

# Spectral sensitivities of the human cones

Andrew Stockman, Donald I. A. MacLeod, and Nancy E. Johnson

*Department of Psychology, University of California, San Diego, La Jolla, California 92093-0109*

Received June 12, 1992; accepted May 24, 1993; revised manuscript received June 21, 1993

Transient chromatic adaptation produced by an abrupt change of background color permits an easier and closer approach to cone isolation than does steady-state adaptation. Using this technique, we measured middle-wavelength-sensitive (M-) cone spectral sensitivities in 11 normals and 2 protanopes and long-wavelength-sensitive (L-) cone spectral sensitivities in 12 normals and 4 deuteranopes. Although there is great individual variation in the adapting intensity required for effective isolation, there is little variation in the shape of the M- and L-cone spectral-sensitivity functions across subjects. At middle and long wavelengths, our mean spectral sensitivities agree extremely well with dichromatic spectral sensitivities and with the M- and L-cone fundamentals of Smith and Pokorny [Vision Res. 15, 161 (1975)] and of Vos and Walraven [Vision Res. 11, 799 (1971)], both of which are based on the CIE (Judd-revised) 2° color-matching functions (CMF's). But the agreement with the M-cone fundamentals of Estévez [Ph.D. dissertation, Amsterdam University (1979)] and of Vos *et al.* [Vision Res. 30, 936 (1990)], which are based on the Stiles-Burch 2° CMF's, is poor. Using our spectral-sensitivity data, tritanopic color-matching data, and Stiles's  $\pi_3$ , we derive new sets of cone fundamentals. The consistency of the proposed fundamentals based on either the Stiles-Burch 2° CMF's or the CIE 10° large-field CMF's with each other, with protanopic and deuteranopic spectral sensitivities, with tritanopic color-matching data, and with short-wavelength-sensitive (S-) cone spectral-sensitivity data suggests that they are to be preferred over fundamentals based on the CIE 2° CMF's.

**Key words:** Color vision, cone fundamentals, color matching, spectral sensitivity, cones, luminance, dichromacy

## 1. INTRODUCTION

More than a century of research effort has been devoted to the determination of the cone spectral sensitivities on which normal color vision depends. Though a degree of consensus now obtains, there are substantial differences among the prevailing cone-sensitivity estimates.

In principle, all that we require to measure cone spectral sensitivities in the normal observer is to find conditions under which vision depends on only a single cone type. Such isolation is difficult to achieve across the entire visible spectrum, however, because the spectral sensitivities of the three cone types [particularly those of the middle-wavelength-sensitive (M) cones and long-wavelength-sensitive (L) cones] overlap extensively. Many workers have used steady chromatic adaptation in an attempt to isolate the cones (for example, Refs. 1 and 2), but there are *a priori* grounds for supposing that this strategy will be unsuccessful.<sup>3</sup> In our companion paper<sup>4</sup> we report the development and validation of a technique of isolating the M and L cones in the normal human eye that uses transient adaptation. Spectral sensitivity is measured following an exchange of background color from blue to deep red for M-cone isolation and from deep red to blue for L-cone isolation (see also Ref. 5). Here we apply this technique to estimate the M-cone spectral sensitivity in 2 protanopes and 11 normals and the L-cone spectral sensitivity in 4 deuteranopes and 12 normals. We compare the average spectral sensitivities that we obtain with other estimates of the protanopic and deuteranopic spectral sensitivities and with tritanopic color matches to derive new M- and L-cone fundamentals. In the color space defined by the CIE 2° color-matching functions (CMF's), our results are broadly consistent with the fundamentals of Smith and Pokorny.<sup>6</sup> In the color space defined by the Stiles-

Burch<sub>1955</sub> 2° CMF's and in the color space defined by the CIE<sub>1964</sub> 10° CMF's, we propose new cone fundamentals to replace the current Stiles-Burch<sub>1955</sub>-based estimates, which overestimate M-cone sensitivity in the red part of the spectrum. Comparisons with other data, such as tritanopic color-matching data and large-field, 10° CMF's, suggest that the cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° estimates are to be preferred over versions based on the CIE 2° CMF's.

### A. Dichromats and Normals

A traditional method of estimating the M- and L-cone spectral sensitivities is the use of protanopes and deuteranopes, since these dichromatic observers behave as if they possess only a single visual pigment in the long-wavelength spectral range. This makes possible a direct and straightforward measurement of the longer-wavelength cone spectral sensitivity, merely by the use of conditions under which the short-wavelength-sensitive (S) cones do not contribute to sensitivity. If dichromacy reflects the loss of one of the three cone types in the normal observer,<sup>7,8</sup> then, with the S cones disadvantaged, the protanopic spectral sensitivity should be that of the normal's M cones, and the deuteranopic spectral sensitivity should be that of the normal's L cones.

This approach is valid only if protanopia and deuteranopia are truly reduced forms of normal trichromacy, in which one of the two longer-wavelength photopigments is absent and the other is identical to that in the normal observer. Doubts about this "loss" hypothesis could be entertained on three main grounds.

First, many protanopes and deuteranopes show some residual anomalous trichromacy when their peripheral retinas are stimulated.<sup>9-11</sup> Second, microspectrophotometric absorption spectra (for example, Ref. 12) predict

much greater sensitivity at the ends of the spectrum than is observed in dichromats [see Fig. 11(a) below]. Third, the classic "field sensitivities" obtained by Stiles<sup>13</sup> from normal eyes are broader than dichromatic spectral sensitivities and are somewhat like the sensitivities inferred from microspectrophotometry (MSP) (see Fig. 3 of Ref. 14).

There is, on the other hand, also strong support for the loss hypothesis. First, though most are weakly trichromatic in their peripheral retinas, protanopes and deuteranopes are dichromatic in the central 2° of vision (where we make our measurements). Second, suction electrode recordings yield data that are much closer to dichromat sensitivities than are microspectrophotometric data [see Ref. 15 and Fig. 11(b) below]. Third, unlike Stiles's field-sensitivity measurements, many other cone isolation experiments,<sup>1-5,16,17</sup> including Stiles's high-intensity "test sensitivity" measurements,<sup>18</sup> have yielded spectral sensitivities in the normal observer that are nearly protanopic or deuteranopic. Fourth, comparisons between normal and anomalous trichromatic color matches support the loss hypothesis.<sup>19</sup>

In this paper we compare cone spectral sensitivities in normals and in dichromats obtained under precisely the same conditions of adaptation. Our results support the loss hypothesis of dichromacy.

### B. Color-Matching Functions and the Fundamental Spectral Sensitivities

The normal observer can match any spectral light to a mixture of three fixed-color primary lights (one of which may have to be added to the spectral light for completion of the match). An observer's color-matching behavior can therefore be described by the three functions that relate the matching intensities of the three primary lights to the wavelength of the spectral test light. These are known as the CMF's. Typically, they are defined for equal-energy spectral lights.

When a trichromatic color match is made by an observer with just three types of cone, it is a match at the cone level: the total quantal catch produced by the three primaries in each of the three cone types is the same as the quantal catch produced by the spectral test light. If we knew the sensitivity of each of the three cone types to the three primary lights, we could reconstruct the cone spectral sensitivities from the three CMF's by a simple linear transformation. Those nine sensitivities, however, are unknown.

In this paper we first estimate the M- or the L-cone sensitivities directly. Any cone-sensitivity estimate must be expressible as a linear combination of the CMF's, with weights given by the relative sensitivity of that cone to the three primaries. Accordingly, we next fit our cone spectral-sensitivity estimates with linear combinations of two of the standard sets of 2° CMF's: the CIE<sub>Judd</sub> and the Stiles-Burch<sub>1955</sub> CMF's (which are discussed in more detail below). We use the results and data from other sources to evaluate the differences between these CMF's: a crucial issue is which set of CMF's is the most appropriate as the basis for deriving the cone sensitivities.

### C. Individual Variability

At short wavelengths much of the individual variation in the corneally measured cone sensitivities arises from differences in the densities of the yellow pigments in the

macula and lens. To minimize uncertainty about these factors, we measured the macular and lens pigment densities in most of our subjects.

There is also a slight but significant individual variation in the cone pigment spectra themselves. With the identification of the genes that code the M- and L-cone photopigments, and the finding that there is more than one genotype for each cone type,<sup>20,21</sup> the study of the variability in  $\lambda_{\max}$  (the wavelength of maximum sensitivity) has taken on renewed interest.

As discussed above, measuring M- or L-cone spectral sensitivities (and their  $\lambda_{\max}$ ) is easier if protanopes or deuteranopes rather than normals are used. The most extensive data on the variability in the  $\lambda_{\max}$  of dichromats comes from work done at the University of Michigan. Alpern and Pugh<sup>22</sup> reported that the L-cone-sensitivity curves in a group of eight deuteranopes varied in spectral position over a total range of 7.4 nm, with a standard deviation estimated from their Fig. 9(C) of ~2.4 nm. Alpern,<sup>23</sup> analyzing the results from Alpern and Wake<sup>24</sup> and Bastian,<sup>25</sup> estimated the range of  $\lambda_{\max}$  in 38 protanopes to be 12.4 nm and the range in 38 deuteranopes to be 6.4 nm. These ranges are large, yet the standard deviations of the  $\lambda_{\max}$  calculated from Fig. 1 of Ref. 23 are only 2.3 nm for the protanopes and 1.6 nm for the deuteranopes.

For the normal observer, MacLeod and Webster<sup>26</sup> and Webster and MacLeod<sup>27</sup> found that the individual variation in the 10° CMF's of Stiles and Burch<sup>28</sup> implied a standard deviation in  $\lambda_{\max}$  for 49 observers of only 1.5 nm or slightly less for L-cone sensitivities and 0.9 nm for M-cone sensitivities; and they found comparable standard deviations in  $\lambda_{\max}$  for the 10 observers making up the Stiles-Burch 2° color-matching functions<sup>27</sup> (see also Ref. 29).

Thus psychophysical data from normals and dichromats suggest only a limited variability in the cone spectra. MSP of cones from the eyes of seven persons, however, suggests a greater variability, with standard deviations in  $\lambda_{\max}$  of 3.5 and 5.2 nm, respectively, for 45 M and 58 L cones in humans.<sup>12</sup> Presumably the excess variability in MSP either does not appear under the conditions of natural vision or else represents variation among cones in each individual rather than among different individuals. In fact, the distribution of  $\lambda_{\max}$  values in Fig. 1 of Ref. 30 suggests that the standard deviation of the mean  $\lambda_{\max}$  values among the seven subjects is roughly 2.4 and 3.7 nm for the M- and L-cones, respectively, suggesting that some of the variability found in the MSP data is within subjects. Suction electrode recordings from single cones in the monkey *Macaca fascicularis* are in better agreement with psychophysical measures of variability with standard deviations of  $\lambda_{\max}$  of only 1.0 nm for the L cones and 1.3 nm for the M cones<sup>15</sup>; and, in a limited sample of 5 L cones from a single human male, Schnapf *et al.*<sup>31</sup> report a standard deviation of 0.9 nm.

The question of whether variability in the absorption spectra is continuous or discrete is of considerable theoretical interest. Much has been made of the bimodal distribution of Rayleigh matches reported by Neitz and Jacobs,<sup>32</sup> which has since become a quadrimodality.<sup>33</sup> Unfortunately, two other recent studies have produced only unimodal distributions of Rayleigh matches.<sup>34,35</sup> Nevertheless, there is evidence to support the original

claim of Neitz and Jacobs<sup>32</sup> that there is a polymorphism of the L-cone-pigment gene that translates into a shift of  $\lambda_{\max}$  of  $\sim 3$  nm.<sup>2,36</sup> Despite claims to the contrary,<sup>37</sup> it remains that the Stiles–Burch 10° data, which represent the most extensive set of individual color-matching data, are consistent with a unimodal variation in  $\lambda_{\max}$  with a relatively small standard deviation.<sup>38</sup> This result suggests that the idea of defining cone fundamentals or color-matching functions of a standard or average observer is still useful and valid.

## 2. GENERAL METHODS

### A. Apparatus

The optical apparatus was a four-channel, Maxwellian-view system, described in more detail in the companion paper.<sup>4</sup> One channel provided the test field, and two others provided the primary background fields. A fourth channel provided an auxiliary violet background that was used to suppress the S cones under M-cone-isolation conditions. Each subject was positioned in the apparatus by means of a dental mouth bite.

### B. Stimuli

The sizes of the test and field stimuli were defined by circular field stops. The observer foveally fixated the center of the 4°-diameter background field, upon which a 2°-diameter test field was superimposed.

Test and field wavelengths were selected by use of interference filters with half-bandwidths of from 7 to 11 nm, with the exception of the deep-red background field, which was produced by a Wratten #70 gelatin cutoff filter and two heat-absorbing filters (HA3 glass).

#### 1. Adaptational Procedure

To achieve cone isolation, we alternated a red, 678-nm background and a blue, 485-nm background at 0.5 Hz. The blue background was chosen to desensitize the M cones selectively, and the deep-red background was chosen to desensitize the L cones selectively. The target field, flickering at 17 Hz, was presented during the 500 ms immediately following the transition from one field (which we refer to as the preceding field) to the second (which we refer to as the concurrent field). The preceding and concurrent fields were blue and deep red, respectively, for M-cone isolation and deep-red and blue, respectively, for L-cone isolation. The choice of background wavelengths and the specifics of the adaptational procedure are discussed in more detail in the companion paper.<sup>4</sup> There we report that measurement of sensitivity just after the exchange of two colored fields is more successful in producing cone isolation than measurement after either a steady field or a flashed field.

#### 2. Sensitivity Measurement

In the following experiments we determined sensitivity by measuring the threshold for detecting 17-Hz, square-wave flicker. The method of adjustment was used. The subject varied the intensity of the flickering 2° target field by rotating a circular variable neutral-density wedge until he or she was satisfied that the flicker was just at threshold. Six settings were made for each condition. The subject was instructed to alternate the direction of the initial

excursion of the wedge after each setting. The rationale for the use of a rapidly flickering test stimulus is discussed elsewhere.<sup>4</sup>

### C. Calibration

All light source and spectral filter combinations were calibrated with a spectroradiometer (EG&G) that had itself been calibrated against a reference mercury lamp and a reference light source. Calibrations of the radiant fluxes of test and background fields were obtained at regular intervals with a conventional radiometer/photometer (EG&G) that had been cross calibrated with a silicon photodiode (United Detector Technology) independently calibrated (by Optronics, Inc.) with a precision of 2% traceable to the National Institute of Standards and Technology. The test intensities are given below in  $\log_{10}$  quanta  $\text{sec}^{-1} \text{deg}^{-2}$ , and background intensities are given in  $\log_{10}$  trolands (Td). Each narrow-band stimulus is characterized by an equivalent wavelength, which is the wavelength of a monochromatic light that has the same effect on the cone type of interest when it is equated in energy to the narrow-band light. The equivalent wavelengths calculated for these stimuli assumed the Smith–Pokorny cone fundamentals, as described in the companion paper.<sup>4</sup> Revised equivalent wavelengths based on the quite similar cone sensitivities that were ultimately derived differ only by inconsequential amounts: resulting errors were less than 0.25 nm in equivalent wavelength, or less than 1% (0.004 log unit) if expressed in terms of sensitivity. These corrections have been neglected. We made minor adjustments to the measured L-cone spectral sensitivities to correct for changes resulting from photopigment bleaching (see Ref. 4 for details).

### D. Subjects

We performed the most-extensive measurements on three of the color-normal subjects, who were also the experimenters (AS, JAV, and NEJ). The other subjects did not know the purpose of the experiments. Trichromacy or dichromacy was established by Rayleigh matches and by the Farnsworth–Munsell 100-hue test carried out with use of central vision. We required that our dichromats be able to make a side-by-side match between a yellow light and a mixture of red and green lights by adjusting only the intensity of the yellow, whatever the ratio of red to green light in the mixture. The majority of our subjects could accommodate without corrective lenses. Of those who could not, two wore colorless contact lenses during the experiment and a third used a corrective lens placed just in front of his eye.

## 3. RESULTS AND DISCUSSION

### A. Flicker Threshold Spectral Sensitivity As a Function of the Intensity of the Concurrent Background

#### 1. Introduction

In our previous study we found that at sufficiently high luminances the spectral sensitivities of three normal observers closely approached an M-cone spectral sensitivity after an exchange of background color from blue to deep red and an L-cone sensitivity after an exchange of background color from deep red to blue.<sup>4</sup> The purpose of this first experiment was to test whether M- and L-cone iso-

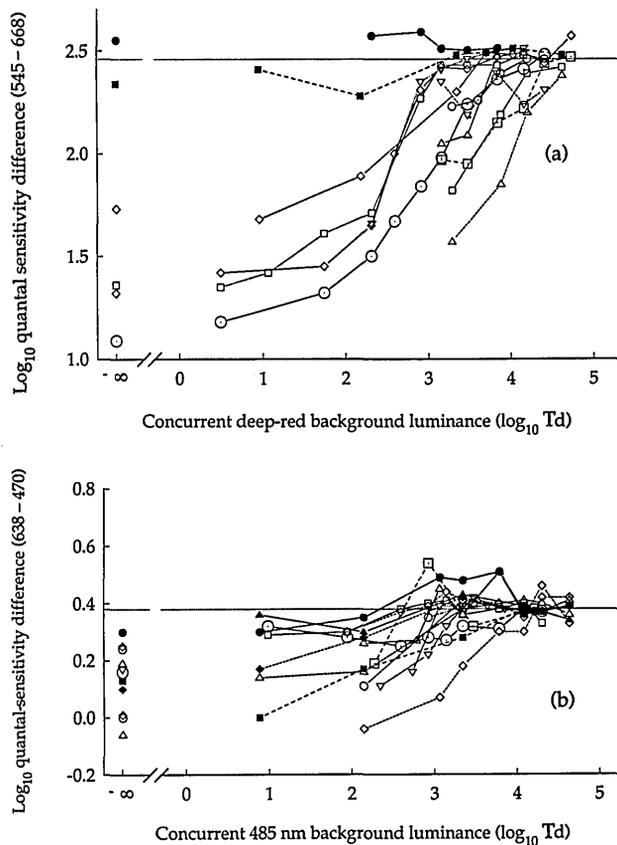


Fig. 1. Cone isolation for nine male color normals (open symbols), two female color normals (dotted symbols), and two male protanopes (filled symbols). (a) M-cone isolation: The difference in  $\log_{10}$  sensitivity for detecting 545- and 668-nm, 17-Hz flicker following an exchange of background from 485 to 678 nm plotted as a function of the 678-nm background luminance. The horizontal line is the Smith-Pokorny M-cone sensitivity. (b) L-cone isolation: The difference in  $\log_{10}$  sensitivity for detecting 638- and 470-nm, 17-Hz flicker following an exchange of background from 678 to 485 nm plotted as a function of the 485-nm background luminance. The horizontal dotted line at +0.38 is the mean 638-470 nm sensitivity difference obtained in Subsection 3.B (see Table 1 below). The data for each subject have been vertically shifted to align each subject's asymptotic 638-470-nm spectral sensitivity with that value. (In contrast, the average 638-470-nm sensitivity difference under M-cone isolation conditions was  $-0.86 \log_{10}$  unit.)

lation could also be achieved in a larger group of naïve subjects and, if it could, then to use the results for choosing appropriate background luminances for the complete spectral-sensitivity determinations described in Subsection 3.B.

## 2. Methods

For the M-cone-isolation conditions, test lights of 545 and 668 nm were used, and for the L-cone isolation conditions lights of 638 and 470 nm were used. Target wavelengths of 470 and 668 nm were chosen because they are close to those at which L-cone isolation and M-cone isolation, respectively, should be poorest (see Ref. 4). For the shorter-wavelength test light under the M-cone-isolation conditions, 545 nm was preferred to 470 nm, mainly because in the fovea the sensitivity to 470-nm light is affected by macular pigmentation and lens pigmentation, both of which show considerable individual variation. Because of this individual variation, the asymptotic 638-

470-nm L-cone-sensitivity difference varies considerably among subjects. In contrast, the 545-668-nm M-cone asymptote is almost unaffected by macular pigmentation and is only slightly affected by lens pigmentation. Other sources of variability are assessed in Appendix B.

## 3. Results

Figure 1(a) shows the difference in  $\log_{10}$  sensitivity for detecting 545- and 668-nm, 17-Hz flicker measured as a function of the luminance of the concurrent deep-red background. Results are shown for nine male color normals, two female color normals, and two male protanopes. The Smith-Pokorny cone spectral-sensitivity functions shown throughout this paper are calculated from Ref. 6 with use of the Judd<sup>39</sup> and Vos<sup>40</sup> modified CIE 2° CMF's (see Table I of Ref. 40).

For nearly all our subjects, the 545-668-nm sensitivity difference closely approaches or reaches the expected M-cone spectral-sensitivity difference as the concurrent 678-nm background luminance is increased. There are two important features of the results shown in Fig. 1(a). First, the asymptotic 545-668-nm sensitivity difference seems to be common to all our subjects: none of them has a 545-668-nm sensitivity difference that significantly exceeds the Smith-Pokorny M-cone spectral sensitivity. Second, although there is a common asymptote, there is considerable variation in the luminance of the concurrent, 678-nm background needed for reaching it. In fact, the range is from as low as 3.0  $\log_{10}$  photopic Td to as high as 4.5  $\log_{10}$  photopic Td.

Figure 1(b) shows the difference in  $\log_{10}$  sensitivity for detecting 638- and 470-nm flicker following background exchange. Results are shown for nine male color normals, two female color normals, and four male deuteranopes. Because of individual variability in macular and lens pigmentation at 470 nm, we cannot assume that the Smith-Pokorny L-cone estimate of the 638-470-nm sensitivity difference is valid for our subjects. The upper horizontal dotted line in Fig. 1(b) is the average 470-638 nm sensitivity difference for all 15 subjects obtained in the spectral-sensitivity determinations described in Subsection 3.B. To compensate for differences in prereceptor filtering, we have vertically shifted each subject's data by an amount that brings his or her asymptotic 470-638-nm spectral sensitivity into alignment with the average asymptotic 470-638-nm spectral sensitivity. In Subsection 3.B we estimate the macular and lens pigment for a group of these subjects. After correction of the individual spectral-sensitivity data to a peak macular density of 0.35 and typical lens density (when we refer to the peak macular density, we are referring to the macular density at 460 nm, the peak of the macular spectrum), the average spectral sensitivities that we derive agree well with other cone-sensitivity estimates (see Figs. 2, 5, and 6 below).

Adaptation has comparatively little effect on the 638-470-nm sensitivity differences shown in Fig. 1(b), because the spectral-sensitivity change from the standard photopic luminosity curve ( $V_\lambda$ ) to a pure L-cone sensitivity amounts to a shift of only 0.32  $\log_{10}$  unit at these wavelengths. One interesting feature of these data is that the 638-470-nm spectral sensitivity increases with concurrent 485-nm background luminance in deuteranopes as well as in color normals, presumably because 470-nm, 17-Hz

flicker is detected by the S cones (or even by the rods) at low background luminances.

## B. M- and L-Cone Spectral Sensitivities

### 1. Introduction

In this experiment we determined the 17-Hz flicker-detection spectral sensitivities following an exchange of background color (1) from blue to deep red to determine M-cone spectral sensitivity in 11 color normals and 2 protanopes and (2) from deep red to blue to determine L-cone spectral sensitivity in 12 color normals and 4 deuteranopes. Nine of the color normals made both the M- and the L-cone spectral-sensitivity measurements. Three others made only the L-cone measurements, and two others only the M-cone measurements.

Two important sources of variability in the shapes of corneally measured cone spectral sensitivities are individual differences in the densities of lens and macular pigmentation. These prereceptor filters absorb mostly at short wavelengths. Individual differences are large: in studies using more than 10 subjects, macular pigment density has been found to vary from 0.0 to 1.2 at 460 nm,<sup>41-43</sup> and lens pigment density by approximately  $\pm 25\%$  of the mean density implied by the CIE 1951 scotopic luminosity function (see Ref. 44; the variability estimate given in Ref. 44 was based on the individual scotopic luminosity data of Crawford<sup>45</sup>). These large individual variations in lens and macular pigmentation can obscure whether cone isolation has been attained at short wavelengths, and they are the main source of observer sampling error in the estimation of the cone sensitivities. To mitigate these problems, we undertook independent measurements of the density of lens and macular pigmentation in 11 of our subjects. We use the measurements below to make small corrections to our mean data in order to make them representative of typical levels of prereceptor pigmentation.

### 2. Methods

*Spectral-sensitivity determination.* Ten test wavelengths were used. Six settings were made at each test wavelength. Two separate spectral-sensitivity determinations were carried out for each subject: the first in ascending order of test wavelength and the second in descending order. Subjects AS, NEJ, and JAV carried out four separate determinations, for which the order of test wavelengths was ascending, descending, descending, and ascending.

The M-cone data were obtained following an exchange of background from 485 to 678 nm. The average luminance of the preceding 485-nm background was  $3.15 \log_{10}$  Td and that of the concurrent 678-nm background  $3.95 \log_{10}$  Td. Although we are comparatively insensitive to high-frequency flicker detected by the S cones, we are easily able to resolve 17-Hz S-cone flicker at high enough intensities (see, for example, Refs. 46 and 47). Under the conditions of our experiment we found an S-cone contribution to the detection of both 442- and 470-nm, 17-Hz flicker under M-cone-isolation conditions. We suppressed this unwanted contribution by adding a steady, violet, 418-nm auxiliary background of  $9.68 \log_{10}$  quanta  $\text{sec}^{-1} \text{deg}^{-2}$  ( $1.20 \log_{10}$  Td) to the exchange backgrounds. No auxiliary background was needed for the L-cone-isolation conditions.<sup>4</sup>

The L-cone data were obtained following an exchange of background from 678 nm (average luminance,  $3.35 \log_{10}$  Td) to 485 nm (average luminance,  $4.05 \log_{10}$  Td).

*Macular pigment density determination.* We estimated macular pigment density by comparing 17-Hz flicker-detection sensitivities at 470 and 545 nm at an eccentricity of  $10^\circ$  and centrally. Relative to 545 nm, the difference in log relative sensitivity at 470 nm between these eccentricities was taken to be our estimate of macular pigment density, which could then be suitably scaled for other wavelengths with the standard templates tabulated by Wyszecki and Stiles.<sup>48</sup> So that regional variations in the relative sensitivity of different cone types would not upset the estimate, the macular estimate was performed under M-cone-isolation conditions for 11 of the subjects and as an additional control under both M- and L-cone-isolation conditions for our three main subjects (AS, JAV, and NEJ). A number of previous studies estimated macular pigment density by isolating the same cone mechanism in the fovea and parafovea in this way (for example, Ref. 13).

Macular pigment density was determined experimentally in only 11 of our 20 subjects, yet we needed to make macular pigment density adjustments to the spectral-sensitivity data averaged across all our subjects. We obtained an estimate of the unknown macular pigment densities by comparing the spectral sensitivities of the 9 subjects in the unknown group with the spectral sensitivities of the 11 subjects in whom the macular density was known. This was done as part of the analysis of the factors that underlie the individual variation in the corneal cone sensitivities, described in Appendix B. That analysis yielded the macular pigment density required for a best fit to each subject's sensitivity data. The macular pigment absorption curve assumed was the one tabulated in Ref. 48. While subjects may differ somewhat in their macular pigment absorption spectra (see, for example, Ref. 49), the general validity of the Wyszecki-Stiles estimate is supported by our own analysis in Fig. 9(c) below.

*Lens pigment density determination.* We estimated lens pigmentation by measuring 2-Hz scotopic flicker thresholds for test wavelengths of 413 and 545 nm at an eccentricity of  $10^\circ$  in the temporal retina and by assuming that individual variation in the ratio of the two sensitivities reflects lens absorption in the violet (essentially the method of Ref. 50). This assumption neglects possible individual differences in the optical density of rhodopsin itself, but these can play only a minor role. The test fields were  $2^\circ$  in diameter, and no background was used. Each run was preceded by 40 min of dark adaptation. The sensitivity difference between 413 and 545 nm, averaged from two or more runs, was compared with the standard  $V_\lambda'$  scotopic luminosity function [Table I(4.3.2) of Ref. 48] at those two wavelengths.

### 3. Results

Table 1 lists the means and standard deviations of the 17-Hz flicker-detection spectral sensitivities before any corrections for macular or lens pigment density. An analysis of the factors that underlie the individual variation in these data is presented in Appendix B.

Before these mean data are compared with other estimates of the cone spectral sensitivities, it is desirable first

**Table 1. Means and Standard Deviations of the M- and L-Cone Spectral Sensitivities Obtained with the Exchange Procedure**

Wavelength (nm)	M-Cone ( $n = 13$ )		L-Cone ( $n = 16$ )	
	Log Sensitivity	Standard Deviation	Log Sensitivity	Standard Deviation
442	-0.985	0.175	-1.262	0.177
470	-0.641	0.155	-0.963	0.178
500	-0.262	0.101	-0.519	0.113
516	-0.098	0.067	-0.169	0.072
545	0.000	0.019	-0.003	0.042
576	-0.128	0.070	0.000	0.036
600	-0.552	0.046	-0.095	0.044
617	-0.938	0.042	-0.255	0.051
638	-1.498	0.036	-0.587	0.040
668	-2.463	0.035	-1.330	0.053

to adjust them to typical macular and lens pigment densities. We found that the average peak macular density (i.e., the density at 460 nm calculated from our data at 470 nm by use of the Wyszecki–Stiles standard macular pigment template) in the 11 subjects measured was 0.32, with a standard deviation of 0.23 across observers. The average lens density was 99% of that implied by the standard  $V_{\lambda}'$  scotopic luminosity function, with a standard deviation of 23%. Our average data thus required practically no adjustment for idiosyncrasies of lens pigmentation, with corrections approaching 0.01  $\log_{10}$  unit only in the deep violet. Since such small corrections are visually insignificant, only macular pigment corrections to our data are considered in the remainder of this paper. According to the analysis described in Subsection 3.B.2, the mean macular pigment density for all subjects who made M-cone measurements was 0.30, and for those who made L-cone measurements it was 0.34.

*What is the typical macular density for a 2° field?* In making comparisons between our data and cone fundamentals based on the 2° CMF's, it is important that we have a good estimate of the typical macular density for a 2°-diameter field, so that we can use the measured macular densities to correct the spectral sensitivities of our observers to typical density values. The peak macular density (at 460 nm) most often assumed is the 0.5 value given by Wyszecki and Stiles.<sup>48</sup> This value, however, may not be appropriate for a 2° field. Most macular pigment density determinations, including those on which Wyszecki and Stiles based their estimate, were carried out with fields smaller than 2°. The chief exception was the study by Bone and Sparrock,<sup>42</sup> which gave a mean peak density of 0.53, but this value is probably inflated by scotopic intrusion in their peripheral measurements (see Ref. 51, p. 7). Of the other studies that actually note the field size, both Wald<sup>41</sup> (0.50 peak) and Stiles<sup>13</sup> (0.50 peak) used a 1°-diameter field; and, more recently, Pease *et al.*<sup>43</sup> (0.77 peak) used a 0.67°-diameter field. Since macular density falls off rapidly with eccentricity,<sup>49</sup> it seems likely that the typical effective density of macular pigment for a 2° field is less than the 0.50 peak value assumed by Wyszecki and Stiles. But how much less?

Our own macular density measurements suggest a mean peak density (at 460 nm) for a 2°-diameter field of 0.32, or

64% of the density assumed by Wyszecki and Stiles.<sup>48</sup> Other evidence suggests that this value may be typical. Smith and Pokorny<sup>6</sup> measured the macular densities for 2°-diameter fields in four deuteranopes and five protanopes. Although they subsequently adjusted their data to a peak density of 0.53, the measured densities were only 0.26–0.38 for the protanopes and 0.146–0.85 for the deuteranopes. The mean peak macular density for their nine subjects (from their Fig. 3) is  $\sim 0.36$ . This value compares well with the mean of 0.32 for our eleven subjects.

The foregoing experimental estimates assume negligible macular pigmentation in the peripheral retinal region (10° eccentricity in our case) that was used for comparison with the macular area, and they could be underestimates if macular pigmentation does extend substantially beyond the macula. Reassuringly, however, high-performance liquid chromatography data on human eyes suggest a negligible density at an eccentricity of 10° (Ref. 52, Table 2 and p. 847). Moreover, Baylor *et al.*<sup>15</sup> found that comparisons between psychophysical and electrophysiological spectral sensitivities suggested a peak macular pigment density of 0.29 for a 2° field. Consideration of the shapes of the absorption spectra also supports a value close to 0.35. Vos<sup>51</sup> concluded that a macular density of 0.35 yielded the smoothest inferred cone pigment absorption spectra for cone sensitivities based on the CIE<sub>Judd</sub> 2° CMF's. In similar analyses undertaken by us, the macular densities that yielded absorption spectra best described by low-order polynomials was generally even lower than 0.35 for cone sensitivities derived from the Stiles–Burch<sub>1955</sub> 2° CMF's, but the estimates depended on the candidate cone spectral sensitivity, on the lens absorption spectrum assumed, and on the fitting criterion adopted. The macular density that yielded the closest approach to a common shape (on a log wavelength or relative-frequency basis<sup>53,54</sup>) for the visual pigment absorption spectra was 0.35 or slightly higher, again with considerable dependence on the details of the analysis.

Provisionally, then, we assume 0.35 to be the typical peak macular density for a 2° field. This assumption requires a comparatively small adjustment to our mean data (by 0.045 and 0.014  $\log_{10}$  unit at 470 nm for our M- and L-cone data, respectively).

*Comparisons with other estimates.* The mean spectral-sensitivity data adjusted to a peak macular density of 0.35 are shown in Fig. 2 as filled circles. In each panel, our data are shown twice, displaced vertically for clarity.

The upper curves in both panels are the Smith–Pokorny<sup>6</sup> (solid curves) and the Vos–Walraven (dashed curves) cone estimates based on the CIE<sub>Judd</sub> 2° CMF's. (In general, when we refer to the Vos–Walraven cone fundamentals, we are referring to the Vos–Walraven fundamentals<sup>55</sup> modified by Walraven<sup>56</sup> and Vos<sup>40</sup>.) The lower curves are the Vos *et al.*<sup>57</sup> (solid curves) and the Estévez<sup>58</sup> (dashed curves) cone estimates based on the Stiles–Burch<sub>1955</sub> 2° CMF's. These four cone estimates are derived from dichromatic and trichromatic color-matching data. Their derivation is discussed below.

At wavelengths greater than 500 nm, both of the CIE<sub>Judd</sub>-based cone estimates (upper curves) describe our data extremely well. At shorter wavelengths, the agreement is poorer, yet the Smith–Pokorny fundamentals are still

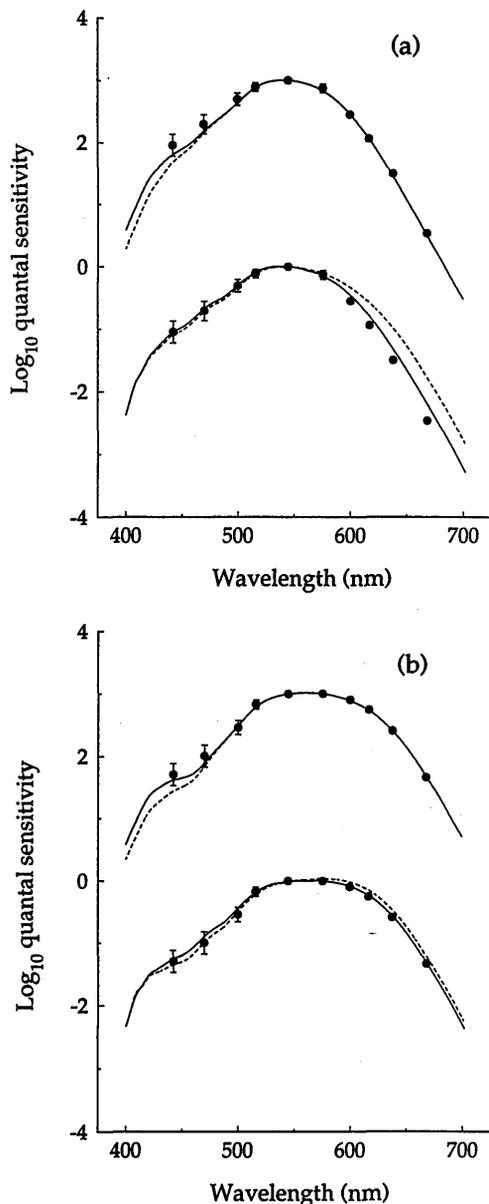


Fig. 2. Average 17-Hz flicker-detection spectral sensitivities under (a) M-cone or (b) L-cone isolation conditions, adjusted to a typical peak macular pigment density of 0.35 (filled circles). The error bars are  $\pm 1$  standard deviation across subjects. The upper comparison in each panel is with the  $CIE_{Judd}$ -based cone fundamentals of Smith and Pokorny<sup>6</sup> (solid curves) and of Vos and Walraven<sup>55</sup> (dashed curves); the lower comparison is with the Stiles-Burch<sub>1955</sub>-based cone fundamentals of Vos *et al.*<sup>57</sup> (solid curves) and Estévez<sup>58</sup> (dashed curves).

within 1 standard deviation of our mean data. The Vos-Walraven estimates are substantially less sensitive at short wavelengths than any of the other cone estimates shown in Fig. 2.

The Stiles-Burch<sub>1955</sub>-based cone estimates (lower curves) agree well with our adjusted data at short wavelengths. At the long-wavelength end of the spectrum, however, the M-cone estimates of both Estévez<sup>58</sup> and Vos *et al.*<sup>57</sup> are clearly too sensitive to describe our data. The Estévez M-cone estimate deviates from our data (and from the  $CIE_{Judd}$ -based estimates) by nearly 0.4  $\log_{10}$  unit (a factor of 2.5) at long wavelengths. The Vos *et al.* function agrees

somewhat better than the Estévez function, but like the Estévez function it is too sensitive in the orange and red. As we show in the Subsection 3.C, these discrepancies are due not to inconsistencies between our data and the standard Stiles-Burch<sub>1955</sub> 2° observer but rather to less-than-optimal choices of the weighting coefficients in the proposals of Vos *et al.* and of Estévez. With more appropriate choices, the Stiles-Burch<sub>1955</sub> 2° CMF's can fit our own and other relevant data fairly well (see Fig. 4 below).

### C. Linear Combinations of the $CIE_{Judd}$ and Stiles-Burch<sub>1955</sub> 2° CMF's Best-Fitting Our Data

#### 1. Introduction

The color matches of a normal observer can be described by three CMF's, each of which represents the energy of one of the primaries required for matching a spectrum of monochromatic test lights of unit energy. A set of CMF's can be linearly transformed from one triad of primaries to any other, including imaginary primaries such as the  $x, y, z$  primaries adopted by the CIE, and including as a special case the cone, or fundamental, spectral sensitivities. Since they are the basis of trichromatic color matches, the cone spectral sensitivities must be a linear combination of the CMF's. We next ask how well our data can be represented by linear combinations of the CMF's.

There are three major derivations of the CMF's for foveal vision, as follows.

**$CIE_{1931}$  2° color-matching functions.** The  $CIE_{1931}$  2° CMF's,<sup>59</sup> which form the basis for virtually all practical colorimetry, are based on the chromaticity coordinates obtained by Guild<sup>60</sup> and by Wright.<sup>61</sup> Chromaticity coordinates, however, provide only a relative measure of the ratios of the three primaries needed for matching each spectrum color, whereas CMF's specify absolute energy values. In order to reconstruct the CMF's from the Wright<sup>61</sup> and Guild<sup>60</sup> data, it was assumed that the  $CIE_{1924}$   $V_\lambda$  photopic luminosity function<sup>62</sup> is a linear combination of the three CMF's (see Ref. 48 for a description of the reconstruction and for the tabulated values). Because they are seriously in error at short wavelengths (see below), we do not consider the original  $CIE_{1931}$  2° CMF's further in this section but return to them in Subsection 3.F below.

**$CIE_{Judd}$  2° color-matching functions.** It has long been clear that the  $CIE_{1924}$   $V_\lambda$  that was used to construct the  $CIE_{1931}$  2° CMF's seriously underestimates sensitivity at wavelengths below 460 nm. Judd<sup>39</sup> proposed a revised version of  $V_\lambda$  to overcome this problem and derived a new set of CMF's [see Table 1(5.5.2) of Ref. 48]. Subsequently, Vos made additional corrections to Judd's revision below 410 nm and incorporated the infrared color reversal described by Brindley<sup>63</sup> to produce the modified version of the  $CIE_{Judd}$  2° CMF's used here (Table 1 of Ref. 40). The Judd-Vos  $V_\lambda$  is the modified luminosity function  $V_M(\lambda)$  recently adopted by the CIE.

The validity of the  $CIE_{1931}$  and the  $CIE_{Judd}$  2° CMF's depends on the assumption that  $V_\lambda$  is a linear combination of the color-matching functions. This assumption was tested by Sperling, who measured chromaticity coordinates and luminosity functions and found deviations from additivity as high as 0.1  $\log_{10}$  unit in the violet, blue, and far-red parts of the spectrum between a flicker photo-

**Table 2. Linear Combinations of the CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's Best Fitting Our Data<sup>a</sup>**

Best-Fitting Parameters	Macular Density Adjustments			Smith-Pokorny <sup>6</sup>
	(A) None	(B) Adjusted to Peak of 0.35	(C) Adjusted to Peak of 0.50	
M-Cone				
$a_M$	-0.154709	-0.154503	-0.154048	-0.155140
$b_M$	0.456840	0.456840	0.456840	0.456840
$c_M$	0.041610	0.039281	0.035455	0.032860
rms <sup>b</sup>	0.130279	0.099126	0.050188	—
L-Cone				
$a_L$	0.138148	0.140398	0.156838	0.155140
$b_L$	0.543120	0.543120	0.543120	0.543120
$c_L$	-0.024874	-0.025833	-0.032081	-0.032860
rms <sup>b</sup>	0.086869	0.084282	0.086217	—

<sup>a</sup>The coefficients  $a_M$  through  $c_L$  refer to  $M_\lambda = a_M\bar{x} + b_M\bar{y} + c_M\bar{z}$ ;  $L_\lambda = a_L\bar{x} + b_L\bar{y} + c_L\bar{z}$ , where  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  are the Judd<sup>39</sup> and Vos<sup>40</sup> modified CIE 2° CMF's and  $M_\lambda$  and  $L_\lambda$  are the cone sensitivities.

<sup>b</sup>Root-mean-square fitting errors in log<sub>10</sub> sensitivity.

metric  $V_\lambda$  and the CMF's (and even larger deviations if  $V_\lambda$  was measured by brightness matching).<sup>64</sup> This suggests, as Estévez has pointed out,<sup>58</sup> that the use of the CIE  $V_\lambda$  function to construct the CIE 2° CMF's could introduce sizable errors, particularly since the derivation of the CIE  $V_\lambda$  was not limited to flicker photometric measurements.<sup>62,65</sup>

The validity of the CIE  $V_\lambda$ , itself, is also questionable. The uncertainty surrounding it is illustrated by the fact that the values from the different studies that were averaged to define it diverged by as much as a hundredfold in the violet.<sup>62,66</sup> The substantial modifications to the CIE  $V_\lambda$  subsequently introduced by Judd and by Vos are confined mainly to wavelengths below 460 nm, but even above that wavelength (where Judd retained the original CIE<sub>1924</sub> luminosity values) the CIE  $V_\lambda$  function seems not to have been carefully tested or validated. If the original CIE<sub>1924</sub> luminosity values are too low at and above 460 nm (as well as at shorter wavelengths at which Judd increased the luminosity values), then the Judd modification creates a standard observer whose sensitivity is too low at 460 nm and who could thus be roughly characterized as having artificially high macular pigment density (see Ref. 67, p. 171). Indeed, the CIE<sub>Judd</sub> 2° data do seem to deviate in this way from data of typical real observers, such as our subjects, the Stiles-Burch<sub>1955</sub> 2° data, and other relevant data (see Subsection 3.F).

*Stiles-Burch 2° color-matching functions.* There is no good reason that CMF's should be reconstructed with the use of  $V_\lambda$  in the way that the CIE<sub>1931</sub> and CIE<sub>Judd</sub> 2° CMF's were, because something better exists: the directly measured Stiles-Burch<sub>1955</sub> 2° CMF's.<sup>67</sup> Estévez<sup>58</sup> argued that these CMF's, which are based on data from 10 observers, are to be preferred over the CIE 2° CMF's, and Pugh and Sigel<sup>68</sup> noted that they are more consistent with Stiles's  $\pi$ -mechanism sensitivities than are the CIE 2° functions. The Stiles-Burch<sub>1955</sub> 2° CMF's are tabulated in Table I(5.5.3) of Ref. 48.

## 2. Methods

Using a curve-fitting program (SigmaPlot), we determined the best-fitting linear combination of either the CIE<sub>Judd</sub> or the Stiles-Burch<sub>1955</sub> 2° CMF's to describe our data. For each set of CMF's we carried out three types of fit: (A) with no macular pigment adjustments, (B) with our

data adjusted to a peak macular density of 0.35, and (C) with our data adjusted to a peak macular density of 0.50.

The fits minimized the sums of the squares of the deviations of the predicted from the observed log<sub>10</sub> sensitivity values, each deviation being divided by the standard deviation of the observed values among our observers (see Table 1). This gives less weight to the short-wavelength measurements. For the appropriateness of the rms deviation of log<sub>10</sub> sensitivity from prediction as a criterion of goodness of fit, see Ref. 68.

## 3. Results

*CIE<sub>Judd</sub> 2° color-matching functions.* Table 2 lists the best-fitting linear combinations of the CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's for the three types of fit (A–C) described above. In descending order,  $a_M$  to  $c_L$  are the M-cone  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  weights and the L-cone  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  weights, respectively. The row labeled rms gives the root-mean-square error in log<sub>10</sub> sensitivity for each fit. The column on the far right is the Smith-Pokorny solution.<sup>6</sup> To aid the reader in making comparisons, we have normalized our solutions, so that the weight on  $\bar{y}$  is the same as for Smith-Pokorny. This normalization also makes the sum of the M- and L-cone sensitivities a rough approximation to the Judd-Vos  $V_\lambda$  function.

Figure 3 illustrates the best-fitting linear combinations given in Table 2. Figure 3(a) shows the best-fitting solutions that describe our mean data adjusted to a peak macular density of 0.35.

The three panels in Fig. 3(b) show the logarithmic differences between the M-cone (dotted squares) or L-cone (dotted circles) data and the best-fitting linear combinations of  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$ . Panels (A), (B), and (C) correspond to the best-fitting solutions listed in columns (A), (B), and (C), respectively, of Table 2. Panel (B) corresponds to the fit shown by the curves and filled circles in Fig. 3(a).

Above 500 nm the residuals for all of the fits shown in Fig. 3 are small (<0.04 log<sub>10</sub> unit). At shorter wavelengths the fit to the data adjusted to a peak macular density of 0.50 is clearly better than the fits to the unadjusted data or to the data adjusted to a peak macular density of 0.35. This could mean either that macular density of 0.50 is in fact typical and that the CIE<sub>Judd</sub> 2° CMF's are representative or else, as we have suggested above, that the CIE<sub>Judd</sub> 2°

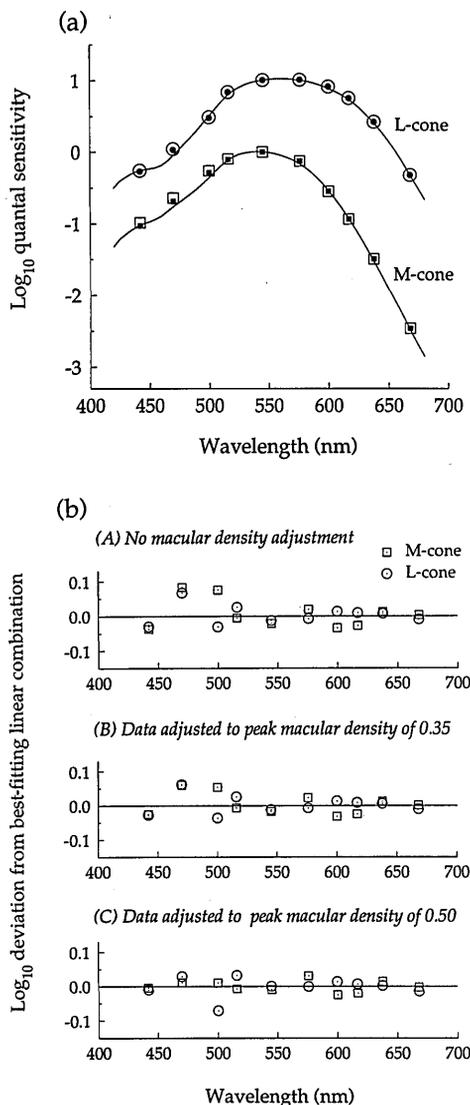


Fig. 3. (a) Best-fitting linear combinations of the CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's (continuous curves) that describe the adjusted data of Fig. 2 (small filled symbols; large open symbols are data before adjustment). (b) Logarithmic differences between the best-fitting linear combinations of  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  and our M-cone (dotted squares) or L-cone (dotted circles) data with (A) no macular pigment adjustments, (B) data adjusted to a peak macular density of 0.35; and (C) data adjusted to a peak macular density of 0.50.

observer is too insensitive in the region near 460 nm where macular absorption is most prominent.

*Stiles-Burch*<sub>1955</sub> 2° color-matching functions. Table 3 lists the best-fitting linear combinations of the Stiles-Burch<sub>1955</sub>  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  2° CMF's for the three types of fit. The far-right column is the Vos *et al.*<sup>57</sup> solution. Our solutions have been normalized, so that the weight on  $\bar{g}$  is the same as for Vos *et al.*

Figure 4 illustrates the best-fitting linear combinations tabulated in Table 3. Figure 4(a) shows the best-fitting solutions that describe our mean data adjusted to a peak macular density of 0.35. Panels (A), (B), and (C) of Fig. 4(b) show the best-fitting solution listed in columns (A), (B), and (C), respectively, of Table 3.

As in the case of the CIE<sub>Judd</sub> 2° CMF's, the residuals at wavelengths greater than 500 nm in Fig. 4 are small (<0.05 log<sub>10</sub> unit). But at shorter wavelengths the fits to the unadjusted data and to the data adjusted to a peak macular density of 0.35 are now better than the fit to the data adjusted to a peak macular density of 0.50.

We have already argued that the CIE<sub>Judd</sub> 2° standard observer has artificially high macular pigment density because of Judd's corrections to the CMF's (see above). Yet how certain can we be that the lower, average macular pigmentation of the 10 Stiles-Burch observers is typical for a 2° field? It is reassuring that in a separate brightness matching experiment, Stiles and Burch<sup>67</sup> found that the same 10 observers had short-wavelength sensitivities comparable with those of 18 other observers who also were tested. As Stiles and Burch observed, this makes it statistically unlikely that the 10 observers had exceptional pigmentation.<sup>67</sup> Our cone-sensitivity data support this through their consistency with the Stiles-Burch<sub>1955</sub> 2° CMF's.

#### D. Consistency with Protanopic and Deuteranopic Spectral Sensitivities

##### 1. Introduction

In this section we evaluate cone fundamentals based on the CIE<sub>Judd</sub> 2° and the Stiles-Burch<sub>1955</sub> 2° CMF's by comparing them with protanopic and deuteranopic spectral sensitivities. We choose not to use the color-confusion characteristics of dichromats in making these comparisons, because such data are strongly influenced by individual differences in the prereceptor absorption of the

**Table 3. Linear Combinations of the Stiles-Burch<sub>1955</sub>  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  2° CMF's Best Fitting Our Data<sup>a</sup>**

Best-Fitting Parameters	Macular Density Adjustments			Vos <i>et al.</i> <sup>57</sup>
	(A) None	(B) Adjusted to Peak of 0.35	(C) Adjusted to Peak of 0.50	
<b>M-Cone</b>				
$a_M$	0.042516	0.042955	0.043897	0.068090
$b_M$	1.765640	1.765640	1.765640	1.765640
$c_M$	0.171802	0.155559	0.128663	0.144690
rms <sup>b</sup>	0.090062	0.081216	0.111832	—
<b>L-Cone</b>				
$a_L$	0.346373	0.348928	0.367282	0.355120
$b_L$	1.219960	1.219960	1.219960	1.219960
$c_L$	0.069698	0.067896	0.057294	0.072090
rms <sup>b</sup>	0.094698	0.103592	0.111832	—

<sup>a</sup>The coefficients  $a_M$  through  $c_L$  refer to  $M_\lambda = a_M \bar{r} + b_M \bar{g} + c_M \bar{b}$ ;  $L_\lambda = a_L \bar{r} + b_L \bar{g} + c_L \bar{b}$ , where  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  are the Stiles-Burch 2° CMF's.

<sup>b</sup>Root-mean-square fitting errors in log<sub>10</sub> sensitivity.

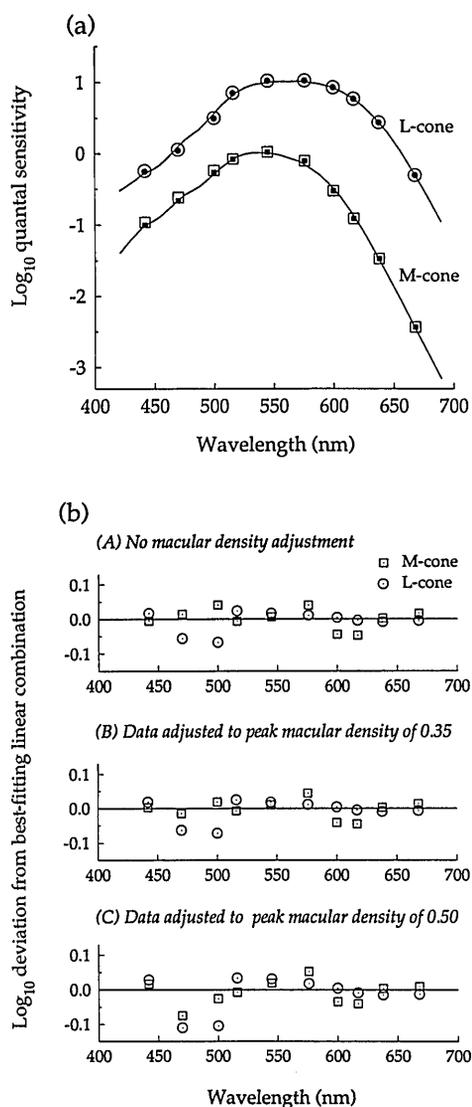


Fig. 4. (a) Best-fitting linear combinations of the Stiles-Burch<sub>1955</sub>  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  2° CMF's (continuous curves) that describe the adjusted data of Fig. 2 (filled symbols). The open symbols are the data before adjustment. (b) Logarithmic differences between the best-fitting linear combinations of  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  and M-cone (dotted squares) or L-cone (dotted circles) data with (A) no macular pigment adjustments, (B) data adjusted to a peak macular density of 0.35, and (C) data adjusted to a peak macular density of 0.50.

blue primary. Spectral-sensitivity data are less affected by, and are more easily corrected for, individual variations in prereceptor absorption and can also be averaged straightforwardly (unlike the chromaticity coordinates of the confusion points frequently used to characterize dichromatic vision, which cannot be meaningfully averaged across observers).

## 2. Dichromat Spectral Sensitivities

For these comparisons we have replotted the protanopic and deuteranopic spectral sensitivities of Pitt<sup>69</sup> from Table 4(5.14.2) of Ref. 48, of Hecht from Fig. 4 of Ref. 70, of Willmer from Figs. 3 and 5 of Ref. 71, and of Hsia and Graham from Table 1 of Ref. 72, as well as the spectral sensitivities from Figs. 3 and 4 of a more-recent study by Smith and Pokorny.<sup>6</sup> The Smith-Pokorny mean data are

plotted with no macular corrections. This is equivalent to an average peak macular density of approximately 0.35 (see above). We also show the average protanopic spectral sensitivities ( $n = 2$ ) and deuteranopic spectral sensitivities ( $n = 4$ ) from the present study adjusted to peak macular density of 0.35.

In our study we were careful to minimize any S-cone contribution by adding an auxiliary violet adapting field. Such precautions were not generally taken in the older studies. The data of Pitt<sup>69</sup> and Hecht,<sup>70</sup> which were obtained with direct brightness matching, may be subject to S-cone intrusion.<sup>73</sup> The data of Willmer,<sup>71</sup> which were obtained in the tritanopic foveola with a 0.13°-diameter target, and the data of Hsia and Graham,<sup>72</sup> which were obtained with a very brief, 4-ms, 0.7°-diameter flash, are less likely to be influenced by S cones; but their data are likely to show evidence of high macular pigmentation, since both studies used test flashes much smaller than 2°. The most-useful data at short wavelengths are those of Smith and Pokorny,<sup>6</sup> because they were obtained in the presence of a violet background so that the S cones were suppressed and because the mean macular pigment density of the subjects is known. It is reassuring that, when corrected to the same macular density values, the Smith-Pokorny dichromat data and our own dichromat data are similar.

Figures 5 and 6 reveal that the deuteranopes of Pitt and of Hecht are significantly more sensitive in the blue and violet than are the cone fundamentals based on either the CIE<sub>Judd</sub> [Fig. 5(b)] or the Stiles-Burch<sub>1955</sub> [Fig. 6(b)] 2° CMF's and more sensitive than the deuteranopic data of Smith and Pokorny and of the present study. This increased sensitivity could be due in part to S-cone intrusion.

## 3. CIE<sub>Judd</sub>-Based Cone Fundamentals

Three proposed cone fundamentals based on the CIE<sub>Judd</sub> 2° CMF's are shown in Fig. 5: those based on our data, on the Smith-Pokorny<sup>6</sup> estimates, and on the Vos-Walraven<sup>55</sup> estimates.

Our CIE<sub>Judd</sub>-based cone fundamentals shown in Fig. 5 agree well with the Smith-Pokorny and the Vos-Walraven fundamentals at wavelengths longer than 500 nm. In that region the agreement between the dichromat spectral sensitivities and the CIE<sub>Judd</sub>-based cone fundamentals is extremely good. Below 500 nm, however, the three sets of fundamentals differ substantially. At these wavelengths the dichromat data favor our version of the CIE<sub>Judd</sub>-based cone fundamentals. The sole exception is the data of Hsia and Graham, which favor the Smith-Pokorny fundamentals; these data, however, were obtained with a small 0.7° field and so are likely to reflect a higher macular pigment density than those for 2° fields. The Vos-Walraven M- and L-cone fundamentals both seem far too insensitive in the violet.

## 4. Stiles-Burch<sub>1955</sub>-Based Cone Fundamentals

Three candidate cone estimates based on the Stiles-Burch<sub>1955</sub> 2° CMF's are shown in Fig. 6: those based on our data, on the Vos *et al.*<sup>57</sup> estimates, and on the Estévez<sup>58</sup> estimates.

At short and middle wavelengths, our Stiles-Burch<sub>1955</sub>-based fundamentals shown in Fig. 6 are in almost exact

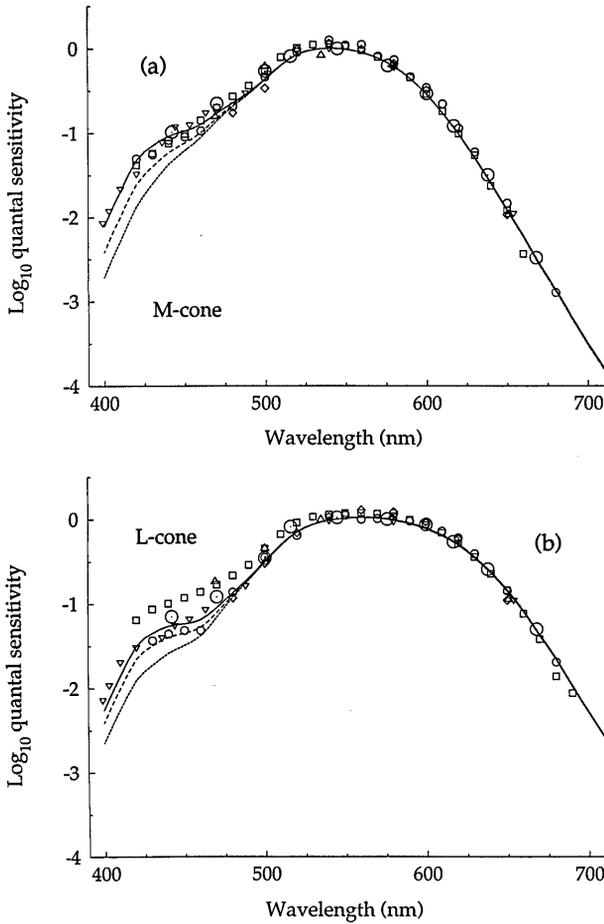


Fig. 5. Comparisons of the CIE<sub>Judd</sub>-based cone fundamentals of Vos and Walraven<sup>55</sup> (short-dashed curves), Smith and Pokorny<sup>6</sup> (long-dashed curves), and the present study (solid curves; column B of Table 2) with the dichromat data of Pitt<sup>69</sup> (squares), Hecht<sup>70</sup> (triangles), Willmer<sup>71</sup> (diamonds), Hsia and Graham<sup>72</sup> (circles), and Smith and Pokorny<sup>6</sup> (inverted triangles). The large dotted circles are the mean protanopic and deuteranopic data from the present study. (a) M-cone fundamentals and protanopes, (b) L-cone fundamentals and deuteranopes.

agreement with the Vos *et al.*<sup>57</sup> fundamentals. The Estévez<sup>58</sup> fundamentals are slightly less sensitive at short wavelengths, yet all three sets of Stiles-Burch<sub>1955</sub>-based fundamentals fall within the range of the dichromat spectral sensitivities from short wavelengths up to nearly 600 nm. At longer wavelengths, however, there are large discrepancies among the M-cone fundamentals. The Estévez M-cone fundamental is considerably more sensitive than either our M-cone fundamental or the Vos *et al.* M-cone fundamental. And, though it is closer to our estimate, the Vos *et al.* M-cone fundamental, too, is significantly more sensitive at longer wavelengths. The protanopic spectral sensitivities shown in Fig. 6 provide compelling support for our M-cone fundamental: they are clearly inconsistent with both the Vos *et al.* and the Estévez M-cone fundamentals. At long wavelengths, the deuteranopic spectral sensitivities agree well with all three Stiles-Burch<sub>1955</sub>-based L-cone fundamentals, although the Estévez L-cone fundamental, like his M-cone fundamental, seems too sensitive.

The differences between the Estévez M-cone fundamental and the protanopic spectral sensitivities shown in

Fig. 6 are remarkably large, especially since the fundamental is reportedly based on data from protanopes.<sup>58</sup> The Estévez M-cone fundamental has had a long and varied history. So far, it has appeared in three different versions. In his Ph.D. dissertation Estévez<sup>58</sup> based his first M-cone estimate on a protanopic confusion point of  $r_{pc} = 1.100$ ,  $g_{pc} = -0.102$ , which is consistent with a neutral point (for source B) of 495 nm. This first Estévez M-cone fundamental is the one shown in Fig. 6(a). In Ref. 48 Estévez proposed a new protanopic confusion point of  $r_{pc} = 1.025$ ,  $g_{pc} = -0.025$ , but unhappily the Estévez M-cone fundamental actually tabulated in Table 3(8.2.5) of Ref. 48 and adopted by many more recent investigators is quite inconsistent with that choice of confusion point. [The M-cone fundamental that is tabulated by Wyszecki and Stiles<sup>48</sup> is similar at long wavelengths to the Vos *et al.*<sup>57</sup> estimate shown in Fig. 6(a).] The M-cone fundamental corresponding to the (1.025, -0.025) confusion point in Ref. 48 is tabulated by Stockman<sup>74</sup> and by Stockman and Mollon in Table A1 of Ref. 3. Remarkably, at long wavelengths this M-cone fundamental is nearly identical to the estimate based on our spectral sensitivity data (see also Ref. 3, in which this fundamental is compared with other spectral-sensitivity data). It seems ironic that the only version of the Estévez M-cone fun-

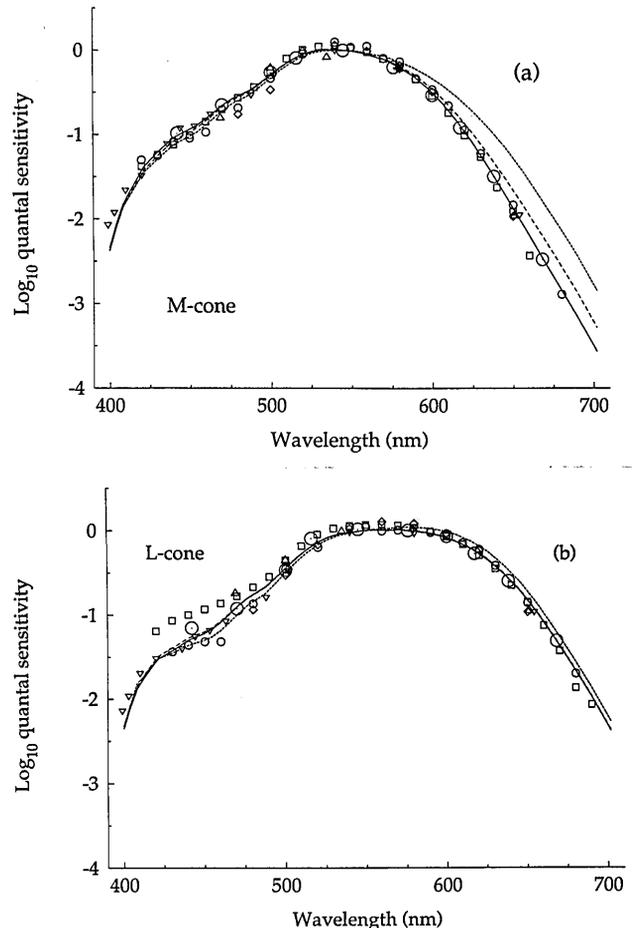


Fig. 6. Comparison of Stiles-Burch<sub>1955</sub>-based cone fundamentals of Estévez<sup>58</sup> (short-dashed curves), Vos *et al.*<sup>57</sup> (long-dashed curves), and the present study (solid curves; column B of Table 3) with the dichromat data. Other details as for Fig. 5.

damental that is actually consistent with protanopic spectral-sensitivity data was disowned by him in the note added in proof in Ref. 75, p. 266, in which it is stated that "O. Estévez has informed us that the protanopic confusion loci on which his calculations were based are printed incorrectly in [Ref. 48]." In that note a confusion point at (1.0381, -0.0388) is introduced as the basis of the tables in Ref. 48, but no empirical support for that choice of confusion point (or for the corresponding tabulated values<sup>48</sup>) is given there or elsewhere.

The smaller deviations in the case of the Vos *et al.*<sup>57</sup> M-cone fundamental (which implies a protanopic confusion point of  $r_{pc} = 1.040$ ,  $g_{pc} = -0.040$ ) are also curious, because Vos *et al.* chose this function specifically to fit protanopic spectral sensitivities (including the data of Pitt,<sup>69</sup> Hecht,<sup>70</sup> and Hsia and Graham<sup>72</sup> shown here). Inspection of Fig. 2 of Ref. 57 reveals that the protanopic data being fitted all fall substantially (by as much as 0.2 log<sub>10</sub> unit) below the fitted curve at long wavelengths. Clearly another Stiles-Burch<sub>1955</sub>-based M-cone fundamental, for instance the one proposed here, can provide a much better fit to the data.

## E. Consistency with Tritanopic Color Matches

### 1. Introduction

The small standard deviations of our measurements at middle and long wavelengths (see Table 1) fix the relative weights of the CIE<sub>Judd</sub>  $\bar{x}$  and  $\bar{y}$  2° CMF's and the Stiles-Burch<sub>1955</sub>  $\bar{r}$  and  $\bar{g}$  2° CMF's (see Tables 2 and 3) with some precision. At short wavelengths, however, where the CIE<sub>Judd</sub>  $\bar{z}$  2° CMF and the Stiles-Burch<sub>1955</sub>  $\bar{b}$  2° CMF become important, the standard deviations of our measurements are relatively large, so that we cannot be as confident of the best-fitting  $\bar{z}$  and  $\bar{b}$  coefficients. In this section we optimize the  $\bar{z}$  and  $\bar{b}$  coefficients by making them consistent with Wright's tritanopic color-matching data.<sup>76</sup>

Wright's data take the form of chromaticity coordinates and luminosity functions for seven tritanopes measured with use of a 1.33°-diameter field. The tabulated tritanopic CMF's, however, like the CMF's of the CIE, are synthesized from the chromaticity coordinates and luminosity data. Thus we use only the chromaticity coordinates in the following analysis. An advantage of using WDW coordinates (named WDW after W. D. Wright, who devised them) is that they are independent of prereceptor and intensity calibration errors that depend on wavelength.

Modifying our cone estimates so that they are consistent with tritanopic color matches is sensible only if the tritanope has the normal's M and L cones but lacks the normal's S cones. If this loss hypothesis of tritanopia is correct, Wright's tritanopic chromaticity coordinates should be predictable from the normal's M- and L-cone spectral sensitivities or, if the cone sensitivities are unknown, from the normal's CMF's (since the cone sensitivities are a linear combination of the CMF's). Alpern<sup>77</sup> found that the tritanopic chromaticity coordinates of Wright's subjects were poorly predicted by their confusion loci and the CIE<sub>1931</sub> (or CIE<sub>Judd</sub>) 2° CMF's. However, Estévez<sup>58</sup> showed that Wright's tritanopic chromaticity coordinates are more consistent with the Stiles-Burch<sub>1955</sub> 2° CMF's, suggesting that the loss hypothesis is valid but

that the CIE<sub>1931</sub> 2° CMF's may be in error at short wavelengths. The following analysis is consistent with that conclusion.

### 2. Methods

To refine our M- and L-cone fundamentals based on the CIE<sub>Judd</sub> 2° CMF's at short wavelengths, we fixed the weights of the  $\bar{x}$  and the  $\bar{y}$  CMF's given in column (B) of Table 2 and independently varied the M- and L-cone weights of the  $\bar{z}$  CMF to find the best least-squares fit to Wright's chromaticity coordinates. Similarly, to refine our cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's, we fixed the weights of the  $\bar{r}$  and the  $\bar{g}$  CMF's given in column (B) of Table 3 and varied the weights of the  $\bar{b}$  CMF.

### 3. CIE<sub>Judd</sub>-Based Fundamentals

Figure 7(a) shows the tritanopic chromaticity coordinates for the 480-nm primary ( $g_\lambda$ ) calculated from the CIE<sub>Judd</sub>-

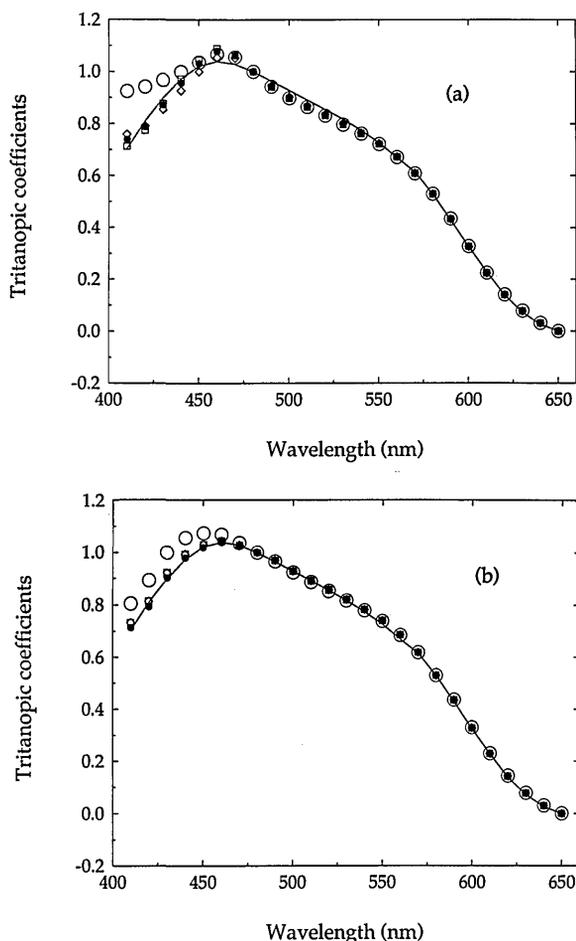


Fig. 7. Comparison of Wright's<sup>76</sup> tritanopic  $g_\lambda$  coefficients (solid curves) and predictions from (a) the CIE<sub>Judd</sub>-based M- and L-cone fundamentals of Vos and Walraven<sup>55</sup> (open squares), Smith and Pokorny<sup>6</sup> (open diamonds), and the initial estimate from the present study [open circles; column (B) of Table 2] with (b) the Stiles-Burch<sub>1955</sub>-based cone fundamentals of Estévez<sup>58</sup> (open squares), Vos *et al.*<sup>57</sup> (open diamonds), and the initial estimate from the present study [open circles; column (B) of Table 3]. The filled circles show the effects of (a) modifying the CIE<sub>Judd</sub> cone fundamentals presented in column (B) of Table 2 by varying the  $\bar{z}$  coefficient and (b) modifying the Stiles-Burch<sub>1955</sub> cone fundamentals presented in column (B) of Table 3 by varying the  $\bar{b}$  coefficient to best describe the Wright coefficients (see text for details).

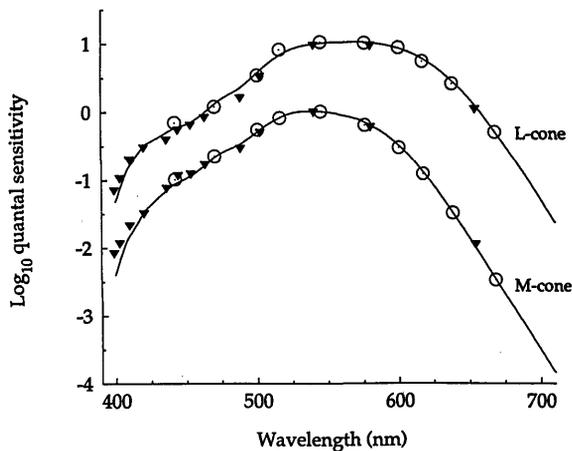


Fig. 8. Comparison of final Stiles–Burch<sub>1955</sub>-based cone fundamentals (solid curves; columns 2, 3, and 4 of Table 8 below) with protanopic and deuteranopic spectral sensitivities from Smith and Pokorny<sup>6</sup> (triangles) and from the present study (dotted circles).

based fundamentals of Smith and Pokorny<sup>6</sup> and of Vos and Walraven<sup>55</sup> and from the cone fundamentals based on our data adjusted to 0.35 peak macular density.

Though our candidate fundamentals of Table 2, column (B), and of Fig. 5 predict Wright's  $g_\lambda$  as well as do the other fundamentals above 480 nm, they do poorly at short wavelengths. The fit can be considerably improved by adjustment of the coefficients defining our cone fundamentals, as shown by the filled circles. The required adjustments to the equations given in column (B) of Table 2 are  $-0.006797\bar{z}$  for the L-cone fundamental and  $-0.008718\bar{z}$  for the M-cone fundamental. These reduce the rms error from 0.055 to 0.018.

Our revised CIE<sub>Judd</sub> 2°-based fundamentals predict Wright's chromaticity coordinates as well as (if not slightly better than) do both the Smith–Pokorny and the Vos–Walraven fundamentals. However, reducing the  $\bar{z}$  coefficients to improve the agreement with tritanopic color matches has the unwanted effect of decreasing the sensitivities of our M- and L-cone fundamentals at short wavelengths, taking the fundamentals farther away from the protanopic and deuteranopic spectral sensitivities shown in Fig. 5. Unfortunately, then, consistency with tritanopic color matches is gained at the expense of consistency with protanopic and deuteranopic spectral sensitivities.

The most noticeable feature of Fig. 7(a) is that none of the M- and L-cone fundamentals based on the CIE<sub>Judd</sub> CMF's accurately predicts the tritanopic chromaticity coordinates. Typically, Wright's  $g_\lambda$  is underestimated near 430 and 510 nm and overestimated near 460 nm. These differences suggest an essential incompatibility between tritanopic color matches on the one hand and the color matches of the CIE<sub>Judd</sub> 2° standard observer (and matches predicted by derivatives of the CIE<sub>Judd</sub> 2° observer, such as the MacLeod–Boynton<sup>78</sup> color space) on the other (see also Alpern<sup>77</sup> and Estévez<sup>58</sup>).

#### 4. Stiles–Burch<sub>1955</sub>-Based Cone Fundamentals

Figure 7(b) shows the tritanopic chromaticity coordinates predicted from the Stiles–Burch<sub>1955</sub>-based fundamentals of Vos *et al.*<sup>57</sup> and Estévez<sup>58</sup> and from the cone fundamen-

als of column (B) of Table 3 and Fig. 6, based on our data adjusted to 0.35 peak macular density. The fundamentals of Vos *et al.* and Estévez predict Wright's  $g_\lambda$  better than do the fundamentals of column (B) of Table 3 below 480 nm. However, the best-fitting adjustments to the  $\bar{b}$  coefficients given in column (B) of Table 3, though small ( $+0.005454\bar{b}$  for the L-cone fundamental and  $-0.011334\bar{b}$  for the M-cone fundamental), reduce the rms error from 0.039 to only 0.007. The fit to Wright's data is now marginally better than for either the Vos *et al.* or the Estévez fundamentals. Clearly the Stiles–Burch<sub>1955</sub> 2°-based cone fundamentals shown in Fig. 7(b) agree with Wright's tritanopic color-matching data much better than do the CIE<sub>Judd</sub>-based cone fundamentals shown in Fig. 7(a).

In Fig. 8 the revised cone fundamentals based on the Stiles–Burch<sub>1955</sub> 2° CMF's, modified for consistency with tritanopic color matches, are compared with the protanopic and deuteranopic data of Smith and Pokorny<sup>6</sup> and from our own study. We show only these two sets of data, because in both studies the macular densities were measured, and S-cone intrusion was minimized by the use of violet backgrounds. As in Figs. 5 and 6, the dichromat data plotted in Fig. 8 are consistent with a peak macular density of 0.35.

Adjusting the  $\bar{b}$  coefficients to improve the consistency of our candidate Stiles–Burch<sub>1955</sub>-based fundamentals with tritanopic matches has the effect of slightly increasing the short-wavelength sensitivity of the L-cone fundamental and slightly decreasing the sensitivity of the M-cone fundamental. The modified fundamentals still agree well with the protanopic and deuteranopic spectral-sensitivity functions. Thus the Stiles–Burch<sub>1955</sub>-based fundamentals of Fig. 8 are consistent with tritanopic color matches as well as with protanopic and deuteranopic spectral sensitivities. These revised fundamentals are specified and tabulated in columns 2, 3, and 4 of Table 8 below, and we adopt them as a basis for analysis in the remainder of this paper.

#### F. Derivation of M- and L-Cone Fundamentals Based on the CIE<sub>Judd</sub> and the CIE<sub>1931</sub> 2° CMF's and on the CIE<sub>1964</sub> 10° CMF's: How Consistent Are the Different Sets of CMF's?

##### 1. Introduction

In this section we derive the linear combinations of the CIE<sub>1931</sub> 2° and the CIE<sub>Judd</sub> 2° CMF's that best fit the revised cone fundamentals based on the Stiles–Burch<sub>1955</sub> 2° CMF's (Fig. 8 and Appendix A). This is the best way to reveal the nature and extent of any inconsistency between these sets of CMF's. To allow for possible differences in prereceptor filtering, we also derive the best-fitting linear combinations of the CIE<sub>1931</sub> and the CIE<sub>Judd</sub> 2° CMF's, also allowing lens and macular pigment densities to vary as fitting parameters. We chose the revised Stiles–Burch<sub>1955</sub>-based cone fundamentals of Fig. 8 and Table 8 below (columns 2, 3, and 4), as the standard set of fundamentals because of their consistency with deuteranopic and protanopic spectral sensitivities, with tritanopic color matching, and with our own spectral-sensitivity data measured in normals. The differences between the CIE<sub>1931</sub>, the CIE<sub>Judd</sub>, and the Stiles–Burch<sub>1955</sub> 2° CMF's have been analyzed by Smith *et al.*,<sup>79</sup> who concluded that the different CMF's are essentially equivalent except for variations in

prereceptor absorption. To the extent that this is true, the differences between our Stiles–Burch<sub>1955</sub>-based cone fundamentals and the linear combinations of the CIE<sub>Judd</sub> or CIE<sub>1931</sub> 2° CMF's that best describe them should disappear if we allow for possible differences in lens and macular pigmentation.

Finally, we derive the linear combinations of the CIE<sub>1964</sub> 10° CMF's that best fit the proposed cone fundamentals based on the Stiles–Burch<sub>1955</sub> 2° CMF's. The CIE<sub>1964</sub> 10° CMF's are based mainly on the 10° CMF's of Stiles and Burch<sup>28</sup> and to a lesser extent on the 10° CMF's of Speranskaya.<sup>80</sup> The 10° CMF's of Stiles and Burch, like their 2° functions, have the advantage over the CIE 2° functions that they were measured directly and thus do not depend on unnecessary photometric assumptions. We expect the 10° CMF's to reflect a lower macular pigment density than the 2° functions, since macular pigmentation declines with eccentricity. Since Stiles and Burch instructed their subjects to ignore the central 1° or 2° of vision where macular density is greatest<sup>28</sup> and Speranskaya presented a 10° field with the central 2° removed,<sup>80</sup> the macular density for the 10° CMF's will be less than that for a complete 10° field. We also expect the 10° CMF's to reflect a narrowing of the cone spectral sensitivities, since cones become shorter and broader with increasing eccentricity,<sup>81</sup> thus reducing the axial photopigment density in the cone outer segment. After correction for only macular and lens differences, the consistency between the CIE<sub>1964</sub> 10° CMF's and the Stiles–Burch<sub>1955</sub> 2° CMF's is good.

The fits given in this section are useful also because they yield candidate M- and L-cone sensitivities that are based on the CIE<sub>1931</sub> 2°, the CIE<sub>Judd</sub> 2°, and the CIE<sub>1964</sub> 10° CMF's instead of on the Stiles–Burch<sub>1955</sub> 2° CMF's. These fits may be preferred in some cases because of their ties to the functions customarily used in practical colorimetry, for instance, when cone excitations must be estimated from the CIE<sub>1931</sub> 2° ( $x, y$ ) chromaticity coordinates or ( $\bar{x}, \bar{y}, \bar{z}$ ) tristimulus values.

## 2. Methods

The fits were performed from 400 to 710 nm in 5-nm steps and minimized the mean-squared logarithmic difference between the functions. Thus the deviations expressed as a proportion or percentage are given the same weight at all wavelengths. For spectral lights, observed under conditions in which Weber's law holds, this index of goodness of fit properly represents the visual significance of the deviations.

For the reasons stated above, we carried out two types of fit: (A) we fitted the Stiles–Burch<sub>1955</sub>-based cone fundamentals, with no macular or lens pigment adjustments; and (B) we fitted the Stiles–Burch<sub>1955</sub>-based cone fundamentals, with the macular and lens densities allowed to vary in 0.01 steps as fitting parameters.

In addition, for the CIE<sub>1964</sub> 10° CMF's: (C) we fitted the Stiles–Burch<sub>1955</sub>-based cone fundamentals, with the photopigment, macular, and lens densities allowed to vary as fitting parameters. To carry out fit (C), we first converted the corneal Stiles–Burch<sub>1955</sub> 2°-based cone sensitivities to the photoreceptor level by removing the effects of lens pigmentation and macular pigmentation. For the prereceptoral filters we used the van Norren–Vos lens pigment template (multiplied by 1.16 for a small pupil size)

and the Wyszecki–Stiles standard macular pigment template. Assuming the axial photopigment density for the 2° Stiles–Burch<sub>1955</sub> cone fundamentals to be 0.40, we next calculated the absorbance spectrum for the photopigment in question. From the absorbance spectrum, we could calculate back to the corneal spectral sensitivity for any axial photopigment density (see Subsection 3.H for more details and a discussion of photopigment density estimates).

## 3. Results

Table 4 gives the linear combinations of the CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's that best fit the proposed fundamentals based on the Stiles–Burch<sub>1955</sub> 2° CMF's. The solutions have been normalized, so that the  $\bar{y}$  coefficient is the same as in Table 2. Column (A) lists the best-fitting linear combinations of CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$ , with no macular or lens density adjustments; these coefficients specify the CIE<sub>Judd</sub>-based cone fundamentals that are optimally consistent with the Stiles–Burch<sub>1955</sub>-based fundamentals shown in Fig. 8. Column (B) lists the best-fitting linear combinations when optimal macular and lens density adjustments to the CIE<sub>Judd</sub> cone fundamentals are permitted: the optimal adjustments are a reduction of 0.115 in peak macular density and a reduction of only 0.017 in lens density at 400 nm (as if the CIE<sub>Judd</sub> 2° observer had more macular density and slightly more lens density than the Stiles–Burch<sub>1955</sub> 2° observer). Smith *et al.*,<sup>79</sup> however, concluded that a reduction of 0.04 in peak macular density and an increase in lens density of 0.35 at 400 nm is required for making the CIE<sub>Judd</sub> 2° color-matching functions consistent with the Stiles–Burch<sub>1955</sub> 2° CMF's. The differences between these estimates are due in part to our adoption of (1) van Norren and Vos's modification to the Wyszecki–Stiles lens template and (2) Vos's modification to  $V_\lambda$  in the extreme violet: if we repeat the analysis, using the original CIE<sub>Judd</sub> 2° CMF's used by Smith *et al.*<sup>79</sup> [from Table 1(5.5.2) of Ref. 48] and the Wyszecki–Stiles lens template, we find that the CIE<sub>Judd</sub>-based cone fundamentals must be reduced in macular density by 0.13 at peak

**Table 4. Linear Combinations of the CIE<sub>Judd</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's That Best Fit the Proposed Stiles–Burch<sub>1955</sub>-Based Estimates of the M- and L-Cone Sensitivities (Appendix A)<sup>a</sup>**

Best-Fitting Parameters	Best-Fitting Density Adjustments	
	(A) None	(B) Macular and Lens <sup>b</sup>
M-Cone		
$a_M$	−0.156007	−0.154721
$b_M$	0.456840	0.456840
$c_M$	0.034803	0.033515
rms <sup>c</sup>	0.039294	0.022747
L-Cone		
$a_L$	0.099974	0.140664
$b_L$	0.543120	0.543120
$c_L$	−0.018539	−0.028216
rms <sup>c</sup>	0.037683	0.029959

<sup>a</sup>The coefficients  $a_M$  through  $c_L$  refer to  $M_\lambda = a_M \bar{x} + b_M \bar{y} + c_M \bar{z}$ ;  $L_\lambda = a_L \bar{x} + b_L \bar{y} + c_L \bar{z}$ , where  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  are the Judd<sup>39</sup> and Vos<sup>40</sup> modified CIE 2° CMF's and  $M_\lambda$  and  $L_\lambda$  are the linear combinations yielding the best fits to the Stiles–Burch<sub>1955</sub>-based cone fundamentals proposed in Appendix A.

<sup>b</sup>Reduction of 0.115 in peak macular density and 0.017 in lens density at 400 nm applied to the CIE<sub>Judd</sub> 2° CMF's.

<sup>c</sup>Root-mean-square fitting errors in log<sub>10</sub> sensitivity.

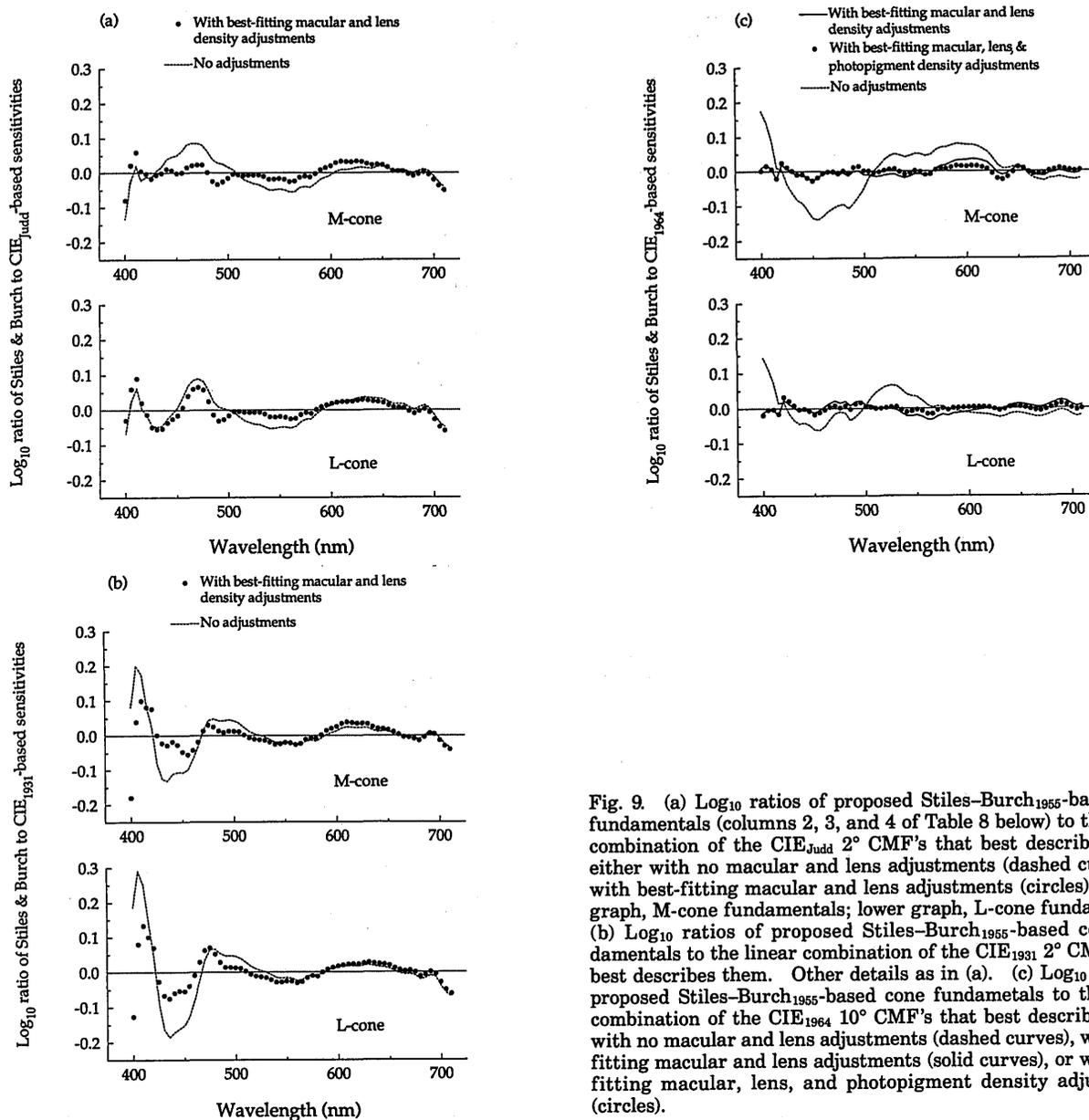


Fig. 9. (a) Log<sub>10</sub> ratios of proposed Stiles–Burch<sub>1955</sub>-based cone fundamentals (columns 2, 3, and 4 of Table 8 below) to the linear combination of the CIE<sub>Judd</sub> 2° CMF's that best describes them, either with no macular and lens adjustments (dashed curves) or with best-fitting macular and lens adjustments (circles). Upper graph, M-cone fundamentals; lower graph, L-cone fundamentals. (b) Log<sub>10</sub> ratios of proposed Stiles–Burch<sub>1955</sub>-based cone fundamentals to the linear combination of the CIE<sub>1931</sub> 2° CMF's that best describes them. Other details as in (a). (c) Log<sub>10</sub> ratios of proposed Stiles–Burch<sub>1955</sub>-based cone fundamentals to the linear combination of the CIE<sub>1964</sub> 10° CMF's that best describes them, with no macular and lens adjustments (dashed curves), with best-fitting macular and lens adjustments (solid curves), or with best-fitting macular, lens, and photopigment density adjustments (circles).

and increased in lens density by 0.31 at 400 nm for optimal consistency with the Stiles–Burch<sub>1955</sub>-based cone fundamentals. Presumably the remaining difference in inferred macular pigmentation arises because our fits were to the logarithms of the M- and L-cone fundamentals, whereas those of Smith *et al.* were to the logarithms of the three CMF's transformed to a common set of primaries, a procedure that introduces a somewhat arbitrary element into the comparison that depends on the choice of the primary wavelengths.

Figure 9(a) shows the difference in log<sub>10</sub> sensitivity between our cone fundamentals based on the Stiles–Burch<sub>1955</sub> 2° CMF's and the best-fitting approximations to them based on the CIE<sub>Judd</sub> 2° CMF's, both for the fits made with and without the optimal macular and lens density adjustments.

Without density adjustments, the differences between the Stiles–Burch<sub>1955</sub>-based cone fundamentals and the linear combinations of the CIE<sub>Judd</sub> 2° CMF's that best de-

scribe them are typically less than ~0.1 log<sub>10</sub> unit. When best-fitting macular adjustments are added, the differences are reduced, particularly in the case of the M-cone fundamental, but systematic and visually significant differences remain throughout the spectrum. Above 480 nm, these differences are similar (though not identical) for M and for L cones, suggesting that they could arise because of photometric or radiometric inconsistencies between the two CMF determinations: between 540 and 640 nm, for example, the best-fitting CIE<sub>Judd</sub> 2° CMF's fall slightly more steeply than the Stiles–Burch<sub>1955</sub>-based cone fundamentals. At shorter wavelengths, there are differences that follow a quite-different pattern for M than for L cones. Notably, between 435 and 465 nm, the change in the ratio of M- to L-cone sensitivity differs by ~0.1 log<sub>10</sub> unit in the two cases. When arbitrary macular and lens density adjustments are made, the differences between the CIE<sub>Judd</sub> 2° and the Stiles–Burch<sub>1955</sub> 2° standard observers do not appear large in a direct comparison of the under-

**Table 5. Linear Combinations of the CIE<sub>1931</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's That Best Fit the Proposed Stiles-Burch<sub>1955</sub> 2°-Based Estimates of the M- and L-Cone Sensitivities (Appendix A)<sup>a</sup>**

Best-Fitting Parameters	Best-Fitting Density Adjustments	
	(A) None	(B) Macular and Lens <sup>b</sup>
<b>M-Cone</b>		
$a_M$	-0.151530	-0.150522
$b_M$	0.456840	0.456840
$c_M$	0.042963	0.036119
rms <sup>c</sup>	0.056125	0.036886
<b>L-Cone</b>		
$a_L$	0.150241	0.159517
$b_L$	0.543120	0.543120
$c_L$	-0.015598	-0.025780
rms <sup>c</sup>	0.080911	0.041885

<sup>a</sup>The coefficients  $a_M$  through  $c_L$  refer to  $M_\lambda = a_M\bar{x} + b_M\bar{y} + c_M\bar{z}$ ;  $L_\lambda = a_L\bar{x} + b_L\bar{y} + c_L\bar{z}$ , where  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  are the CIE<sub>1931</sub> 2° CMF's and  $M_\lambda$  and  $L_\lambda$  are the linear combinations yielding the best fits to the Stiles-Burch<sub>1955</sub>-based cone fundamentals proposed in Appendix A.

<sup>b</sup>Reduction of 0.020 in peak macular density and 0.57 in lens density at 400 nm applied to the CIE<sub>1931</sub> 2° CMF's.

<sup>c</sup>Root-mean-square fitting errors in log<sub>10</sub> sensitivity.

lying CMF's.<sup>79</sup> Yet they imply essential differences in the color matches of the two observers that are visually significant and too large to be accounted for by individual variability (see Fig. 1 of Ref. 67). This analysis therefore provides, at best, qualified support for the conclusion of Smith *et al.*<sup>79</sup> that the differences between these CMF's are due mainly to lens and macular pigmentation, especially since, when these comparisons are made, inappropriate *ad hoc* adjustments in assumed prereceptoral filter densities can help to compensate for photometric or other inconsistencies.

Table 5 lists the linear combinations of the CIE<sub>1931</sub>  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$  2° CMF's that best fit our cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's. Column (A) specifies the latter straightforwardly as a best-fitting linear com-

ination of  $\bar{x}$ ,  $\bar{y}$ , and  $\bar{z}$ . The coefficients in column (A) are the appropriate ones for estimating the cone excitations when only the CIE<sub>1931</sub> tristimulus values are available. When macular and lens densities are allowed to vary as fitting parameters [column (B)], the best fit is obtained by reducing the peak macular density of the CIE<sub>1931</sub> 2° observer by only 0.02 at peak and lens density by 0.57 at 400 nm (this implies that the CIE<sub>1931</sub> 2° observer has approximately the same macular density but much more lens density than the Stiles-Burch<sub>1955</sub> 2° observer). As in the case of the CIE<sub>Judd</sub> CMF's (see above), these values agree only approximately with those of Smith *et al.*,<sup>79</sup> who concluded that an increase of 0.11 in peak macular density and a reduction in lens density of 0.39 at 400 nm are required for making the CIE<sub>1931</sub> 2° CMF's consistent with the Stiles-Burch<sub>1955</sub> 2° CMF's.

Figure 9(b) shows the difference in log<sub>10</sub> sensitivity between our Stiles-Burch<sub>1955</sub>-based cone fundamentals and the best-fitting approximations to them based on the CIE<sub>1931</sub> 2° CMF's. Without macular and lens adjustments, the fits at short wavelengths are poor. Adding the best-fitting macular and lens adjustments reduces the differences, but because the lens densities thereby attributed to the CIE<sub>1931</sub> 2° standard observer are unreasonably high, the significance of this is questionable: presumably the short-wavelength aberrations of the standard CIE<sub>1924</sub> luminosity function are due to photometric error rather than to exceptionally high lens pigmentation. This comparison indicates that the macular pigmentations of the CIE<sub>1931</sub> 2° observer and of the Stiles-Burch<sub>1955</sub> 2° observer are similar, which supports the suggestion (above) that the increase in effective macular pigmentation created by Judd's modification to the CIE<sub>1931</sub> 2° observer may be inappropriate.

Table 6 lists the linear combinations of the CIE<sub>1964</sub>  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  10° CMF's that best fit our proposed Stiles-Burch<sub>1955</sub>-based cone fundamentals. Column (A) specifies our 2° cone sensitivities as a best-fitting linear combination of  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$ . When macular and lens densities are allowed to vary as fitting parameters [column (B)], one

**Table 6. Linear Combinations of the CIE<sub>1964</sub>  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  10° CMF's That Best Fit the Proposed Stiles-Burch<sub>1955</sub> 2°-Based Estimates of the M- and L-Cone Sensitivities (Appendix A)<sup>a</sup>**

Best-Fitting Parameters	Best-Fitting Density Adjustments			
	(A) None	(B) Macular and Lens <sup>b</sup>	(C) Macular, Lens, and Photopigment <sup>c</sup>	(D) Luminance-Constrained Best Fit to (C) <sup>d</sup>
<b>M-Cone</b>				
$a_M$	-0.158975	-0.161721	-0.163185	-0.163504
$b_M$	0.456840	0.456840	0.456840	0.456840
$c_M$	0.034339	0.034447	0.034074	0.033559
rms <sup>e</sup>	0.069234	0.015521	0.010756	—
<b>L-Cone</b>				
$a_L$	0.288707	0.176588	0.155200	0.140330
$b_L$	0.543120	0.543120	0.543120	0.543120
$c_L$	-0.055388	-0.033326	-0.030040	-0.028803
rms <sup>e</sup>	0.038313	0.013883	0.008648	—

<sup>a</sup>The coefficients  $a_M$  through  $c_L$  refer to  $M_\lambda = a_M\bar{x}_{10} + b_M\bar{y}_{10} + c_M\bar{z}_{10}$ ;  $L_\lambda = a_L\bar{x}_{10} + b_L\bar{y}_{10} + c_L\bar{z}_{10}$ , where  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  are the 10° CMF's and  $M_\lambda$  and  $L_\lambda$  are the linear combinations yielding best fits to the Stiles-Burch<sub>1955</sub>-based cone fundamentals proposed in Appendix A.

<sup>b</sup>Increase of 0.195 peak macular density and reduction of 0.168 lens density at 400 nm applied to the CIE<sub>1964</sub> CMF's.

<sup>c</sup>Best-fitting photopigment density adjustment from an assumed photopigment density of 0.40 in the 2° observer to 0.30 in the 10° observer and best-fitting macular and lens density adjustments (an increase of 0.210 peak macular density and a reduction of 0.185 lens density at 400 nm applied to the CIE<sub>1964</sub> 10° CMF's).

<sup>d</sup>Sensitivities best fitting column (C) with the constraint that their weighted sum be  $\bar{y}_{10}$  (see text for details).

<sup>e</sup>Root-mean-square fitting errors in log<sub>10</sub> sensitivity.

obtains the best fit by increasing the peak macular density of the CIE<sub>1964</sub> 10° observer by 0.195 at peak (see also Fig. 2.6 of Ref. 58) and reducing lens density by 0.168 at 400 nm (as if the CIE<sub>1964</sub> 10° observer had less macular and more lens pigment than the Stiles–Burch<sub>1955</sub> 2° observer). When photopigment density as well as macular and lens densities is allowed to vary as fitting parameters [column (C)], the best fit requires a reduction in photopigment density for the CIE<sub>1964</sub> 10° observer from an assumed density of 0.40 for the Stiles–Burch<sub>1955</sub> 2° observer to 0.30, an increase in the peak macular density of the CIE<sub>1964</sub> 10° observer by 0.210 at peak, and a reduction in lens density by 0.185 at 400 nm.

The coefficients in column (C) generate our best estimates of the M- and L-cone sensitivities for a large (10°) field. We calculated corresponding cone sensitivities for a 2° field from these large-field cone sensitivities by using the estimated changes in macular density (from 0.28 to 0.70 times the Wyszecki–Stiles template) and photopigment density (from 0.30 to 0.40) in going from a 10° to a 2° field. These sensitivities are tabulated in columns 5, 6, and 7 of Table A (see also Subsection 3.I and Section 4 below).

Figure 9(c) shows the difference in log<sub>10</sub> sensitivity between the proposed Stiles–Burch<sub>1955</sub>-based cone fundamentals and the best-fitting approximations to them based on the CIE<sub>1964</sub> 10° CMF's. As expected, without macular adjustments the fits at short wavelengths are poor. With macular and lens adjustments the average (M + L) rms deviations are reduced from 0.0538 to 0.0147. If we also correct for changes in photopigment density, the rms deviation falls to 0.0097.

The adjustment of macular pigment density needed for reconciling these two sets of CMF's is substantial, naturally so in view of the difference in field size. Fortunately, the 10 subjects who made the 2° matches also participated in the 10° experiments, and comparison of the 10° matches of those 10 observers and those of the remaining 39 observers in that investigation (as reported by Stiles<sup>82</sup>) makes it clear that the 10 subjects did not differ substantially from the others in macular pigmentation. More troublesome is the indication (also reflected in Stiles's analysis of the differences between the 10° matches) that the 10 observers of the 2° study may have had less lens pigmentation than the other 10° observers. This could suggest that a small lens density correction might make the Stiles–Burch 2° CMF's more representative. On the other hand, it is reassuring that the short-wave luminosity functions of the 10 observers of the 2° study agreed with those of 18 other observers.<sup>67</sup> Moreover, the results of Smith and Pokorny<sup>6</sup> with dichromats (see Fig. 8) suggest a deviation in, if anything, the opposite direction.

### G. S-Cone Sensitivity and Rod Intrusion in the Stiles–Burch<sub>1955</sub> 2° Color-Matching Functions

Since the results considered thus far favor the Stiles–Burch<sub>1955</sub> 2° CMF's as the basis for computation of the M- and L-cone sensitivities, we now ask whether they can also yield a plausible S-cone sensitivity. Stiles's  $\pi_3$  field sensitivity<sup>13</sup> is probably the most-accurate psychophysical estimate of the S-cone sensitivity obtained by chromatic adaptation in normal eyes. The S cones are comparatively easy to isolate because they preserve their sensitivity well in the presence of long-wavelength adapting fields.

As shown in Fig. 10, this is reflected in the low field sensitivity of  $\pi_3$  in the green-to-red spectral range, where its sensitivity falls by more than a factor of 10 per 1000 cm<sup>-1</sup> in wave number. Psychophysical test sensitivities for S cones in the normal eye, for instance those found by Stockman *et al.*,<sup>47</sup> are quite consistent with the  $\pi_3$  field sensitivity until M- and L-cones intrude, at wavelengths longer than ~540 nm. If  $\pi_3$  is an approximate measure of S-cone sensitivity, it should be possible to fit it with an appropriate linear combination of the Stiles–Burch<sub>1955</sub> 2° CMF's.

In the case of the S cones, however, no appeal to other criteria, such as  $\pi_3$  or data from dichromats, is really necessary for estimating the cone spectral sensitivity. The trichromatic CMF's themselves provide evidence that one cone type has negligible sensitivity in the yellow spectral range (as well as at the red primary wavelength). In the range 555–595 nm, the test light has to be mixed with a small amount of the blue primary in order to match a suitable mixture of the red and green primaries; and, significantly, the amount of blue primary required is simply proportional to the amount of green primary. This is the behavior expected if one of the cone types determining the match is sensitive only to the blue and green primary lights in the matching field and not to the red primary or to the test lights because, in that case, the blue primary (on one side of the field) must simply match the effect of the green primary (on the other side of the field) for those cones. The ratio of the energies of blue and green required for a match in this spectral range will therefore be constant and will be inversely proportional to the cone sensitivities for those two primaries. Thus one can con-

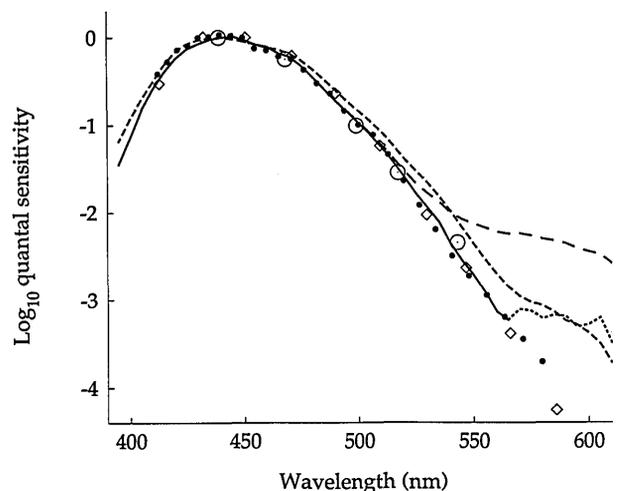


Fig. 10. Comparisons among S-cone spectral-sensitivity estimates. Psychophysical data: Stiles's  $\pi_3$  field sensitivity (filled circles) from Table 2(7.4.3) of Ref. 48 and unpublished mean 5-Hz test sensitivities for two of our subjects (dotted circles); details as for subject AS, 5-Hz data, Fig. 1 of Stockman *et al.*<sup>47</sup> S-cone fundamentals: Stiles–Burch<sub>1955</sub>-based estimate (long-dashed curve) of Vos *et al.*<sup>57</sup> CIE<sub>Judd</sub>-based estimate (short-dashed curve) of Vos and Walraven<sup>55</sup> and of Smith and Pokorny<sup>6</sup>; and linear combination of the Stiles–Burch<sub>1955</sub>  $\bar{g}$  and  $\bar{b}$  2° CMF's (solid curve) that best fits  $\pi_3$  up to 565 nm; beyond 565 nm (dashed extension of solid curve) the CMF's do not define S-cone sensitivity with useful precision. Monkey data: suction electrode recordings (diamonds) from Baylor *et al.*,<sup>15</sup> shifted 400 cm<sup>-1</sup> to shorter wavelengths and corrected for macular and lens densities and for axial photopigment density (see text).

struct the entire spectral-sensitivity function simply by combining the green and blue CMF's in that ratio. In the Stiles-Burch<sup>1955</sup> 2° CMF's the ratio of blue to green energy is constant at  $\sim 0.0157$  for lights of 555–595 nm. The corresponding cone sensitivity,  $\bar{b} + 0.0157\bar{g}$ , is a good candidate S-cone fundamental inasmuch as it follows  $\pi_3$  quite closely in the spectral range up to 550 nm. For the S-cone fundamental, we chose a slightly higher coefficient of  $0.0165\bar{g}$  in order to fit  $\pi_3$  up to 565 nm: this choice minimizes the mean-squared error in fitting the logarithm of the  $\pi_3$  sensitivities over that range.

In contrast, most previous Stiles-Burch<sup>1955</sup>-based S-cone fundamentals, such as that of Vos *et al.*<sup>57</sup> (our Fig. 10, long-dashed curve) or Smith *et al.*,<sup>79</sup> deviate implausibly both from the data and from the expected shape for a visual pigment absorption spectrum in the yellow-green (530–570 nm) range. S-cone fundamentals based on the CIE<sub>Judd</sub> 2° CMF's such as those of Vos and Walraven<sup>55</sup> or of Smith and Pokorny<sup>6</sup> (our Fig. 10, short-dashed curve) show a similar excess of sensitivity in this range (see also Fig. 9 of Ref. 83) partly because the long-wavelength-spectrum locus standardized by the CIE systematically avoids the color-matching data on which it is based<sup>58,59</sup>: the resulting errors in the inferred S-cone sensitivity, though small in linear terms, exceed a factor of 2 in the red-green spectral range. Pugh and Sigel,<sup>68</sup> however, proposed an S-cone sensitivity similar to the present one, based on a fit to  $\pi_3$  with the Stiles-Burch CMF's.

In the yellow and orange (Fig. 10, dashed extension of the continuous solid curve), the CMF's do not define the S-cone sensitivity with useful precision for two reasons. First, the S-cone excitations produced by these test lights are close to the minimum detectable energies for the S-cone system.<sup>84,85</sup> Second, the derived sensitivity in this range is a small difference between two approximately equal measured quantities ( $0.165\bar{g}$  and  $\bar{b}$ , the value of  $\bar{b}$  being negative), so a small percentage error in either  $\bar{b}$  or  $\bar{g}$  can drastically alter the inferred sensitivity. Rather than retaining the function derived from the CMF's in this spectral range, it is much more reasonable for one to suppose that the logarithm of S-cone sensitivity continues to decline approximately linearly with wave number in the way suggested by  $\pi_3$ , by objective measurements of visual pigment spectra, and by the electrophysiological action spectra reported by Baylor *et al.*<sup>15</sup> With an appropriate spectral shift (see Subsection 3.H below), the latter agree well with the psychophysical data.

At still longer wavelengths, the amounts of blue required in the matches increase again and become disproportionate to the amounts of the green primary. This is not expected for a three-cone system, but, as Stiles has pointed out,<sup>82</sup> it is qualitatively understandable if rod intrusion occurs, with an effect equivalent to adding some white light to the half-field that contains the (scotopically dominant) green primary. (The effect is greater in the red because the scotopic contrast exhibited by the matching field increases with increasing test wavelength, and the scotopic field luminances are much less in the deep-red part of the spectrum.) The energy of this equivalent added white that is attributable to rod intrusion can be inferred from the amount of excess blue required in the match, and the values of  $\bar{g}$  and  $\bar{r}$  as well as  $\bar{b}$  can be corrected for the intrusion by subtracting the tristimulus values of the equivalent

white from the (signed) CMF's if the green primary is positive (in the opposite half-field from that of the test light) or by adding them if it is negative.

By design, this correction makes the implied S-cone sensitivities at long wavelengths small. The effect of the correction on the M- and L-cone sensitivities depends on the assumed color of the scotopic white, but fortunately it is small in any case. The only potentially significant effect is a reduction in the M-cone sensitivity in the deep red, and even this is practically negligible (less than 0.05 log<sub>10</sub> unit) for wavelengths less than 700 nm. Moreover, corrections based on the added-white model (whether it is an equal-energy white or, for example, an equal-quanta-per-unit-wave number white) appear excessive in that they implausibly distort the M-cone sensitivity beyond 720 nm and eliminate the reversal of the spectrum locus at long wavelengths. Presumably the effect of rod excitation in the 2° field is more akin to the addition of a distinctly bluish stimulus than to the addition of a white. We therefore have not felt the need to incorporate any rod-intrusion correction in the figures or tables of this paper.

## H. Comparisons of Psychophysically Derived Measurements with Microspectrophotometric and Electrophysiological Measurements

### 1. Introduction

The psychophysically derived M- and L-cone fundamentals can be compared with objective measurements of single-cone outer segments obtained either by MSP or by suction electrode recordings.

In MSP one compares the spectral transmission of a small measuring beam (passing transversely through the outer segment of a single cone) with that of a reference beam (passing outside the cone) to derive the absorption spectrum of the outer segment (Ref. 86, for example). Microspectrophotometric measurements, however, are subject to systematic distortions that are due to wavelength-dependent factors such as light scattering, absorption by substances other than visual pigment (including photoproducts), and focusing errors.<sup>87</sup> Many of these problems can be avoided or reduced if, instead of an absorption spectrum, an action spectrum is measured. This is accomplished in suction electrode recordings, in which a single human or primate cone outer segment is drawn inside a small glass electrode and its electrical response to lights of different wavelength recorded (for example, Refs. 15 and 88).

Both the suction electrode and MSP measurements, however, have employed light stimuli that were passed transversely through the outer segment rather than axially as in normal vision. This introduces two difficulties. First, it is not clear how the interaction between light and the photoreceptor modifies the axial action spectrum. Second, the axial visual pigment density is much higher than the transverse density. Thus, relative to the transverse spectral-sensitivity measurements, the axial spectral sensitivity is broadened by self-screening.

### 2. Methods

The corneal spectral sensitivities were constructed from the low-density suction electrode action spectrum, or the MSP absorbance spectrum  $A_\lambda$ , as follows. First, the ac-

tual fraction of incident light absorbed by the photoreceptor for axially incident lights of different wavelength (the absorption spectrum  $J_\lambda$ ) was determined; this fraction depends on the peak axial optical density  $D$  of the photopigment in the outer segment.  $J_\lambda$  is related to  $D$  and to  $A_\lambda$  by the following equation (see Knowles and Dartnall,<sup>89</sup> p. 56), which implies a broadening of the absorption spectrum relative to the low-density absorption spectrum when the density  $D$  becomes sufficiently high:

$$J_\lambda = 1 - 10^{-DA_\lambda}$$

Second, we derived the corneal sensitivity from the absorption spectrum ( $J_\lambda$ ) by allowing for prereceptor filtering. The densities that we assumed were 100% of the van Norren-Vos lens pigment density for a small pupil (1.68 at 400 nm) and 70% of the Wyszecki-Stiles macular pigment (0.35 peak).

The value of  $D$  required for conversion from the absorbance to the absorption spectra is uncertain. Evidence about  $D$  can be obtained by a comparison of spectral sensitivity or color matching when the concentration of the photopigment is dilute to when it is in its normally high concentration. This evidence can be collected psychophysically by a comparison of data obtained (i) under bleached versus unbleached conditions or (ii) for obliquely versus axially presented lights. Data can also be obtained (iii) objectively by MSP or by retinal densitometry.

(i) *Bleaching.* In seven color-normal observers the changes in color matches accompanying bleaching indicated a mean photopigment density of 0.51.<sup>90</sup> In a single normal observer, Terstiege<sup>91</sup> obtained differences that were consistent with a higher photopigment density of 0.7–0.9, and, also in a single observer, Wyszecki and Stiles<sup>92</sup> found differences that suggested lower-density values of 0.44 for the L cones and 0.38 for the M cones. Two studies used dichromatic observers. Miller<sup>93</sup> estimated the density for the deuteranope to be 0.5–0.6 and that for the protanope to be 0.4–0.5, and Smith and Pokorny<sup>94</sup> found mean photopigment densities of 0.4 for four deuteranopes and 0.3 for three protanopes. Recently Burns and Elsner suggested mean photopigment densities of 0.48 for the L cones and only 0.27 for the M cones of six observers (see Table 1 of Ref. 95).

(ii) *Oblique presentation.* The change in color of monochromatic lights when they are obliquely incident upon the retina can be well described by a self-screening model in which the effective photopigment density is less for oblique incidence (but see Ref. 96). Such analyses have yielded higher estimates of photopigment density of between 0.69 and 1.0,<sup>97,98</sup> generally for a 1° field.

(iii) *Objective measures.* MSP suggests a specific density in the macaque of  $0.015 \pm 0.004 \mu\text{m}^{-1}$  for the M cones and  $0.013 \pm 0.002 \mu\text{m}^{-1}$  for the L cones.<sup>86</sup> If we assume a foveal-cone outer segment length of  $35 \mu\text{m}$ ,<sup>81</sup> these values give axial photopigment densities of approximately 0.5 (see also Ref. 14). Retinal densitometry gives a density value of 0.35 for the M cones<sup>99</sup> and 0.41 for the L cones.<sup>100,101</sup>

With the exception of the results obtained by Terstiege,<sup>91</sup> bleaching measurements yield mean density values in the range 0.3–0.6, Stiles–Crawford analyses in the range 0.7–1.0, and objective measures in the range 0.35–0.50. We have decided to base our estimate of  $D$  mainly on the

bleaching and objective measures and so choose a value of 0.40. There is clearly a good deal of uncertainty in the choice of  $D$ . On the basis of the available evidence, values much lower than 0.35, such as the value of 0.27 assumed by Baylor *et al.*,<sup>15</sup> seem implausible, but for completeness we also consider the photopigment density of 0.27 in our comparison with suction electrode data.

The bleaching data reviewed above suggest a lower density for M than for L cones. But the other evidence contradicts this. Notably, with oblique presentation, spectral lights of 548 nm ( $\pm 5$  nm standard error of the mean) retain the same appearance when obliquely incident upon the retina, while longer wavelengths appear redder and shorter ones greener.<sup>98,102–104</sup> If we assume that the M- and L-cone densities are the same at the invariant wavelength, as the self-screening model requires, this means that the peak densities must be similar, or at any rate not substantially greater for the L than for the M cones ( $D_L = D_M - 0.04 \pm 0.026$  standard error of the mean). A similarity in peak photopigment densities is also supported by MSP.<sup>86</sup> Further evidence on this point comes from the comparison between large-field and small-field CMF's: when we repeated the analysis shown by Fig. 9(c), allowing independent variation of visual pigment density for M and L cones, the required density changes with field size were not substantially different.

If short-wavelength-absorbing photoproducts are reducing the densities inferred from the bleaching experiments, they would do this more for the M than for the L cones, and this could explain the discrepancy. We therefore assume the M- and L-cone densities to be the same.

### 3. Results

Figure 11(a) shows the human MSP data of Dartnall *et al.*<sup>12</sup> (from their Table 2) and the rhesus monkey MSP data of Bowmaker *et al.*<sup>86</sup> (from their Table 4). Both sets of data are adjusted to a peak photopigment density of 0.40 and are corrected for lens pigment (1.68 at 400 nm) by use of 1.16 times the van Norren-Vos<sup>44</sup> (open pupil) template, and for macular pigment (0.35 at peak) by use of the standard Wyszecki–Stiles<sup>48</sup> templates (see above). The continuous curves are our cone fundamentals (see columns 2, 3, and 4 in Table 8 below) given as quantal sensitivities.

The agreement between the human MSP data and our cone fundamentals is notably poor, particularly for the M-cone data. Discrepancies of this magnitude suggest that MSP is of little value in defining cone spectral sensitivities.

Figure 11(b) shows the cynomolgus monkey suction electrode recordings of Baylor *et al.*<sup>15</sup> (from their Table 1) adjusted to a peak photopigment density of either 0.40 or their assumed density of 0.27 and corrected for the lens and macular pigment densities (see Subsection 3.H.2). Again, the continuous curves are the cone fundamentals of Table 8, expressed on a quantal basis.

The monkey suction electrode spectra are closer to our fundamentals than are the human MSP spectra. Nevertheless, the suction electrode spectra adjusted to a peak photopigment density of 0.27, the value derived by Baylor *et al.*<sup>15</sup> from their comparisons with CMF's, are broader than our cone fundamentals at long wavelengths. In contrast, at short wavelengths the macular and lens adjustments bring the monkey suction electrode data tolerably

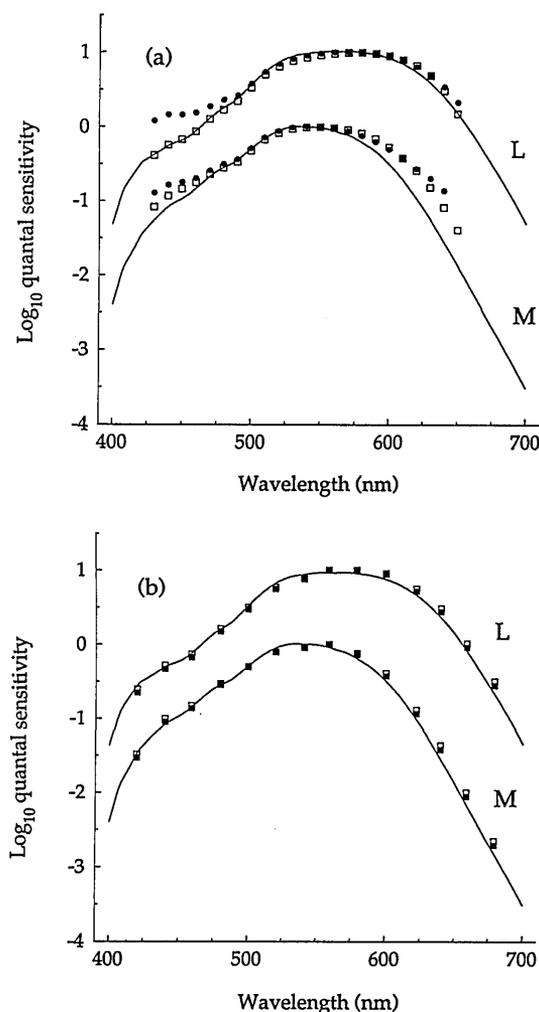


Fig. 11. Comparisons of proposed Stiles-Burch<sub>1955</sub>-based cone fundamentals (solid curves, from Appendix A) and MSP and suction electrode spectra. (a) Human MSP data (circles) from Table 2 of Dartnall *et al.*<sup>12</sup> and rhesus monkey MSP data (open squares) from Bowmaker *et al.*,<sup>86</sup> both adjusted to a peak photopigment density of 0.40 and corrected for typical lens and macular pigmentation (see text). (b) Cynomolgus monkey suction electrode spectra from Baylor *et al.*,<sup>15</sup> adjusted to a peak photopigment density of 0.40 (open squares) or 0.27 (filled squares), and corrected for typical lens and macular densities.

close to our fundamentals; this sustains the assumption that the macular and lens pigment densities in the Stiles-Burch<sub>1955</sub> 2° observer are not atypical.

The peak photopigment density of 0.27 chosen by Baylor *et al.*<sup>15</sup> is almost certainly less than the true optical density of the photopigment in cone outer segments of the central 2° of vision. The value of 0.40 has much better experimental support (see above). With this optical density, the M- and L-cone suction electrode spectra are too broad to describe our cone fundamentals at long wavelengths; they are also too broad to account for (1) our own psychophysical data from dichromats and normals, (2) most other dichromat data (see Figs. 5 and 6), and (3) the CIE<sub>Judd</sub>-based cone fundamentals derived by Smith and Pokorny<sup>6</sup> and by Vos and Walraven.<sup>55</sup>

How can this apparent inconsistency be understood? One possibility is that macaque and human pigments are not the same.<sup>105,106</sup> Alternatively (or in addition), a more-

elusive factor may be at work. Light is transmitted along the photoreceptor in patterns called waveguide modal patterns (see Fig. 6 of Ref. 107). The fraction of the power of each modal pattern that is transmitted inside the photoreceptor to its power outside the photoreceptor decreases with the wavelength of the incident light, so that, in principle, the structure of the photoreceptor can change its spectral sensitivity (see, for example, Refs. 98 and 108–110). It is difficult to know precisely how waveguide factors will influence the spectral sensitivity for axially incident light in the human fovea, since many of the relevant quantities, such as the refractive indices inside and outside the cone outer segment, are uncertain. If we assume values of 1 μm for the diameter of a human foveal-cone outer segment<sup>81</sup> and 1.39 and 1.35, respectively, for the refractive indices inside and outside the cone outer segment (Fig. 6.11 of Ref. 110), standard formulas [Eq. (7a) and Fig. 9 of Ref. 109] suggest a loss of spectral sensitivity for mode  $\eta_{11}$  (the most important mode for axially incident light) of  $\sim 0.2 \log_{10}$  unit for red light relative to violet. Adjustments of this magnitude would bring the suction electrode data and the cone fundamentals shown in Fig. 11(b) into much closer agreement, without the need for spectral shifts. Although we cannot be certain of the importance of waveguide factors, it is clear that the interaction between the photoreceptor and the incident light must be considered in any reconstruction of the axial spectral sensitivity from transverse measurements (see Ref. 110, Sec. 6.4.3).

In the case of the S cones, there is a more-pronounced mismatch between macaque electrophysiology and human psychophysics. With our standard corrections (0.35 peak macular density, 1.68 lens density at 400 nm, and 0.40 photopigment density), a shift of 400 cm<sup>-1</sup> or  $\sim 8$  nm to shorter wavelengths is required for bringing the macaque data (open diamonds, Fig. 10) into agreement with the human psychophysical estimates. In this case, the evidence from MSP supports a difference of this magnitude between the macaque and the human S-cone pigments.<sup>12,111</sup>

### I. Action Spectra of the Cone Photopigments

After correction for prereceptor filtering and adjustment to an infinitely low photopigment density, candidate cone fundamentals must yield plausible cone photopigment action spectra.

Figure 12 shows action spectra derived from the cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's (columns 2, 3, and 4 of Table 8 below) by assuming 1.16 times the van Norren-Vos<sup>44</sup> lens pigment density template (i.e., their standard, open-pupil template adjusted for a small pupil), 0.70 times the Wyszecki-Stiles<sup>48</sup> macular pigment template, and a photopigment density of 0.40 (see above). Though it is not ideal (see below), the van Norren-Vos lens template, based on the differences between the scotopic luminosity function and the rhodopsin photopigment spectrum, was clearly preferable to the Wyszecki-Stiles lens template, which generated action spectra with a marked discontinuity in the violet.

It can be seen that there are small irregularities in the action spectra, especially in the case of the S-cone spectrum at short wavelengths; these may reflect experimental error in the pilot Stiles-Burch<sub>1955</sub> 2° data.

Figure 13 shows cone action spectra derived from the

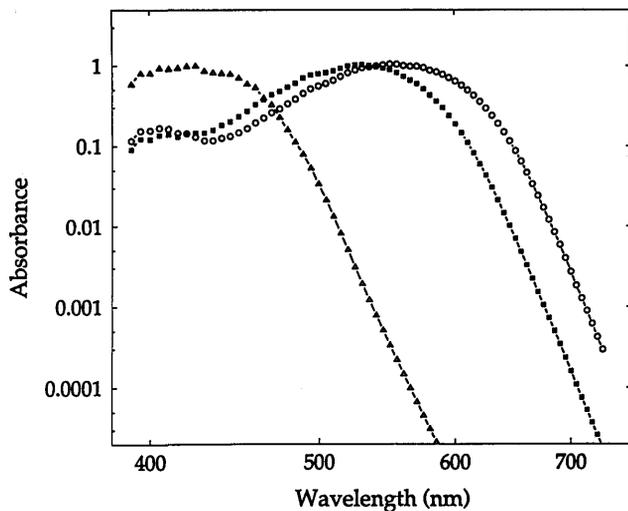


Fig. 12. S-cone (triangles), M-cone (squares), and L-cone (circles) action spectra derived from the cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's (Table 8 below) by assuming 1.16 times the van Norren-Vos (open pupil) lens pigment template, 0.70 times the Wyszecki-Stiles macular pigment template, and a photopigment density of 0.40.

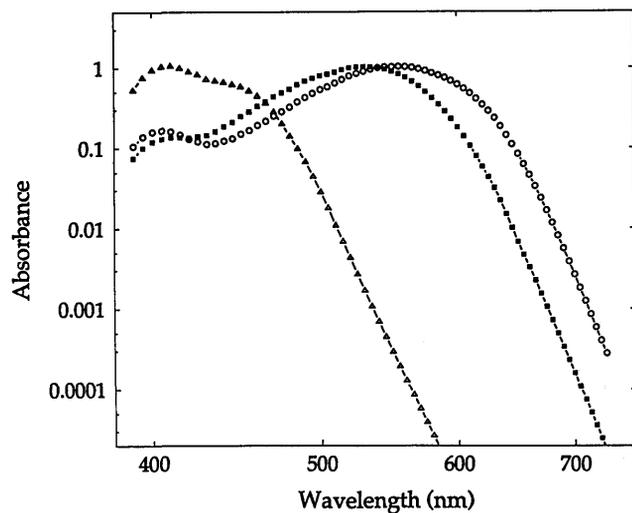


Fig. 13. S-cone (triangles), M-cone (squares), and L-cone (circles) action spectra derived from the cone fundamentals based on the CIE<sub>1964</sub> 10° CMF's [column (C) of Table 6] by assuming 1.28 times the van Norren-Vos (open pupil) lens pigment template, 0.28 times the Wyszecki-Stiles macular pigment template, and a photopigment density of 0.30.

cone fundamentals based on the CIE<sub>1964</sub> 10° CMF's [column (C) of Table 6] by assuming 1.28 times the van Norren-Vos lens pigment template, 0.28 times the Wyszecki-Stiles macular pigment template, and a photopigment density of 0.30. These are the values that optimize the consistency between the 2° and the 10° CMF's [see Table 6 and Fig. 9(c)].

The CIE<sub>1964</sub> 10° S-cone fundamental used to derive the action spectrum shown in Fig. 13 was chosen in a fashion similar to that for the proposed 2° S-cone fundamental (see above). The 1964  $\bar{z}_{10}$  function can hardly be an accurate representation of the S-cone sensitivity in a 10° field: it is broader than the 2° S-cone function shown in Fig. 10 (perhaps for consistency with the CIE 1931  $\bar{z}$  function) and shows an inflection to accommodate its increased

sensitivity in the green before being artificially truncated in the yellow. Fortunately, the 10° data of Stiles and Burch, like their 2° data, show proportionality between the energies of the blue and green primaries in the yellow-green; the suggested ratio of green primary to blue primary is ~0.0105 (rather than 0.0165 for their 2° CMF's), consistent with the expected effects of reductions in macular and visual pigment density. (The CIE<sub>1964</sub>  $\bar{z}_{10}$  differs considerably from the data of Stiles and Burch in this range, probably because of rod intrusion in the Speranskaya data, which were collected at lower intensities.) We adopted as the 10° S-cone spectral sensitivity the linear combination of  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  coefficients that best described  $\bar{b} + 0.0105\bar{g}$  in the range from 390 to 540 nm, where  $\bar{b}$  and  $\bar{g}$  are the Stiles-Burch 10° CMF's. The fit minimized the mean-squared logarithmic difference between the functions. The best-fitting coefficients were 0.040557 $\bar{x}_{10}$ , -0.019683 $\bar{y}_{10}$ , +0.486195 $\bar{z}_{10}$ . These provide a plausible estimate of the S-cone spectral sensitivity up to 520 nm, at which point data and curve are both already decreasing exponentially with wave number. Beyond 520 nm the decimal logarithm of the S-cone spectral sensitivity (adjusted to unity peak) can be extended with the following exponential, which has the same gradient as the function used to extend the 2° S-cone fundamental: 10402.1/ $\lambda$  - 21.7185 (where  $\lambda$  is in nanometers).

The S-cone action spectrum in Fig. 13 has a pronounced short-wavelength hump peaking at ~410 nm. This hump is unlikely to reflect the true pigment shape and must therefore reflect errors either in the CIE<sub>1964</sub> 10° CMF's or in the macular pigment or the lens pigment density spectra used to calculate the pigment curves. If we assume that the CIE<sub>1964</sub> CMF's are correct, the most likely source of error at such short wavelengths is the lens spectrum, especially since the results shown in Fig. 9(c) support the correctness of the macular pigment template adopted from Wyszecki and Stiles.<sup>48</sup> We therefore adjusted the standard lens pigment template of van Norren and Vos<sup>44</sup> in order to improve the shape of the cone action spectra. Two procedures were used.

In the first procedure, A, we adjusted the van Norren-Vos lens template to smooth both the 2°- and the 10°-based cone fundamentals. Figure 14 shows the resulting CIE<sub>1964</sub> 10°-based spectra and the Stiles-Burch<sub>1955</sub> 2°-based spectra. The lens adjustment is shown as Adjustment A in Fig. 16 below. As expected from Fig. 9(c), the 2°- and the 10°-based M- and L-cone spectra agree remarkably well. But, although the overall agreement between the two S-cone spectra is good, small differences remain that cannot be removed by prereceptor filter adjustments. These differences are due, in part, to the irregularities in the 2° function.

In the second procedure, B, we adjusted the lens template shape to smooth only the 10°-based cone photopigment action spectra, thus ignoring (on the grounds of their reduced reliability) the 2° spectra. We chose the adjustments to minimize the differences between the S-cone action spectrum and the L- and M-cone spectra when they were shifted to superimpose upon a log<sub>10</sub>-wavelength plot. This method depends on the assumption that the spectra are approximately shape invariant when the appropriate scale is used (see, for example, Refs. 53 and 54).

Figure 15 shows the CIE<sub>1964</sub> 10°-based spectra derived

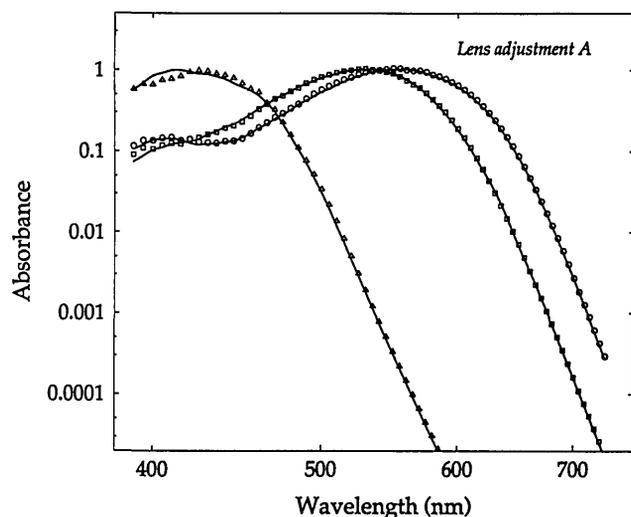


Fig. 14. Cone action spectra derived from the cone fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's (symbols) and CIE<sub>1964</sub> 10° CMF's (curves). Details as in Figs. 12 and 13, except that Adjustment A (see Fig. 16 below) was made to the van Norren-Vos lens pigment template.

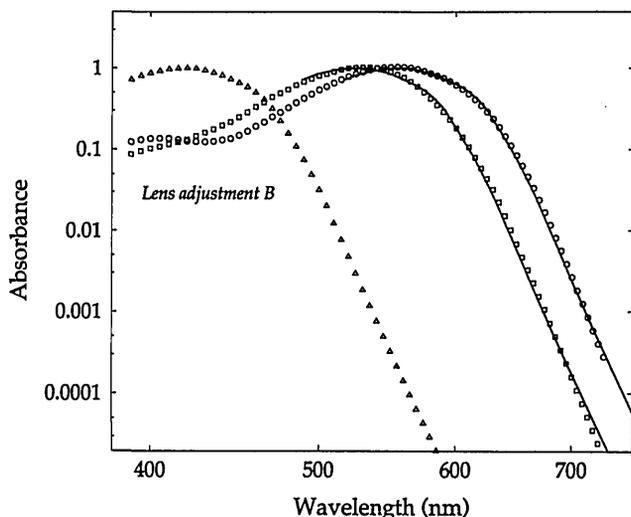


Fig. 15. Cone action spectra derived from the cone fundamentals based on the CIE<sub>1964</sub> 10° CMF's (symbols). Details as in Fig. 13, except that Adjustment B (see Fig. 16 below) was made to the van Norren-Vos lens pigment template. The S-cone pigment curve is shown shifted laterally to align with the M- and L-cone curves (solid curves).

by use of the adjusted lens pigment. The S-cone action spectrum is shown shifted laterally to align with M- and L-cone curves. With this correction to the van Norren-Vos lens template, which is shown as Adjustment B in Fig. 16, the action spectra are very similar. (In Figs. 14 and 15, a small adjustment of  $< \pm 0.023$  in density was made to the Wyszecki-Stiles template shape in the region between 490 and 520 nm. This has the effect of removing the small irregularity in the 2° and 10° pigment curves that can be seen in Figs. 12 and 13 at ~510 nm.)

Lens adjustments A and B shown in Fig. 16 are very similar. Both adjustments yield a convincing rhodopsin action spectrum when used to correct the scotopic  $V_l$  luminosity function to the photoreceptor level. Because of its consistency with the 10° cone fundamentals and the regularity of the resulting pigment template, we favor Adjust-

ment B over A. The open-pupil lens pigment densities based on Adjustment B applied to the van Norren-Vos lens template are given in Table 7.

Even with the adjusted lens template, the shape invariance represented in Fig. 15 is only approximate, since the L-cone shape is slightly broader than either the M- or the S-cone shapes. Yet this difference is increased if Barlow's<sup>112</sup> fourth-root-of-wavelength scale is used instead of log wavelength; and the use of a wave-number scale produces opposite but larger mismatches in width. Thus the CIE<sub>1964</sub> CMF's suggest that, of these three scales, the log wavelength scale gives the best approximation to shape invariance.

Since the action spectra derived from the 2° and the

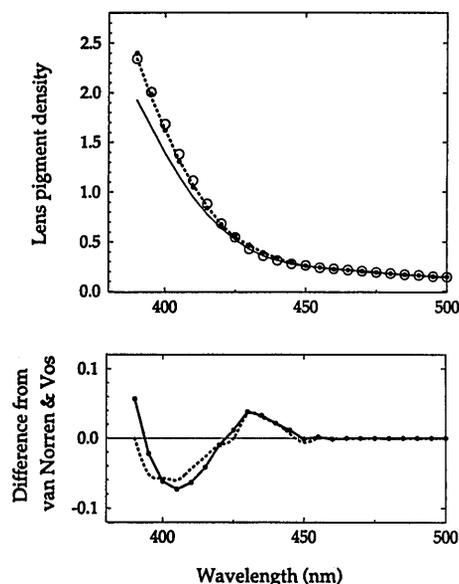


Fig. 16. Upper panel, Comparison of the Wyszecki-Stiles lens pigment template (solid curve), the van Norren-Vos template (open circles), and two adjustments to the van Norren-Vos template. Lower panel, Comparison of adjustments to the van Norren-Vos lens pigment template. Both panels: Dashed curve, Adjustment A; filled circles, Adjustment B. All templates shapes are for a small pupil.

**Table 7. Proposed Lens Pigment Densities for a Standard Observer with a Completely Open Pupil<sup>a</sup>**

Wavelength (nm)	Density
390	2.069
395	1.711
400	1.397
405	1.127
410	0.905
415	0.724
420	0.582
425	0.480
430	0.403
435	0.338
440	0.289
445	0.250
450	0.224
455	0.207
460	0.194

<sup>a</sup>For a small pupil, multiply the densities by 1.16; for densities at  $\lambda > 460$  nm, use Table II(2.4.6) of Ref. 48. The tabulated densities are based on Adjustment B to the van Norren-Vos lens pigment template shape.<sup>44</sup>

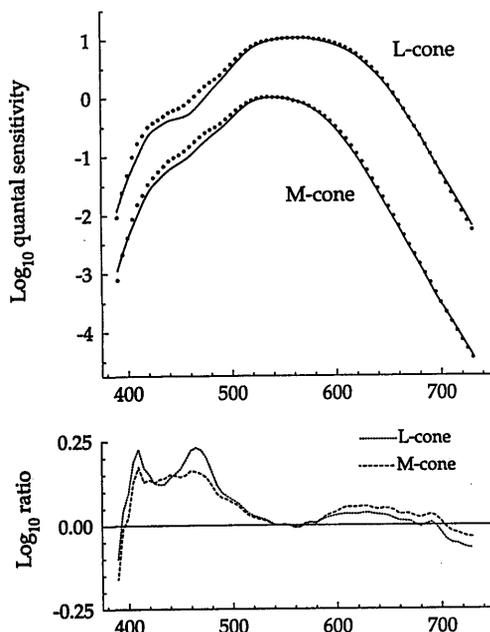


Fig. 17. Upper panel, Comparison of the CIE<sub>Judd</sub>-based 2° cone fundamentals of Smith and Pokorny<sup>6</sup> (curves) and the proposed fundamentals based on the Stiles-Burch<sub>1955</sub> 2° CMF's (circles) given in columns 2, 3, and 4 of Table 8 below. Lower panel, Differences between the M-cone (dashed curves) and the L-cone (dotted curve) fundamentals.

10° CMF's are virtually indistinguishable except in the far violet part of the spectrum, we propose an alternative specification of the 2° cone fundamentals that is based not on the Stiles-Burch<sub>1955</sub> 2° CMF's but instead on the CIE<sub>1964</sub> 10° CMF's. There are several advantages in doing this:

1. The 10° CMF's are based on data obtained from many more individuals than are the 2° CMF's and are therefore likely to be more representative of the average population.
2. The 2° CMF's are recognized as pilot data, whereas the 10° CMF's are an internationally accepted standard.
3. The use of the 10° CMF's to derive the 2° cone fundamentals removes minor imperfections in the fundamentals that are traceable to the 2° CMF's and that are probably due to experimental error.

To derive the 2° fundamentals from the 10° CMF's, we started with the 10° cone fundamentals [column (C) of Table 6] and corrected them to action spectra by using the values referred to above (1.28× lens and 0.28× macular density and a photopigment density of 0.30). We then recalculated the corneal cone spectral sensitivities by reversing the calculation and using the same lens density but 2° density values for the other parameters (0.70× macular density and a photopigment density of 0.40). The resulting sensitivities are tabulated in columns 5, 6, and 7 of Table 8 below. The only substantial and systematic discrepancies between these and the sensitivities of columns 2, 3, and 4 are in the far violet, where the sensitivity is lower for the CIE<sub>1964</sub> observer. This is due in part to a slightly higher lens density in the average CIE<sub>1964</sub> observer than in the Stiles-Burch<sub>1955</sub> observer (see above). Here the 2° cone fundamentals based on the Stiles-Burch<sub>1955</sub> CMF's are intermediate between those based on the CIE<sub>1964</sub> and those based on the CIE<sub>Judd</sub> CMF's.

#### 4. DISCUSSION

The proposed new sets of fundamentals based on either the Stiles-Burch<sub>1955</sub> 2° CMF's or the CIE<sub>1964</sub> 10° CMF's are consistent with each other, with protanopic and deuteranopic spectral sensitivities, with tritanopic color matches, and with the isolated cone spectral sensitivities of normal observers. The differences between the proposed cone sensitivities and those of Smith and Pokorny,<sup>6</sup> illustrated in Fig. 17, are small enough to be colorimetrically insignificant in most situations in which only broadband spectra are of interest but big enough to alter materially the predicted visual effects of spectral or narrow-band stimuli. The Stiles-Burch<sub>1955</sub>- or the CIE<sub>1964</sub>-based M- and L-cone sensitivity curves have a shallower peak: spectral sensitivity in the orange is greater by 10–15% or 0.05  $\text{log}_{10}$  unit (relative to the spectral peak), while in the blue, near 460 nm, it is greater by ~50%. Another substantial difference appears in the deep red, where the rate at which sensitivity drops is greater for the Stiles-Burch<sub>1955</sub>- or the CIE<sub>1964</sub>-based cones by approximately a factor of 2 per 100 nm.

The above differences follow a fairly similar pattern for M and L cones and could be attributable to calibration or photometric error. But there are also minor, colorimetric differences: the proposed S-cone-sensitivity curve is lower by a factor of 2 in the green (see Fig. 10), a difference not closely paralleled by differences in the other cone sensitivities; and the proposed M- and L-cone sensitivities maintain a more-constant ratio below 490 nm. The latter difference illustrates how even a small change in the assumed cone sensitivities can have theoretical consequences: the suggestion that the L cones have a greater density of macular pigmentation than the M cones<sup>6</sup> derives from shape differences that are mostly specific to the CIE<sub>Judd</sub>-based sensitivities.

##### A. Dichromacy As a Reduced Form of Normal Vision

Our test sensitivity measurements show that, under suitable regimes of chromatic adaptation, the normal's spectral sensitivity can become protanopic or deuteranopic. This gives further support to the loss hypotheses for protanopia and deuteranopia and supports the use of dichromatic data in the derivation of the normal cone sensitivities. The test spectral sensitivities from dichromats and normals are narrower than Stiles's  $\pi_4$  and  $\pi_5$  field sensitivities (see also, for example, Refs. 13 and 113) or than the sensitivities from MSP [see Fig. 12(a)]. It might be possible to suppose that the cones of normal observers have the broad spectra indicated by MSP and that the spectrally narrow sensitivities found under cone-isolation conditions are due to inhibitory interactions (but see Ref. 4), but this could not explain the finding of equally narrow spectral sensitivities in dichromats.

##### B. Choice between 2° Color-Matching Functions

At middle and long wavelengths, our spectral-sensitivity data are fairly consistent with both the Stiles-Burch<sub>1955</sub> and the CIE<sub>Judd</sub> 2° CMF's and do not usefully distinguish between them. At short wavelengths, much depends on what the typical macular pigmentation for a 2° field is assumed to be. If a peak macular density of 0.35 (at 460 nm) is assumed, our adjusted data are more consis-

tent with the Stiles–Burch<sub>1955</sub> 2° CMF's. Yet, if a peak macular density of 0.50 is assumed, our adjusted data are more consistent with the CIE<sub>Judd</sub> 2° CMF's. We believe that the evidence discussed above (in particular, the macular density measurements of Smith and Pokorny<sup>6</sup> and of the present study) points to the lower peak density of 0.35 as being typical for a 2° field. Thus we favor the Stiles–Burch<sub>1955</sub> 2° CMF's. As Stiles and Burch noted,<sup>67</sup> it is statistically unlikely that the subjects in their 2° study (along with the 18 other subjects shown to have similar spectral sensitivity) have atypical macular density. Comparison of the 10° CMF's of the 10 observers who participated in the 2° study with the larger group investigated later is quite reassuring on this point. In contrast, the apparent macular density of the CIE<sub>Judd</sub> 2° observer may be inflated by the corrections made to the faulty CIE<sub>1924</sub>  $V_\lambda$  function by Judd.<sup>39,67</sup>

Most other evidence also supports the choice of the Stiles–Burch<sub>1955</sub> 2° CMF's over the CIE<sub>Judd</sub> 2° CMF's. To summarize: (1) the Stiles–Burch<sub>1955</sub> 2° CMF's were measured directly and do not depend on unnecessary photometric assumptions; (2) the Stiles–Burch<sub>1955</sub> 2° CMF's are more consistent with tritanopic color matches, and those Stiles–Burch<sub>1955</sub>-based cone fundamentals that are consistent with tritanopic color matches are also consistent with deuteranopic and protanopic spectral sensitivities; (3) the Stiles–Burch<sub>1955</sub> 2° CMF's are more consistent with the CIE<sub>1964</sub> 10° CMF's, (4) the Stiles–Burch<sub>1955</sub> 2° CMF's are more consistent with Stiles's  $\pi$  mechanisms<sup>68</sup>; and (5) the CIE<sub>Judd</sub> 2° CMF is quite artificially constructed at long wavelengths. These arguments have been made before (for example, Ref. 58). They strongly suggest that the Stiles–Burch<sub>1955</sub> 2° CMF's should be the preferred 2° CMF's for color-vision modeling. This has to be weighed against the drawback that the Stiles–Burch functions have no connection with the clearly erroneous CIE<sub>1931</sub> 2° CMF's on which most practical colorimetry is based. Partly to counter this problem, we have proposed 2° cone fundamentals based on the CIE<sub>1964</sub> CMF's (see Subsection 3.I and Appendix A).

### C. S Cones and Luminance

It has long been clear that the S cones play a more-restricted role in vision than do the other cones (see Ref. 114 for a discussion). Although the S cones clearly contribute to our perception of color, photometric data suggest that the S-cone influence on luminance, measured by, for example, flicker photometry, is slight.<sup>115–117</sup> Indeed, several models of postreceptoral organization<sup>118,119</sup> postulate that the S cones have little or no access to the visual pathways that are relevant for such tasks as rapid flicker detection or flicker photometry. Although some experimental tests support this point of view,<sup>2,120</sup> it is now clear that the S cones can provide a small, negative contribution to luminance.<sup>47,121,122</sup> This small contribution, however, has been demonstrated only under moderate-to-extreme conditions of chromatic adaptation, and it may be insignificant under the conditions under which the CMF's were derived. It should be recalled, however, that saturated blues and violets have a brightness (assessed by direct comparison) that exceeds their luminance (assessed by an additive photometric measure such as flicker photometry), and S cones have been shown to influence brightness matches (Ref. 73, but see Ref. 123).

### D. CIE<sub>1964</sub>-Based Cone Sensitivities and $\bar{y}_{10}$

The 1964 10° data are unusual in that the  $\bar{y}_{10}$  function is based on experimental flicker matches made by most of the subjects at the primary wavelengths. This provides us with an opportunity to consider the relationship of the different cone types to a luminance estimate ( $\bar{y}_{10}$ ) reconstructed from flicker photometric matches at the three primary wavelengths. The 10° M- and L-cone sensitivities specified in column (C) of Table 6, though chosen without any reference to luminosity data, sum almost exactly to  $\bar{y}_{10}$  (a minimal negative S-cone contribution is needed for an exact reconstruction of  $\bar{y}_{10}$ ). M- and L-cone sensitivities that sum exactly to  $\bar{y}_{10}$  are specified in column (D) of Table 6. They were obtained by a least-squares best logarithmic fit to the unconstrained M- and L-cone sensitivities of column (C) of Table 6, with the constraint that the new M- and L-cone sensitivities should sum exactly to  $\bar{y}_{10}$ . A further constraint was added: although we obtained the best fit with sensitivities such that 29.85% of the luminance of an equal-energy white was attributable to the M cones and 70.15% to the L cones, we obtained the constrained M- and L-cone sensitivities of column (D) of Table 6 by holding these percentages to 30% and 70%, respectively. This additional constraint has negligible consequences for the cone sensitivities, and it is potentially convenient for the construction of a constant-luminance chromaticity diagram,<sup>78</sup> since it places the white point in such a diagram at exactly  $r$  [or  $L/(L + M)] = 0.70$ . In spite of these constraints, the constrained cone sensitivities agree closely with the unconstrained ones, with an rms error of 0.002 for M and 0.003 for L cones, although significant differences do exist, particularly in the deep violet. However, a luminance estimate ( $\bar{y}_{10}$ ) that is reconstructed from flicker photometric matches made at only three primary wavelengths (by assuming that luminance is a linear combination of the CMF's) may differ systematically from a luminance estimate based entirely on flicker photometry (see above and Fig. 3 of Ref. 64). The 2° cone fundamentals calculated from the 10° CIE<sub>1964</sub> CMF's given in Table 8 (columns 5, 6, and 7) are based on the unconstrained [column (C) of Table 6] rather than on the constrained [column (D) of Table 6] functions.

### E. Relation between Objective and Subjective Sensitivity Measures

The comparisons shown in Subsection 3.H imply that there are small but significant differences between the transversely measured macaque suction electrode data and the axially measured corneal spectral sensitivities of normal and dichromatic humans.

The differences at short wavelengths are small, suggesting that our assumptions about typical lens and macular densities for a 2° field are appropriate. The differences at long wavelengths are larger. One possible cause, suggested by DeMarco *et al.*,<sup>106</sup> is that the macaque and the human photopigments differ in  $\lambda_{max}$ . Although there is some support for this argument in the case of the L-cone pigment, there is little support in the case of the M-cone pigment.<sup>105</sup> Moreover, if a photopigment density of 0.40 is used to construct the corneal spectral sensitivities from the suction electrode data, a density for which there seems to be good experimental support (see above), the required

spectral shifts are close to 4 or 5 nm, much larger than the shifts in  $\lambda_{\max}$  allowed by suction electrode and MSP data.<sup>105</sup>

Even with the improbably low density of 0.27 assumed by Baylor *et al.*,<sup>15</sup> the electrophysiological M-cone data deviate systematically from the psychophysical data reviewed here and fit only the M-cone fundamental of Estévez, which, as we have seen, has no clear empirical support and is inconsistent with much psychophysical evidence.

We have speculated that waveguide effects might account for some of the differences between (axial) psychophysical and (transverse) suction electrode spectral sensitivities. There is no strong psychophysical evidence to support this proposal, but uncertainties about the interaction between light and photoreceptor are such that there is no reason to expect the axial and transverse sensitivities to be identical.

## APPENDIX A: PROPOSED 2° CONE FUNDAMENTALS BASED ON THE STILES-BURCH<sub>1955</sub> 2° CMF'S OR ON THE CIE<sub>1964</sub> 10° CMF'S

Columns 2, 3, and 4 of Table 8 give logarithms of proposed S-cone ( $S_\lambda$ ), M-cone ( $M_\lambda$ ), and L-cone ( $L_\lambda$ ) fundamentals based on the Stiles-Burch<sub>1955</sub>  $\bar{r}$ ,  $\bar{g}$ , and  $\bar{b}$  2° CMF's [Table I(5.5.3) of Ref. 48] according to the following equations:

$$\begin{aligned} L_\lambda &= 0.214808\bar{r} + 0.751035\bar{g} + 0.045156\bar{b}, \\ M_\lambda &= 0.022882\bar{r} + 0.940534\bar{g} + 0.076827\bar{b}, \\ S_\lambda &= 0.000000\bar{r} + 0.016500\bar{g} + 0.999989\bar{b} \end{aligned} \quad (\lambda \leq 525 \text{ nm}).$$

The S-cone sensitivities have been extended at  $\lambda > 525$  nm by use of the following function:

$$\log_{10} S_\lambda = 10,402.1/\lambda - 21.549,$$

where  $\lambda$  is the wavelength in nanometers. By adding columns 2 and 3 with weights equal to 0.68273 for  $L_\lambda$  and 0.35235 for  $M_\lambda$ , we can obtain a reasonable approximation to the shape of the CIE modified  $V_\lambda$  function [ $V_M(\lambda)$ ].

Columns 5, 6, and 7 give logarithms of proposed cone sensitivities based on the  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  10° CMF's of the CIE<sub>1964</sub> supplementary standard observer (Table I(3.3.2) of Ref. 48], derived from the following transformation for large-field cone sensitivities and adapted for small-field application through the transformations described below (see also Subsection 3.I):

$$\begin{aligned} L_\lambda &= 0.236157\bar{x}_{10} + 0.826427\bar{y}_{10} - 0.045710\bar{z}_{10}, \\ M_\lambda &= -0.431117\bar{x}_{10} + 1.206922\bar{y}_{10} + 0.090020\bar{z}_{10}, \\ S_\lambda &= 0.040557\bar{x}_{10} - 0.019683\bar{y}_{10} + 0.486195\bar{z}_{10} \end{aligned} \quad (\lambda \leq 520 \text{ nm}).$$

The S-cone sensitivities have been extended at  $\lambda > 520$  nm by use of the following function:

$$\log_{10} S_\lambda = 10,402.1/\lambda - 21.7185.$$

We calculated the 2° cone fundamentals, using the above equations, by (1) converting the above 10° cone fundamentals to action spectra, assuming 1.28 times the (open pupil) van Norren-Vos<sup>44</sup> lens template, 0.28 times the Wyszecki-

Stiles<sup>48</sup> macular template, and a photopigment density of 0.30, and then (2) converting the action spectra to 2° cone fundamentals, assuming the same lens densities, 0.70 times the macular template, and a photopigment density of 0.40 (see text for details). We extended the Wyszecki-Stiles macular template beyond 400 nm by assuming densities of 0.0425 at 395 nm and 0.0000 at 390 nm. Since the 2° cone fundamentals tabulated in columns 5, 6, and 7 are based on the CIE<sub>1964</sub> CMF's instead of the Stiles-Burch<sub>1955</sub> CMF's, they are consistent with a slightly higher lens density than those tabulated in columns 2, 3, and 4 (see Subsections 3.F and 3.I).

The tabulated M- and L-cone sensitivities can be extended into the infrared, where self-screening is negligible, by use of the above linear equations in  $\bar{x}_{10}$ ,  $\bar{y}_{10}$ , and  $\bar{z}_{10}$  multiplied by wavelength-independent scaling factors of 1.103 for M and 1.102 for L.

All coefficients given above have been scaled so that the interpolated peak cone sensitivities are equal to 1.

## APPENDIX B: NATURE AND EXTENT OF INDIVIDUAL VARIATION IN OUR SAMPLE

Normal variation in the corneal cone spectral sensitivities appears to be traceable to variation in a limited number of identifiable factors. The importance of lens and macular pigmentation has long been recognized, but recent analyses suggest that receptor factors such as variation in  $\lambda_{\max}$  and variability in cone pigment density are also important (see above).

We now show that these factors account well for the small individual variation in our cone sensitivities, with standard deviations for each factor that are as small as the smallest current psychophysical estimates. This is further evidence that the isolation procedure was successful. If our isolation procedure had failed in some observers but not in others, our variability estimates would have been inflated.

To analyze the nature of the individual variation in our data set, we adopted the mean spectral transmittances for lens and macular pigment tabulated by Wyszecki and Stiles<sup>48</sup> and allowed the densities of these pigments to vary independently by an observer-dependent factor that was independent of wavelength. To introduce receptor variation, we first derived the absorbance spectrum for each cone type by (1) correcting our average measured quantal spectral sensitivity, using the mean prereceptor spectral transmittance for lens and macula, and (2) allowing for self-screening, with an assumed density of 0.45 at the spectral peak of each cone pigment. The absorption spectra for individual observers were then allowed to vary by a displacement (independent for each cone type) from the mean shape along the  $\log_{10}$  wavelength (or log wave-number) axis. Such a displacement, which is almost equivalent to a more complex proposal made by Barlow,<sup>112</sup> provides an excellent account of species variations in visual pigment spectra<sup>53,54</sup> and has been used successfully to model individual variation in normal human trichromatic matches.<sup>27</sup> Finally, for each observer the densities of the two cone pigments were allowed to vary together. In all, then, five parameters—lens and macular pigment density, M- and L-cone  $\lambda_{\max}$ , and cone pigment density—were varied for a least-squares fit to the measured log sensitivities obtained under M- and L-cone isolation conditions.

**Table 8. Proposed 2° Cone Fundamentals Based on the Stiles-Burch<sub>1955</sub> 2° CMF's or on the CIE<sub>1964</sub> 10° CMF's**

Wavelength (nm)	Stiles-Burch 2°		Stiles-Burch 2°		CIE <sub>1964</sub> 10°-Based 2°		CIE <sub>1964</sub> 10°-Based 2°	
	L-Cone Fundamental	M-Cone Fundamental	S-Cone Fundamental	L-Cone Fundamental	M-Cone Fundamental	S-Cone Fundamental	L-Cone Fundamental	S-Cone Fundamental
390	-3.2197	-3.2606	-1.9156	-3.5037	-3.5967	-2.1038	-3.5967	-2.1038
395	-2.7931	-2.8206	-1.5073	-3.0445	-3.1245	-1.6412	-3.1245	-1.6412
400	-2.4874	-2.5269	-1.2053	-2.6515	-2.7147	-1.2413	-2.7147	-1.2413
405	-2.1744	-2.1953	-0.8810	-2.3204	-2.3631	-0.8994	-2.3631	-0.8994
410	-1.9401	-1.9428	-0.6433	-2.0576	-2.0726	-0.6216	-2.0726	-0.6216
415	-1.7991	-1.7768	-0.4452	-1.8795	-1.8560	-0.4200	-1.8560	-0.4200
420	-1.6526	-1.5888	-0.2809	-1.7576	-1.6883	-0.2777	-1.6883	-0.2777
425	-1.5789	-1.4695	-0.1640	-1.6575	-1.5418	-0.1740	-1.5418	-0.1740
430	-1.5159	-1.3623	-0.0992	-1.5695	-1.4113	-0.0953	-1.4113	-0.0953
435	-1.4531	-1.2650	-0.0485	-1.4872	-1.2951	-0.0370	-1.2951	-0.0370
440	-1.3853	-1.1708	-0.0160	-1.4161	-1.1968	-0.0058	-1.1968	-0.0058
445	-1.3411	-1.1084	-0.0008	-1.3620	-1.1209	-0.0017	-1.1209	-0.0017
450	-1.3014	-1.0537	-0.0367	-1.3116	-1.0561	-0.0222	-1.0561	-0.0222
455	-1.2452	-0.9877	-0.0832	-1.2585	-0.9962	-0.0535	-0.9962	-0.0535
460	-1.1669	-0.9035	-0.1042	-1.1860	-0.9220	-0.0902	-0.9220	-0.0902
465	-1.0791	-0.8188	-0.1745	-1.1045	-0.8404	-0.1272	-0.8404	-0.1272
470	-0.9857	-0.7332	-0.2122	-1.0138	-0.7533	-0.1863	-0.7533	-0.1863
475	-0.9029	-0.6599	-0.3084	-0.9238	-0.6733	-0.2767	-0.6733	-0.2767
480	-0.8362	-0.6047	-0.4366	-0.8613	-0.6239	-0.4042	-0.6239	-0.4042
485	-0.7770	-0.5562	-0.5671	-0.7910	-0.5674	-0.5402	-0.5674	-0.5402
490	-0.6994	-0.4916	-0.6959	-0.7267	-0.5170	-0.6791	-0.5170	-0.6791
495	-0.6048	-0.4137	-0.8125	-0.6342	-0.4405	-0.8046	-0.4405	-0.8046
500	-0.5087	-0.3345	-0.9371	-0.5277	-0.3488	-0.9243	-0.3488	-0.9243
505	-0.4114	-0.2515	-1.0627	-0.4272	-0.2633	-1.0485	-0.2633	-1.0485
510	-0.3262	-0.1819	-1.2088	-0.3380	-0.1892	-1.2068	-0.1892	-1.2068
515	-0.2504	-0.1205	-1.3755	-0.2622	-0.1284	-1.3635	-0.1284	-1.3635
520	-0.1852	-0.0684	-1.5477	-0.1976	-0.0793	-1.5313	-0.0793	-1.5313
525	-0.1354	-0.0336	-1.7360	-0.1484	-0.0459	-1.7112	-0.0459	-1.7112
530	-0.0974	-0.0112	-1.9224	-0.1101	-0.0239	-1.8918	-0.0239	-1.8918
535	-0.0722	-0.0015	-2.1058	-0.0773	-0.0069	-2.0710	-0.0069	-2.0710
540	-0.0560	-0.0011	-2.2859	-0.0542	-0.0002	-2.2510	-0.0002	-2.2510
545	-0.0385	-0.0001	-2.4626	-0.0382	-0.0022	-2.4277	-0.0022	-2.4277
550	-0.0233	-0.0034	-2.6361	-0.0261	-0.0099	-2.6012	-0.0099	-2.6012
555	-0.0152	-0.0174	-2.8065	-0.0142	-0.0205	-2.7716	-0.0205	-2.7716

*Table continued*

Table 8. Continued

Wavelength (nm)	Stiles-Burch 2°		Stiles-Burch 2°		CIE <sub>1964</sub> 10°-Based 2°		CIE <sub>1964</sub> 10°-Based 2°	
	L-Cone Fundamental	M-Cone Fundamental	S-Cone Fundamental	M-Cone Fundamental	L-Cone Fundamental	M-Cone Fundamental	S-Cone Fundamental	M-Cone Fundamental
560	-0.0143	-0.0414	-2.9738	-0.0054	-0.0054	-0.0369	-2.9389	-0.0369
565	-0.0101	-0.0652	-3.1382	-0.0008	-0.0008	-0.0617	-3.1033	-0.0617
570	-0.0013	-0.0872	-3.2997	-0.0005	-0.0005	-0.0952	-3.2648	-0.0952
575	-0.0023	-0.1262	-3.4584	-0.0057	-0.0057	-0.1389	-3.4235	-0.1389
580	-0.0108	-0.1792	-3.6143	-0.0140	-0.0140	-0.1906	-3.5794	-0.1906
585	-0.0189	-0.2321	-3.7676	-0.0219	-0.0219	-0.2469	-3.7327	-0.2469
590	-0.0307	-0.2933	-3.9183	-0.0337	-0.0337	-0.3120	-3.8834	-0.3120
595	-0.0495	-0.3708	-4.0665	-0.0525	-0.0525	-0.3882	-4.0316	-0.3882
600	-0.0744	-0.4582	-4.2122	-0.0777	-0.0777	-0.4748	-4.1773	-0.4748
605	-0.1055	-0.5529	-4.3554	-0.1092	-0.1092	-0.5711	-4.3205	-0.5711
610	-0.1443	-0.6598	-4.4964	-0.1478	-0.1478	-0.6771	-4.4615	-0.6771
615	-0.1914	-0.7792	-4.6350	-0.1946	-0.1946	-0.7924	-4.6001	-0.7924
620	-0.2472	-0.9050	-4.7714	-0.2491	-0.2491	-0.9139	-4.7365	-0.9139
625	-0.3123	-1.0370	-4.9056	-0.3101	-0.3101	-1.0334	-4.8707	-1.0334
630	-0.3877	-1.1789	-5.0377	-0.3815	-0.3815	-1.1594	-5.0028	-1.1594
635	-0.4723	-1.3295	-5.1677	-0.4688	-0.4688	-1.3073	-5.1328	-1.3073
640	-0.5641	-1.4825	-5.2957	-0.5663	-0.5663	-1.4670	-5.2608	-1.4670
645	-0.6645	-1.6355	-5.4217	-0.6690	-0.6690	-1.6345	-5.3868	-1.6345
650	-0.7761	-1.7917	-5.5458	-0.7795	-0.7795	-1.8047	-5.5109	-1.8047
655	-0.8990	-1.9512	-5.6679	-0.8992	-0.8992	-1.9615	-5.6330	-1.9615
660	-1.0304	-2.1141	-5.7882	-1.0267	-1.0267	-2.1137	-5.7533	-2.1137
665	-1.1681	-2.2785	-5.9067	-1.1609	-1.1609	-2.2722	-5.8718	-2.2722
670	-1.3099	-2.4412	-6.0235	-1.3016	-1.3016	-2.4327	-5.9886	-2.4327
675	-1.4536	-2.5996	-6.1385	-1.4490	-1.4490	-2.5949	-6.1036	-2.5949
680	-1.5994	-2.7550	-6.2518	-1.6010	-1.6010	-2.7574	-6.2169	-2.7574
685	-1.7486	-2.9125	-6.3635	-1.7556	-1.7556	-2.9185	-6.3285	-2.9185
690	-1.9024	-3.0719	-6.4735	-1.9126	-1.9126	-3.0793	-6.4386	-3.0793
695	-2.0647	-3.2353	-6.5819	-2.0712	-2.0712	-3.2415	-6.5470	-3.2415
700	-2.2334	-3.4003	-6.6889	-2.2312	-2.2312	-3.4031	-6.6539	-3.4031
705	-2.4006	-3.5629	-6.7942	-2.3925	-2.3925	-3.5636	-6.7593	-3.5636
710	-2.5580	-3.7191	-6.8982	-2.5540	-2.5540	-3.7226	-6.8632	-3.7226
715	-2.7084	-3.8690	-7.0006	-2.7145	-2.7145	-3.8796	-6.9657	-3.8796
720	-2.8674	-4.0206	-7.1016	-2.8744	-2.8744	-4.0350	-7.0667	-4.0350
725	-3.0243	-4.1705	-7.2013	-3.0338	-3.0338	-4.1890	-7.1664	-4.1890
730	-3.1791	-4.3186	-7.2995	-3.1922	-3.1922	-4.3414	-7.2646	-4.3414

Our measurements were made at only 10 wavelengths, but the displaced spectra have to be continuous functions of wavelength. To construct these, we first extrapolated the derived mean dilute absorption spectra to 430 and 680 nm (using spectra derived from the cone sensitivities of Smith and Pokorny<sup>6</sup> to bridge the 10-nm gap at each end of the spectrum) and then fitted the resulting 12  $\log_{10}$  absorption values with a four-component Fourier series in  $\log_{10}$  wavelength. The accuracy of these fits was well within experimental error, with an rms error of less than 0.01  $\log_{10}$  unit.

The first attempt to fit the individual sensitivities with this model was not a complete success: it yielded acceptable fits, but the parameter values required were quite variable and frequently implausible. Moreover, the parameter values were in many cases strongly correlated: large but approximately canceling deviations in different parameter values were being selected to obtain slight improvements in the fit of model to data.

Our recourse was to repeat the analysis, this time discouraging the choice of implausible parameter values in cases in which more-plausible ones would do almost as well. This had to be done judiciously, since by constraining the parameters too tightly we would underestimate their variance, defeating the purpose of the analysis. Our procedure was to take equal account, in this second analysis, of (1) the likelihood of an observer's data, given the parameter values being considered for that observer, and (2) the likelihood of those parameter values themselves, as given by the rather broad distributions that emerged from the first analysis. In other words, we identified the most-plausible set of parameter values for each subject, assuming that the subjects came from a population with parameter values distributed as in the first analysis. We accomplished this by minimizing the sum of two terms: (1) the sum of the squares of the errors of prediction, each error being divided first by the rms error of prediction from the first analysis, and (2) the sum of the squares of the five parameter values themselves, each expressed as a normal deviate using the mean and standard deviation obtained for each parameter in the first analysis. The distributions that now emerged were much tighter than those from the first analysis, with standard deviations approximately threefold smaller; it follows that the weak constraint on the parameter values that was imported from the first analysis was not strong enough to cause a serious underestimation of parameter variance in the second analysis. The errors of prediction were only minimally increased in this second, constrained analysis: the rms error of prediction of the individual sensitivities was 0.05  $\log_{10}$  unit, and the irregularity in the spectral variation of these residuals suggested that most of this was due to experimental error. Correlations between parameter values were now generally less than 0.4 (the only exception being a negative correlation between the fitted densities for lens and macular pigmentation).

The obtained standard deviations for our observers were

Peak macular pigment peak density	0.11
Lens density at 400 nm	0.42
Peak density for cone pigments	0.07
Peak absorption wavelength, M cones	0.38 nm
Peak absorption wavelength, L cones	1.02 nm

These values are of limited reliability, being based on limited data from a relatively small sample, but they are comparable in magnitude with estimates from other sources (see above). Failures of isolation would presumably be reflected in inflated estimates of  $\lambda_{\max}$  variability, so it is encouraging that our standard deviations for peak wavelength actually fall slightly below other estimates (for example, Ref. 27).

The constraint imported from the first analysis, weak though it was, could have caused an underestimate of the standard deviations in the second analysis. In an independent approach to check this, we determined the deviation of each measured log sensitivity from the value expected on the basis of the observers' mean sensitivity and the mean sensitivity of all observers at the wavelengths in question, and we modeled the covariances of these quantities for different pairs of test wavelengths as the sum of contributions from the factors listed above. We found the contribution of each factor in the manner reported by Webster and MacLeod,<sup>27</sup> by calculating the derivative of log sensitivity with respect to each observer parameter and multiplying this by the standard deviation of the parameter; we then estimated the standard deviations by optimizing the fit to the covariance matrix. The implicit assumption that the different factors vary independently among observers is supported by the results reported by Webster and MacLeod.<sup>27</sup> The required standard deviations were indeed somewhat higher than the tabulated values in the case of the spectral shifts, with values of 1.0 nm for the M cones and 1.76 nm for the L cones. Moreover, these data could be fitted almost as well without the allowance of any variation in cone pigment density; in that case, the spectral-shift standard deviation remained at 1.0 nm for the M cones but increased to 2.6 nm for the L cones.

In addition to the well-documented variations in macular pigment density, our results support the earlier psychophysical indications that the cone sensitivities themselves vary among individuals, with a jitter of the order of 1-nm standard deviation in spectral position. Such jitter might limit the usefulness of an estimate of the M- or L-cone sensitivity based on averaged data, but the variability indicated here is not enough to make this a serious concern in most contexts. For individual observers, the ratio of long- to short-wavelength sensitivity would exhibit a standard deviation of only  $\sim 0.03 \log_{10}$  unit; the means for our observers would have standard errors of only  $\sim 0.01 \log_{10}$  unit.

## ACKNOWLEDGMENTS

This study was supported by National Science Foundation grants BNS 86-09217, BNS 88-12401, and IBN 92-10046 and by National Institutes of Health grant EY 01711. We thank Jeff Vivien for experimental assistance and Bob Boynton, Rhea Eskew, Ted Sharpe, and Charles Stromeyer for comments.

## REFERENCES

1. G. Wald, "The receptors of human color vision," *Science* **145**, 1007-1016 (1964).
2. A. Eisner and D. I. A. MacLeod, "Flicker photometric study of chromatic adaptation: selective suppression of cone inputs by colored backgrounds," *J. Opt. Soc. Am.* **71**, 705-718 (1981).

3. A. Stockman and J. D. Mollon, "The spectral sensitivities of the middle- and long-wavelength cones: an extension of the two-colour threshold technique of W. S. Stiles," *Perception* **15**, 729-754 (1986).
4. A. Stockman, D. I. A. MacLeod, and J. A. Vivien, "Isolation of the middle- and long-wavelength-sensitive cones in normal trichromats," *J. Opt. Soc. Am. A* **10**, 2471-2490 (1993).
5. P. E. King-Smith and J. R. Webb, "The use of photopic saturation in determining the fundamental spectral sensitivity curves," *Vision Res.* **14**, 421-429 (1974).
6. V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," *Vision Res.* **15**, 161-171 (1975).
7. T. Young, *Lectures on Natural Philosophy* (Johnson, London, 1807), Vol. II.
8. A. König and C. Dieterici, "Die Grundempfindungen und ihre Intensitäts-Vertheilung im Spectrum," *Sitz. Akad. Wiss. Berlin* **1886**, 805-829 (1986).
9. H. M. O. Scheibner and R. M. Boynton, "Residual red-green discrimination in dichromats," *J. Opt. Soc. Am.* **58**, 1151-1158 (1968).
10. A. L. Nagy, "Large-field substitution Rayleigh matches of dichromats," *J. Opt. Soc. Am.* **70**, 778-783 (1980).
11. M. E. Breton and W. B. Cowan, "Deuteranomalous color matching in the deuteranopic eye," *J. Opt. Soc. Am.* **71**, 1220-1223 (1981).
12. H. J. A. Dartnall, J. K. Bowmaker, and J. D. Mollon, "Human visual pigments: microspectrophotometric results from the eyes of seven persons," *Proc. R. Soc. London Ser. B* **220**, 115-130 (1983).
13. W. S. Stiles, "Further studies of visual mechanisms by the two-colour threshold technique," *Coloquio Prob. Opt. Vision* **1**, 65-103 (1953).
14. J. K. Bowmaker and H. J. A. Dartnall, "Visual pigments of rods and cones in the human retina," *J. Physiol. (London)* **298**, 501-512 (1980).
15. D. A. Baylor, B. J. Nunn, and J. L. Schnapf, "Spectral sensitivity of the cones of the monkey *Macaca fascicularis*," *J. Physiol. (London)* **390**, 145-160 (1987).
16. H. L. De Vries, "The fundamental response curves of normal and abnormal dichromatic and trichromatic eyes," *Physika* **14**, 367-380 (1948).
17. G. S. Brindley, "The effects on colour vision of adaptation to very bright lights," *J. Physiol. (London)* **122**, 332-350 (1953).
18. W. S. Stiles, "Foveal threshold sensitivity on fields of different colors," *Science* **145**, 1016-1018 (1964).
19. D. I. A. MacLeod and M. Hayhoe, "Three pigments in normal and anomalous color vision," *J. Opt. Soc. Am.* **64**, 92-96 (1974).
20. J. Nathans, D. Thomas, and S. G. Hogness, "Molecular genetics of human color vision: the genes encoding blue, green and red pigments," *Science* **232**, 193-202 (1986).
21. J. Nathans, T. P. Piantanida, R. L. Eddy, T. B. Shows, and S. G. Hogness, "Molecular genetics of inherited variation in human color vision," *Science* **232**, 203-210 (1986).
22. M. Alpern and E. N. Pugh, "Variation in the action spectrum of erythrolabe among deuteranopes," *J. Physiol. (London)* **266**, 613-646 (1977).
23. M. Alpern, "Variation in the visual pigments of human dichromats and normal human trichromats," in *Frontiers of Visual Science: Proceedings of the 1985 Symposium*, National Research Council Committee on Vision, ed. (National Academy Press, Washington, D.C., 1987).
24. M. Alpern and T. Wake, "Cone pigments in human deutan color vision defects," *J. Physiol. (London)* **266**, 595-612 (1977).
25. B. L. Bastian, "Individual differences among the photopigments of protan observers," Ph.D. dissertation (University of Michigan, Ann Arbor, Mich., 1976).
26. D. I. A. MacLeod and M. A. Webster, "Factors influencing the color matches of normal observers," in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983), pp. 81-92.
27. M. A. Webster and D. I. A. MacLeod, "Factors underlying individual differences in the color matches of normal observers," *J. Opt. Soc. Am. A* **5**, 1722-1735 (1988).
28. W. S. Stiles and J. M. Burch, "NPL colour-matching investigation: final report," *Opt. Acta* **6**, 1-26 (1959).
29. V. C. Smith, J. Pokorny, and S. J. Starr, "Variability of color mixture data—I. Interobserver variability in the unit coordinates," *Vision Res.* **16**, 1087-1094 (1976).
30. J. K. Bowmaker, J. D. Mollon, and G. H. Jacobs, "Microspectrophotometric results for Old and New World primates," in *Colour Vision*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983).
31. J. L. Schnapf, T. W. Kraft, and D. A. Baylor, "Spectral sensitivity of human cone photoreceptors," *Nature (London)* **325**, 439-441 (1987).
32. J. Neitz and G. H. Jacobs, "Polymorphism of the long-wavelength cone in normal human colour vision," *Nature (London)* **323**, 623-625 (1986).
33. J. Neitz and G. H. Jacobs, "Polymorphism in normal human colour vision and its mechanism," *Vision Res.* **30**, 621-636 (1990).
34. G. Jordan and J. D. Mollon, "Two kinds of men?" *Invest. Ophthalmol. Vis. Sci. Suppl.* **29**, 164 (1988).
35. M. Lutze, N. J. Cox, V. C. Smith, and J. Pokorny, "Genetic studies of variation in Rayleigh and photometric matches in normal trichromats," *Vision Res.* **30**, 149-162 (1990).
36. J. Winderickx, D. T. Lindsey, E. Sanocki, S. Y. Teller, A. G. Motulsky, and S. S. Deeb, "A Ser/Ala polymorphism in the red photopigment underlies variation in colour matching among colour-normal individuals," *Nature (London)* **356**, 431-433 (1992).
37. J. Neitz and G. H. Jacobs, "Polymorphism of cone pigments among color normals: evidence from color matching," in *Colour Deficiencies IX*, B. Drum and G. Verriest, eds. (Kluwer, Dordrecht, The Netherlands, 1989), pp. 27-34.
38. M. A. Webster, "Reanalysis of  $\lambda_{max}$  variations in the Stiles-Burch 10° color-matching functions," *J. Opt. Soc. Am. A* **9**, 1419-1421 (1992).
39. D. B. Judd, "Report of U.S. Secretariat Committee on Colorimetry and Artificial Daylight," in *Proceedings of the Twelfth Session of the CIE, Stockholm*, Technical Committee No. 7 (Bureau Central de la CIE, Paris, 1951).
40. J. J. Vos, "Colorimetric and photometric properties of a 2-deg fundamental observer," *Color Res. Appl.* **3**, 125-128 (1978).
41. G. Wald, "Human vision and the spectrum," *Science* **101**, 653-658 (1945).
42. R. A. Bone and J. M. B. Sparrock, "Comparison of macular pigment densities in the human eye," *Vision Res.* **11**, 1057-1064 (1971).
43. P. L. Pease, A. J. Adams, and E. Nuccio, "Optical density of human macular pigment," *Vision Res.* **27**, 705-710 (1987).
44. D. van Norren and J. J. Vos, "Spectral transmission of the human ocular media," *Vision Res.* **14**, 1237-1244 (1974).
45. B. H. Crawford, "The scotopic visibility function," *Proc. Phys. Soc. London Section B* **62**, 321-334 (1949).
46. G. S. Brindley, J. J. Du Croz, and W. A. H. Rushton, "The flicker fusion frequency of the blue-sensitive mechanism of colour vision," *J. Physiol. (London)* **183**, 497-500 (1966).
47. A. Stockman, D. I. A. MacLeod, and D. D. DePriest, "The temporal properties of the human short-wave photoreceptors and their associated pathways," *Vision Res.* **31**, 189-208 (1991).
48. G. Wyszecki and W. S. Stiles, *Color Science*, 2nd ed. (Wiley, New York, 1982).
49. F. Viénot, "Can variation in macular pigment account for the variation of colour matches with retinal position?" in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983), pp. 107-116.
50. K. H. Ruddock, "The effect of age upon colour vision II. Changes with age in light transmission of the ocular media," *Vision Res.* **5**, 47-58 (1965).
51. J. J. Vos, "Literature review of human macular absorption in the visible and its consequences for the cone receptor primaries" (Institute for Perception, Netherlands Organization for Applied Scientific Research, Soesterberg, The Netherlands, 1972).
52. R. A. Bone, J. T. Landrum, L. Fernandez, and S. L. Tarsis, "Analysis of the macular pigment by HPLC: retinal distribution and age study," *Invest. Ophthalmol. Vis. Sci.* **29**, 843-849 (1988).

53. R. J. W. Mansfield, "Primate photopigments and cone mechanisms," in *The Visual System*, A. Fein and J. S. Levine, eds. (Liss, New York, 1985).
54. E. F. MacNichol, "A unifying presentation of photopigment spectra," *Vision Res.* **26**, 1543-1556 (1986).
55. J. J. Vos and P. L. Walraven, "On the derivation of the foveal receptor primaries," *Vision Res.* **11**, 799-818 (1971).
56. P. L. Walraven, "A closer look at the tritanopic confusion point," *Vision Res.* **14**, 1339-1343 (1974).
57. J. J. Vos, O. Estévez, and P. L. Walraven, "Improved color fundamentals offer a new view on photometric additivity," *Vision Res.* **30**, 936-943 (1990).
58. O. Estévez, "On the fundamental database of normal and dichromatic color vision," Ph.D. dissertation (Amsterdam University, Amsterdam, 1979).
59. CIE, *Commission Internationale de l'Eclairage Proceedings, 1931* (Cambridge U. Press, Cambridge, 1932).
60. J. Guild, "The colorimetric properties of the spectrum," *Philos. Trans. R. Soc. London Ser. A* **230**, 149-187 (1931).
61. W. D. Wright, "A re-determination of the trichromatic coefficients of the spectral colours," *Trans. Opt. Soc.* **30**, 141-164 (1928-1929).
62. CIE, *Commission Internationale de l'Eclairage Proceedings, 1924* (Cambridge U. Press, Cambridge, 1926).
63. G. S. Brindley, "The colour of light of very long wavelength," *J. Physiol. (London)* **130**, 35-44 (1955).
64. H. G. Sperling, "An experimental investigation of the relationship between colour mixture and luminance efficiency," in *Visual Problems of Colour* (Her Majesty's Stationery Office, London, 1958), Vol. 1, pp. 249-277.
65. K. S. Gibson and E. P. T. Tyndall, "Visibility of radiant energy," *Sci. Papers Bur. Stand.* **19**, 131-191 (1923).
66. Y. Le Grand, *Light, Colour and Vision*, 2nd ed. (Chapman & Hall, London, 1968).
67. W. S. Stiles and J. M. Burch, "Interim report to the Commission Internationale de l'Eclairage Zurich, 1955, on the National Physical Laboratory's investigation of colour-matching," *Opt. Acta* **2**, 168-181 (1955).
68. E. N. Pugh and C. Sigel, "Evaluation of the candidacy of the  $\pi$ -mechanisms of Stiles for color-matching fundamentals," *Vision Res.* **18**, 317-330 (1978).
69. F. H. G. Pitt, *Characteristics of Dichromatic Vision*, Medical Research Council Special Report Series No. 200 (His Majesty's Stationery Office, London, 1935).
70. S. Hecht, "Brightness, visual acuity and color blindness," *Doc. Ophthalmol.* **3**, 289-306 (1949).
71. E. N. Willmer, "Further observations on the properties of the central fovea in colour-blind and normal subjects," *J. Physiol. (London)* **110**, 422-446 (1950).
72. Y. Hsia and C. H. Graham, "Spectral luminosity curves for protanopic, deutanopic, and normal subjects," *Proc. Natl. Acad. Sci. (USA)* **43**, 1011-1019 (1957).
73. L. E. Marks, "Blue-sensitive cones can mediate brightness," *Vision Res.* **14**, 1493-1494 (1974).
74. A. Stockman, "The spectral sensitivities of the middle- and long-wavelength cone mechanisms," Ph.D. dissertation (University of Cambridge, Cambridge, 1983).
75. B. J. Nunn, J. L. Schnapf, and D. A. Baylor, "Spectral sensitivity of single cones in the retina of *Macaca fascicularis*," *Nature (London)* **309**, 264-266 (1984).
76. W. D. Wright, "The characteristics of tritanopia," *J. Opt. Soc. Am.* **42**, 509-521 (1952).
77. M. Alpern, "Tritanopia," *Am. J. Optom. Physiol. Opt.* **53**, 340-349 (1976).
78. D. I. A. MacLeod and R. M. Boynton, "Chromaticity diagram showing cone excitation by stimuli of equal luminance," *J. Opt. Soc. Am.* **69**, 1183-1186 (1979).
79. V. C. Smith, J. Pokorny, and Q. Zaidi, "How do sets of color-matching functions differ?" in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983).
80. N. I. Speranskaya, "Determination of spectrum color coordinates for twenty-seven normal observers," *Opt. Spectrosc. (USSR)* **7**, 424-428 (1959).
81. S. L. Polyak, *The Retina* (U. Chicago Press, Chicago, Ill., 1941).
82. W. S. Stiles, "The average colour matching functions for a large matching field," in *Visual Problems of Colour* (Her Majesty's Stationery Office, London, 1958), Vol. 1, pp. 209-247.
83. H. R. Blackwell and O. M. Blackwell, "Rod and cone receptor mechanisms in typical and atypical congenital achromatopsia," *Vision Res.* **1**, 62-107 (1961).
84. W. S. Stiles, *Mechanisms of Colour Vision* (Academic, London, 1978).
85. E. N. Pugh and J. D. Mollon, "A theory of the  $\pi_1$  and  $\pi_3$  color mechanisms of Stiles," *Vision Res.* **20**, 779-788 (1979).
86. J. K. Bowmaker, H. J. A. Dartnall, J. N. Lythgoe, and J. D. Mollon, "The visual pigments of rods and cones in the rhesus monkey *Macaca mulatta*," *J. Physiol. (London)* **274**, 329-348 (1978).
87. E. F. MacNichol, J. S. Levine, R. J. W. Mansfield, L. E. Lipetz, and B. A. Collins, "Microspectrophotometry of visual pigments in primate photoreceptors," in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983), pp. 13-38.
88. D. A. Baylor, B. J. Nunn, and J. L. Schnapf, "The photo-current, noise and spectral sensitivity of rods of the monkey *Macaca fascicularis*," *J. Physiol. (London)* **357**, 575-607 (1984).
89. A. Knowles and H. J. A. Dartnall, "The photobiology of vision," in *The Eye*, H. Davson, ed. (Academic, London, 1977), Vol. 2B.
90. M. Alpern, "Lack of uniformity in colour matching," *J. Physiol. (London)* **288**, 85-105 (1979).
91. H. Terstiege, "Untersuchungen zum Persistenz- und Koefizientesatz," *Farbe* **16**, 1-120 (1967).
92. G. Wyszecki and W. S. Stiles, "High-level trichromatic color matching and the pigment-bleaching hypothesis," *Vision Res.* **20**, 23-37 (1982).
93. S. S. Miller, "Psychophysical estimates of visual pigment densities in red-green dichromats," *J. Physiol. (London)* **223**, 89-107 (1972).
94. V. C. Smith and J. Pokorny, "Psychophysical estimates of optical density in human cones," *Vision Res.* **13**, 1199-1202 (1973).
95. S. A. Burns and A. E. Elsner, "Color matching at high luminances: photopigment optical density and pupil entry," *J. Opt. Soc. Am. A* **10**, 221-230 (1993).
96. M. Alpern, H. Kitahara, and G. H. Fielder, "The change in color matches with retinal angle of incidence of the colorimeter beams," *Vision Res.* **27**, 1763-1778 (1987).
97. P. L. Walraven and M. A. Bouman, "Relation between directional sensitivity and spectral response curves in human cone vision," *J. Opt. Soc. Am.* **50**, 780-784 (1960).
98. J. M. Enoch and W. S. Stiles, "The colour change of monochromatic light with retinal angle of incidence," *Opt. Acta* **8**, 329-358 (1961).
99. W. A. H. Rushton, "The density of chlorolabe in the foveal cones of a protanope," *J. Physiol. (London)* **168**, 360-373 (1963).
100. P. E. King-Smith, "The optical density of erythrolabe determined by retinal densitometry using the self-screening method," *J. Physiol. (London)* **230**, 535-549 (1973).
101. P. E. King-Smith, "The optical density of erythrolabe determined by a new method," *J. Physiol. (London)* **230**, 551-560 (1973).
102. W. S. Stiles, "The luminous efficiency of monochromatic rays entering the eye pupil at different points and a new colour effect," *Proc. R. Soc. London Ser. B* **123**, 90-118 (1937).
103. M. Alpern, K. Kitahara, and R. Tamaki, "The dependence of the colour and brightness of a monochromatic light upon its angle of incidence on the retina," *J. Physiol. (London)* **338**, 651-668 (1983).
104. P. L. Walraven, "The Stiles-Crawford effects in normal and anomalous color vision," in *Ophthalmic and Visual Optics*, Vol. 3 of 1993 OSA Technical Digest Series (Optical Society of America, Washington, D.C., 1993), pp. 118-121.
105. G. H. Jacobs, "Variations in colour vision in non-human primates," in *Inherited and Acquired Colour Vision Deficiencies*, D. H. Foster, ed. (CRC, Boca Raton, Fla., 1991), pp. 1127-1144.
106. P. DeMarco, J. Pokorny, and V. C. Smith, "Full-spectrum cone sensitivity functions for X-chromosome-linked anoma-

- lous trichromats," *J. Opt. Soc. Am. A* **9**, 1465–1476 (1992).
107. J. M. Enoch, "Optical properties of the retinal receptors," *J. Opt. Soc. Am.* **53**, 71–85 (1963).
108. J. M. Enoch, "Nature of the transmission of energy in the retinal receptors," *J. Opt. Soc. Am.* **51**, 1122–1126 (1961).
109. A. W. Snyder, "Photoreceptor optics—theoretical principles," in *Photoreceptor Optics*, A. W. Snyder and R. Menzel, eds. (Springer-Verlag, Berlin, 1975), pp. 38–55.
110. B. R. Horowitz, "Theoretical considerations of the retinal receptor as a waveguide," in *Vertebrate Photoreceptor Optics*, J. M. Enoch and F. L. Tobey, eds. (Springer-Verlag, Berlin, 1981), pp. 217–300.
111. J. K. Bowmaker, "Cone visual pigments in monkeys and humans," in *Advances in Photoreception: Proceedings of a Symposium on the Frontiers of Visual Science*, National Research Council Committee on Vision, ed. (National Academy Press, Washington, D.C., 1990).
112. H. B. Barlow, "What causes trichromacy? A theoretical analysis using comb-filter spectra," *Vision Res.* **22**, 635–643 (1982).
113. R. M. Boynton, "Contributions of threshold measurements to color-discrimination theory," *J. Opt. Soc. Am.* **53**, 165–178 (1963).
114. J. D. Mollon, "Color vision," *Ann. Rev. Psychol.* **33**, 41–85 (1982).
115. H. E. Ives, "Studies in the photometry of lights of different colours. I. Spectral luminosity curves obtained by the equality of brightness photometer and flicker photometer under similar conditions," *Philos. Mag. Ser. 6* **24**, 149–188 (1912).
116. E. Schrödinger, "Über das Verhältnis der Vierfarben zur Dreifarben-theorie," *Sitzungsberichte, Akad. Wiss. Wien Math-Naturwis. Kl., Abt. 2a* **134**, 471 (1925).
117. R. Luther, "Aus dem Gebiet der Farbreizmetrik," *Z. Tech. Phys.* **8**, 540–558 (1927).
118. G. L. Walls, "A branched-pathway schema for the color-vision system and some of the evidence for it," *Am. J. Ophthalmol.* **39**, 8–23 (1955).
119. S. L. Guth, J. V. Alexander, J. I. Chumbly, C. B. Gillman, and M. M. Patterson, "Factors affecting luminance additivity at threshold," *Vision Res.* **8**, 913–928 (1968).
120. W. Verdon and A. J. Adams, "Short-wavelength-sensitive cones do not contribute to mesopic luminosity," *J. Opt. Soc. Am. A* **4**, 91–95 (1987).
121. A. Stockman and D. I. A. MacLeod, "An inverted S-cone input to the luminance channel: evidence for two processes in S-cone flicker detection," *Invest. Ophthalmol. Vis. Sci. Suppl.* **28**, 92 (1987).
122. J. Lee and C. F. Stromeyer III, "Contribution of human short-wave cones to luminance and motion detection," *J. Physiol. (London)* **413**, 563–593 (1989).
123. P. Whittle, "The brightness of coloured flashes on backgrounds of various colours and luminances," *Vision Res.* **13**, 621–638 (1973).