the cone system is substantially less sensitive than the rod system but has greater spatial acuity. Further increases in illumination through 9.3 td bring about progressive improvements in the contrast sensitivities of both systems to middle and high spatial frequencies, with the cone system showing the greater improvement. Above 9.3 td rod sensitivity begins to decline, as would be expected from the onset of saturation, while cone sensitivity continues to improve. These changes are summarized in Fig. 4, which shows how sensitivities to gratings of optimal spatial frequency (0.92 c/deg for rods, 2.77 c/deg for cones) vary with the mean level of illumination. These results show the rod system to be more sensitive than has hitherto been supposed: at its most

sensitive it can detect a 2% change in illumination.

The contrast sensitivity curve obtained with *achromatic* gratings, which excite rod and cone systems together, would be expected to envelop the contrast sensitivity curves obtained with rod-isolating and cone-isolating gratings. The 2.9 td panels in Fig. 3 show results obtained with achromatic gratings. For both observers the curve obtained with such gratings (squares) closely follows the envelope of the other two curves except where rod and cone sensitivities are the same (at 3 c/deg), where the overall sensitivity is clearly higher, as would be expected. This result validates our procedure for calculating equivalent contrast.

#### *Interpretation of contrast sensitivity curves*

At all levels of illumination the cone system has appreciably better spatial acuity than the rod system. At 2.9 td, parameter  $r_c$  in equation (1) is for rods about 2.7 times its value for cones. If the contrast sensitivity curve is taken to represent the properties of a notional receptive field we are led to conclude that receptive fields of the rod system are larger than those of the cone system. This idea is not readily reconciled with physiological observations, and it conflicts with abundant psychophysical evidence that the spatial contrast sensitivity function describes the activity of multiple underlying mechanisms. A more attractive interpretation of our results is that each contrast sensitivity curve (rod or cone) represents the envelope of the sensitivities of a number of underlying mechanisms, and that over the range of low and middle spatial frequencies where both rod and cone systems can be excited their signals travel in the same pathways. However, only cones have access to the pathways subserving the detection of high spatial frequencies.

An informal observation corroborates this idea. Contrast thresholds of rod and cone systems were always measured concurrently for a single spatial frequency, yet although the stimuli that isolated one or the other system were temporally juxtaposed, they could never be reliably distinguished. This observation prompted a more thorough examination of the discriminability of patterns seen by rods and cones.

#### *The appearance of patterns seen by rods and cones*

The first experiment was an attempt to establish whether the gratings seen by rods can under

any circumstances be distinguished from those seen by cones. Because we did not know in which ways a grating detected via rods might be distinguished from one detected via cones our experiment was designed to permit the observer to use any potential cue.

With the usual arrangement of the two-alternative forced-choice trial, the observers had to indicate whether or not two suprathreshold gratings differed. On half the trials the members of the pair were identical rod-isolating gratings; on the other half of the trials the rod-isolating grating was paired with a cone-isolating grating of the same spatial and temporal frequency. The rod and cone stimuli would be discriminable if their apparent contrasts differed, so to control for this the cone-isolating grating appeared at one of nine different contrasts selected randomly from trial to trial. The range covered a factor of two (M.D.) or three (P.L.) in contrast, centered on the contrast that appeared equal to that of the standard rod-isolating grating. Thus, if variations in apparent contrast were the only cue that reliably distinguished the two classes of grating, we should find that as the apparent contrasts become more nearly equal, the two types of grating become indistinguishable. The gratings used in this experiment had a spatial frequency of 2.77 c/deg and moved at 4 Hz; the mean level of illumination was 4.7 td for M.D. and 7.4 td for P.L. Rod-isolating gratings appeared with a contrast of 0.14 for M.D. and 0.10 for P.L. In a single experimental run there were 720 trials, on half of which both stimuli were identical rod-isolating gratings. On the other trials the rod-isolating grating was paired equally often with one of the nine cone-isolating gratings. Figure 5 shows, for M.D. (A) and P.L. (B), how the discriminability of rod-isolating and cone-isolating gratings depended upon the contrast of the cone-isolating pattern. Results are averaged from two experimental runs. When the apparent contrasts of the rod- and cone-isolating gratings differ the patterns are reliably distinguished, but when the contrasts appear equal the patterns are indistinguishable. Thus we infer that signals from the two classes of receptor lose their separate identities in some common pathway.

Prolonged viewing of a high-contrast grating reduces sensitivity to gratings of similar spatial frequency viewed subsequently (Blakemore and Campbell, 1969). If rod and cone signals do indeed travel in a common pathway, and are indistinguishable at central sites, adaptation to

a grating seen only through rods should reduce by the same amount the detectability of subsequently viewed gratings seen with either rods or cones. Similarly, an adapting grating seen only through cones should equally affect the detectability of test gratings seen with either rods or cones. Thresholds for test gratings (either rod- or cone-isolating, 2.77 c/deg, moving at 4 Hz) were measured by M.D. and P.L. before and after adaptation to gratings (either rod- or cone-isolating) of 20% contrast viewed for 1 min. Mean illumination was 4.7 td. Table

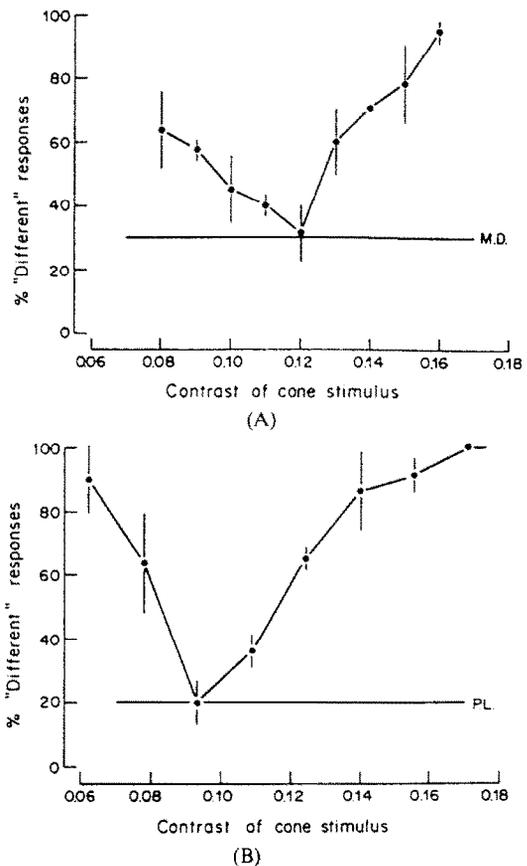


Fig. 5. Discriminability of "cone-isolating" and "rod-isolating" gratings. The observer had to decide whether two gratings presented sequentially were identical or different. Half the pairs contained identical "rod-isolating" gratings, while the other half contained pairs of "rod-isolating" and "cone-isolating" gratings. Results for M.D. are shown in (A); those for P.L. in (B). The contrast of all "rod-isolating" gratings was constant at 14% (M.D.) or 10% (P.L.) while the contrasts of "cone-isolating" gratings were varied over a range centered on the contrast apparently equal to that of the "rod-isolating" grating. The false positive rate for identical rod stimulus pairs was 30% (M.D.) or 20% (P.L.) and is indicated by the horizontal lines. The gratings were of spatial frequency 2.77 c/deg, drifted at 4 Hz, and had a mean illumination of 4.7 td. A ninth point for P.L., indicating 100% discrimination at a cone contrast of 0.19, is not shown. Error bars represent standard errors.

Table 1. Factors by which thresholds increased after adaptation (SEM for all values shown &lt;0.2)

Adapting gratings	Test gratings	
	Rod-isolating	Cone-isolating
Rod-isolating	2.1 (M.D.) 1.9 (P.L.)	1.8 (M.D.) 1.7 (P.L.)
Cone-isolating	1.7 (M.D.) 2.0 (P.L.)	1.9 (M.D.) 2.1 (P.L.)

1 shows that both sorts of adapting grating raised threshold substantially, for both test gratings. Moreover, each adapting grating had similar effect upon the visibility of both tests.

## DISCUSSION

### *Sensitivity of rods*

Our results show that the highest rod contrast sensitivity (near 50, contrast threshold 0.02) is attained for gratings of about 1 c/deg when the level of illumination is close to 20 scot td. This sensitivity is higher than has been found previously. With increment threshold measurements obtained using a 9 deg test patch of long duration, viewed on a background of long wavelength, Aguilar and Stiles found that the Weber fraction of the rod system was about 0.1 (Aguilar and Stiles, 1954; Fig. 6). Using a similar technique for isolating rods, Conner found that the greatest sensitivity to a large disc flickering at 4 Hz was six, while maximal sensitivity reached was about ten using 9 Hz stimuli (Conner, 1982; Fig. 7).

The spatial configuration of the stimulus is undoubtedly relevant: the band-pass characteristic of the contrast sensitivity curve suggests that sensitivity to large uniform targets will be lower (by perhaps a factor of two) than to gratings of optimal spatial frequency. The other possibly important factor is the spectral composition of the stimuli. Several reports (Makous and Booth, 1974; Makous and Peeples, 1979) show that when rods are isolated by large adapting backgrounds of long-wavelength, threshold may be higher than is found when the test stimulus is seen against a scotopically equal background of shorter wavelength that has less effect upon cones. These factors together probably explain why in our experiments rod sensitivity was relatively higher than was found by Aguilar and Stiles (1954) and by Conner (1982). In this connection it is interesting that the spatial contrast sensitivity curves obtained in the present experiments are very like those of a

rod monochromat studied by Hess and Nordby (1986). However, it is more difficult to reconcile the present estimates of sensitivity with those found for normal observers by Daitch and Green (1969). They used achromatic gratings presented with an abrupt onset and offset and found that the contrast sensitivity of the rod system did not exceed 10 (Daitch and Green, 1969; Fig. 1, 0.0 log td). We do not know what accounts for the discrepancy. Figure 3 shows that the peak sensitivity of the rod system begins to decline at levels of illumination above 20 scot. td—a slightly lower level than has usually been thought to characterize the onset of saturation. However, Conner (1982) showed that this depends upon temporal frequency, and our results are consistent with his observation that for stimuli flickering at temporal frequencies near 4 Hz, the scotopic system begins to saturate at 20–50 scot. td.

### *Convergence of rod and cone pathways*

Many ganglion cells receive input from both rods and cones (Gouras and Link, 1966; Boycott and Dowling, 1969), yet the spatial properties of rod and cone vision differ (Fig. 3). The natural interpretation is that rod and cone receptive fields differ in size, but the physiological evidence shows no marked change in the spatial organization of receptive fields following the transition from rod to cone vision (Enroth-Cugell *et al.*, 1977; Gouras, 1967). Our results are consistent with an alternative arrangement whereby some ganglion cells with small receptive fields receive inputs only from cones, while others, with larger receptive fields, receive inputs from both rods and cones. In these units, the scotopic and photopic receptive fields are identical. This is not to say that under all circumstances the rod and cone signals in this pathway will be indistinguishable. Non-linearities might arise before the point at which signals are combined, and distinctive distortion products might make the time-courses of rod and cone responses identifiable. No such non-linearities are evident in our results, nor in others that examined the combination of rod and cone signals from flickering uniform fields, but our experiments did not explore a wide range of temporal frequencies or a wide range of suprathreshold contrasts.

The division of information into two pathways, one carrying signals from both rods and cones, the other from cones only, probably does not reflect the morphological and physiological

distinction between the two major classes of ganglion cell that project to different laminae of LGN in macaque (Wiesel and Hubel, 1966; Dreher *et al.*, 1976; Leventhal *et al.*, 1981; Perry *et al.*, 1984; Derrington *et al.*, 1984). Although Boycott and Dowling (1969) found that in the central retina the "midget" ganglion cells (which almost certainly correspond to  $P_\beta$  class of Perry *et al.*, and provide the sole afferent input to parvocellular laminae of the LGN) mostly received input from single bipolar cells which, in turn, were usually in contact with single cones, Wiesel and Hubel (1966) found some parvocellular neurons driven by rods as well as by cones. Thus, although the midget/ $P_\beta$  system in the fovea may be driven exclusively by cones, it seems that in the near peripheral retina some of the larger  $P_\beta$  ganglion cells also receive input from rods. There is good evidence that many of the larger  $P_\alpha$  ganglion cells that project principally to magnocellular LGN receive inputs from rods (Gouras and Link, 1966; Wiesel and Hubel, 1966). We cannot at this stage say how these classes of cell contribute to the contrast sensitivities measured in our experiments.

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