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Human cone spectral sensitivities: a progress report

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Abstract

The spectral sensitivities of the short (S-), middle (M-) and long (L-) wave-sensitive cones have been measured in normal trichromats and in dichromats and monochromats of known genotype. For the S-cone sensitivities, three blue-cone monochromats and five normals were used; for the M-cone sensitivities, nine protanopes (three with a single L1M2 gene, three with a single L2M3 gene, one with both an L1M2 and an M gene, and two with both an L2M3 and an M gene); and for the L-cone sensitivities, 22 deuteranopes (five with a single L(ala^{180}) gene and 17 with a single L(ser^{180}) gene). We compare existing cone spectral sensitivity estimates with these results and with tritanopic color matches. The new findings are more consistent with the cone fundamentals of Stockman et al. (JOSA 1993(A10), 2491) than with those of Smith and Pokorny (Vision Research 1975(15), 161). The discrepancies that we find, however, are sufficient to warrant the replacement of both sets.

Keywords: Cone spectral sensitivity; Photopigment genes; Photopigments; Human color vision; Color matching functions; Deuteranopes; Protanopes; Tritanopes; Blue-cone monochromats

1. Introduction

Human trichromatic color vision depends on three types of cones, each of which produces a univariant, color-blind output signal, but with different spectral sensitivity. They are referred to as long-, middle- and short-wavelength-sensitive (L, M and S), according to the part of the visible spectrum to which they are most sensitive. A precise knowledge of the cone spectral sensitivities is essential for understanding and modeling both normal and reduced forms of color vision and visual processing.

1.1. Monochromats, dichromats and normal observers

Since the spectral sensitivities of the cones overlap extensively, the isolation and measurement of cone spectral sensitivities is most easily achieved in individuals who lack one or more of the cone types. Following in this tradition, we have obtained: L-cone spectral sensitivities in deuteranopes, who lack M-cones; M-cone spectral sensitivities in protanopes, who lack L-cones; and S-cone spectral sensitivities in blue-cone monochromats, who lack both M- and L-cones [1]. Lastly, as a test of the validity of candidate M- and L-cone spectral sensitivity estimates, we have measured color matches in a tritanope, who lacks S-cones.

The use of monochromatic and dichromatic observers to define normal cone spectral sensitivities requires that their color vision be a reduced form of normal color vision [2]; that is, their surviving cones must have the same spectral sensitivities as their counterparts in the normal trichromat. While we can be more secure in this assumption, since it is now possible to sequence the photopigment genes of our observers (see below), it remains important to compare the spectral sensitivities of dichromats and monochromats with those of normals, before using them to define normal spectral sensitivity. For example, we found that with central fixation the S-cone spectral sensitivity function measured in blue-cone monochromats is slightly narrower than the same function measured in normals, probably because they fixate extrafoveally, where the S-cone photopigment density is lower than in the fovea [1]. Though the differences are small, it suggests the need to adjust

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blue-cone monochromat data to normal photopigment density values before their inclusion with normal data. Recent foveal optical reflectance measurements suggest that deuteranopes and protanopes also have lower foveal M- and L-cone photopigment optical densities than normals [3]. The mainly color normal M-cone data of Stockman et al. [4] however, agree well at long wavelengths with the protanope data reported here, which suggests that the two groups have similar M-cone photopigment optical densities (see Fig. 6). The corresponding L-cone comparison is complicated by the L(ser^{180}) and L(ala^{180}) polymorphism (see below.)

For normal M- and L-cone spectral sensitivities, we rely on the measurements of Stockman et al. [4], who used a transient adaptation technique to isolate the M or the L cones [5]. Normal S-cone spectral sensitivities were measured in five trichromats from 390 to $\sim$540 nm by selectively adapting the M- and L-cones with an intense yellow background [1]. In addition, we measured tritanopic color matches in normals, under adaptation conditions that induce temporary tritanopia.

1.2. Molecular genetics

An important aspect of this work is that the M- and L-cone photopigment genes of the dichromat observers have been sequenced by Jeremy Nathans (personal communication) and those of the blue-cone monochromat observers by Nathans et al. [6,7]. Moreover, with the exception of three protanopes, who have two M-cone photopigment genes, the dichromats had only a single M- or L-cone photopigment gene. Using single-gene dichromats, greatly simplifies the interpretation of the spectral sensitivity data. Of the twenty two single-gene deuteranopes, five had alanine at position 180 of their L-cone photopigment gene (L(ala^{180})) and 17 had serine at position 180 (L(ser^{180})). L(ala^{180}) and L(ser^{180}) are the two normally occurring L-cone photopigment gene polymorphisms. Of the nine protanopes, three had a single L1M2 gene, three had a single L2M3 gene, one had both an L1M2 and an M gene, and two had both an L2M3 and a M gene. The nomenclatures L1M2 and L2M3 indicate the site at which the hybrid genes change from being L-cone photopigment genes to M-cone photopigment genes. The numbers refer to the six exons that make up the photopigment gene. Thus, for L2M3, the change from L to M occurs between exons 2 and 3. Since the first exons of the L and M photopigment genes are identical, L1M2 is a de facto M photopigment gene. The spectral sensitivities of protanopes with a single L1M2 and protanopes with a single L2M3 photopigment gene are practically indistinguishable. Therefore, we have combined the data from the L1M2 and L2M3 groups. This accords with *in vitro* studies of recombinant pigment produced in tissue culture cells, which report a shift in the peak of the absorbance spectra of the two genotypes of 0.2 nm [8] or 0.0 nm [9]. A shift of 0.2 nm is within the measurement error.

1.3. Color matching and cone spectral sensitivities

Trichromacy is evident in our ability to match any light to a mixture of three other suitably-chosen 'primary' lights of fixed wavelength. The results of a matching experiment carried out by Stiles and Burch [10] and plotted for equal-energy test lights spanning the visible spectrum are shown in Fig. 1. The three functions are the relative intensities of the red (645 nm), green (526 nm) and violet (444 nm) primary lights required to match the test light, λ. They are referred to as the red, green and blue color matching functions (CMFs), respectively, and written, $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$.

Although the CMFs shown in Fig. 1 are for primaries of 645, 526 and 444 nm, the $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ CMFs (or tristimulus values, as they are also known) can be linearly transformed to other sets of real primary lights, to imaginary primary lights, such as the X, Y and Z primaries favored by the CIE and to the fundamental or cone primaries. Each transformation is accomplished by multiplying the CMFs by a 3×3 matrix. Our ultimate goal is to determine the unknown 3×3 matrix that will transform the $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ CMFs to the three cone spectral sensitivities: $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$ (cone) fundamental CMFs.

Color matches between the test and mixture fields are determined at the cone level; i.e. the two fields produce identical quantal catches in the S-, M- and L-cones. Thus, for matched fields, the following relationships apply:

$$\bar{l}_R\bar{r}(\lambda) + \bar{l}_G\bar{g}(\lambda) + \bar{l}_B\bar{b}(\lambda) = \bar{l}(\lambda);$$

$$\bar{m}_R\bar{r}(\lambda) + \bar{m}_G\bar{g}(\lambda) + \bar{m}_B\bar{b}(\lambda) = \bar{m}(\lambda); \quad \text{and}$$

$$\bar{s}_R\bar{r}(\lambda) + \bar{s}_G\bar{g}(\lambda) + \bar{s}_B\bar{b}(\lambda) = \bar{s}(\lambda); \qquad (1)$$

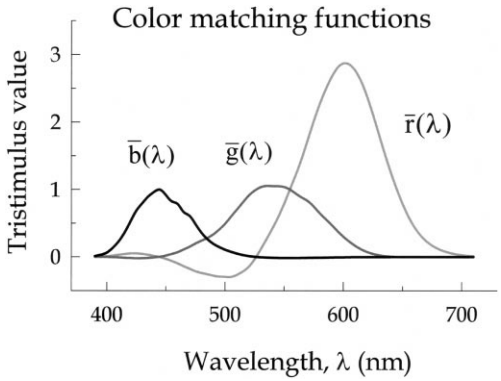

Fig. 1. The amounts of each of the three primaries or tristimulus values required to match monochromatic lights of equal energy spanning the visible spectrum are known as the red, $\bar{r}(\lambda)$, green, $\bar{g}(\lambda)$ and blue, $\bar{b}(\lambda)$ color matching functions. The data are from Stiles and Burch [10].

where $\bar{l}_R$, $\bar{l}_G$ and $\bar{l}_B$ are, respectively, the L-cone sensitivities to the red, green and blue primary lights and similarly $\bar{m}_R$, $\bar{m}_G$ and $\bar{m}_B$ are the M-cone sensitivities to the primary lights and $\bar{s}_R$, $\bar{s}_G$ and $\bar{s}_R$ are the S-cone sensitivities. We know $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ and we assume that $\bar{s}_R$ is effectively zero for a long-wavelength red primary, since the S-cones are insensitive to the red primary light at the radiances used in color-matching experiments. (The radiance of the spectral light λ, which is also known, is equal in energy units throughout the spectrum and therefore can be discounted).

There are therefore eight unknowns required for the linear transformation:

$$\begin{pmatrix} \bar{l}_R & \bar{l}_G & \bar{l}_B \\ \bar{m}_R & \bar{m}_G & \bar{m}_B \\ 0 & \bar{s}_G & \bar{s}_B \end{pmatrix} \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} = \begin{pmatrix} \bar{l}(\lambda) \\ \bar{m}(\lambda) \\ \bar{s}(\lambda) \end{pmatrix}. \quad (2)$$

Moreover, because we are often unconcerned about the absolute sizes of $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$, the eight unknowns collapse to just five:

$$\begin{pmatrix} \bar{l}_R/\bar{l}_B & \bar{l}_G/\bar{l}_B & 1 \\ \bar{m}_R/\bar{m}_B & \bar{m}_G/\bar{m}_B & 1 \\ 0 & \bar{s}_G/\bar{s}_B & 1 \end{pmatrix} \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} = \begin{pmatrix} k_l\,\bar{l}(\lambda) \\ k_m\,\bar{m}(\lambda) \\ k_s\,\bar{s}(\lambda) \end{pmatrix} \quad (3)$$

where the absolute values of $k_l(1/\bar{l}_B)$, $k_m(1/\bar{m}_B)$ and $k_s(1/\bar{s}_B)$ remain unknown. However, in practice k_l, k_m and k_s might be picked for some purpose, such as scaling $k_l\bar{l}(\lambda)$, $k_m\bar{m}(\lambda)$ and $k_s\bar{s}(\lambda)$ to peak at unity.

Our preferred method of obtaining the five unknowns is to measure the spectral sensitivities $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$ directly in either monochromats, dichromats or trichromats and then find the best fitting linear combination of $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ that describes each function. This approach also allows us to take into account differences in macular, lens and, if necessary, photopigment optical density between our observers and the mean observer represented by the CMFs. The S-cone spectral sensitivity, in addition, can be derived directly from the CMFs [11,4].

The validity of the linear transformation in Eq. (3), of course, depends not only on determining the correct unknowns, but also on the accuracy of the CMFs themselves. There are several CMFs that could be used to derive the cone spectral sensitivities. For the central 2-deg of vision, the main candidates are the Stiles and Burch, [10] and the Judd [12] and Vos [13] corrected CIE 1931 functions [14]. Additionally, the 10-deg CMFs of Stiles and Burch [15], which form the basis of the CIE 1964 large-field colorimetric observer, can be corrected to correspond to 2-deg macular and photopigment densities, as can the CIE 1964 10-deg CMFs.

Previous estimates of the cone spectral sensitivities are linear transformations of the Judd, Vos modified CIE 2-deg CMFs (e.g. [16,17]), the Stiles and Burch 2-deg CMFs (e.g. [18,19,4]), or the CIE 1964 10-deg CMFs [4]. Those that we will propose are a linear transformation of either the Stiles and Burch 2-deg CMFs or the Stiles and Burch [15] 10-deg CMFs adjusted to 2-deg. We prefer either the 2-deg or 10-deg Stiles and Burch CMFs because they were directly measured and are uncontaminated by changes introduced by standards committees. In contrast, the CIE functions were constructed from the relative color matching data of Wright [20] and Guild [21] with the assumption that the CMFs must be a linear combination of the 1924 CIE $V(\lambda)$ function [14]. Not only is the validity of the $V(\lambda)$ curve questionable, even after the corrections of Judd and Vos have been applied, but so too is the assumption that $V(\lambda)$ must be a linear combination of the CMFs [22,18]. Moreover, there are real differences between the CIE 1931 2-deg color matching data and the Stiles and Burch [10] 2-deg data between 430 and 490 nm, which can be clearly seen in Fig. 1 of Stiles and Burch [10].

The Smith and Pokorny [17] cone fundamentals have become the unofficial standard for cone spectral sensitivities. They were closely based on the fundamentals of Vos and Walraven [16], but with the crucial difference that $V(\lambda)$ was assumed to be equal to $\bar{l}(\lambda)+\bar{m}(\lambda)$ rather than to $\bar{l}(\lambda)+\bar{m}(\lambda)+\bar{s}(\lambda)$.

In this paper, we compare the normal, dichromat and monochromat spectral sensitivities and tritanopic color matching data with the Smith and Pokorny [17] fundamentals and with the Stockman et al. [4] fundamentals. Our data favor the Stiles and Burch 2-deg CMF and the CIE 1964 10-deg CMF based S-, M- and L-cone fundamentals of Stockman, MacLeod and Johnson at short wavelengths and their S-cone fundamental at middle wavelengths. Both sets of fundamentals are consistent with each other and with the dichromat L- and M-cone spectral sensitivities at middle- and long-wavelengths. But both are inconsistent with the blue-cone monochromat S-cone spectral sensitivities at long-wavelengths.

2. Methods

Measurements were made on a conventional Maxwellian-view optical system. The test target was 2-deg in diameter and was presented in the center of a 16-deg diameter background field. Target wavelengths were selected by a Jobin Yvon H-10 monochromator with 0.5 mm slits, the spectral output of which was a triangular function of wavelength with a full width at half maximum (FWHM) of 4 nm. A glass cut-off filter (Schott OG550) that blocked short wavelengths, but transmitted wavelengths longer than 550 nm, was placed in the target beam for wavelengths above 560

nm. Target wavelengths were randomly varied in 5 nm steps. Field wavelengths were selected by a Jobin Yvon H-10 monochromator, with 2 mm slits, providing half bandwidths of ~16 nm, or by three cavity, blocked interference filters with FWHMs of between 7 and 11 nm. The spectral sensitivities were measured with central fixation (and for the S-cone measurements, also at an eccentricity of 13-deg in the temporal retina).

The radiant fluxes of test and background fields were measured in situ at the plane of the observers' pupil. Extensive calibrations were conducted at both sites where the spectral sensitivities were measured: Freiburg and Tübingen. In Freiburg, the radiant fluxes were measured with a radiometer (United Detector Technology, Model S370 Optometer); in Tübingen with a calibrated silicon photodiode (Model SS0-PD50-6-BNC, Gigahertz-Optics, Puchheim, Germany) and a picoammeter (Model 486, Keithley). We carried out our additional calibration checks. Both instruments were cross-calibrated against: (1) a silicon photodetector supplied by Gigahertz-Optics (Puchheim, Germany), which was calibrated against the German National Standard (Braunsweig); and (2) a recently calibrated radiometer (Graseby, Model S370 Optometer) transported from San Diego, the calibration of which was traceable to the US National Standard. The two devices agreed to within 0.01 $\log_{10}$ unit from 400 to 700 nm.

The monochromators and interference filters were also calibrated in situ. In Freiburg, the spectral calibrations were carried out with a Photo Research, PR-704 spectroradiometer (Spectra-Scan, Chatsworth, CA) and in Tübingen with an Instrument Systems CAS-140 Spectroradiometer (Instrument Systems GmbH, Compact Array Spectrometer, München, Germany). The resolution of the Freiburg instrument was better than 0.5 nm; and that of the Tübingen instrument was better than 0.2 nm. The wavelength scales of the two spectroradiometers and the Jobin-Yvon monochromators were calibrated against a low pressure mercury source (Model 6035, LOT-Oriel GmbH., Darmstadt, Germany).

For the S-cone measurements in normals, we presented a single target field on an intense yellow (580 nm) background field of 12.10 log quanta s^{-1} deg^{-2} (5.93 log photopic td or 5.47 log scotopic td). The target was square-wave flickered at 1 Hz. The background field, which was chosen to selectively adapt the M- and L-cones in normals, also saturated the rods. For measurements in blue-cone monochromats, the target was presented on an orange (620 nm) background of 11.24 log quanta s^{-1} deg^{-2} (4.68 log photopic td or 3.36 log scotopic td), which was chosen to saturate the rods. The subjects' task was to set the threshold for detecting the flicker as a function of target wavelength. Five settings at each target wavelength were made on each of four runs.

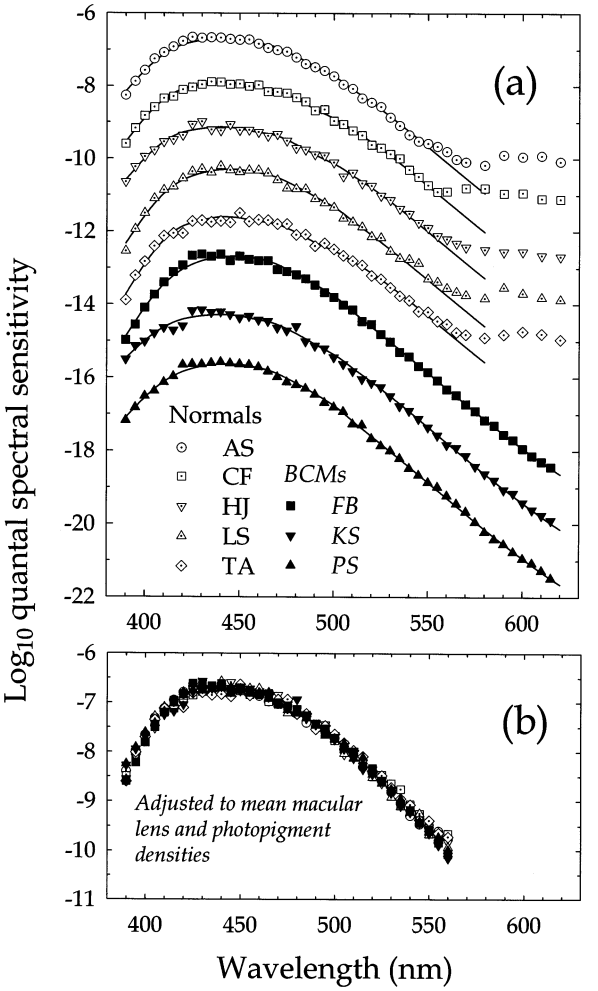

Fig. 2. (a): Individual 1-Hz spectral sensitivities obtained with central fixation, under S-cone isolation conditions. Each data set, except that for AS, has been displaced vertically for clarity: by −1.2 (CF), −2.0 (HJ), −3.8 (LS), −4.0 (TA), −6.3 (FB), −8.1 (KS) and −9.7 (PS) log units, respectively. Dotted symbols denote observers with normal color vision: AS (circles), CF (squares), HJ (inverted triangles), LS (triangles) and TA (diamonds). Filled symbols denote blue-cone monochromats: FB (squares), KS (inverted triangles) and PS (triangles). The continuous lines drawn through the data are macular and lens corrected versions of our proposed S-cone fundamental based on the Stiles and Burch [15] 10-deg CMFs adjusted to 2-deg. (b): Individual data corrected to typical normal macular, lens and photopigment densities and aligned with the mean. See Stockman et al. [1] for details of the density corrections.

For the M- and L-cone measurements, two targets were presented on a violet (430 nm) field of 11.00 log quanta s^{-1} deg^{-2} (3.08 log photopic td or 4.71 log scotopic td), which saturated the rods and prevented the S-cones from contributing to the measurements. S-cone-mediated detection was also disadvantaged by the flicker rate and the task [23,24]. Sensitivity was measured by heterochromatic flicker photometry. A reference target of 560 nm was alternated at a rate of 25 Hz (or, in some of the early longer-wavelength measurements, at 16 Hz), in opposite phase with a superim-

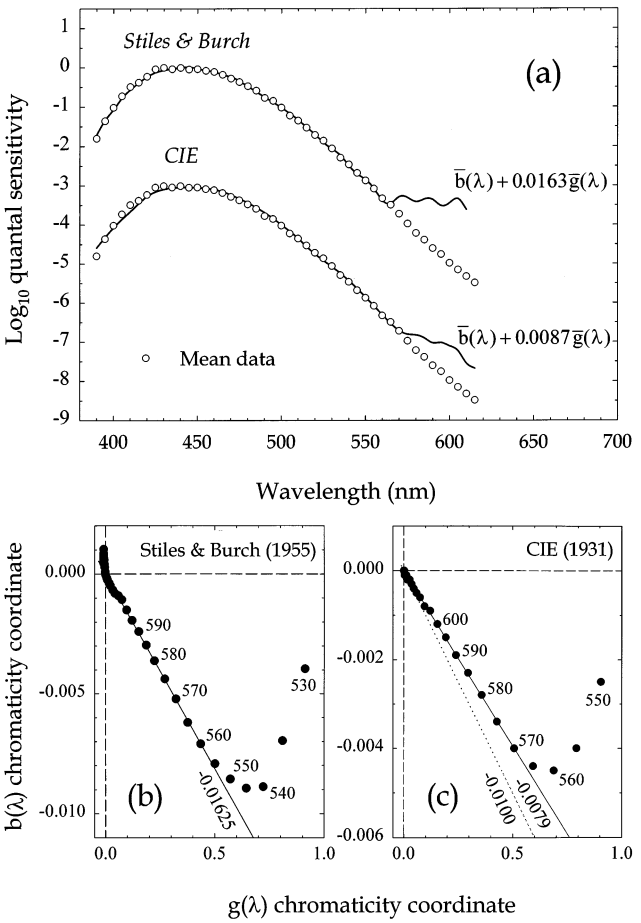

Fig. 3. (a): Mean central data shown twice separated by 3 $\log_{10}$ units (open circles) and linear combinations of the Stiles and Burch [10] 2-deg $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs ($\bar{b}(\lambda)+0.0163\bar{g}(\lambda)$, continuous line, upper function) and the Judd, Vos modified CIE 1931 2-deg $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs ($\bar{b}(\lambda)+0.0087\bar{g}(\lambda)$, continuous line, lower function) that best fit them (≤ 565 nm), after applying adjustments in lens and macular pigment densities. (b): Stiles and Burch [10] $g(\lambda)$ chromaticity coordinates plotted against the $b(\lambda)$ chromaticity coordinates (filled circles). The best-fitting straight line from 555 nm to long-wavelengths (continuous line) has a slope of -0.01625. (c): CIE 1931 2-deg $g(\lambda)$ chromaticity coordinates plotted against the $b(\lambda)$ chromaticity coordinates (filled circles). The best-fitting line from 565 nm to 600 nm (solid line) has a slope of -0.0079. The $\bar{z}(\lambda)$ CMF or Smith and Pokorny S fundamental implies the dotted line with a slope of -0.0100.

posed test target, the wavelength of which was varied from 400 to 680 nm. The flicker was square-wave. The reference was set to 0.2 $\log_{10}$ unit above flicker threshold and the subjects' task was to adjust the radiance of the variable-wavelength target until the flicker percept disappeared or was minimized. Five settings at each target wavelength were made on each of between two to eight runs.

Tritanopic matches were made on 420-nm backgrounds of varying radiance. Two vertically-bisected 2-deg half fields were juxtaposed to make a circular bipartite field. One half field, the standard field was illuminated by a high-pressure 100-W Hg lamp (Osram) filtered by 3-cavity interference filters (Ealing) designed to transmit only either the 404.7 or the 435.8-nm Hg lines. The Hg lines in a high-pressure lamp, however, are broadened and shifted to longer wavelengths (see [25]). Moreover, the nominal '435.8-nm' interference filter that we used skewed the spectral distribution to longer wavelengths by an additional 1.4 nm. The spectral 'lines' produced by our 100-W lamp are actually centered on 405.2 and 438.2 nm. The other half-field, the test field, was illuminated by a high-pressure 75-W Xe lamp (Osram). Its wavelength was selected by the Jobin Yvon H-10 monochromator and could be adjusted by the subject. The standard half-field was set to either 0.6 or 0.9 $\log_{10}$ unit above its contrast threshold. The subjects' task was then to adjust the wavelength and radiance of the test field so that it matched the standard field. If a perfect match in color and brightness was not possible, a record was made and the subject proceeded to make the closest possible match. The use of nearly monochromatic Hg lines makes the wavelength matches more or less independent of prereceptoral filtering by the macular and lens pigmentation. Such pigmentation, which can vary substantially between observers, alters the spectral energy distributions of broad-band short-wavelength lights, but not of spectral lines.

3. Results and discussion

3.1. S-cone spectral sensitivities

To define the S-cone spectral sensitivity in terms of $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$there is just one unknown, $\bar{s}_G/\bar{s}_B$, thus:

$$\frac{\bar{s}_G}{\bar{s}_B}\bar{g}(\lambda)+\bar{b}(\lambda)=k_s\bar{s}(\lambda). \quad (4)$$

We used two methods to find this value. First, we directly measured S-cone spectral sensitivity and then found the linear combination of the $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs that best describes it. We made measurements in five subjects with normal color vision and in three blue-cone monochromats, who lack functioning L- and M-cones. S-cone spectral sensitivity was measured centrally and at 13° in the periphery. This enabled us to estimate individual differences in macular and photopigment density. Separately, we estimated the lens density of each observer.

Fig. 2(a) shows the individual central spectral sensitivity curves for the normal trichromats (dotted symbols) and blue-cone monochromats (BCM, filled symbols). There is good overall agreement between the shapes of these curves until 540 nm, after which the M- and L-cones take over target detection in normals, but

not in blue-cone monochromats. Individual differences are evident at short wavelengths, which are mainly due to variations in lens and macular pigmentation, and other differences are evident at middle wavelengths (below 540 nm). These are greatly reduced by adjusting the data to mean macular, lens and photopigment densities (Fig. 2b).

Fig. 3(a) shows the mean central S-cone spectral sensitivities (open circles) plotted twice, separated by 3 $\log_{10}$ units. The sensitivities are the mean of the normal and blue-cone monochromat data below 540 nm and the mean of the blue-cone monochromat data from 540 to 615 nm. No density adjustments were made to the normal data before averaging. The blue-cone monochromat data, which was consistent with an unusually low central macular density and photopigment density, were adjusted to the mean normal macular and photopigment densities before averaging (for details, see [1]). Superimposed on the upper instance of the mean data is the linear combination of the Stiles and Burch [10] 2-deg $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs that best fits the data below 565 nm after making best-fitting adjustments to the lens and macular pigment density. The best-fitting value of $\bar{s}_G/\bar{s}_B$ with density adjustments is 0.0163, so that $\bar{s}(\lambda)$ in the Stiles and Burch [10] 2-deg space equals $0.0163\bar{g}(\lambda)+\bar{b}(\lambda)$. This function produces an excellent fit to the data up to 565 nm. According to the fit, our subjects' average lens pigment is 0.17 lower in density at 400 nm and their average macular pigment is 0.06 lower in density at 460 nm than the corresponding densities of the mean Stiles and Burch [10] 2-deg observer. The actual lens and macular density spectra used for these and later analyses are tabulated elsewhere [1]. The macular spectrum we used to make the adjustments is based on measurements by Bone et al. [26], while the lens spectrum is a version of the van Norren [27] spectrum slightly modified at short-wavelengths for consistency with the S-cone measurements and color matching data [1]. Both are similar to conventional spectra.

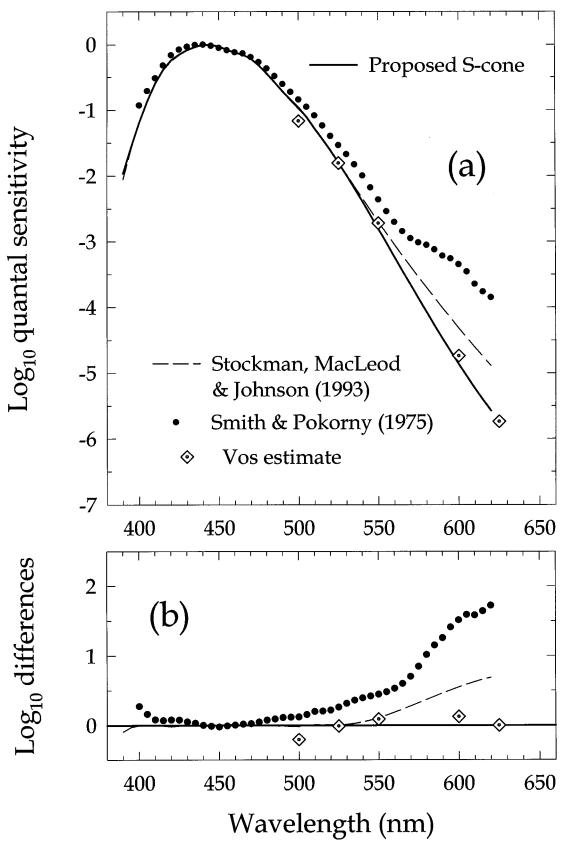

Fig. 4. (a): Comparison between the proposed S-cone spectral sensitivity function (continuous line), the Judd, Vos modified CIE 1931 $\bar{z}(\lambda)$ CMF or Smith and Pokorny [17] S-cone fundamental (filled circles) and the Stockman et al. [4] S-cone fundamental (dashed line). The extension suggested by Vos (personal communication) is shown by the dotted diamonds. (b): Differences between the proposed fundamental and the other functions.

Superimposed on the lower instance of the mean data is the best-fitting linear combination of the Judd, Vos modified CIE 1931 2-deg $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs with adjustments in lens and macular pigment density. The value of $\bar{s}_G/\bar{s}_B$ is 0.0087, so that in the CIE space equals $0.0087\bar{g}(\lambda)+\bar{b}(\lambda)$. The agreement with the Judd, Vos modified CIE 1931 2-deg function is poor at short-wavelengths. According to this fit, our subjects have an average lens pigment 0.16 lower in density at 400 nm and an average macular pigment 0.42 lower in density at 460 nm than the mean Judd, Vos modified CIE 1931 2-deg observer. The macular adjustment of 0.42 is implausibly large for mean data and reflects underlying problems with the CIE data at short-wavelengths Stockman et al. [4].

Using the method explained in Stockman et al. [4], we can also derive $\bar{s}_G/\bar{s}_B$ directly from the color matching data (see also [11]). This derivation depends on the longer wavelength part of the visible spectrum being effectively tritanopic for lights of the radiances typically used in color-matching experiments. Thus, target wavelengths longer than about 560 nm, as well as the red primary, are below S-cone threshold, in contrast to the green and blue primaries, which are above S-cone threshold. Targets longer than 560 nm can be matched for the L- and M-cones by a mixture of the red and green primaries, but a small color difference typically remains, because the S-cones detect the field containing the green primary. To complete the match for the S-cones, a small amount of the blue primary must be added to the mixture field opposite to the green primary. The sole purpose of the blue primary is to balance the effect of the green primary on the S-cones. Thus, the ratio of green to blue primary should be negative and fixed at $\bar{s}_G/\bar{s}_B$, the ratio of the S-cone spectral sensitivity to the two primaries.

Fig. 3(b) shows the Stiles and Burch [10] green, $g(\lambda)$ and $b(\lambda)$ blue, 2-deg chromaticity coordinates, which

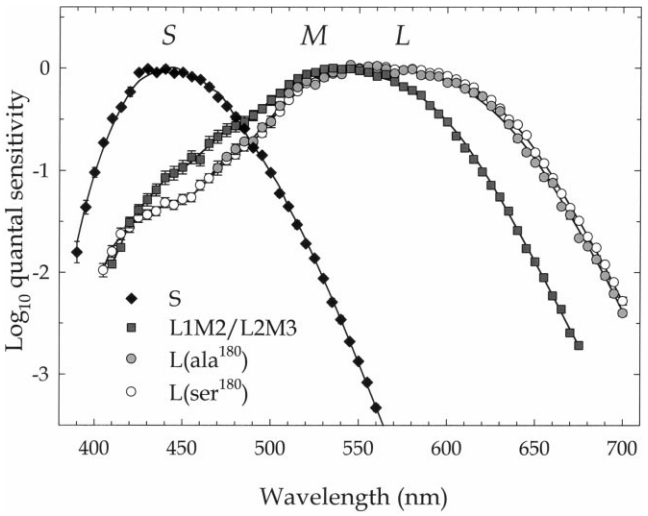

Fig. 5. Mean M-cone spectral sensitivities for nine protanopes with single L1M2 or L2M3 photopigment genes or with multiple L1M2 or L2M3 and M photopigment genes (gray squares); mean L-cone spectral sensitivities for five deuteranopes with a single L(ala^{180}) photopigment gene (gray circles) and 15 deuteranopes with a single L(ser^{180}) photopigment gene (white circles); and mean S-cone spectral sensitivities (black diamonds) for normals and blue-cone monochromats <540 nm and for blue-cone monochromats alone from 540–615nm (see also Fig. 3). The continuous lines are linear combinations of the Stiles and Burch [10] 2-deg CMFs adjusted in lens and macular density.

are related to the CMFs by $g(\lambda)=\bar{g}(\lambda)/[\bar{r}(\lambda)+\bar{g}(\lambda)+\bar{b}(\lambda)]$ and by $g(\lambda)=\bar{g}(\lambda)/[\bar{r}(\lambda)+\bar{g}(\lambda)+\bar{b}(\lambda)]$. As expected, the function above ~ 555 nm follows a straight line relationship. It has a slope of -0.01625, which implies that $\bar{s}_G/\bar{s}_B$ is 0.01625. Reassuringly, it is similar to the value obtained from the direct spectral sensitivity measurements, given above. Fig. 3(c) shows comparable CIE 1931 2-deg data. In this case, mainly because the primaries are different, the slope is shallower at only -0.0079, so that $\bar{s}_G/\bar{s}_B$ equals 0.0079 in the CIE 1931 2-deg space. Notice that the value of $\bar{s}_G/\bar{s}_B$ of 0.0100, which was adopted by Smith and Pokorny [17] and Vos and Walraven [16] to define $\bar{s}(\lambda)$ (and is also the CIE $\bar{z}(\lambda)$ CMF), completely misses the chromaticity coordinates. It is not the optimal value for $\bar{s}(\lambda)$ in the CIE space.

The value of $\bar{s}_G/\bar{s}_B$ of 0.0079 is similar to the value of 0.0087 obtained from direct spectral sensitivity measurements. Given the speculative adjustments made by the CIE to the original data [20,21] on which the CIE chromaticity coordinates are based (see [1]), we consider the value based on the spectral sensitivity measurements to be more reliable.

On the basis of color matching data at wavelengths below 540 nm (1), 560 nm (2) or 565 nm (3)[1], the mean S-cone data between 540 and 615 nm Stockman et al. [1] have proposed three S-cone functions derived from: (1) the Stiles and Burch [15], 10-deg functions adjusted to 2-deg; (2) the Stiles and Burch [10], 2-deg functions and (3) the Judd, Vos modified CIE 1931 2-deg functions. Of these we prefer (1), but we propose (3) as a replacement in the CIE space. The values of $\bar{s}_G/\bar{s}_B$ that we adopt are: 0.01625 in the Stiles and Burch 2-deg space, 0.0087 in the CIE 2-deg space and, taking into account similar considerations, 0.0106 in the Stiles and Burch 10-deg space.

Fig. 4(a) compares our proposed S-cone fundamental (1), which is based on the Stiles and Burch [15] 10-deg CMFs adjusted to 2-deg (continuous line), with the Stockman et al., [4] function (dashed line) and the Smith and Pokorny, [17] function (filled circles). The differences between the functions are shown in Fig. 4(b). The overall agreement between the proposed S-cone function and the Judd, Vos modified CIE 1931 based Smith and Pokorny [17] S-cone function is poor. The agreement with the Stockman, MacLeod and Johnson fundamental is good from 390 to 540 nm, but beyond 540 nm, after which the color matching functions no longer usefully define the S-cone fundamental, their fundamental has been wrongly extrapolated.

The suggestion that the Stockman, MacLeod and Johnson function was too shallow at long-wavelengths was originally made by Vos (private communication), who offered the modification indicated by the dotted diamonds. His guess, however, was based on a theoretical model of photopigment sensitivity at long wavelengths [28], which has no currently accepted basis.

3.2. M- and L-cone spectral sensitivities

The definition of the M- and L-cone spectral sensitivities in terms of $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ and requires knowledge of four unknowns (in addition to the two scaling constants):

$$\frac{\bar{m}_R}{\bar{m}_B}\bar{r}(\lambda)+\frac{\bar{m}_G}{\bar{m}_B}\bar{g}(\lambda)+\bar{b}(\lambda)=k_m\bar{m}(\lambda), \quad \text{and} \tag{5}$$

$$\frac{\bar{l}_R}{\bar{l}_B}\bar{r}(\lambda)+\frac{\bar{l}_G}{\bar{l}_B}\bar{g}(\lambda)+\bar{b}(\lambda)=k_l\bar{l}(\lambda). \tag{6}$$

To find $\bar{m}_R/\bar{m}_B$, $\bar{m}_G/\bar{m}_B$, $\bar{l}_R/\bar{l}_B$ and $\bar{l}_G/\bar{l}_B$ we rely on direct measurements in normals and in dichromats. For normals, we used the measurements of Stockman et al., [4], who exploited the transient adaptation technique of Stockman et al. [5] to obtain M- and L-cone isolation. Briefly, isolation was achieved by measuring sensitivity immediately following an exchange of background color: M-cone isolation following a blue to red background transition; and L-cone isolation following a red to blue transition. The Stockman et al. [4] data remain useful because they represent mainly normal measure-

[1] The highest wavelength depends on the range over which the particular CMFs, which we have labelled (1), (2) and (3), usefully define S-cone sensitivity.

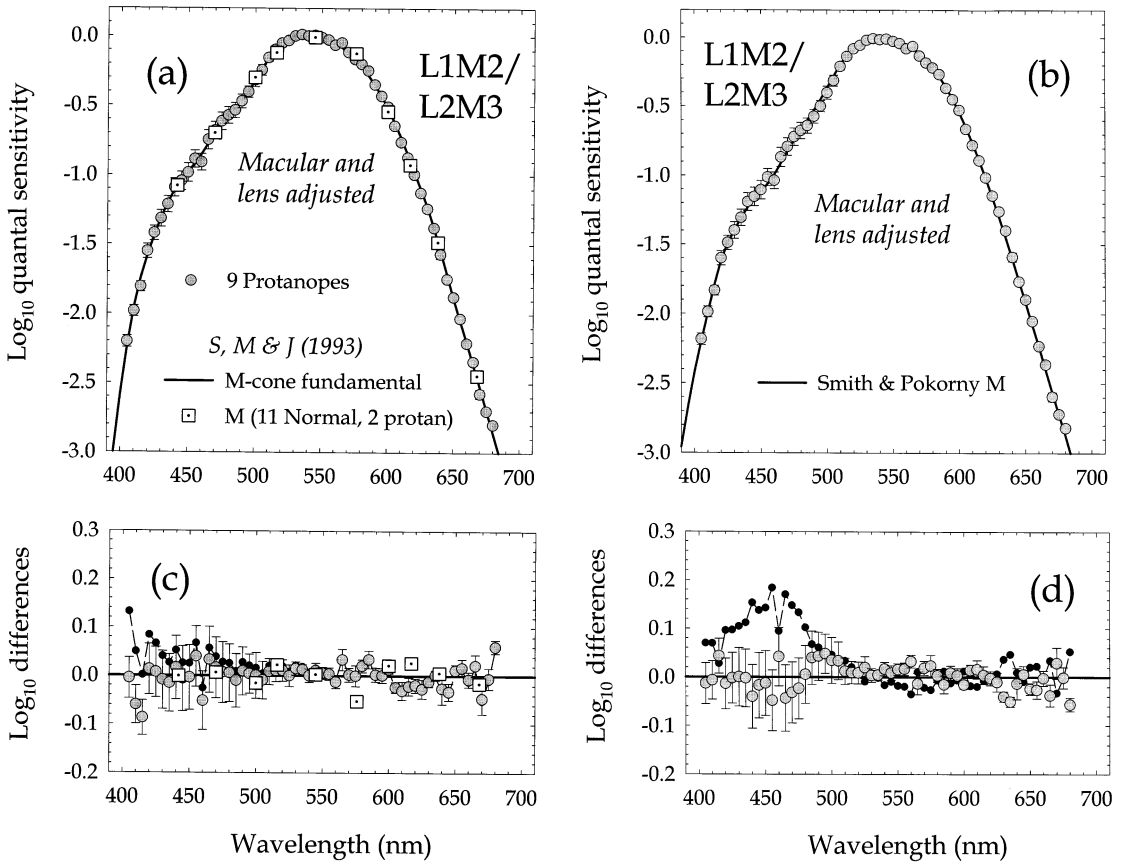

Fig. 6. (a): Mean protanope data (gray circles) and mean M-cone data (dotted squares) from [4] adjusted in macular and lens density to best fit the Stockman et al. [4] M-cone fundamental (continuous line). (b): Mean protanope data (gray circles) adjusted in macular and lens density to best fit the Smith and Pokorny [17] M-cone fundamental (continuous line). (c): Residuals from (a). Differences between the mean protanope data and the Stockman, MacLeod and Johnson M-cone fundamental (gray circles) and between the mean M-cone data from Stockman, MacLeod and Johnson and their M-cone fundamental (dotted squares). Also shown are the differences between the mean protanope data and the Stockman et al. [4] M-cone fundamentals before macular and lens adjustments (small filled circles). (d): Residuals from (b). Differences between the mean protanope data and the Smith and Pokorny M-cone fundamental (gray circles). Also shown are the differences between the mean protanope data and the Smith and Pokorny M-cone fundamental before macular and lens adjustments (small filled circles).

ments that can be compared with dichromat measurements[2] (see dotted symbols in Figs. 6–8).

A straightforward way of estimating the L and M-cone spectral sensitivities is to measure them in dichromats, who lack one of the longer wavelength cone pigments—under conditions that suppress the S-cones—either in protanopes who lack the L-cone photopigment, or in deuteranopes who lack the M-cone photopigment. Dichromats have been used to estimate cone spectral sensitivities many times before (e.g. [29–32,17,33,34]. These earlier studies, however, did not have the present-day advantage of being able to sequence the photopigment genes of their dichromatic observers and to determine exactly the genotype; i.e. whether their observers have normal or hybrid genes and whether they have single or multiple instances of the X-chromosome-linked photopigment genes.

Fig. 5 shows the mean dichromat data for the nine protanopes (gray squares), the five deuteranopes with L(ala^{180}) (gray circles) and the 15 deuteranopes with L(ser^{180}) of the 17 who made measurements throughout the spectrum (white circles). The mean S-cone data obtained from the normal and blue-cone monochromat observers are also shown (black diamonds).

Fig. 6 compares the mean data for the L1M2/L2M3 protanope observers (gray circles) with the Stockman et al. [4] 2-deg M-cone fundamental based on the CIE 1964 10-deg CMFs (continuous lines, a, c) and with the Smith and Pokorny [17] M-cone fundamental (continuous lines, b, d). In both cases, the lens and macular pigment densities of the mean L1M2/L2M3 observer have been adjusted to best fit the fundamentals. According to these fits, the L1M2/L2M3 observers' average macular pigment is 0.02 lower in density at 460 nm and their average lens pigment is 0.11 lower in density

[2] They are also the basis, at short and long-wavelengths, of the Stockman, MacLeod and Johnson fundamentals. At short-wavelengths the Stockman, MacLeod & Johnson fundamentals are based on Wright's [36] tritanopic color matching data.

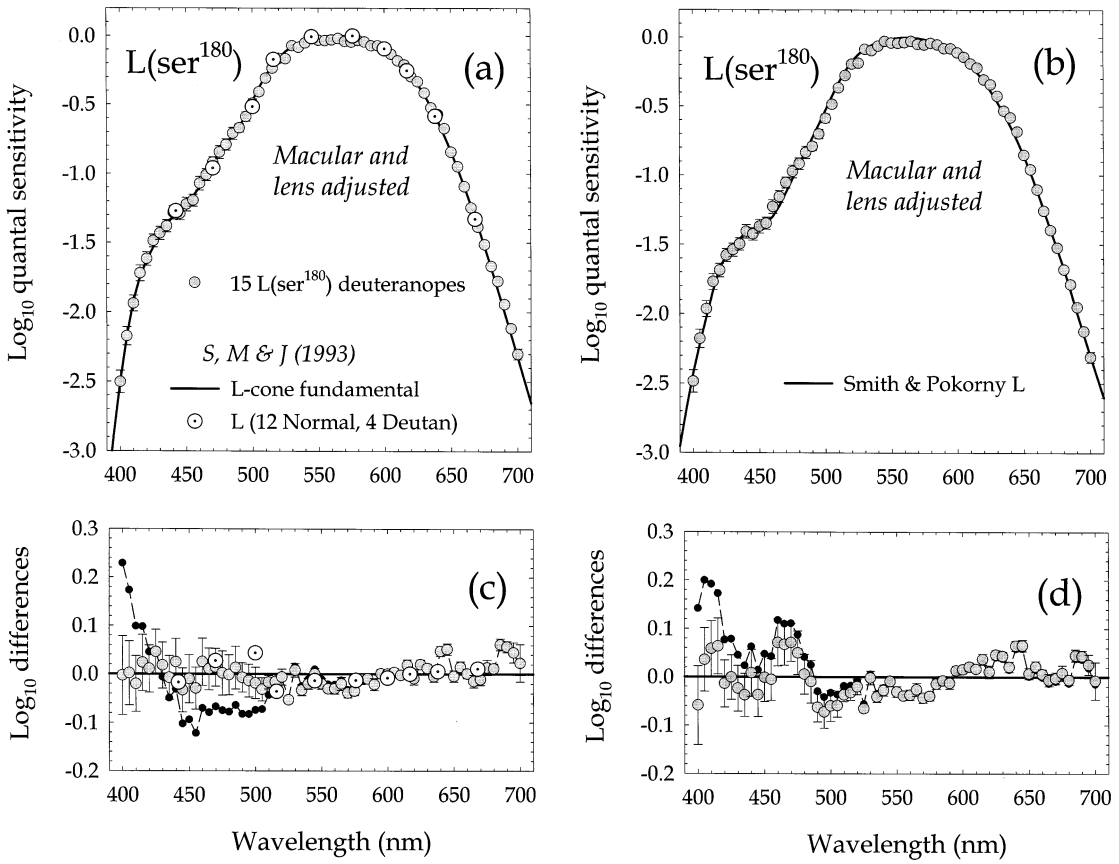

Fig. 7. (a): Mean L(ser^{180}) data (gray circles) and mean L-cone data (dotted circles) from Stockman et al. [4] adjusted in macular and lens density to best fit the Stockman et al. [4] L-cone fundamental (continuous line). (b): Mean L(ser^{180}) data (gray circles) adjusted in macular and lens density to best fit the Smith and Pokorny [17] L-cone fundamental (continuous line). (c): Residuals from (a). Differences between the mean L(ser^{180}) data and the Stockman, MacLeod and Johnson L-cone fundamental (gray circles) and between the mean L-cone data from Stockman, MacLeod and Johnson and their L-cone fundamental (dotted circles). Also shown are differences between the mean L(ser^{180}) data and the Stockman, MacLeod and Johnson L-cone fundamental before macular and lens adjustments (small filled circles). (d): Residuals from (b). Differences between the mean L(ser^{180}) data and the Smith and Pokorny M-cone fundamental (gray circles). Also shown are the differences between the mean L(ser^{180}) data and the Smith and Pokorny L-cone fundamentals before macular and lens adjustments (small filled circles).

at 400 nm than the corresponding densities of the mean Stockman et al. [4] observer; whereas the L1M2/L2M3 observers' average macular pigment is 0.14 lower in density at 460 nm and their average lens pigment is 0.02 lower at 400 nm in density than the values of the mean Smith and Pokorny [17] observer. Also shown in panels a and c are the mean data of Stockman, MacLeod and Johnson (dotted squares) for eleven normals and two protanopes adjusted in macular and lens density (see [4]). The residuals are shown in the corresponding lower panels (c) and (d), for the Stockman et al. [4] and Smith and Pokorny [17] fundamentals, respectively. The filled circles in the lower panels show the differences between the fundamentals and the mean L1M2/L2M3 data before any adjustments in macular and lens density.

After macular and lens adjustment, the agreement between the mean L1M2/L2M3 data and both the Stockman et al. [4] and the Smith and Pokorny [17] M-cone fundamentals is good (gray circles). Moreover, the best-fitting lens and macular adjustments are plausible and suggest that the Stockman et al. [4] observer has a lower macular pigment density, but higher lens pigment density than the Smith and Pokorny [17] observer (see also [10,35]. A small undulation can be seen in Fig. 6(d) between 450 and 510 nm (gray circles) for the Smith and Pokorny [17], M-cone fundamental, but the differences are small.

Fig. 7 shows comparisons between the mean data for the L(ser^{180}) observers (gray circles) and the Stockman et al. [4] 2-deg L-cone fundamental based on the CIE 1964 10-deg CMFs (continuous lines, a, c) and the Smith and Pokorny, [17] L-cone fundamental (continuous lines, b, d). As in Fig. 6, the lens and macular pigment densities of the mean L(ser^{180}) observer have been adjusted to best fit the fundamentals. According to these fits, the L(ser^{180}) observers' average macular pigment is 0.13 higher in density at 460 nm and their average lens pigment is 0.27 lower in density at 400 nm than the densities of the average Stockman et al. [4] observer; whereas the L(ser^{180}) observers' average mac-

ular pigment is 0.03 lower in density at 460 nm and their average lens pigment is 0.20 lower in density at 400 nm than the densities of the Smith and Pokorny [17] observer. Also shown are the mean data of Stockman et al. [4] for 12 normals and four deuteranopes (dotted circles). The residuals are shown in the corresponding lower panels (b) and (d). The filled circles in the lower panels show the differences between the fundamentals and the mean L(ser^{180}) data before any adjustments in macular and lens density.

After macular and lens adjustment (gray circles), the agreement between the mean L(ser^{180}) data and the Stockman et al. [4] L-cone fundamental is good; as is the agreement between the mean L-cone data from Stockman, MacLeod and Johnson and their L-cone fundamental (dotted circles). The agreement between the mean L(ser^{180}) data and the Smith and Pokorny, [17] L-cone fundamentals is poorer at short wavelengths (see Fig. 7(d)). In both cases, the differences at longer wavelengths suggest that the λ_{max} of the L(ser^{180}) observers is shifted to slightly longer wavelengths than the L-cone fundamentals. Again, the best-fitting lens and macular adjustments are plausible and again they suggest that the Stockman et al. [4] observer has a lower macular pigment density, but higher lens pigment density than the Smith and Pokorny [17] observer. This accords with our measurements of the lens and macular pigment densities in our dichromat observers (unpublished observations). Comparisons suggest that the L1M2/L2M3 observers have on average a lower macular density and higher lens density than the L(ser^{180}) observers.

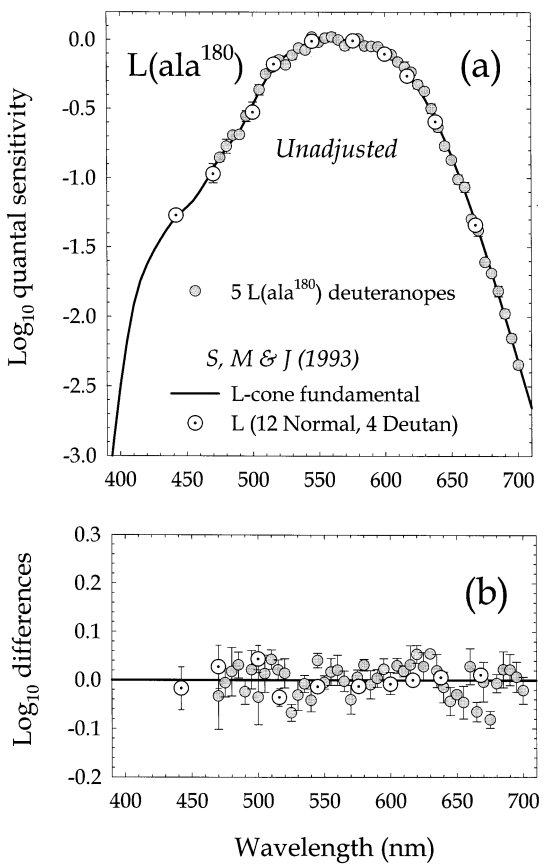

Fig. 8. (a): Mean L(ala^{180}) data (gray circles) and mean L-cone data (dotted circles) from Stockman et al. [4] compared with the Stockman et al. [4] L-cone fundamental (continuous line) without any macular or lens density adjustments. (b): Residuals from (a). Differences between the mean L(ala^{180}) data and the Stockman, MacLeod and Johnson L-cone fundamental (gray circles) and between the mean L-cone data from Stockman, MacLeod and Johnson and their L-cone fundamental (dotted circles).

Fig. 8 shows comparisons between the mean data for the five L(ala^{180}) deuteranope observers (gray circles) and the Stockman et al. [4] L-cone fundamental based on the CIE 1964 10-deg CMFs (continuous lines, a, b). No lens and macular pigment density adjustments have been made, partly because the mean for the five observers begins at 470 nm, since only two out of our five subjects made measurements at short wavelengths. The agreement is fairly good, but the differences at longer wavelengths suggest that the λ_{max} of the L(ala^{180}) observers is shifted to slightly shorter wavelengths than the Stockman et al. [4] L-cone fundamental.

Instead of just comparing the dichromat data with other fundamentals, we can use them to generate new fundamentals directly. That is, we can use them to determine the unknowns in the matrix transformation. Fig. 9 shows the linear combination of the Stiles and Burch [10] 2-deg CMFs that best fits the mean protanope data (Panels a, c) and the mean L(ser^{180}) data (Panels b,d) with best-fitting macular and lens density adjustments. In both cases, the fit is good throughout the spectrum.

For the L1M2/L2M3 data, the best-fitting values are $\bar{m}_R/\bar{m}_B = 0.29089$ and $\bar{m}_G/\bar{m}_B = 12.24415$ and the best-fitting densities suggest that the L1M2/L2M3 observers' average macular pigment is 0.03 lower in density at 460 nm and their average lens pigment is 0.09 higher in density at 400 nm than the densities of the mean Stiles and Burch [10] observer. For L(ser^{180}), the best-fitting values are $\bar{l}_R/\bar{l}_B = 5.28554$ and $\bar{l}_G/\bar{l}_B = 16.80098$ and the best-fitting densities suggest that the L(ser^{180}) observers' average macular pigment is 0.08 higher in density at 460 nm and their average lens pigment is 0.07 lower in density at 400 nm than the Stiles and Burch [10] observer. The Stiles and Burch [10] 2-deg CMF based fundamentals of Stockman et al., [4] use $\bar{m}_R/\bar{m}_B = 0.29784$, $\bar{m}_R/\bar{m}_B = 12.24223$, $\bar{l}_R/\bar{l}_B = 4.75702$ and $\bar{l}_G/\bar{l}_B = 16.63201$. The differences between the dichromat-based fundamentals and the Stockman et al., [4] fundamentals are small.

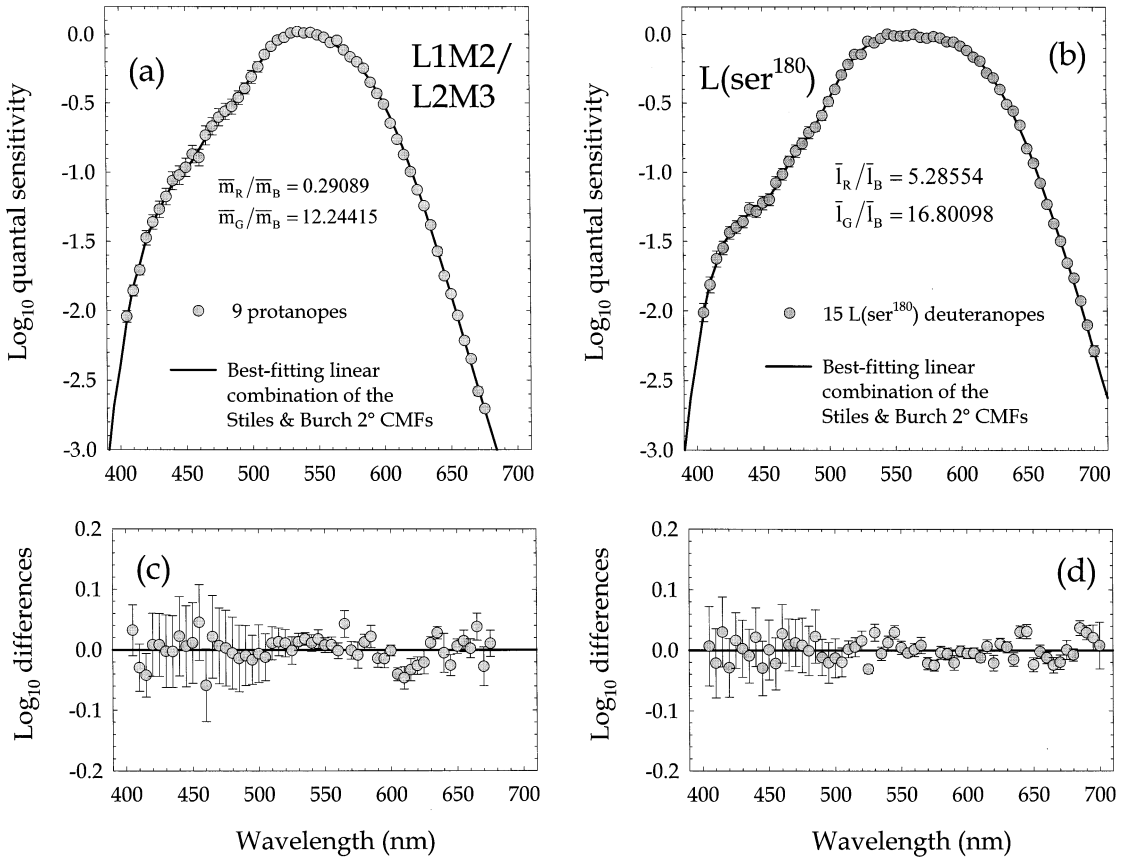

Fig. 9. (a): Mean protanope data (gray circles) and best-fitting linear combinations of the Stiles and Burch [10] 2-deg CMFs with best-fitting lens and macular adjustments (continuous line). (b): Mean L(ser^{180}) data (gray circles) and best-fitting linear combinations of the Stiles and Burch 2-deg CMFs with best-fitting lens and macular adjustments (continuous line). (c): Residuals from (a). (d): Residuals from (b).

3.3. Tritanopic color matches

The dichromat M- and L-cone spectral sensitivities shown in Figs. 6 and 7 do not clearly favor either the fundamentals of Smith and Pokorny [17] or the fundamentals of Stockman et al. [4]. Real differences between the two sets of fundamentals at short-wavelengths do exist, but they are obscured by uncertainties about the macular and lens pigment densities of each group of observers. This problem is confounded by the use of the M-(protanopic) and L-(deuteranopic) cone spectral sensitivities, since they are necessarily obtained in different groups of observers with different mean lens and macular densities.

Tritanopic matches provide a useful way of testing between the candidate fundamentals. Since tritanopes lack S-cones, their color matches should be approximately predicted by any plausible L- and M-cone spectral sensitivity estimates[3].

The continuous lines in both panels of Fig. 10 show Wright's [36] tritanopic data in the form of the $g(\lambda)$ WDW coordinates (the WDW $r(\lambda)$ coordinates are simply $1-g(\lambda)$)[4]. Spectral lights that are confused by tritanopes are represented by any two points on the curve with the same $g(\lambda)$ value.

Pokorny and Smith [37] suggested that a way of testing between the Smith and Pokorny [17] and the Stockman et al. [4] fundamentals would be to determine the spectral lights that tritanopes confused with the short-wavelength Hg lines. We induced tritanopia in normals by presenting targets on intense violet backgrounds. Under such conditions, six normals and one tritanope match, on average, the 405-nm line with 556.6 nm and 438-nm 'line' with 493.7 nm, as indicated by the inverted triangles. We emphasize that these are preliminary averages. A detailed analysis is in progress.

Fig. 10(a) shows the $g(\lambda)$ function predicted by the Stockman et al. [4] 2-deg L- and M-cone fundamentals based on the CIE 1964 10-deg CMFs (dotted circles).

[3] Of course, because individual tritanopes might be R(ser^{180}), or R(ala^{180}), or have hybrid genes, individual matches might differ from the mean matches by several nanometers.

[4] WDW coordinates are a form of chromaticity coordinates devised by W. D. Wright. They are calculated by first normalizing $r(\lambda)$ and $g(\lambda)$ to be equal at 582.5 nm, and then normalizing $g(\lambda)$ and $b(\lambda)$ to be equal at 494.0 nm. This double normalization produces chromaticity data that are independent of variations in prereceptoral filtering. For tritanope data, only the first normalization applies.

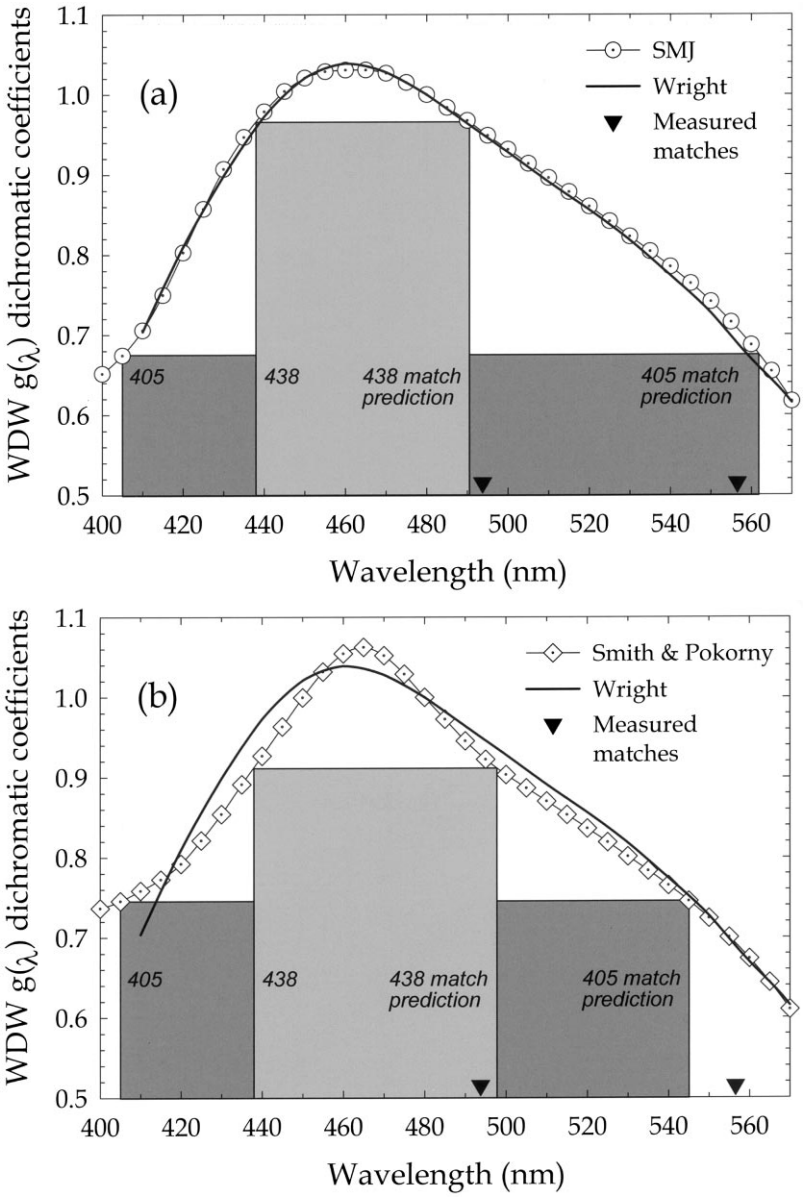

Fig. 10. (a): Comparison between Wright's [36] tritanopic WDW coefficients (continuous line) and the tritanopic coefficients calculated from the Stockman et al. [4] 2-deg M- and L-cone fundamentals based on the CIE 1964 10-deg CMFs (dotted circles). The matches to the 405 and 438-nm lights predicted by the Stockman et al. [4] fundamentals are indicated by the light gray rectangle (438 nm) and by the dark gray rectangle (405 nm) that underlies it. The right edge of each rectangle is aligned with the wavelength for which the $g(\lambda)$ value is the same as for the left edge. Thus, the right edge of the light gray rectangle is the 438-nm match prediction and the right edge of the dark gray rectangle the 405-nm match prediction. The mean matches of six normal observers and one tritanopic observer are indicated by the inverted triangles. (b): Comparison between the WDW $g(\lambda)$ coefficients (continuous line), the tritanopic coefficients calculated from the Smith and Pokorny [17] M- and L-cone fundamentals (dotted diamonds). The matches to the 405 and 438-nm lights predicted by the Smith and Pokorny [17] fundamentals are indicated by the light gray rectangle (438 nm) and by the dark gray rectangle (405 nm) that underlies it. Other details as (a).

Not surprisingly, since Stockman et al. [4], chose their fundamentals to be consistent with Wright's data, the agreement with Wright's $g(\lambda)$ function (continuous line) is good down to 410 nm, after which Wright's measurements end. However, the measured 405-nm match, which is beyond the range of Wright's data, is ~ 5 nm shorter than the Stockman et al. [4] prediction, while the measured 438-nm match is ~ 3 nm longer. The agreement for the 405-nm match is better for the version of the Stockman et al. [4] 2-deg fundamentals based on the Stiles and Burch [10] 2-deg CMFs.

Fig. 10(b) shows the $g(\lambda)$ function predicted by the Smith and Pokorny [17] fundamentals (dotted diamonds). In contrast to CIE 1964 10-deg and Stiles and Burch 2-deg and 10-deg based fundamentals, the Smith and Pokorny [17] predictions agree poorly with Wright's data. The problem lies in the Judd, Vos modified CIE 2-deg CMFs, which, as others have

pointed out before, are inconsistent with the tritanopic color matching data [38,18]. The measured 438 nm match is about 4 nm shorter than the Smith and Pokorny [17] prediction, while the 405 nm match is ~12 nm longer.

4. Conclusions

The Stockman et al. [4] S-, M- and L-cone fundamentals agree fairly well with data from protanopes, deuteranopes, tritanopes, blue-cone monochromats and normal trichromats. The need for improvements, however, to the M- and L-cone fundamentals is suggested by the tritan confusion pairs. S-cone sensitivity is also overestimated at wavelengths longer than 540 nm.The Smith and Pokorny [17] M- and L-cone fundamentals also agree fairly well with the data from protanopes and deuteranopes. Their M- and L-cone functions, however, are clearly inconsistent with the tritanopic color matches of Wright [36] and with the tritan confusions established for the 405-nm Hg line. The Smith and Pokorny [17] S-cone fundamental agrees poorly with the S-cone spectral sensitivity measurements. Moreover, it is not the optimal fundamental in the CIE Judd, Vos space, on which it is based (see Fig. 3c).

The comparisons shown in Fig. 7 suggest that the L(ser^{180}) observers have a slightly longer λ_{max} than the normal observers represented by the Stockman et al. [4] and the Smith and Pokorny [17] L-cone fundamentals. In contrast, the comparisons shown in Fig. 8 suggest that the L(ala^{180}) observers have a slightly shorter λ_{max} than the normal observers. These results imply that the mean normal λ_{max} lies between the L(ala^{180}) and L(ser^{180}) values, which is entirely expected since the normal population should be a mixture of the two polymorphic variants of the normal L-cone pigment gene. The differences are small, however. An analysis of our L(ala^{180}) and L(ser^{180}) dichromat data indicates a λ_{max} difference between the two genotypes of only ~2.7 nm [39], which is at the lower end of the range of indirect psychophysical estimates of 2.6–4.3 nm inferred from Rayleigh-type matches (e.g. [40,41]) and less than estimates of 5–7 nm inferred from electro-retinographic action spectra (e.g. [42]).

We are now working on new versions of the cone fundamentals based on the data presented here. Several issues will be important: for example, how to combine the L(ala^{180}) and L(ser^{180}) data to produce a normal L-cone fundamental; and how to define luminance in the Stiles and Burch [10,15] color spaces.

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