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## COLOR VISION FROM ROD AND LONG-WAVE CONE INTERACTIONS: CONDITIONS IN WHICH RODS CONTRIBUTE TO MULTICOLORED IMAGES

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**Abstract**—Two different color-separation images, each illuminated with different wavelengths of light, were combined to make a multicolored image. Experiments that measured the action spectra of the receptor mechanisms responding to one of the color-separation images show that the rods interact with the long-wave cones to produce the multicolored image. A second experiment used the different directional sensitivities of rods and cones (the Stiles-Crawford effect) to determine the conditions in which the multicolored images are generated by the rod-cone interactions, and to determine the conditions in which the colors are produced by cone-cone interactions.

One of the principal research interests in our laboratory has been the study of complex *multicolored* images. There are two conditions needed to produce a multicolored image. The first condition is that one must have two sets of spectrally independent information. An example of what we mean by two sets of spectral information is a pair of color-separation photographs, i.e. two pictures of the same scene made with photographic systems that respond to different portions of the visible spectrum (see Fig. 1). The second necessary condition is that the different sets of spectral information must be sent to the eye by two discriminably different wavelengths of light.

Until recently, it has been assumed that the two different sets of spectral information must be processed by a minimum of two different *cone* systems. Rods were thought to be completely independent from the cones and not to be involved in color vision. There is much psychophysical evidence to support this assumption of rod-cone independence (von Kries, 1895; Hecht, 1937; Stiles, 1949; Alpern, 1965; Westheimer, 1970). Nevertheless, there exist experiments that show that the rods and cones, acting together, can generate color. Willmer (1949) observed that the color blue could be produced by placing a yellow or red light adjacent to a light that was below cone threshold. Blackwell and Blackwell (1961) noted that individuals suffering from a rare visual defect, blue cone monochromacy, were able to make color discriminations between long and short wavelengths, presumably on the basis of signals from their blue cones and their normal rods. These observers identified wavelengths from 400 to 450 nm as blue, from 450 to 470 nm as gray, and wavelengths longer than 470 nm as yellow. After selective chromatic adaptation at photopic levels, Stabell and Stabell (1965) found that lights too weak to stimulate cones appeared colored. They have performed a variety of different experiments with these color after-effects, including recent experiments that show that the after-effects

have the same spectral sensitivity as the scotopic luminosity curve (Stabell and Stabell, 1975).

In 1969, McCann and Benton showed that under appropriate conditions rods can be as much a part of the production of color sensations as the cones. They illuminated a complex multicolored scene with two narrow bands of wavelengths (546 and 656 nm), choosing the intensity of 546 nm light such that it was above threshold for only the rods. The 656 nm light was at a radiance level such that the long-wave cones were the only cone mechanism above threshold. This combination produced a variety of color sensations that was identical, except for brightness and sharpness, to color sensations produced when two narrow-band illuminants (656 and 495 nm) were each above cone threshold. To demonstrate that the cones were unable to respond to the image viewed in 546 nm light alone, they showed that the highest radiance in the 546 nm image was nearly two log units below cone threshold as measured by three techniques: the rod-cone break in the dark adaptation curve, a discontinuity in the rate of change of the sharpness of the image, and the radiance at which the 546 nm light changed from producing a colorless image to producing a slightly green image.

In the McCann and Benton study, measurements to determine whether rods or cones were responding to a stimulus were made with each illuminant viewed alone. In this paper, we will examine the properties of the receptor systems responding when *both* illuminants are viewed simultaneously. A dark-adapted observer studied a color image made by the additive superposition of images produced by two different color-separation transparencies. Each transparency was illuminated by a separate Maxwellian-view monochromator. One transparency, taken with a red filter, was illuminated with 656 nm light at an intensity that just allowed the observer to see reddish forms and shapes. The experimenter used a wavelength between 400 and 600 nm to illuminate the second transparency, taken through a green filter. The addition of the second color-separation image, illuminated by a shorter wavelength, changed the reddish image to a multicolored image. The observer adjusted

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the intensity of the shorter wavelength until the variety of colors produced by the combined images was in optimum color balance—neither too warm (too reddish) nor too cool (too blue-green). If the rods are responding to the short wavelengths illuminating the green-separation image, then at each wavelength the radiance chosen by the observer for optimum color should be characteristic of the rods; the action spectrum of optimum color should have the same shape as the scotopic luminosity curve.

In the second experiment, the observer was asked to make similar optimum color judgements in which he again adjusted the intensity of the light illuminating the green-separation transparency. Instead of changing the wavelength illuminating this slide, the experimenter changed the angle of incidence of the light on the retina by alternately inserting and removing a prism in the optical path of the monochromator. The rods are known to be insensitive to changes in the angle of incidence while the cones respond much less efficiently to light striking them obliquely (Stiles-Crawford effect). Therefore, if the rods are responding to the green-separation image, the observer should choose the same intensity for optimum color, regardless of the angle of incidence. Only when the light illuminating the middle-wavelength slide exceeds cone threshold should the observer require more light for optimum color when the beam strikes the receptors obliquely.

The results of these two experiments confirm the finding that the rods can interact with long-wave cones to produce a variety of color sensations when there is insufficient light to excite middle- and short-wave cones. The experiments also define further the conditions under which the rods are color receptors.

#### METHODS

##### *Apparatus*

These experiments were performed with an image monochromator similar to the one described by Land (1959b). This instrument (see Fig. 2) was called an image monochromator because photographic transparencies were

mounted in the light beam, after the monochromator grating system narrowed the waveband. The images from different monochromators were superimposed with semi-silvered mirrors. The transparencies could be adjusted horizontally and vertically and rotated until the images from different monochromators were precisely superimposed. The filaments of the tungsten sources (6 V, 18 A CPR lamp) were imaged in the plane of the observer's pupil by the telescope mounted on the casing of the monochromator. The filament image at the pupil was 1 mm square. The observer's head was positioned by a bite bar mounted on the casing of the instrument below the telescope. The positioning of the bite bar could be translated in three perpendicular directions. In the first experiment, all measurements were made while the filament was centered on the observer's natural pupil. In the second experiment, a prism was alternately inserted into and removed from the optical system such that when the prism was in place the image of the filament was horizontally displaced 2.6 mm on the temporal side of the pupil. This change in pupil entry produced no detectable change in the position of the image on the retina; in fact, at scotopic levels, the observer could not detect whether or not the prism was in place.

The intensity of each beam could be varied independently by means of a variable transformer which controlled the voltage across each filament. For large reductions in the amount of light, we used Wratten neutral density filters. The spectral absorption curve of each neutral filter was measured on a Cary spectrophotometer, and these measurements were included in our calibrations. At wavelengths below 500 nm we used additional scavenger filters to insure that the light reaching the eye was composed of only a narrow band of wavelengths. These filters were necessary because at low voltages the output of a tungsten bulb is very weak in the 400–500 nm region of the spectrum. In spite of these precautions some scattered light from other wavelengths may have affected our measurements for the short wavelengths.

Using the incident-light photometer we measured the irradiance at each experimental wavelength over the whole range of bulb voltages employed in our experiments. The measurements were made with a clear slide, equal in area to the experimental slides; thus, these measurements represent an upper limit on the amounts of light coming from all regions of the experimental slides. These measurements, corrected for the spectral characteristics of the photodiode and Wratten neutral density filters, were then converted

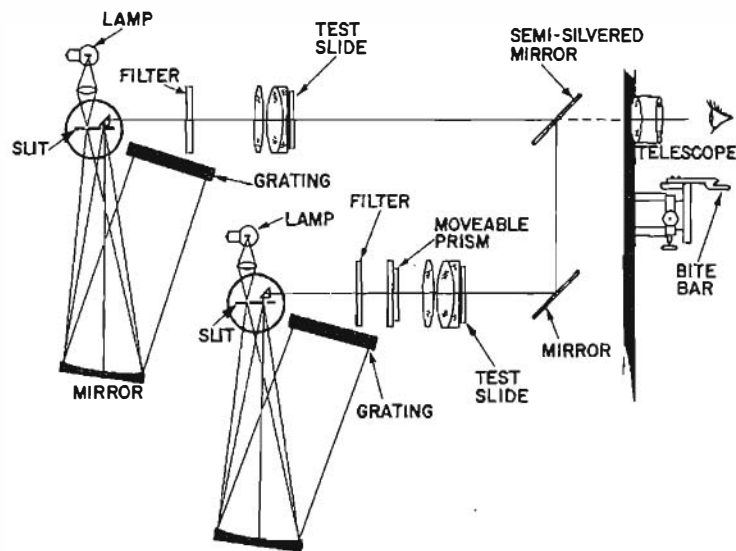
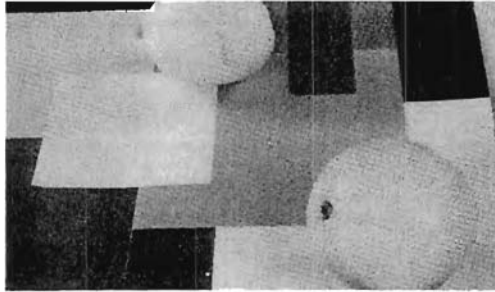


Fig. 2. A schematic diagram of two image monochromators used in these experiments.

**LONG-WAVE RECORD**



**MIDDLE-WAVE RECORD**

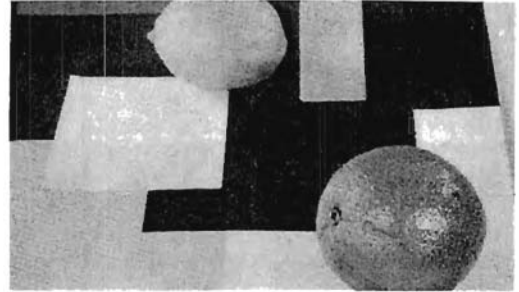


Fig. 1. Copies of the color-separation transparencies used in the experiments.

to irradiance ( $\mu\text{W}/\text{cm}^2$ ). Repeated measurements were made during the course of the experiment to check the bulbs for aging and any other systematic changes. We used a Tektronix spectrum analyzer to calibrate the wavelength indicator dial on the monochromator and to measure the bandwidth of light (7 nm at half height).

Two color-separation transparencies of the same scene were used in these experiments. One transparency, called the *long-wave record*, was taken with a red (Wratten 24) filter in front of the camera, and the second transparency, called the *middle-wave record*, was taken with a green (Wratten 58) filter (see Land, 1959a, for a description of this technique). When these two slides were superimposed and illuminated at photopic levels with two beams of different wavelength composition, the resulting picture was a bright multicolored image. In these experiments we used a picture with large objects (see Fig. 1) suitable for scotopic resolution. The image subtended  $28^\circ$  by  $16^\circ$ .

The illumination for the long-wave record was always set at the same wavelength (656 nm). The intensity of this beam was varied parametrically; the 656 nm irradiance was constant for each spectral sensitivity curve shown in the Results section. We used at least nine wavelengths between 420 and 600 nm to measure the spectral sensitivity of the mechanism that used the middle-wave information to contribute to color sensations.

### Subjects

The three authors served as subjects; all had good color vision (average scores of 8, 2 and 0 in the Farnsworth 100-Hue Test). For the experiment using the Stiles-Crawford effect, the pupil was dilated by a mixture of two drops of 1% mydriacyl and one drop of 10% phenylephrine solution, administered before the experimental session. The pupil stayed fully dilated for a period of about 2 hr.

## RESULTS

### Part 1: The measurement of spectral sensitivity functions

First, in the control experiments, we used only the middle wavelength separation image illuminated by a number of different wavelengths ranging from 420 to 610 nm. The experimenter presented a wavelength

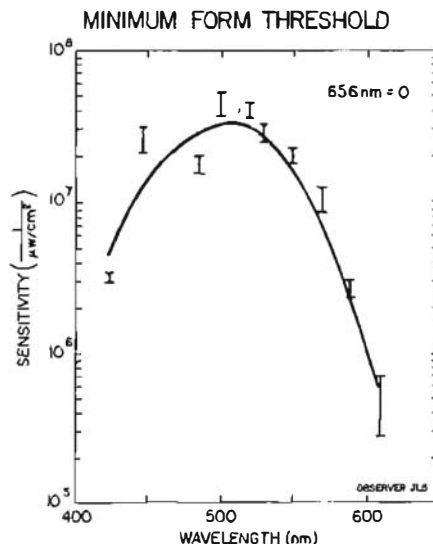


Fig. 3. A graph of *minimum form threshold* as a function of wavelength. This judgement has the same spectral sensitivity as the scotopic luminosity curve drawn as the solid line. The vertical lines represent the mean  $\pm 1$  S.E.M.

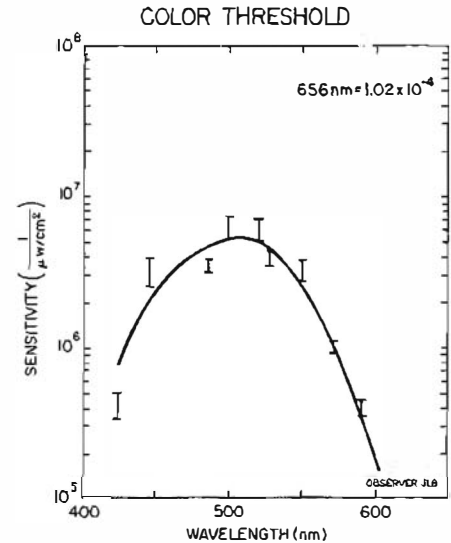


Fig. 4. A graph of *color threshold* as a function of wavelength. This judgement also has the same spectral sensitivity as the scotopic luminosity curve (solid line).

and the observer chose an intensity of that wavelength such that he could just see very faint forms. Under these conditions the observer can see several areas with different lightnesses but cannot necessarily identify objects. We called this judgement *minimum form threshold*. The minimum form threshold data, shown in Fig. 3, are plotted as sensitivity (l/irradiance at the cornea) vs wavelength.

The vertical bars represent  $\pm 1$  S.E.M. The solid curve is the CIE scotopic luminosity curve (LeGrand, 1957). *Minimum form threshold* has the same spectral sensitivity as the scotopic luminosity curve. We believe that the small deviations from the scotopic curve below 500 nm are due to stray light of longer wavelengths. The cause is the very low output of wavelengths below 500 nm when the voltage of the lamps is low. At higher radiance levels these deviations disappear.

Next, the experimenter turned on the second monochromator and projected the long-wave image, illuminated with 656 nm light, in superposition with the middle-wave separation image. The 656 nm beam was set at a very low intensity ( $1.02 \times 10^{-4} \mu\text{W}/\text{cm}^2$ ) allowing just enough light so that the long-wave record was visible in 656 nm light alone. The entire image appeared reddish. As in the first experiment, the wavelength illuminating the middle-wave record was variable. Without the knowledge of the observer, the experimenter chose a wavelength and asked the observer to increase the intensity of that wavelength until the combined image just produced a sensation of many colors. We call this judgement *color threshold*. At color threshold the observer could faintly see an image of reds, blue-greens, and yellows. In Fig. 4 color-threshold sensitivity is plotted as a function of wavelength. Again we find that this curve fits the scotopic luminosity curve.

In the third part of this experiment, we slightly increased the intensity of the 656 nm light to  $1.6 \times 10^{-3} \mu\text{W}/\text{cm}^2$ . This time the observer was asked to adjust the intensity of the wavelength illuminating the middle-wave record until the multi-

colored image was neither too warm (too red) nor too cool (too blue-green). We call this judgement *optimum color*. When the observer sets the short-wave light for optimum color, he sees a larger variety of colors including whites, reds, yellows, dark and light blue-greens, browns, and oranges. The top curve in Fig. 5 is a plot of optimum color sensitivity as a function of wavelength: this curve, the wavelength-irradiance distribution for optimum color judgement, also fits the scotopic luminosity curve. We then substantially increased the intensity of the 656 nm light to  $2.6 \mu\text{W}/\text{cm}^2$  and repeated the optimum color judgements. At this level of light the optimum-color sensitivity curve no longer fits the scotopic luminosity function. The bottom curve in Fig. 5 shows that this sensitivity curve is much broader than the scotopic curve, indicating cone response to the middle-wave separation image.

In Fig. 6 we replotted the four graphs already discussed and added four more. The ordinate was changed from sensitivity to its reciprocal, the irradiance necessary for threshold. The reason for this change, which inverts the scotopic luminosity curve, is to allow comparison of these curves to a pair of dark-adaptation curves. The ordinate, which is the same for both graphs, is irradiance at the cornea. On the left we plot the threshold for 510 nm light as a function of time after light adaptation. We used two types of light adaptation sources. In the first adaptation experiment the subject's eye was light adapted by six strobe flashes, at 15 sec intervals, viewed through half a ping-pong ball. The subject then chose the intensity of 510 nm light that was just visible every 30 sec for half an hour. These threshold measurements were made with the middle-wave

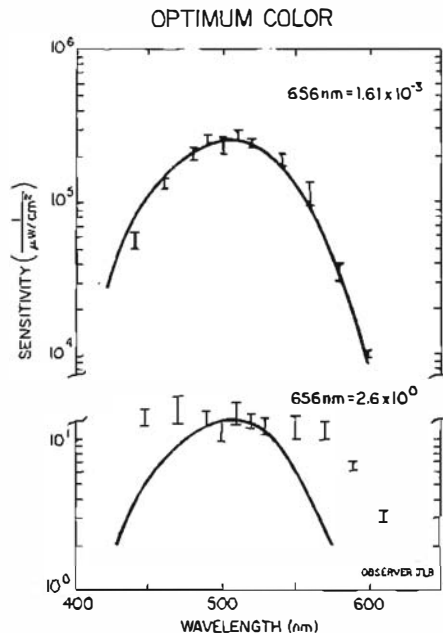


Fig. 5. A pair of graphs of *optimum color* as a function of wavelength. When the 656 nm light was set at  $1.61 \times 10^{-3} \mu\text{W}/\text{cm}^2$  the optimum color judgements had the same spectral sensitivity as the scotopic luminosity curve. When the 656 nm light was set at  $2.6 \mu\text{W}/\text{cm}^2$ , the optimum color judgements had a very different spectral sensitivity curve.

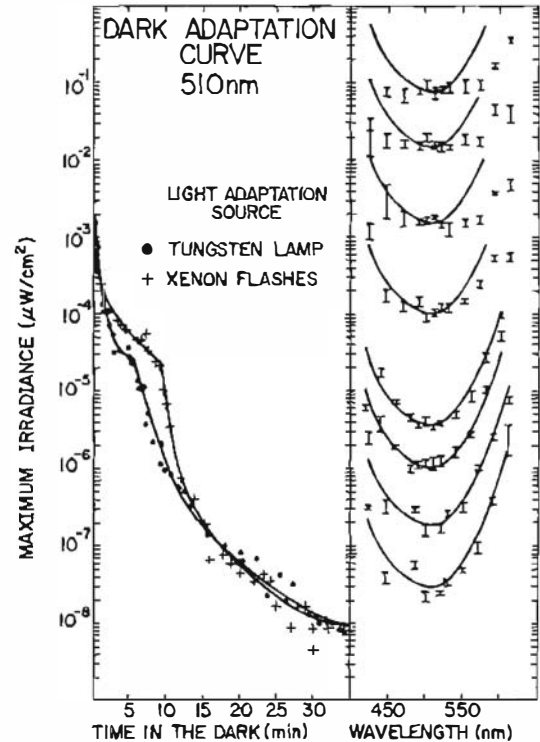


Fig. 6. A composite of all the action spectra we recorded, as well as a pair of dark adaptation curves. Here the data are plotted as threshold irradiance instead of the reciprocal, sensitivity. The bottom four curves on the right fit the rod action spectrum while the four curves above them do not. The change from fit to non-fit occurs at the same irradiance as the rod-cone break in the dark-adaptation curve.

record in place. In the second adaptation experiment we used a projector with a 1000-W tungsten lamp as the light-adapting stimulus. The projector illuminated the ping-pong ball in front of the observer's eye. The duration of light adaptation was 5 min. The two curves, one for each light-adapting source, show slightly different rates of recovery of sensitivity, but both curves show a rod-cone break at approximately the same irradiance. We can take the value of the breaks in the curves as the irradiance of 510 nm light at which the rods become more sensitive than the cones.

When the observer's judgements of optimum color are based on rod and long-wave cone interactions, then the necessary irradiances illuminating the middle-wave record should have an action spectrum similar to that of the rods. The data should no longer fit the reciprocal of the scotopic luminosity function when the optimum color judgements depend on interactions between the long-wave cones and other cones. The bottom curve on the right, *minimum form threshold vs wavelength*, has the same action spectrum as the rods. The next curve is *color threshold*, and it also fits the rod action spectrum. All the remaining curves above these are *optimum color* measurements. The first two optimum color curves have the same action spectrum as the rods, and the irradiance of 510 nm light for these curves is less than the 510 nm irradiance at which the rod-cone break was measured in the dark adaptation curves. The irradiance of

510 nm light in the third optimum color curve is above the rod-cone break. At this intensity, the longer wavelength portion of the curve does not fit the rod action spectrum. Above the rod-cone break, the changes in the shape of the action spectra are more noticeable in the short wavelength region. It is this region which appears to fit the rod function at irradiances above the break; for more than a log unit above the rod-cone break the values for threshold on the short wavelength side fall on the scotopic luminosity function.

In conclusion, Fig. 6 provides us with data about the levels of irradiance necessary for the cones to contribute to color sensations. These data clearly show that at 510 nm there is a range of irradiances, varying by a ratio of 100 to 1, in which the rods must be the only contributor of the middle-wavelength information necessary for multicolored images.

#### Part II: Rod-cone interactions and the Stiles-Crawford effect

The second set of experiments made use of the Stiles-Crawford effect. Since the double image monochromator system uses Maxwellian-view optics, we can arrange to have all the light illuminating the middle-wave separation image pass through the center of the pupil at position A (see Fig. 7) or pass through the periphery of the pupil at position B. The rods are very nearly as sensitive to light traveling through B along path X as they are to light traveling through

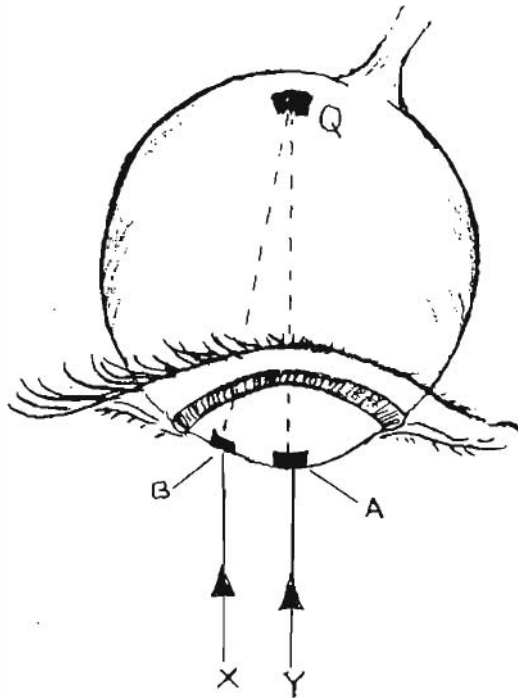


Fig. 7. A diagram of the locations of the images of the filament on the pupil. The double-image monochromator system uses Maxwellian-view optics so that all the light illuminating the green-separation image passes through the center of the pupil at A. With the addition of a prism all the light passes through the periphery of the pupil at B. Light passing through B travels along path X and arrives at the same point Q as light traveling through the center of the pupil and traveling along path Y.

A along path Y. The cones are about 2.5 times more sensitive to light entering through the center of the pupil (through A) than they are to light entering 2.5 mm on the temporal side of center (through B).

In these experiments we used a smaller middle-wave-separation image that subtended  $7^\circ$  by  $16^\circ$ . Instead of using wavelengths from 400 to 600 nm, we used only 510 nm light. As before, the observer adjusted the intensity of the 510 nm light for optimum color, and the experimenter chose whether the light passed through position A or position B in the pupil. The experiment was repeated for many intensities of 656 nm light. If the rods generate the biological signals for color from the green-separation image, we could predict that the observer would choose a very similar intensity of 510 nm light regardless of its optical path to the rods. If the cones are absorbing the light coming from the green-separation image, then the observer should choose 2.5 times more 510 nm light when the light passes through the periphery of the pupil. In Fig. 8 we plot the amount of light chosen by the observer for optimum color vs the amount of 656 nm light coming through the red-separation slide. For low intensities of 656 nm light, the observer chose nearly the same amount of 510 nm light through A as through B. Light passing through position A is plotted as O's, and light passing through position B is plotted as +'s on the graph.

In Fig. 9, we plot the ratio of irradiance through B to the irradiance through A as a function of 510 nm intensity. For a large range of intensities of 510 nm light the ratio of B to A remains slightly greater than 1.0. Then the ratio abruptly changes to 2.5. Over the entire range of this curve the observer reports multicolored images. Below  $10^{-4} \mu\text{W}/\text{cm}^2$  of 510 nm light the rods are generating the biological signals for color sensations from the middle-wave separation image.

A summary of our experimental results is described by the one-dimensional graph in Fig. 10. This graph plots the amount of 510 nm light necessary for the different judgements made by observers already described in the paper. As well, we have included other measurements that are indicators of cone and rod activity. We begin at the bottom with dark-adaptation thresholds, i.e. the minimum amount of light necessary for detecting 510 nm light. Slightly above are the *minimum form threshold* measurements for two observers. With 10 times more light we reach *color threshold* (the amount of 510 nm light which, when combined with  $10^{-4} \mu\text{W}/\text{cm}^2$  of 656 nm light, produces the *color threshold* judgement). At about the same irradiance we find the *distinct form threshold* for 510 nm light alone. *Distinct form threshold* is the irradiance at which the observer is able to see distinctly a variety of lightnesses from white to black.

With 100 times more 510 nm light than that needed for the threshold for a multicolored image, we find grouped together the traditional indicators of cone activity: the break in the dark-adaptation curve for 510 nm light, the intensity at which an observer can detect a difference in brightness between light passing through the center or through the periphery of the pupil, the intensity of 510 nm light that first appeared green in color, the intensity at which the action spectra no longer fit the rod action spectrum, the change in Stiles-Crawford ratio for optimum color, and the

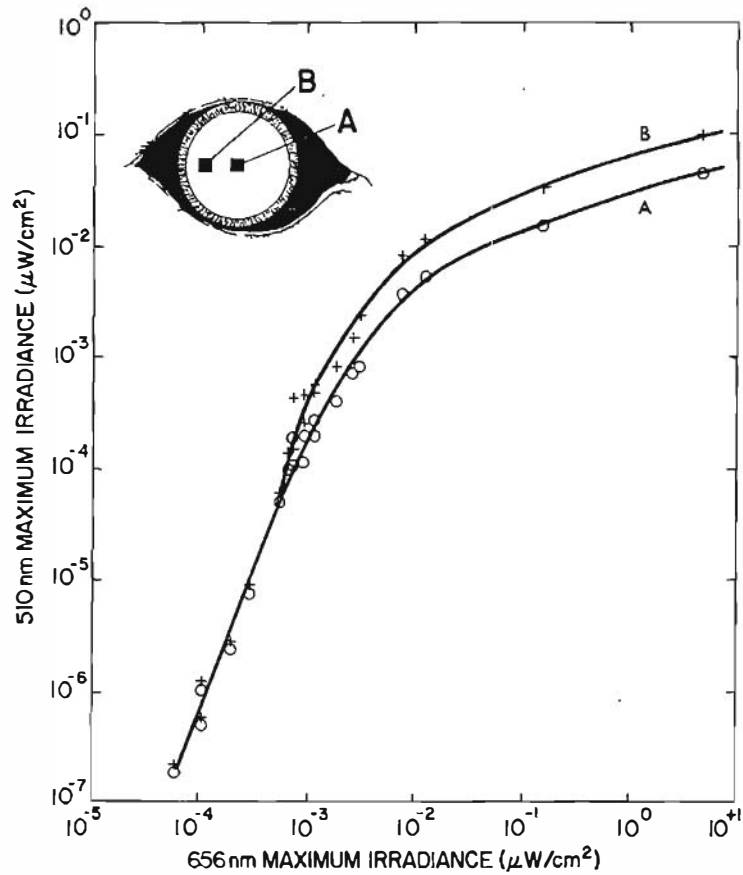


Fig. 8. A graph of irradiance of 510 nm light chosen by the observer for optimum color vs the irradiance of 656 nm light. For low intensities of 656 nm light, the observer chose nearly the same amount of 510 nm light through A as through B. Light passing through position A of the pupil is represented by O's and light passing through position B by +'s on the graph. Above a certain value, the observer chooses higher intensities through the periphery of the pupil in order to make similar optimum color judgements.

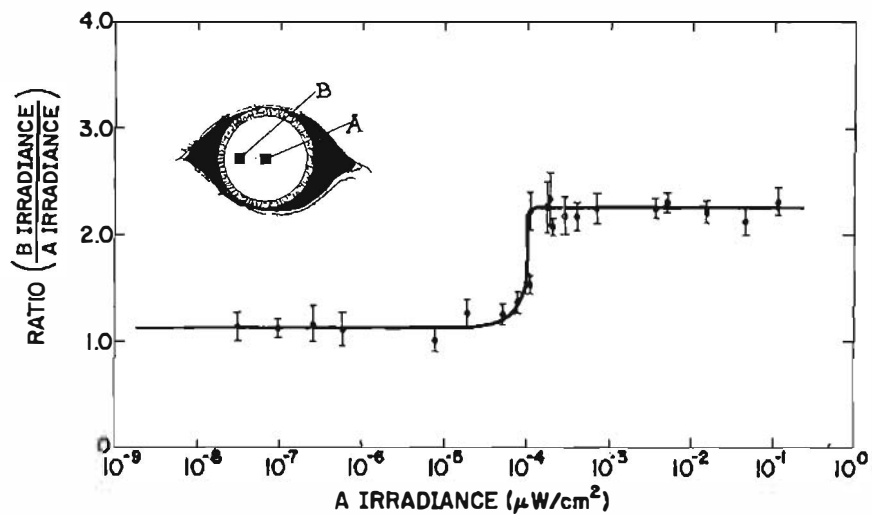


Fig. 9. A graph of the ratio of light through B to light through A as a function of the intensity of the 510 nm light. From  $10^{-9}$  to  $10^{-4} \mu\text{W}/\text{cm}^2$  of 510 nm light the ratio is very slightly greater than 1.0 and then the ratio jumps to a value of 2.5. Over the entire range of this curve the observer reports multicolored images. In the left portion of the curve, the rods are generating the biological signals for colors from the middle-wave separation image; in the right portion the cones are generating the biological color signals from the middle-wave separation image.



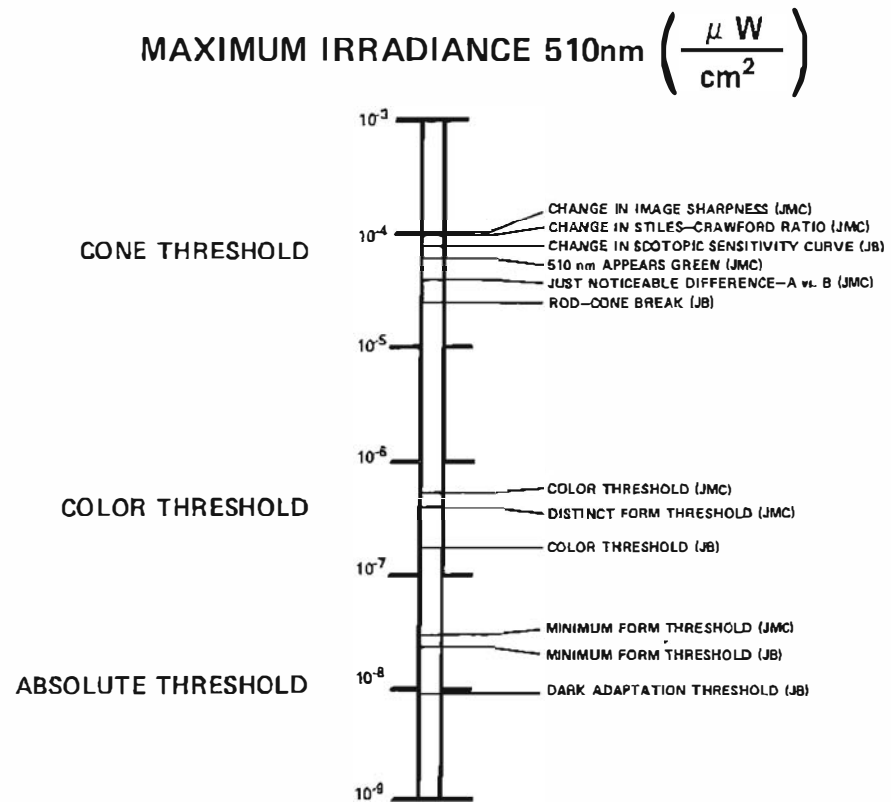


Fig. 10. This figure summarizes the results from all the experiments described in this paper. The change in the Stiles-Crawford ratio, the change in shape of the scotopic sensitivity curve, the change in the image sharpness, and the rod-cone break in dark-adaptation curves are all in agreement and provide a good indicator of cone threshold. All these measurements of the onset of cone activity occur at an intensity of 510 nm light at least 100 times greater than that at which color is first observed.

change in apparent sharpness associated with the greater acuity of the cones. All of the measurements on this graph can be grouped into three categories: cone threshold, color threshold, and absolute threshold. Color threshold for a multicolored image occurs about 10 times above absolute threshold and 100 times below cone threshold.

#### DISCUSSION

At low radiance levels, when only the rods are sensitive enough to be above threshold, a multicolored display appears colorless. This observation, combined with psychophysical evidence for rod-cone independence, is the probable reason that the rods were not considered color receptors. The multicolored display appears colorless at low radiance levels because there is only enough light to excite one set of receptors.

In order to produce a multicolored image, two different visual receptor systems must produce two dif-

ferent sets of responses; for example, the long-wave cones and the rods or the long-wave cones and the middle-wave cones must produce different sets of responses. The two conditions described earlier in this paper (two sets of spectral information illuminated by two discriminably different wavebands) insure that at least two receptor systems receive different sets of information. If only *one* color-separation record is illuminated by *two* wavelengths, the image remains a *single* hue, namely, the color produced by the mixture of two wavelengths. If two different color-separation records are illuminated individually by the same wavelength, this composite image also has only a single hue.

We can illuminate a multicolored display with a single wavelength at 656 nm. The display is reddish as soon as the display is visible. We can increase its intensity from below absolute visual threshold to just above the threshold for the rods and long-wave cones. With ten times more radiance there is sufficient light to exceed also middle-wave cone threshold (Brown and Wald, 1964), and the image still contains a single hue, red<sup>2</sup>. The onset of the middle-wave cones does not produce a multicolored image. With a much greater increase in radiance we might be able to excite all three types of cones and the rods with *only* 656 nm light. Under these conditions the same lightness information produced by only one wavelength is sent to all the receptors, and thus, we do not see a multicolored image.

<sup>2</sup> Helson (1938) reported seeing complementary greenish colors when illuminating a test display with only long-wave light. The greenish colors are associated with areas having lower than average luminance, while areas with higher than average luminance appear reddish, and areas of average luminance appear neutral. These experiments used pre-adaptation to the maximum luminance in the experiment. Analogous results are not found without previous light adaptation or with dark adaptation.

When we look at an image well below cone threshold, the rods produce an image in lightness which is colorless. Lightness is defined as the sensation scale from white to black. McCann (1972) showed that the lightness of an area produced by rods responding to a complex scene does not correspond to the radiance coming from that area. Two areas in this complex image can send identical radiation to the eye, yet one is light and the other is dark. In this respect the rods are similar to the cones: With monochromatic images, above cone threshold, a particular radiance at a point can produce nearly any lightness (Land and McCann, 1971; Land, 1974). Moreover, with three (long-, middle- and short-wavelength) illuminants, all above cone threshold, nearly any color can be produced by a particular wavelength-radiance distribution. Color sensations do not correspond to a particular triplet of radiances (Land, 1964; Land, 1974; McCann, McKee and Taylor, 1976). McCann (1972) showed that very different color sensations, such as red and green, can be generated simultaneously by rod and long-wave cone interactions from identical wavelength-radiance distributions. These colors did not correspond to the wavelength-radiance distribution at a point, but rather corresponded to sets of lightnesses.

Do rods have their own independent color channel, or do they share one or more of the cone channels? The evidence seems to favor the latter possibility. The available physiological data support this notion of shared transmission lines. Anatomical and physiological studies show that the rods share access to the same cells in the visual pathway (Granit, 1944; Barlow, Fitzhugh and Kuffler, 1957; Wiesel and Hubel, 1966; Gouras and Link, 1966; Andrews and Hammond, 1970; Kolb, 1970; Niemyer and Gouras, 1973). While studying the effects of dark adaptation, Wiesel and Hubel (1966) found a monkey geniculate cell in which the rod input substituted for the middle-wave cone signals at low luminance levels. Psychophysical experiments on flicker, increment thresholds, and durations of latency also show a lack of complete rod-cone independence (Walters, 1971; Makous and Boothe, 1974; Frumkes, Sekuler, Barris, Reiss and Chalupa, 1973).

If the rods share the same channels as the blue cones (as suggested by Willmer, 1946; Richards, 1967; and Trezona, 1970), then the color sensations from rod and long-wave cone interactions should be the same as those produced by short- and long-wave interactions above threshold. If the rods share the same channels with the middle-wave cones, then the color sensations should be the same as those produced by middle-wave and long-wave cone interactions. A third hypothesis is that rods share channels with both middle- and short-wave cones. This hypothesis would predict that color sensations produced by rod and long-wave cone interactions would be the same as those produced by wavelengths that excite both middle- and short-wave cone systems.

McCann and Benton (1969) performed an experiment to determine if any combination of wavelengths at radiances above cone threshold can produce the same color sensations as a combination that excites the rods and long-wave cones. They used a double-image monochromator to excite the rods and long-

wave cones in one eye and a second double-image monochromator to excite the cones (two wavelengths, both above cone threshold) in the other eye. The observers reported that 656 nm illumination combined with a record separately illuminated by 495 nm light gave an image that had the same color sensations as the image produced by rods and long-wave cones. Observers said that the only difference between the images in the two monochromators was that some areas in the image above cone threshold appeared somewhat brighter, sharper and slightly more saturated. This result supports the hypothesis that rods are eventually sharing the same color channels with both the middle- and the short-wave cones.

Aguilar and Stiles (1954) used increment threshold measurements to show that the rods continue to function at radiance levels well above cone threshold. This conclusion is supported by large-field ( $10^\circ$ ) colorimetry. In steady-state matching conditions, any wavelength combination can be matched by varying the intensities of at most three primaries. For a  $2^\circ$  field these matches are not altered by changing the luminance of the wavelength to be matched. However, for a  $10^\circ$  field the matches change as a function of luminance (Stiles, 1955). Results of many additivity and related colorimetry tests on large  $10^\circ$  fields have shown serious discrepancies limiting the applicability of large field colorimetry (Trezona, 1970; Clarke, 1973; Trezona, 1974). The usual explanation for this inconsistency is "rod intrusion" in one or more of the cone systems responsible for color vision (Wyszecki and Stiles, 1967). This work in colorimetry supports our contention that the rods contribute to color vision by adding signals to cone channels, and it shows, moreover, that this contribution can occur as well above cone threshold.

Our results provide further evidence that the rods can generate one of the two necessary sets of lightness information for multicolored images. We have shown that the receptor system which interacts with the receptor system responding to the long-wave record illuminated in 656 nm light has the properties expected of the rods. The action spectrum of optimum-color measurements is well fitted by the scotopic sensitivity curve. Moreover, the amount of light required for optimum color judgements is approximately the same regardless of the point of pupil entry, i.e. the Stiles-Crawford effect associated with the cones is not present. The addition of middle-wave record information generated by the rods to information generated from the long-wave image in 656 nm light changes that image from one of a single reddish hue into a multicolored image.

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