Rod-Cone Interactions: Different Color Sensations from Identical Stimuli

Abstract. *Different color sensations were generated by two areas in a complex scene, even though both areas sent to the eye the same 656-nanometer radiance that excited the long-wave cones and the same 546-nanometer radiance that excited only the rods.*

Land (*1*) set up an experiment in which one area appeared red and another area appeared green even though the radiations coming from both areas were identical. The experimental display was a pastel chalk drawing by Jeanne Benton, called the *Street Scene*, which included a green awning on the left side and a red door on the right side. An incandescent lamp with a long-wave filter was placed on the floor near the left side of the display and a second lamp with a middle-wave filter was placed on the right side. The procedure made use of the inverse square law to control the relative amounts of light that fell on the various parts of the display and hence the radiance that came to the observers' eyes from particular areas. In Land's experiments and in those discussed in this report the flux was measured from the central portion of the particular area. In each case, the change of flux from side to side was small because the areas were small. Each area appeared to be uniform in lightness and color. The location of the long-wave light was adjusted so that the same long-wave radiance came to the eye from the center of the awning as from the center of the door. Similarly, the location of the middle-wave light was chosen so that the same middle-wave radiance came from the center of the door as from the center of the awning. Since the long- and middle-wave lamps were the only sources of radiation, the total flux that came from the center of the awning was identical to that from the center of the door. This further implied that the retinal receptors stimulated by those areas must have had identical inputs, since the radiance that came from those areas was identical. The observers, however, reported that the awning and the door produced sensations that were far from identical in long-, in middle-, and in combined long-plus-middle-wave illuminations (*2*). In long-wave light the door appeared very light, and the awning was very dark, near black. In middle-wave light the door was very dark and the awning was very light. In combined long- plus middle-wave illumination the awning was green and the door was red even though the radiation from the awning was identical to that from the door.

Land, in his retinex theory, proposed that the color of objects is determined by the lightnesses in different wave bands (*3*). He proposed that the different kinds of receptors acted as if they were independent sets to form different lightness images for different regions of the visible spectrum. These lightness images are compared to produce color sensations. In the *Street Scene* experiment, for example, the long-wave information is processed by one retinex to form one lightness image and the middle-wave information is processed by a different retinex to form a second lightness image (*4*). Areas that are lighter in long-wave and dark in middle-wave light look red regardless of the radiance-wavelength distribution of the flux coming from them. Areas that look light in middle-wave and dark in long-wave light always look green.

Experiments have shown that color sensations can be generated by the interactions of rods and cones (*5, 6*). McCann and Benton found that when a stimulus that excited only the rods was combined with a stimulus that excited the long-wave cones, observers saw colored images, which, except for brightness and sharpness, were indistinguishable from images seen on two wavebands entirely above cone threshold.

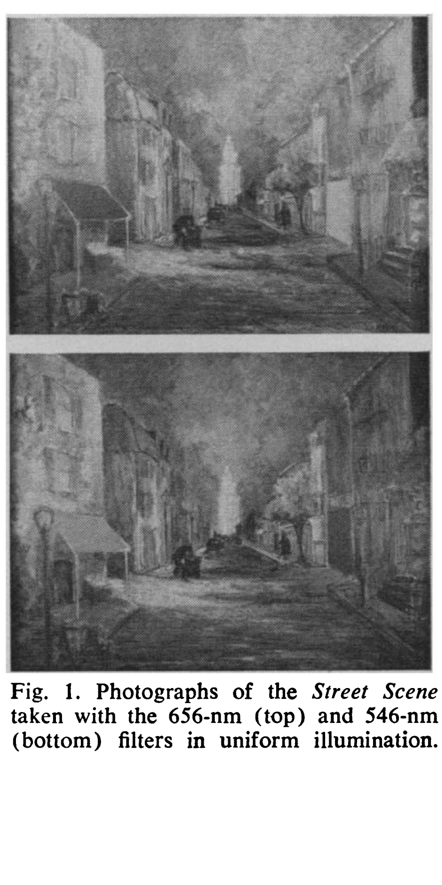

Fig. 1. Photographs of the *Street Scene* taken with the 656-nm (top) and 546-nm (bottom) filters in uniform illumination.

Duplicity theory (*7*) suggests that the rods and cones are completely different systems: one for low-radiance, colorless vision and the other for high-radiance, color vision. The many different properties of images produced by rods and cones have accumulated substantial support for the idea that the rod and cone processes are different (*8*). Nevertheless, McCann and Benton's experiments showed that the lightnesses produced by these different processes can be compared to form color sensations. Repeating Land's *Street Scene* experiment with only rods and long-wave cones provides a test of the hypothesis that color depends on the lightnesses produced by independent systems. Is it possible, in a complex image that excites only the rods, to produce two significantly different lightnesses from areas simultaneously sending the same radiance to the eye? Is it possible to combine such a rod image with an image seen by the long-wave cones, which has different lightnesses produced by areas having the same radiance? Do these areas produce different color sensations? Are the sensations consistent with the hypothesis that colors are determined by the comparison of lightness?

I set up the *Street Scene* display and repeated Land's experiment with only the rods and long-wave cones. I then performed a second similar experiment with a different display and different colored areas. In both experiments I used two projectors with narrow-band interference filters, one 656 nm, the other 546 nm, to illuminate the entire display. I used a series of square photographic transparencies called continuous wedges, which increase in density in one direction. These transparencies allowed the use of projectors as sources of controlled nonuniform illumination. Variable transformers were connected to the projectors to control the brightness of the lamps. The transmission bands of the filters were sufficiently narrow so that change in color temperature of the lamp with changes in transformer settings did not signifi-

Table 1. Radiance measurements in 656-nm and 546-nm illumination in experiment 1.

	Radiances (watts sr^{-1} m^{-2})	
	656 nm	546 nm
Cone threshold	3.0×10^{-7}	1.0×10^{-5}
Brightest area	2.2×10^{-6}	4.9×10^{-6}
Door	6.9×10^{-7}	1.4×10^{-6}
Awning	6.9×10^{-7}	1.4×10^{-6}

Table 2. Munsell chips chosen by the observers to match with the door and the awning in *Street Scene* in experiment 1.

Observer	Door	Awning
MAW	5.0 R 4/14	7.5 G 3/4
JAH	5.0 R 4/12	10.0 GY 3/10
TT	5.0 R 4/9	5.0 G 5/10
JJS	7.5 R 3/10	7.5 G 3/2
JMC	5.0 R 3/12	5.0 G 3/6
WW	5.0 R 4/18	5.0 G 5/10

Table 3. Radiance measurements in 656-nm and 546-nm illumination in experiment 2.

	Radiances (watts sr^{-1} m^{-2})	
	656 nm	546 nm
Cone threshold	3.0×10^{-7}	1.0×10^{-5}
Brightest area	1.6×10^{-6}	4.9×10^{-6}
Left area	5.2×10^{-7}	6.9×10^{-7}
Right area	5.2×10^{-7}	6.9×10^{-7}

Table 4. Munsell chips chosen by the observers to match the left and the right areas of a "Mondrian" in experiment 2.

Observer	Left	Right
TT	2.5 R 7/5	5.0 R 3/3
JAH	2.5 R 8/4	5.0 R 2/6
PV	5.0 YR 7/8	7.5 R 3/6
JMC	2.5 Y 7/8	10.0 R 3/6
MAW	7.5 Y 8/4	10.0 R 3/6
JJS	2.5 Y 8/6	2.5 YR 3/6

cantly affect the wavelength distribution of the light.

Figure 1 is a pair of photographs of the *Street Scene* taken with the 656-nm and 546-nm filters in uniform illumination. The rectangular display subtended 36° by 32° and the door and awning had diagonals that subtended roughly 8° and 6°, respectively. The door reflected a high percentage of long-wave radiation and a low percentage of middle-wave radiation. A wedge transparency was chosen for one projector so that the same radiance at 656 nm came to the eye from the awning and the door. Similarly, another wedge was placed on the projector so that the same radiance at 546 nm came to the eye from the awning and the door. Therefore, when both projectors were turned on together, exactly the same composite stimulus was coming from the center of both the awning and the door.

The remaining problem was to adjust the radiance from the display so that it excited only the rods and long-wave cones. Since the relative radiance at various points in the display was controlled by the position of the wedge transparencies, we could adjust the overall output of the lamps without disturbing the radiance identity of the awning and the door. In earlier work (*6*), McCann and Benton performed three different experiments to determine the upper limit of rod sensitivity that was still below cone threshold. The first experiment measured the recovery of threshold sensitivity to 546-nm and 450-nm light following light adaptation. The plot of threshold versus time in the dark is called a dark adaptation curve. The test area was a 4° square placed in the center of a Mondrian-like display. The rest of the display was covered by a curtain so that the observers saw only the 4° square that had the highest reflectance in the entire display. The transition from cones to rods, shown by the break in the dark adaptation curve, was at 1×10^{-5} watt per stradian (sr) per square meter for 546 nm. This result was checked in the second experiment by asking the observer to look for the rapid change in sharpness and the change in color sensation associated with the transition from rods to cones at 546 nm. This apparent change agreed closely with the break in the dark adaptation curves. Using the value for cone threshold determined by the first two experiments, the third test combined the 546- and 450-nm images both above cone threshold. The scene produced many different color sensations: blues, greens, yellows, and browns. The 546-nm and the 450-nm illuminations were separately reduced to below the measured cone thresholds. The combination of these two illuminations produced no variation of color, just a small increase of apparent brightness. This is what we would expect if both the images were exciting only the rods.

In the experiments for this report, I used the 546-nm radiance determined by those three different techniques. I also performed a control experiment to insure that radiances below 1×10^{-5} watt sr^{-1} m^{-2} were below middle-wave-cone threshold in the conditions described in this report. Three of the six observers remeasured the recovery of threshold sensitivity after light adaptation, using procedures described earlier (*6*). They looked at an 8° square area that was illuminated by the 546-nm light used in the experiment. The *Street Scene* was removed from the large black easel and a piece of white paper was placed in the middle of the easel. This insured that the illumination falling on the white paper was identical to that falling on the central areas of the *Street Scene*. For two observers the break in the dark adaptation curve was at 1×10^{-5} watt sr^{-1} m^{-2}. For the third observer the break appeared at 7.0×10^{-6} watt sr^{-1} m^{-2}. The brightest area in the *Street Scene* in 546-nm light was 4.6×10^{-6} watt sr^{-1} m^{-2}. The awning and the door had a radiance of 1.4×10^{-6} watt sr^{-1} m^{-2}. In other words, the awning and the door sent only one-seventh the amount of 546-nm light necessary to obtain a threshold response from the middle-wave cones. Table 1 shows for both wavelengths the cone threshold radiances, the highest radiances from the entire scene, and the radiances from the awning and the door. These radiances show that the entire scene was below cone threshold for 546-nm light and slightly above long-wave cone threshold for 656 nm.

Six observers were asked to view the display first in long-wave, then in middle-wave illumination. The observers were asked to describe the lightnesses of the awning and door as white, light gray, medium gray, dark gray, or black. In 656-nm illumination the observers were asked to describe the lightnesses as grays even though the entire display appeared to be covered with a red wash. In 546-nm illumination the entire display appeared colorless grays, since it was below cone threshold. The observers reported that the awning was dark gray in 656-nm illumination and light gray in 546-nm illumination. They further described the door as being light gray in 656 nm and dark gray in 546 nm. The observers were then asked to describe the color sensations of the two areas in the combined long- plus middle-wave illumination. They reported that the sensations from those two areas were different from each other—green and red—even though the centers of the areas sent identical physical stimuli to the eye. Just as in Land's experiments entirely above cone threshold, the simultaneously identical sets of radiances produce very different color sensations. Again, the apparent lightnesses of the awning—light gray in middle-wave, dark gray in long-wave flux—correspond to the sensation green. The lightnesses of the door—light gray in long-wave, dark gray in middle-wave flux—correspond to the sensation red.

To provide a better description of the color sensations, the observers were asked to study the awning and the door, and then to select from the *Munsell Book of Color* (*9*) a chip that most closely matched their memory of the awning and the door. The *Munsell Book of Color* was viewed with a Standard Illuminant C in an otherwise darkened room. If the observers could not find a suitable chip, they were instructed to estimate the designation of a chip that would match the awning or the door. The Munsell chips chosen are listed in Table 2.

In the second experiment the *Street Scene* was replaced by a multicolored paper display called a "Mondrian." This display was made of matte-surface papers, cut and overlapped to form squares, rectangles, polygons, and other shapes. There were 23 papers and the entire display subtended roughly 36° on a side. The areas studied were rectangular and their diagonals subtended roughly 8°. New wedge transparencies were chosen so that the same flux came to the eye from these two areas in 656-nm light and 546-nm light. As in the first experiment, the entire display was below cone threshold for 546 nm. Table 3 shows that the two areas studied by the observers were one-sixteenth the amount of light necessary to obtain a threshold response from the middle-wave cones.

Six observers were once again used for this experiment. They were asked to describe the lightnesses of the two areas as white, light gray, middle gray, dark gray, or black, first in long-wave and then in middle-wave light. As in the previous variation of the experiment the observers were asked to find the Munsell chips that most closely matched the two areas. The Munsell chips chosen are shown in Table 4. The observers reported that the area on the left in 656-nm illumination was light gray and that in 546-nm illumination was also light gray. The area on the right was middle gray in 656-nm light and dark in 546-nm light. In combined 656- and 546-nm light the observers reported that the area on the left side was yellow and the area on the right was dark brown. Again the identical sets of radiances would not predict this outcome, namely, that the color sensations will be different. However, above cone threshold, yellow areas always appear light in both long- and middle-wave flux. Brown objects always appear dark in both wave bands, but somewhat lighter in long-wave flux.

In two similar experiments the illumination was controlled so that the displays were below cone threshold for 546-nm light and slightly above cone threshold for 656-nm light. The observers saw a variety of colors from the interaction of rods and long-wave cones. In each wave band the illumination was controlled so that the same amount of light came from the particular low-reflectance objects that appeared dark and high-reflectance objects that appeared light. When the rods and long-wave cone images were combined, the observer reported different color sensations—red versus green and yellow versus brown—from areas that were identical physical stimuli. The color sensations produced by these rods and long-wave cone interactions support the hypothesis that lightnesses on independent systems determine color sensations.

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References and Notes

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2. For discussion of mechanisms responsible for identical radiances producing different lightnesses, see E. H. Land and J. J. McCann, *J. Opt. Soc. Amer.* **61**, 1 (1971).
3. E. H. Land, *Amer. Sci.* **52**, 247 (1964).
4. In these experiments I always worked with two wave bands of illumination and hence I only discuss two lightness scales. Land's retinex theory proposes that there are three or four independent lightness images. In other experiments Land has used three projectors with the *Street Scene* experiment. The position of the short-wave footlight was chosen so that the same short-wave flux came from both areas. Both the awning and the door appeared dark in short-wave light.
5. H. Blackwell and O. Blackwell, *Vision Res.* **1**, 62 (1961); B. Stabell, *Scand. J. Psychol.* **8**, 132 (1967).
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10. I thank E. H. Land for comments and advice and Marie Watson for help with the experiments and the report.

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Submarine Seeps: Are They a Major Source of Open Ocean Oil Pollution?

The existence of submarine seeps is often mentioned in discussions of oil pollution. The argument is made that natural seeps might be of equal importance to man's action in fouling the high seas and the beaches, or that marine organisms which have survived these natural seepages will also survive oil pollution caused by man. Therefore, it is important to assess the relative contribution of seeps and of pollution to marine "tar" (crude oil lumps). I believe that an estimate of some reliability is possible.

According to Weeks (*1*), a maximum of 700 billion barrels of the world's ultimate resources of offshore oil is available by primary recovery; as much as 10 percent of this represents natural gas liquids. Thus, 630 billion barrels (or $100{,}000 \times 10^6$ metric tons) is the maximum amount of offshore oil that is a likely source of submarine seeps. The additional 300 billion barrels of oil which are accessible to secondary recovery do not contribute to seepage; in fact, the estimate of 630 billion barrels is high, since it includes oil which is not free flowing but can be recovered only by pumping.

Estimates for the amount of petroleum reaching the oceans from all sources vary; an influx of 0.5 percent of the annual oil production has been quoted (*2*). In view of the amount produced in 1970 (2200×10^6 tons), this would amount to 11×10^6 tons. Most estimates range close to that figure, between 1 and 10×10^6 tons (*3*).

For the sake of argument, let us assume that the seepage equals in tonnage the oil pollution from human activity, which we will put at 5×10^6 tons. This would imply that submarine seepage would deplete the ultimate reserves of freeflowing offshore oil in less than 20,000 years.

Crude oils are geologically ancient, and the oil formation potential of the source beds is finite. Petroleum ranges in age from Pliocene (2×10^6 years) to Ordovician and Cambrian (4 to 6×10^8 years). A typical average age may be mid-Eocene (5×10^7 years). If an-