

The Estimation of Cone Spectral Sensitivities*

Methods for estimating the cone spectral sensitivities are reviewed (selectively). Techniques applied to the normal eye include measurement of flicker photometric sensitivity against colored backgrounds; creation of temporary artificial dichromacy by colored bleaches; observations of the afterimages of colored bleaching lights; and transient photopic saturation by flashed backgrounds. Results from these techniques agree well with cone sensitivities estimated from studies of congenital dichromats, and these estimates are further supported by appropriately comparing normal with anomalous trichromatic matches. The indicated sensitivities for red- and green-sensitive cones peak at 566 and 543 nm, respectively. Factor analysis of color-matching functions indicates normal variation of the order of 1-1.5-nm standard deviation.

Introduction

Quantitative analysis of color vision should be based on a good knowledge of the cone spectral sensitivities, since these determine the initial physiological effects of any visual stimulus. The estimation of the spectral sensitivities presents an intriguing problem, in that relevant data of high precision are available (color-matching functions, for example) but the coefficients relating the measured functions to the desired cone sensitivities are uncertain. In cases of defective color vision, this ambiguity is reduced; consequently, our best estimates of the human cone sensitivities are based on data from color-deficient individuals. These estimates make assumptions about the relationship between the color-deficient case and the normal case, usually that a dichromat has two of the normal cone types without the third. Experiments on normal individuals have generally yielded cone-sensitivity estimates in broad agreement with those inferred from data on color deficient, but with substantial disagreement in detail. This article outlines some experi-

ments on normal vision in the red-green range that do provide satisfactory agreement with cone-sensitivity estimates from color-deficient individuals. In addition, I describe a method of deriving cone sensitivities from the color matches of anomalous observers, without invoking the "loss hypothesis" of dichromacy, and I consider the question of normal variation in the cone sensitivities.

Normal Observers

The most persistent effort to infer the cone sensitivities from observations on normal color vision has proceeded by applying principles such as the von Kries coefficient law to the changes in color appearance produced by chromatic adaptation. These efforts have seldom yielded internally consistent results, and the inferred cone sensitivities are implausible both on general grounds and by comparison with the results from color deficient. An example of this is the inference that the short-wavelength-sensitive cones retain substantial sensitivity in the long-wavelength spectral region. This conclusion is based on the increase in saturation of long-wavelength light after adaptation to blue, an increase that can be demonstrated even if the adapting conditions are arranged so that the short-wavelength adapting light effectively stimulates the short-wavelength receptors only. The failure of the von Kries type of analysis in this case is probably traceable to the assumption that stimulation of just one cone type alone always produces the same color sensation, regardless of the conditions of adaptation. If the adaptation induces changes in the visual system at stages where signals from different cone types are combined, that assumption will not be correct. A similar assumption is implicit in the identification of the Stiles π mechanisms¹ with individual cone types. In Stiles' experiments, the spectral sensitivities of red-, green-, and violet-sensitive mechanisms are gauged by the ability of monochromatic steady background fields to reduce an observer's sensitivity to test flashes of appropriately chosen wavelength. The inferred sensitivities should be those of the cones if the only effect of the background field is to reduce the sensitivity of

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each cone type independently. One way to avoid any such questionable assumption might be to estimate the cone sensitivities directly from the spectral sensitivities for test lights, in the presence of fixed adapting fields designed to make the unwanted cone types insensitive. The problem with this direct approach is that complete suppression of the unwanted cone types could not be expected for a large range of test wavelengths. However, the ambiguity created by interaction of different cone types in the detection of the test stimulus can be reduced, if not eliminated, through the use of conditions such as heterochromatic flicker photometry, where visual sensitivity is thought to be simply a linear combination of the underlying cone sensitivities. Eisner and I have recently explored this approach.²

Details of methods and results are given elsewhere.² Test lights were presented as relatively weak increments optically superimposed on a larger steady background field. In the test field, a test light of variable wavelength alternated with a fixed standard at 15 Hz. At each test wavelength, flicker photometric sensitivity was measured by adjusting the intensity of the test light for a flicker photometric null. Background fields were monochromatic, with retinal illuminances typically in the range 1000–10,000 trolands.

For all backgrounds used, the incremental flicker photometric sensitivities satisfy Abney's law. That is, the wavelength dependence of flicker photometric sensitivity (unlike contrast sensitivity for detection of the test field as a steady light) can be described by a linear combination of the color-matching functions, with average deviations of about 0.01 log unit in the red–green spectral range. More surprisingly, sensitivity with a red or orange background closely approximated the sensitivity of the green-sensitive cones, while sensitivity with a green background approximated that of the red-sensitive cones. (Blue-sensitive cones make no contribution to flicker photometric sensitivity.³) Although this is a simple pattern of results, it is also highly unexpected, because the selective suppression of one or the other cone type by appropriately colored backgrounds is up to 100 times greater than Weber's law would predict, even though Weber's law holds for variation of background luminance under these test conditions. Moreover, this exaggerated suppression of red- or green-sensitive cones by colored backgrounds was only evident in tests designed to tap the sensitivity of the "achromatic system" such as flicker photometry, flicker threshold at high frequencies, or minimally-distinct-border sensitivity.⁴ Color discrimination, color appearance, and large-field contrast thresholds showed only the suppression predicted by Weber's law. This behavior can be modeled by a scheme² in which the red- and green-sensitive cones independently feed synergistically into the achromatic system, with a compressive nonlinearity interposed in the pathway from each cone type. The summed, or luminance, signal is fed back to a point prior to the compressive nonlinearity in each pathway, so that the signal from each cone type will be kept from saturating if there is enough feedback. Red backgrounds might fail to provide enough feedback to relieve the strongly excited red-cone pathway from saturation; green backgrounds

might similarly allow saturation of the green-cone pathway.

For most of our normal observers, spectral sensitivities that are asymptotically approached by the data against colored backgrounds are clearly very close to the sensitivities estimated for red- and green-sensitive cones from studies of dichromatic individuals.⁵ Two out of seven observers, however, appear to have red-sensitive cones with spectral sensitivities shifted about 2.5 nm toward long wavelengths. Stiles' π_4 can be rejected as a candidate "green" cone sensitivity since it is substantially more red-sensitive than observers viewing red or orange backgrounds. Stiles' π_5 can also be rejected, since it deviates from the green background data in ways that cannot be attributed to residual contributions from the other cone types (Fig. 1).

Shortly after exposure to a red or green light of bleaching intensity, a normal observer may be temporarily dichromatic, and there is evidence^{6,7} that in this state spectral sensitivity follows closely that of a congenital dichromat (protanope or deuteranope) in the red–green spectral range. The spectral sensitivity we measure in artificial protanopia² agrees well with the flicker photometric sensitivity against orange or red backgrounds. Though these sensitivities differ from π_4 , they are well fit by Stiles' π'_4 (see ref. 1, pp. 240–242).

The similarity of artificial dichromacy, induced by bleaching, to true congenital dichromacy raises the question whether bleaching acts to reduce sensitivity independently within each cone system. This may not be true in general, but under certain conditions, observations of afterimages support the idea.⁸ Afterimages, once faded, are generally revived by a change in color of the background against which they are viewed, but exceptions to this can be found under well-specified conditions. If the eye is bleached with two fields of different color (from the red–green spectral range) placed side by side, then the revived afterimage will be uniform (rather than bipartite) if and only if two conditions are met: The luminances of the two colors in the bleaching field must be set to equality for a mechanism with sensitivity peaking at about 565 nm or else for one peaking

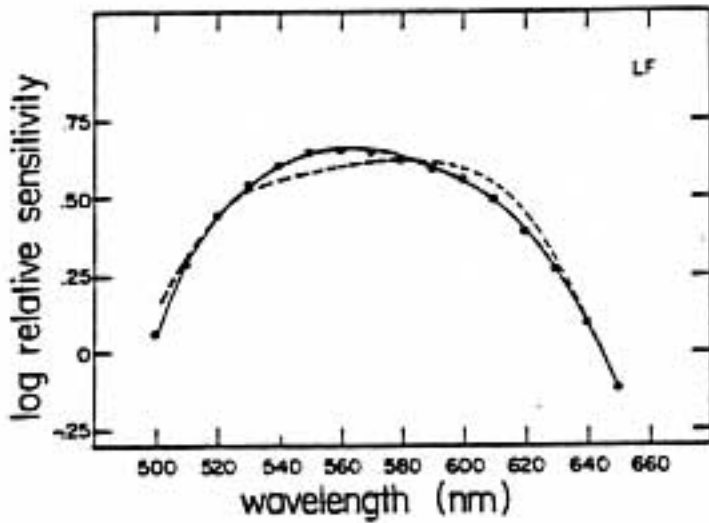


FIG. 1. Red-cone flicker photometric sensitivity (●) with a 500-nm background compared to Vos and Walraven's red-cone (—) and Stiles' π_5 (---) sensitivities.

at about 540 nm, and the background fields whose alternation revives the afterimage must be equated for the other of these two mechanisms. The observations with afterimages are not quite as precise as those with flicker photometry but they nevertheless agree very well with sensitivities from artificial temporary dichromacy or congenital dichromacy. They deviate correspondingly from Stiles' π_4 , but Stiles' π_5 cannot be rejected on the basis of the afterimage data alone.

One other technique that has allowed dichromat-like sensitivities to be observed in the normal eye is King-Smith and Webb's one of transiently overloading the cone systems with background fields of sudden onset.⁹ Thus, convergent evidence from at least four very different techniques supports, with some precision, the attribution of dichromat-like cone sensitivities to the normal eye. The reasons for the slight deviations of the Stiles π_4 and π_5 sensitivities from this pattern remain as a problem for further research.

Color Deficient Observers

While the general agreement between dichromat and normal is gratifying, recent work on dichromats complicates the picture. With large matching fields under strictly photopic conditions, most observers who appear true dichromats with small fields make fairly precise trichromatic matches.¹⁰ Worse still, these are not normal matches but deuteranomalous ones (for deuteranopes) or protanomalous ones (for protanopes). Although the possible role of retinal inhomogeneity, and of variations among individual cones of the same type, needs to be considered carefully, these observations are compelling evidence that the loss hypothesis is not strictly correct and that each dichromat has some anomalous cones in addition to the two types that are more or less normal. This would invalidate the classical procedures for estimating cone sensitivity from dichromatic data, although with luck the involvement of the anomalous cones in the small field dichromatic matches of these observers may prove insufficient for practical purposes. Fortunately it has been possible to estimate the normal cone sensitivities without relying on the loss hypothesis, by using the trichromatic matches of anomalous observers.¹¹ A deuteranomalous observer, for example, will require more green than normal in a red-green mixture to match a spectral yellow. Both this anomalous match and the normal match must be a match for the normal red-sensitive cone pigment, which normal and deuteranomalous observers have in common. The excess green in the anomalous match must therefore be counterbalanced by a reduction in the amount of red, and the amount of red exchanged in this way for the green provides a measure of the relative sensitivity of the red-sensitive cone to these two primaries. When taken together with normal or anomalous color-matching functions, this determines the pigment's spectral sensitivity over the red-green spectral range. Estimates made in this way by Hayhoe and myself¹¹ agree very well with those made on the basis of the loss hypothesis of dichromacy. However, I have recently repeated the analysis using another data

base, the anomaloscope matches of Willis and Farnsworth.¹² The calculated "red" cone spectral sensitivity is acceptable but the "green" cone sensitivity is several times greater than protanopic sensitivity for red light. It is difficult to have much confidence in this implausible result, since the analysis is quite vulnerable to calibration errors that may not have been of concern to the original investigators. More color-matching data for anomalous observers might help to resolve this.

Normal variation in cone spectral sensitivities has been the subject of much recent interest, with ranges in peak wavelength of up to 20 nm in microspectrophotometric data¹³ and in studies of dichromats. M. Webster and I have applied factor analysis to the 10° color-matching functions of Stiles and Burch¹⁴ in an attempt to identify the factors underlying individual differences in normal color matching. Along with a factor for lens pigmentation and another for macular pigmentation we obtain three mutually orthogonal factors, each of which we tentatively identify with the λ_{\max} of one cone type. These factors together account well for the observed individual variations in color matching. The variability in λ_{\max} is not great, however, with standard deviations only about 1.2 nm. This amount of variation would not preclude specification of a "typical normal" cone λ_{\max} to the nearest nanometer. Arguments from the additivity of trichromatic matches¹⁵ suggest that variability among the various cones of an individual observer cannot be much greater than this (standard deviation no greater than 2 nm).

Conclusion

The evidence reviewed points fairly clearly to cone spectral sensitivities similar to the ones inferred from dichromatic data by Vos and Walraven¹⁶ and Smith and Pokorny¹⁷ which have peak sensitivities (energy basis, *in situ*) at about 543 and 566 nm. The two estimates differ mainly in the violet where Vos and Walraven assume some contribution of short-wavelength cones to luminance while Smith and Pokorny assume none. The latter view, besides being simpler, is in better accord with recent evidence.¹²

Acknowledgment

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