[77-JOSA]

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J. opt. Soc. Am., **67**, 119-121, 1977.

Variegated color sensations from rod-cone interactions: Flicker-fusion experiments

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(Received 14 June 1976)

Multicolored images were produced by the combination of two different color-separation images, one illuminated with 656 nm light and the other illuminated with 500 nm light. Flicker-fusion frequency measurements were used to identify the conditions in which the 500 nm light was below cone threshold. Under those conditions the multicolred images were shown to be generated by rod and long-wave cone interactions.

For some time, psychophysical studies have indicated that rod-cone interactions can evoke a limited range of color sensations.[1–3] After selective chromatic adaptation at photopic levels, Stabell and Stabell[4] found that light too weak to stimulate cones appeared as a variety of colors depending on the adapting wavelengths used. McCann and Benton[5] demonstrated the capacity of the rods to interact with the long-wave cones to produce a multicolored image. In that experiment they selectively stimulated the rods with either 450 or 546 nm light well below cone threshold, and they stimulated the long-wave cones with 656 nm light slightly above cone threshold. When dark-adapted observers viewed the combination of the 450 (or 546) and 656 nm light, they reported seeing red, yellow, orange, blue-green, brown, gray, black, and white areas in a display of colored papers when the luminance of the short-wavelength light was set two log units below the level necessary for cone response.

Three independent measurements of the luminance necessary for cone response established that only rods were responding to the shorter wavelengths: the rod-cone breaks in the dark-adaptation curves for the wavelengths used, the change in the rate of change of acuity versus luminance, and the luminance at which a single wavelength changes in appearance from a colorless rod image to either a blue- or a green-colored wash. In further investigations McKee, McCann, and Benton[6] examined the properties of the receptors while *both* illuminants were viewed simultaneously. This series of experiments used the shape of the spectral sensitivity curve of the rods and the Stiles-Crawford directional sensitivities to identify situations in which responses to shorter wavelengths exhibited properties characteristic of the rods.

The experiments described in this Letter use a critical flicker-fusion (CFF) technique to distinguish rod response from cone response. Hecht and Verrijp[7] showed that flicker-fusion frequency varies with illuminance and that the function separates into two branches, one for the rods and another for the cones. At a very low illuminance an image flickering at 4 Hz was above fusion frequency for the rods. As the intensity of the light was increased, higher flicker rates were necessary for fusion. At about 15 Hz a plateau was reached until the illuminance was sufficient to excite cone response. Cone response produced a second branch of the curve that required up to 60 Hz for fusion at very high illuminances.

METHODS

We used two of the three channels in a triple-image Maxwellian-view monochromator to illuminate two color-separation transparencies. The design of the apparatus has been described and illustrated in earlier papers.[6,8] In brief, two black and white photographic transparencies were mounted in the beams of 500 and 656 nm light (see Fig. 1). The two images were superimposed with semisilvered mirrors.

An image designated the red-separation record was photographed on black and white transparency film with a Wratten 26 filter in front of the camera lens. It was placed in one image monochromator and illuminated with 656 nm light. The second image, designated the green-separation record, was taken with a Wratten 58 filter. It was placed in the second image monochromator and illuminated with 500 nm light. The intensity of each beam could be varied independently; for large reductions in the amount of light we used Wratten neutral density filters, and to insure purity of wavelengths we used narrow-band scavenger filters at 656 and 500 nm. The observer's head was positioned by an adjustable bite bar. The filament was imaged in the center of the observer's pupil by the telescope mounted on the casing of the monochromator. The red- and green-separation images subtended 28° by 16°. A two-sector disc painted flat black and mounted on the shaft of a variable-speed motor was used to interrupt the 500 nm light. Motor speed was calibrated using a Strobotac.

The experimenter chose an intensity of 500 nm light and asked dark-adapted observers to adjust the speed of the disc until there was minimal flicker sensation in the field of view. The experimenter had the observer repeat this measurement at least five times. The experimenter then increased the amount of 500 nm light and repeated the measurements. A series of 500 nm intensities was chosen to cover nearly the entire scotopic-photopic range.

RESULTS

We begin with the results for only 500 nm light illuminating the middle-wave image. The experimenter chose an intensity of 500 nm light and asked the observer to adjust the speed of the disc for flicker fusion. The results of flicker-fusion frequency versus 500 nm irradiance for one observer are plotted as open circles in Fig. 2, and the results for a second observer are plotted as open triangles. These results are nearly identical to the Hecht and Verrijp data for 490 nm and show the same two branches for the rod function at low illuminances and cone function at the high illuminances. After each measurement was taken with the 500 nm light alone, the observer was again asked to adjust the speed of the disc chopping the 500 nm light; however, the 500 nm light was now a component of a multicolored image. To do this the experimenter increased the motor speed well above fusion frequency and turned on the 656 nm light illuminating the red-separation image. He then asked the observer to choose an intensity of 656 nm light in combination with 500 nm light that produced a well-balanced multicolored image. Then the observer adjusted the disc speed using the same criterion for flicker fusion. In Fig. 2 the filled circles and triangles, representing data taken with 656 and 500 nm images combined, show that the CFF for the green-separation record of a multicolored image is very nearly the same as that of 500 nm alone (open circles and triangles). The right-hand branch of the curve is identified with the cone response to 500 nm light and the left-hand branch with the rod response. The intersection of the two curves at 3×10^{-3} $\mu W/cm^2$ indicates the minimum 500 nm irradiance associated with cone response to the green-separation image. In order to produce a multicolored image two sets of receptors must respond to two different color-separation images (see Ref. 6). Regardless of the intensity of the 656 nm light alone, the observers do not see a multicolored image. The addition of the green-separation image in 500 nm light is necessary for the observers to report a variety of different hues. When the irradiance is below 3×10^{-3} $\mu W/cm^2$, the rods are the only visual receptors responding to the green-separation image. The observers reported variegated color sensations from the combination of the 656 nm image with the 500 nm image over the entire seven log-unit range of radiances used, that is, from slightly above rod threshold to well above cone threshold. When the irradiance of the 500 nm light was less than 3×10^{-3} $\mu W/cm^2$, the variety of hue sensations was generated by rod and long-wave cone interactions. Above that irradiance more than one type of cone was above threshold and the variety of hues could be generated by either cone-cone or rod-cone interactions.

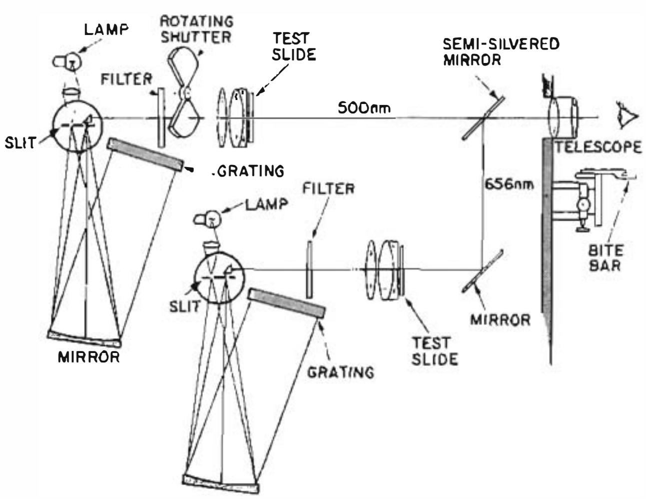

FIG. 1. Diagram of the double-image monochromator with rotating shutter interrupting the 500 nm light.

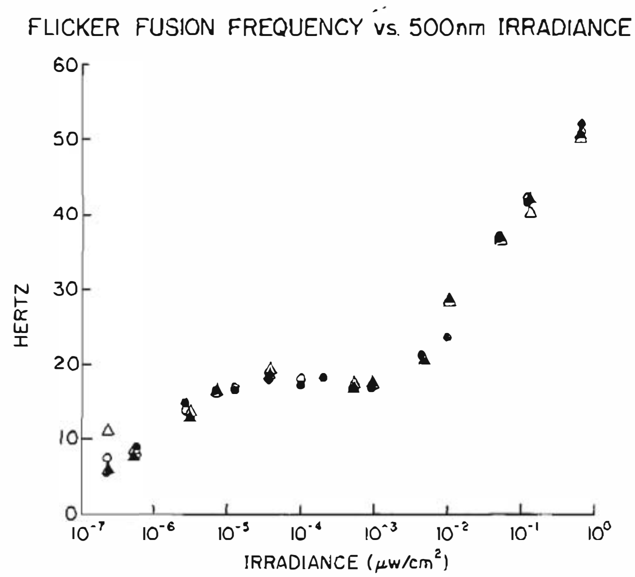

FIG. 2. Open circles and triangles are the flicker-fusion frequency vs 500 nm irradiance data from two observers for 500 nm light alone. Filled circles and triangles are flicker-fusion frequency vs 500 nm irradiance data from the same observers for a multicolored image made by the combination of the green-separation image in 500 nm and the red-separation image in 656 nm.

ACKNOWLEDGMENTS

We wish to thank Marie A. Watson and W. Alan Stiehl for their help in preparation of this manuscript.

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