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JOHN J. McCANN AND JEANNE L. BENTON*  
Research Laboratories, Polaroid Corporation, Cambridge, Massachusetts 02139  
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The duality theory states that cones produce photopic or color vision, whereas the rods produce scotopic or colorless night vision. This paper reports experimental findings which demonstrate the capacity of the rods to interact with the long-wave cones to produce color sensations. Radiances of 346 and 450 nm that excited only the rods, and radiances of 656 nm that excited only the long-wave cones were determined. When the rods and long-wave cones were selectively excited with the minimum radiance necessary to see form, the observers reported seeing a large variety of color sensations. These observers also reported the same variety of color sensations at greater radiances when the rods and long-wave cones were selectively excited. Color sensations produced by the excitation of rods and long-wave cones were independent of the wavelength used to excite the rods. Color sensations produced by rods and long-wave cones were identical, except for slight differences of brightness and sharpness, to the color sensations produced by 656 and 495±5 nm light when both were above cone threshold. Therefore, under the described conditions, the rods can be as much a part of the human color-producing system as the cones. All of the above results can be explained by Land's retina theory of color vision.

INDEX HEADINGS: Vision; Color vision.

THIS work stems from a study of the relationship between being able to see form and being able to see a variety of color sensations in a complex display. As a result of unpublished studies with multicolored displays of varying retinal size and sharpness, Land proposed that if an observer was able to see a variety of forms and lightnesses with each of two different bands of wavelengths, then he could see a variety of color sensations when the two were combined. While he was studying this hypothesis at various radiances he found that it held over a very large range of light adaptations. It was obvious that, after dark adaptation, scotopic vision would have much greater maximum sensitivity than photopic vision. And since scotopic vision is generally considered independent of color-producing

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mechanisms we would expect that after considerable dark adaptation, the rods should generate a colorless image at the minimum radiance necessary to see form. Land fully dark adapted to ensure that both his rods and his cones were in their most sensitive states. He then turned on an incandescent light, controlled by a variable transformer. By slowly increasing the setting of the variable transformer, he could change from having no light to having just enough light to identify forms. Much to his surprise, he could identify nearly all of the colors in a multicolored experimental display.

Our measurements of the energy distribution of the light emitted by the incandescent bulb at this setting of the variable transformer showed that this low-color-temperature light should simultaneously excite both the rods and the long-wave cones. That is, at this color temperature the light had about 1000 times more long-wave radiance than middle-short-wave radiance. This suggested that the rods and the long-wave cones interact to produce color sensations.

Our attention was drawn to the studies of Blackwell and Blackwell of a rare type of color-defective observers, who had only rods and short-wave cones. They found when these observers were shown various wavelengths at a particular radiance for each wavelength, the observer identified wavelengths from 400 to 450 nm as blue, wavelengths from 450 to 470 as gray, and wavelengths longer than 470 nm as yellow. The neurophysiological work of Donner and Rushton, and Wiesel and Hubel also seems relevant. Donner and Rushton found that single ganglion cells in the frog have inputs from both rods and cones. Wiesel and Hubel found that some lateral geniculate cells of rhesus monkeys were connected to both rods and cones.

Our first experiment to test the rod-cone interaction to produce color sensations was to determine at what particular radiance for each wavelength we were exciting the rods or the cones. We used three separate wavelengths, chosen so that each would principally excite only one cone pigment (656, 546, 450 nm). The radiance of a wavelength that excited only the rods can be identified from threshold sensitivity curves. These curves are determined by first exposing the eye to brilliant white light and then measuring the minimum radiance of a particular wavelength that is just visible as the eye recovers from this light adaptation. The rods and cones have different rates of recovery of sensitivity. Although the cones dark adapt much faster than the rods, they are much less sensitive than the completely dark-adapted rods. Thus, the curves of threshold sensitivity for 450 and 546 nm have two segments; one where the threshold is determined by the faster recovery of the cones and the other where the threshold is determined by the slower, but more sensitive, recovery of the rods. The intersection of these segments is called the rod-cone break. We propose that radiances above the rod-cone break can excite both the rods and cones, whereas radiances below the break will excite only the rods. This is based on the assumption that light adaptation will bleach sufficient rod pigments so that the cones will have approached their asymptotic absolute threshold before the rods become more sensitive than the cones.

**EXPERIMENTAL PROCEDURE**

Since we were testing the hypothesis that the rods and the long-wave cones interact to produce color sensations, we constructed a multicolored array of squares and rectangles made from a random selection of matte-surface colored papers. Each paper was positioned so that it was surrounded by a number of different colors. A white square was placed in the center for the threshold-sensitivity measurements. Threshold measurements are usually made with a single area on a dark surround. A large piece of black velour paper was placed over the entire display. A 10-cm square hole was cut in the paper so that the white paper in the center was always visible. The experimenter could measure the threshold sensitivity with a white square and black surround, and he could test color recognition with a multicolored display, using the same test target and the same illumination.

The observer's eye was uniformly light adapted by looking at five 200-W sec xenon flashes (each 1-msec duration); the recovery of sensitivity was measured by varying the illumination until the observer first saw light coming from a white square of paper, 4°8' on a side with a fixation point at its center. The observer measured the recovery of sensitivity for wavelengths of 656, 546 and 450 nm, which were chosen to excite primarily the long-, middle-, and short-wave cone pigments, respectively. Three projectors were used to illuminate the test square, each of which had a narrowband interference filter which maximally transmitted one of the wavelengths. The light output of the projectors was individually regulated by a variable transformer. Changes of color temperature of any one bulb do not significantly change the wavelength output of each projector.

The observer was asked to adjust the variable transformer so that he could just see the white square, thereby measuring his sensitivity. Dark-adaptation experiments are usually performed by asking the observers to set the intensity of the light so that they can just see a flash of light. However, since the experiments were to be done with uninterrupted illumination, these sensitivity measurements were conducted with uninterrupted illumination.

The radiance of each threshold setting, as well as the time of the setting, was recorded. The plot of threshold radiance vs time after light adaptation for three

wavelengths is shown in Fig. 1. These curves represent typical dark-adaptation curves for one of four experienced observers, who performed the experiment four times for each wavelength. The curve for 656 nm has only one segment, indicating that the rods are never more sensitive to 656 nm than the long-wave or red-cone elements. The curve for 546 nm has two segments: The upper segment is associated with the middle-wave or green-cone mechanism, and the lower segment with the rod mechanism. The 450-nm curve shows both cone and rod segments as does the previous curve. Thus, we know the maximum radianc for each of these wavelengths which will selectively excite the rods but not the cones, when the eye is fully dark adapted.

The black velour covering the rest of the multi-colored display was then removed. The fully dark-adapted observer was then asked to increase the radianc of the 656-nm light from darkness until he could just see shapes and forms in the display. This form-threshold radianc is identified by the solid line intersecting the curves in Fig. 1 and is slightly above absolute long-wave-cone threshold. The observer was asked to repeat the procedure for 546- and 450-nm illumination and these form thresholds are also identified by solid lines in Fig. 1.

The observers were then asked to report what they saw when the 656- and 546-nm lights were turned on together, at their form-threshold settings. All four observers reported a large variety of color sensations, which included red, orange, white, yellow, brown, and blue-greens. The observers were then asked to report what they saw when the display was illuminated with 656 and 450 nm at form threshold. They reported that they again saw red, orange, yellow, white, brown, and blue-green areas. Since the reflectance of most of the papers is different for 546 nm than for 450 nm, we would expect the color sensations of most areas to change when the shorter-wavelength illumination is changed from 546 to 450 nm. We found this to be generally true. It is important to note, however, that the overall gamut of color sensations is the same for 656 and 546 nm as for 656 and 450 nm, when the radiances of 546 and 450 nm are both below cone threshold. If 546 and 450 nm were above cone threshold, the overall gamut of color sensations would not be the same for both pairs of wavelengths.

The observers were then asked to report what they saw with 450 plus 546 nm. They saw no colored areas and no color wash over the display. The combination of these two wavelengths produced only a variety of grays which were the mixtures of the apparent lightnesses of each area in the 546-nm with the 450-nm image. This is what we would expect if 546 and 450 nm were exciting only the rods.

We wanted to verify the assumption that the rod-cone break was an accurate measure of the maximum radianc that would excite the rods without exciting the cones. We asked each of the fully dark-adapted observers to increase the radianc until he noticed a difference of the rate of change of acuity with radianc. With 546- and 450-nm illumination, the observers reported that at a particular radianc they observed a marked change of the sharpness of the image with only a small change of radianc. The average radianc readings for observer P.S. are identified by the dotted lines across the curves in Fig. 1. From the work of Hecht and Shlaer, we would expect that this sudden change of acuity would correspond with the change from below cone threshold to cone threshold. The dotted lines in Fig. 1 show that the cone threshold established by this technique is in very close agreement with that established by the rod-cone break of threshold-sensitivity curves. Thus, the observers were certainly well below the middle-wave and short-wave cone thresholds in the above experiment. This led to the next experiment, which tested whether the rods and long-wave cones interact to produce color sensations whenever both are excited.

Each of the observers was again asked to set separately the 546- and 656-nm lights at form threshold for the display. Holding the 656-nm light at form threshold, the experimenter then doubled the radianc of 546-nm light, and the observer reported the same variety of color. The observers reported a slight change of the over-all color balance of the display; however, no area changed its color name. The aesthetic tonal quality could be recaptured by increasing the 656 radianc. The procedure was repeated, each time doubling the radianc of the 546-nm light, and readjusting the 656-nm light, until the 546 radianc was just below cone threshold. Throughout this series, each observer reported that he always saw the same colors and that the only significant change was that the image became sharper and brighter. The procedure was repeated for 450- and 656-nm combination and gave the same results. Thus, the rods and long-wave cones can interact to produce color sensations for all radiances of 546 and 450 nm below cone threshold. The color names reported

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1 S. Hecht, Phys. Rev. 17, 239 (1937).
which describe the color sensations were largely independent of changes of illumination.

Since the reflectance remained constant, change of illumination directly changed the radiance available at the eye. These results show that significant changes of the relative radiances of 656 and 546 nm do not produce significant changes of color sensations produced by the rods and long-wave cones.

**DISCUSSION**

Land proposed a mechanism to explain how color sensations above cone threshold can be independent of both the radiance and the wavelength distribution on the retina. His retinex theory proposes that there are independent image-forming mechanisms, called retinexes, which correspond to the different types of cones in the retina. Each retinex is a separate blackbox that has its own physical input and processed output. The distinction between the lightness of an object and the amount of radiant energy coming from that object is essential for understanding retinex theory. The amount of radiant energy is simply the number of photons per unit area of the scene coming to the eye. This is input. It is entirely physical and is not directly related to the processed output. The processed output, lightness, is the output of a retinal-cerebral process; it is the value from light to dark that we see. The process that analyzes the number of photons per unit area and assigns a lightness is not dependent on the number of photons per unit area coming to the retina from any particular object, but on the pattern of the photon distribution across the entire image. The color sensation of an object is produced by comparing the lightnesses generated by two or more of these independent retinexes.

It is easy to extend the retinex theory to explain the interactions of the rods and long-wave cones. If the rods act as an image-forming black box equivalent to a retinex, then a color sensation is generated by comparing the lightness produced by the rod retinex with the lightness produced by the long-wave cone retinex.

Since the lightness of each object are largely independent of illumination changes, then retinex theory also explains why the color sensations were largely independent of changes of illumination in the previous experiment.

**COLOR SENSATIONS—A FUNCTION OF LIGHTNESS OR WAVELENGTH?**

In the last experiments, the observers reported that 656 and 546 nm gave essentially the same gamut of color sensations as did 656 and 450 nm. However, they reported that a particular object did not always give the same color sensation in the 656- plus 546-nm illumination as it did in the 656- plus 450-nm illumination.

Retinex theory predicts that these differences of color sensations are due to differences of lightnesses. In the experiments described, the reflectances of most areas changed when illuminated with different wavelengths. The lightnesses of most areas also changed with the changes of the wavelength of the illumination. If the lightness of each area in the 546- and 450-nm images were the same, retinex theory predicts that the combination of 656 with 546 nm would give the same sensation as the combination 656 with 450 nm. To test this hypothesis, we used two identical photographs as the lightness scales for 546 and 450 nm. We took three black-and-white photographs of a still-life scene. One photograph was taken through a red Kodak Wratten 24 filter; the other two were taken through a green Kodak Wratten 58 filter. These pictures were placed in a triple-image monochromator similar to the double-image monochromator described by Land. The three pictures were superimposed with semi-silvered mirrors and were observed by maxwellian view. The illumination for each picture was provided by a grating monochromator. The photographs taken with the red filter was illuminated by 656-nm light and the two green photographs were illuminated by 546- and 450-nm light, respectively.

We then set the radiance of the 546-nm light so that it excited only the rods. The observer adjusted the radiance of the 450-nm light so that the image appeared identical to the 546-nm image. We then combined the 656- and 546-nm images and asked the observer to study the colors and describe any changes when we turned off the 546-nm light and turned on the 450-nm light. All three observers reported that they could see no change of color when this substitution was made. The 656- plus 546-nm display was identical with the 656- plus 450-nm display. This experiment, combined with the result that the color sensation of an object was largely independent of changes of radiance, indicates that the lightness of each object, and not the wavelength of the light exciting the rod pigment, is the color-sensation-determining property. Changing the wavelength of illumination in the first experiment changed the apparent lightness and thus affected the color sensations.

**COLOR SENSATIONS WITH RODS AS COMPARED TO COLOR SENSATIONS WITH CONES**

Throughout the preceding sections we simply described the color sensations by their color names. However, the color name red, for example, includes many different sensations. Rather than trying to describe color sensations, we performed an experiment to determine if any combination of wavelengths and radiance above cone threshold produced exactly the same

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color sensations as the combination that excited only the rods and the long-wave cones. If such a combination exists, then the rods can be as much a part of the color-producing mechanism as the cones, since the rods and long-wave cones can produce color sensations identical with those produced with the cones. This, however, would not mean that the rods necessarily play a part in color sensations at radiances above cone threshold.

We used the double-image monochromator to excite the rods and long-wave cones in one eye and another double-image monochromator to excite the cones in the other eye. By alternately examining the images in each eye, the observer could report if the color sensations produced by the rods and long-wave cones were identical with those produced by the cones.

We took four black-and-white transparent photographs of a still-life scene; two were taken through a red Wratten 24 filter and two were taken through a green Wratten 58 filter. One Wratten 58 photograph was placed in one double-image monochromator and illuminated with 546-nm light at a radiance that excited only the rods. A Wratten 24 photograph was placed in the second double-image monochromator and superimposed on the first. This Wratten 24 photograph was illuminated with 656-nm light, so that it excited the long-wave cones and gave the best color balance with the rods. The remaining pair of photographs was placed in the second monochromator, and was illuminated at radiance just above cone threshold. The observer was asked to adjust both the wavelength and the radiance of the light illuminating the Wratten 58 photograph, and to report if any combination appeared identical with the color sensations he saw in the other eye with the rods and the long-wave cones. Careful measurements were made by two experienced observers. Observer 1, in eleven trials, reported that 656 nm combined with a wavelength averaging 495±4 nm gave an image that had all the same color sensations as the image produced by the rods and long-wave cones. Observer 2, in six trials, reported a wavelength averaging 494±4 nm. Both observers said that the differences of the images on the two monochromators were these: Some areas in the image above cone threshold appear somewhat brighter and more saturated, as well as appearing sharper. The observers reported that the maximum difference of chroma corresponded to two steps of Munsell notation, while the maximum difference of value corresponded to one step. No differences of hue were reported. Thus, the color sensations produced by the rods and long-wave cones are very nearly identical to the color sensations produced above cone threshold.

Does the interpretation of these experiments in terms of the retinex theory lead to conclusions about the mechanisms involved? The definition of a retinex states that it is a heuristic mechanism which contains as much of the eye–brain system as is necessary to produce lightness sensations, which are then combined to produce color sensations. Since the rods and the long-wave cones produce variegated color sensations, they must be on separate retinexes. For the rods to constitute a retinex, they would have to be a complete, independent, lightness-forming mechanism. However, the rods might not be entirely independent of the cone retinexes, and for the sake of economy could be a part of the short-wave, middle-wave, or short- and middle-wave retinexes. The first hypothesis states that the rods and short-wave cones combine to form a single image in terms of lightness on the short-wave cone retinex. If we look at an area that appears light on the rods and dark on the long-wave cones, we see that the area is blue-green. And, if we look at an area that appears light on the short-wave cones and dark on the long-wave cones, we see that the area is blue. If the rods and short-wave cones were part of the same retinex, then the same pair of lightnesses on the rods and long-wave cones as on the short-wave cones and long-wave cones should produce the same color sensations. Therefore, the rods are not just a part of the short-wave-cone retinex. The rods produce blue-green, whereas the short-wave cones produce blue. Similarly, the rods could not be part of just the middle-wave-cone retinex, because the rods produce blue-green, whereas the middle-wave cones produce green. If the rods were a part of both the middle- and short-wave-cone retinexes, then a light area on the rods would generate light areas on both the middle- and short-wave-cone retinexes. An area that is light on the middle- and short-wave-cone retinexes but dark on the long-wave cone retinex appears blue-green. Therefore, the rods could be a part of both the middle- and short-wave-cone retinexes.

If the rods are independent of the cones, then there is no reason why the color sensations produced by the rods and the long-wave cones should or should not resemble any other cone interaction. Therefore, logic cannot determine if the rods are a fourth separate retinex or a part of both the middle- and short-wave-cone retinexes.

It is interesting that if the rods are a fourth retinex then they conceivably could generate color sensations different from those generated by the cones. In principle, they could add a new dimension to three-dimensional color space. The above matching experiment, however, shows that the rods do not generate new color sensations but, in fact, generate color sensations that are nearly identical with those generated by the combination of short- and middle-wave cones when interacting with the long-wave cones.

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