Physiologically-based color matching functions

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Abstract

A continuing goal of color science since the establishment of the trichromatic theory of color perception [e.g., 5, 6, 7] has been the accurate determination of the spectral sensitivities of the long-, middle- and short-wavelength-sensitive (L, M and S) cones—also known as the fundamental color matching functions (or CMFs): $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$. These CMFs are the physiological bases of all other CMFs. The cone fundamentals of Stockman and Sharpe [2], which are to be recommended by the CIE Technical Committee 1-36 as an international standard for colorimetry [12], rely on measurements made in both normal trichromats and color deficient observers. These measurements are used to guide the linear combinations of the Stiles & Burch [1] CMFs that define the cone fundamentals.

Introduction

Knowledge of the three cone spectral sensitivity functions is crucial not only for the understanding and modeling of visual function, but also for the practical applications of color matching and color measurement. This short review covers the relationship between color matching and cone spectral sensitivities and then describes the derivation of the "physiologically-relevant" Stockman and Sharpe [2] cone spectral sensitivities.

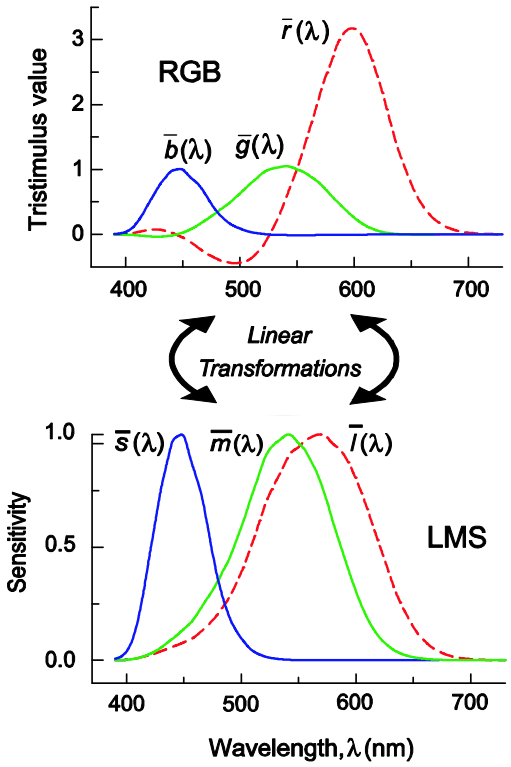

Figure 1 *CMFs can be linearly transformed from one set of primaries to another. Shown here are 10 deg CMFs for real, spectral RGB primaries [1] and LMS cone fundamental primaries [2].*

Normal human photopic vision is trichromatic, a consequence of which is that the color of any light can be defined by just three variables: the intensities of three specially chosen primary lights that match it. The upper panel of Figure 1 shows examples of the $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ colour matching functions or CMFs for **RGB** (red-green-"blue") primaries of 645, 526 and 444 nm. Each CMF defines the amount of that primary required to match monochromatic targets of equal energy. CMFs can be determined without any knowledge of the underlying cone spectral sensitivities. The only restriction on the choice of primary lights is that they must be independent (in the sense that no mixture of two primaries matches the third).

CMFs can be linearly transformed to any other set of real primary lights, and, as illustrated in Fig. 1, to *imaginary* primary lights, such as the **L**, **M** and **S** cone *fundamental* primaries, which are the physiologically important photoreceptor spectral sensitivities, or to the **X**, **Y**, **Z** primaries favoured by the CIE. The three fundamental primaries (or "Grundempfindungen"—fundamental sensations) are the three imaginary primary lights that would uniquely stimulate each of the three cones to yield the $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$ CMFs, the L-, M- and S-cone spectral sensitivity functions. For convenience and precision, cone spectral sensitivities are usually defined in terms of transformed CMFs, rather than as direct sensitivity measurements (such as those shown in Fig. 2).

Derivation of the cone fundamentals

Spectral sensitivity measurements

With the S-cones disadvantaged or suppressed by chromatic adaptation, L- and M-cone spectral sensitivities can be directly measured in deuteranopes, who lack M-cone function, and in protanopes, who lack L-cone function. Figure 2 shows the mean spectral sensitivity data obtained from 17 single-gene L(ser^{180}) deuteranopes with serine at position 180 of their L-cone photopigment opsin gene (open circles), from 5 single-gene L(ala^{180}) deuteranopes with alanine at position 180 (filled squares), and from 9 protanopes (gray diamonds) (for further details, see Refs. [2,3]). An overall L-cone mean was also derived (not shown) to reflect the proportions of the two polymorphic variants in the population [2].

To define a mean S-cone spectral sensitivity, Stockman, Sharpe & Fach [10] measured S-cone spectral sensitivities in three blue-cone monochromats [13-19], known to lack L- and M-cones on genotypical as well as phenotypical grounds, and combined them with S-cone data from normals obtained at short and middle-wavelengths on an intense yellow background field that selectively adapted the M- and L-cones. Their mean S-cone function is shown

in Fig. 2 (filled triangles) and also in the upper panel of Fig. 4 (circles).

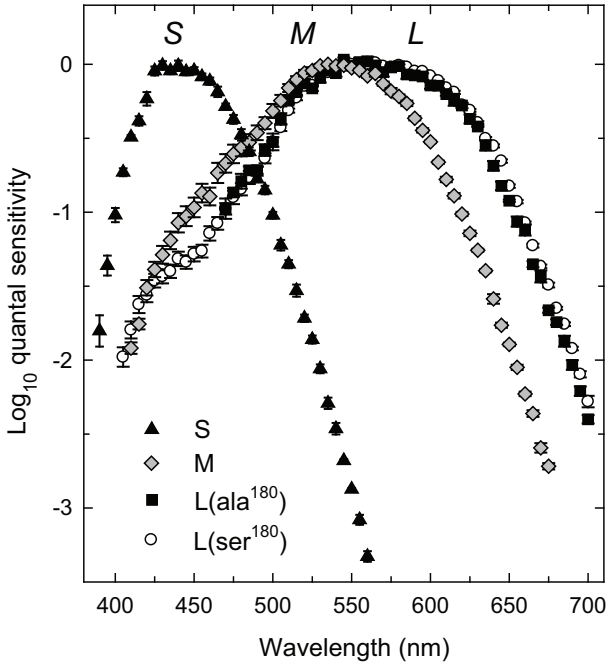

Figure 2 *Mean cone spectral sensitivity data. L-cone data from 17 L(ser^{180}, open circles) and 5 L(ala^{180}, filled squares) deuteranopes measured by Sharpe et al. [3]; M-cone data from 9 protanopes (gray diamonds) measured by Sharpe et al. [3]; and S-cone data from 5 normals and 3 blue-cone monochromats (filled hexagons) measured by Stockman, Sharpe & Fach [10].*

The spectral sensitivities defined as a linear combination of existing CMFs

Although the cone fundamentals could be directly defined by the spectral sensitivity measurements shown in Fig. 2, it is usual to define them in terms of linear combinations of a set of CMFs, which are more precise. All that is required is to find the linear combinations of $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ that best fit each of the three cone spectral sensitivities, $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$, allowing adjustments in the densities of pre-receptoral filtering and photopigment optical density in order to account for differences in the mean densities between different populations and to account for differences in retinal area (see, for discussion, Ref. [20]).

The significance of the best-fitting linear combination can be stated formally. When an observer matches the test and mixture fields in a colour matching experiment, the two fields cause identical absorptions in each of his or her three cones types. The match, in other words, is a match *at the level of the cones*, thus:

$$\begin{aligned} \bar{l}_R\bar{r}(\lambda)+\bar{l}_G\bar{g}(\lambda)+\bar{l}_B\bar{b}(\lambda)&=\bar{l}(\lambda)\\ \bar{m}_R\bar{r}(\lambda)+\bar{m}_G\bar{g}(\lambda)+\bar{m}_B\bar{b}(\lambda)&=\bar{m}(\lambda)\\ \bar{s}_R\bar{r}(\lambda)+\bar{s}_G\bar{g}(\lambda)+\bar{s}_B\bar{b}(\lambda)&=\bar{s}(\lambda) \end{aligned} \quad (1)$$

where $\bar{l}_R$, $\bar{l}_G$ and $\bar{l}_B$ are, respectively, the L-cone sensitivities to the **R**, **G** and **B** primary lights, and similarly $\bar{m}_R$, $\bar{m}_G$ and $\bar{m}_B$ and $\bar{s}_R$, $\bar{s}_G$ and $\bar{s}_B$ are the analogous L-, M- and S-cone sensitivities. Since the S-cones are insensitive in the red part of the spectrum, it can be assumed that $\bar{s}_R$ is effectively zero for a long-wavelength **R** primary. There are therefore eight unknowns required for the linear transformation:

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

Because we are only concerned about the relative shapes 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, but are typically chosen to scale three functions in some way; for example, so that $k_l\bar{l}(\lambda)$, $k_m\bar{m}(\lambda)$ and $k_s\bar{s}(\lambda)$ peak at unity.

Choice of CMFs

Of critical importance in the definition of the cone fundamentals is the choice of CMFs. The ones available vary considerably in quality. The most widely used, the CIE (1931) 2-deg CMFs [21], are the least secure. They are based on the *relative* colour matching data of Wright [22] and Guild [23]. The CIE attempted to reconstruct the *absolute* matching information required for defining three CMFs by assuming that a linear combination of the colour matches must equal the 1924 CIE $V(\lambda)$ function [21, 24]. Aside from uncertainties about the validity of this assumption [e.g., 25], the CIE $V(\lambda)$ curve is far too insensitive at short wavelengths. Moreover, the assumption that $V(\lambda)$ is a linear combination of the CMFs is entirely unnecessary, since CMFs can be measured directly without any recourse to photometric data. The Stiles & Burch [8] 2-deg CMFs are an example of such functions. Although referred to by Stiles as "pilot" data, these CMFs are the most extensive set of directly-measured data for 2-deg vision available, being averaged from matches made by ten observers. They are seldom used.

The most secure and comprehensive set of directly measured colour matching data are the large-field, centrally-viewed 10-deg CMFs of Stiles & Burch [1]. They were measured in 49 subjects from approximately 390 to 730 nm (and in 9 subjects from 730 to 830 nm). They are preferable to the large-field CIE 1964 CMFs, which, although based mainly on the 10-deg CMFs of Stiles & Burch [1], were compromised by the inclusion of the Speranskaya [26] 10-deg data, and by several adjustments carried out by the CIE (see Ref. [2]). The downside of using 10-deg CMFs to model 2-deg spectral sensitivity data is that the spectral sensitivities must be corrected for the differences in pre-retinal filtering and in photopigment optical density between a 2-deg and 10-deg viewing field. However, such adjustments are straightforward once the spectral sensitivities are known (for details and formulae, see Ref.

[20]). For these reasons, the 10-deg CMFs of Stiles & Burch, were chosen as the basis for defining the "physiologically relevant" Stockman and Sharpe [2] cone fundamentals.

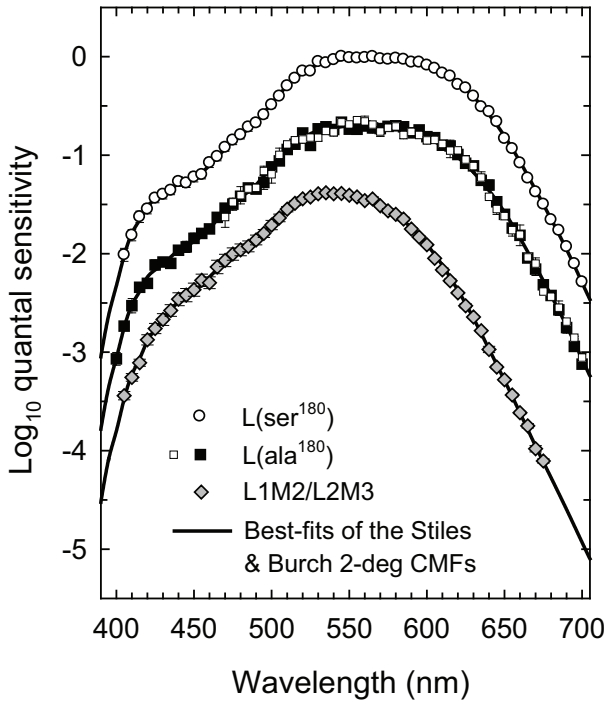

Figure 3 *Fits of the 2-deg CMFs to mean L1M2 & L2M3 protanope data (gray diamonds, n=9), and L(ala^{180}) (filled squares, n=2; open squares n=3) and L(ser^{180}) (open circles, n=17) deuteranope data from Sharpe et al. [4] and the linear combinations of the Stiles & Burch 2-deg CMFs [8] (continuous lines) that best fit each set of dichromat data. The dichromat data have been adjusted in macular and lens density to best fit the CMFs. One group of L(ala^{180}) subjects did not make short-wavelength measurements. Error bars are ±1 standard error of the mean. For best-fitting values, see Stockman & Sharpe [2].*

L- and M-cone fundamentals

The four M- and L-cone unknowns in Eqn. (3), $\bar{l}_R/\bar{l}_B$, $\bar{l}_G/\bar{l}_B$, $\bar{m}_R/\bar{m}_B$, and $\bar{m}_G/\bar{m}_B$, can be estimated by fitting CMFs to the cone spectral sensitivity data, which are shown in Fig. 2. However, since the cone spectral sensitivity data are defined for 2-deg viewing conditions and the CMFs for 10-deg, we employed an intermediate step of fitting the 2 deg data to the Stiles & Burch [8] 2-deg CMFs. Figure 3 shows the linear combinations of the Stiles & Burch 2-deg CMFs that best fit the mean L(ser^{180}) deuteranope data (open circles), L(ala^{180}) deuteranope data (open and filled squares), and L1M2/L2M3 protanope data (gray diamonds) of Sharpe *et al.* [3]. An overall population mean for the L-cone spectral sensitivity function was derived by averaging the L(ser^{180}) and L(ala^{180}) fits after weighting them in ratio of 62 L(ser^{180}) to 38 L(ala^{180}), which is the ratio believed to correspond to normal population incidences (see Table 1 of Ref. [2]).

Having defined the mean L- and M-cone fundamentals in terms of the 2-deg CMFs, they were next defined in terms of linear combinations of Stiles & Burch [1] 10-deg CMFs corrected to 2-deg. These were derived by a curve-fitting procedure in which the linear combinations of the Stiles & Burch 10-deg CMFs were found that, after adjustment to 2-deg macular, lens and photopigment densities, best fit the Stiles & Burch based Stockman & Sharpe 2-deg L- and M-cone fundamentals.

In one final refinement, the relative weights of the blue CMF were fine-tuned for consistency with tritanopic colour matching data [27], from which the S-cones are excluded (for further details, see Ref. [2]). This adjustment is important because of the inevitable uncertainties that arise at short-wavelengths owing to individual differences in pre-retinal filtering.

S-cone fundamental

The S-cone solution requires knowledge of just one unknown, $\bar{s}_G/\bar{s}_B$, which can similarly be estimated by fitting CMFs to the cone spectral sensitivity data. The upper panel of Fig. 4 shows the mean central S-cone spectral sensitivities (circles) measured by Stockman, Sharpe & Fach [10], which were averaged from normal and blue-cone monochromat data below 540 nm and from blue-cone monochromat data alone from 540 to 615 nm. Superimposed on the threshold data is the linear combination of the Stiles & Burch 2-deg $\bar{b}(\lambda)$ and $\bar{g}(\lambda)$ CMFs that best fits the data below 565 nm with best-fitting adjustments to the lens and macular pigment densities.

Using the method explained in Stockman, MacLeod & Johnson [28], the unknown value, $\bar{s}_G/\bar{s}_B$, can also be derived directly from the colour matching data [29]. This derivation depends on the longer wavelength part of the visible spectrum being tritanopic for lights of the radiances typically used in colour-matching experiments. Thus, target wavelengths longer than about 560 nm, as well as the red primary, are invisible to the S-cones. In contrast, the green and blue primaries are both visible to the S-cones. 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 colour 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 blue primary must be added to the field opposite 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.

The lower left panel of Fig. 4 shows the Stiles & Burch [8] green, $g(\lambda)$, and blue, $b(\lambda)$, 2-deg chromaticity coordinates (blue squares). As expected, the function above ~555 nm is a straight line. It has a slope of -0.01625, which implies $\bar{s}_G/\bar{s}_B$ =0.01625, or the same as the value obtained from the direct spectral sensitivity measurements, 0.0163 (upper panel). The lower right panel of Fig. 4 shows the Stiles & Burch [1] green, $g(\lambda)$, and blue, $b(\lambda)$, 10-deg chromaticity coordinates, and the line that best fits the data above 555 nm, which has a slope of -0.0106. Thus, the colour matching data suggest that $\bar{b}(\lambda)+0.0106\,\bar{g}(\lambda)$ is the S-cone fundamental in the Stiles & Burch [1] 10-deg space. The differences between the 2-deg (left panel) and 10-deg (right panel)

coefficients are consistent with changes in preretinal filtering and in photopigment optical density with eccentricity.

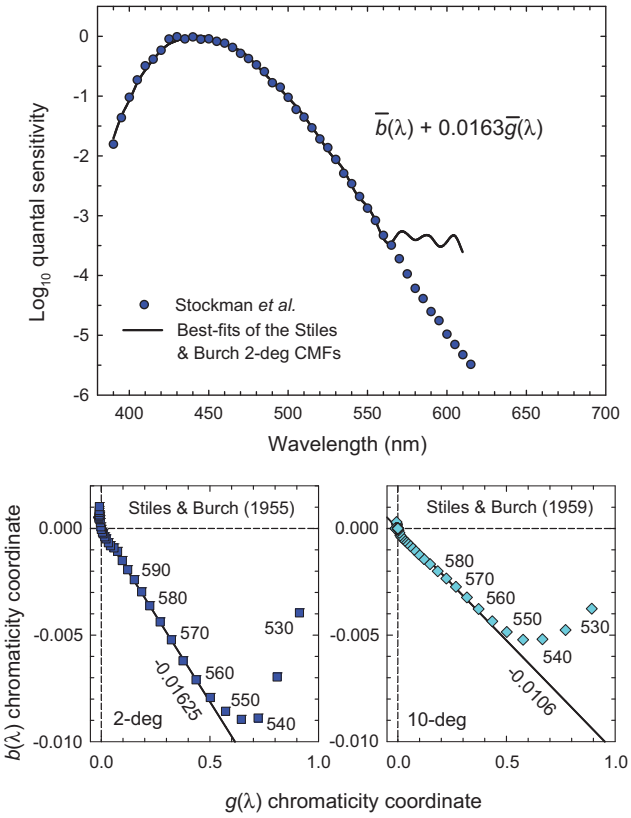

Figure 4 *Top: Mean S-cone data of Stockman, Sharpe & Fach (1999), and linear combination of the Stiles & Burch 2-deg CMFs that best fits them (≤565 nm), after applying lens and macular pigment density adjustments. Bottom left: Stiles & Burch green and blue 2-deg chromaticity coordinates. The best-fitting straight line from 555 nm to long-wavelengths has a slope of -0.01625. Bottom right: Stiles & Burch green and blue 10-deg chromaticity coordinates. The best-fitting straight line from 555 nm to long-wavelengths has a slope of -0.0106.*

Transformation matrix

The transformation matrix for the Stiles and Burch [1] 10-deg RGB CMFs, on which the Stockman & Sharpe cone fundamentals are ultimately based, is given in Eqn. (4):

$$\begin{pmatrix} 2.846201 & 11.092490 & 1 \\ 0.168926 & 8.265895 & 1 \\ 0 & 0.010600 & 1 \end{pmatrix} \quad (4)$$

Because the CMFs are conventionally given in energy units, this transformation yields cone fundamentals in energy units. To convert to quantal units, which are more practical for vision science, multiply by λ^{-1}. The values of k_l, k_m, and k_s in Eqn (3) depend on the desired normalization and on the units (energy or quanta). More details can be found in Stockman, Sharpe & Fach [10] and in Stockman & Sharpe [2].

Figure 5 shows the 2-deg estimates of Stockman & Sharpe [2] (solid lines) compared with those of Smith & Pokorny [9] and with the much earlier estimates by König & Dieterici [11] (coloured triangles). For the L- and M-cone fundamentals, the discrepancies between the Stockman & Sharpe and Smith & Pokorny fundamentals are mainly at shorter wavelengths. The discrepancies between the S-cone fundamentals are more extensive. The fundamentals of König & Dieterici provide a reminder of how close estimates were 120 years ago.

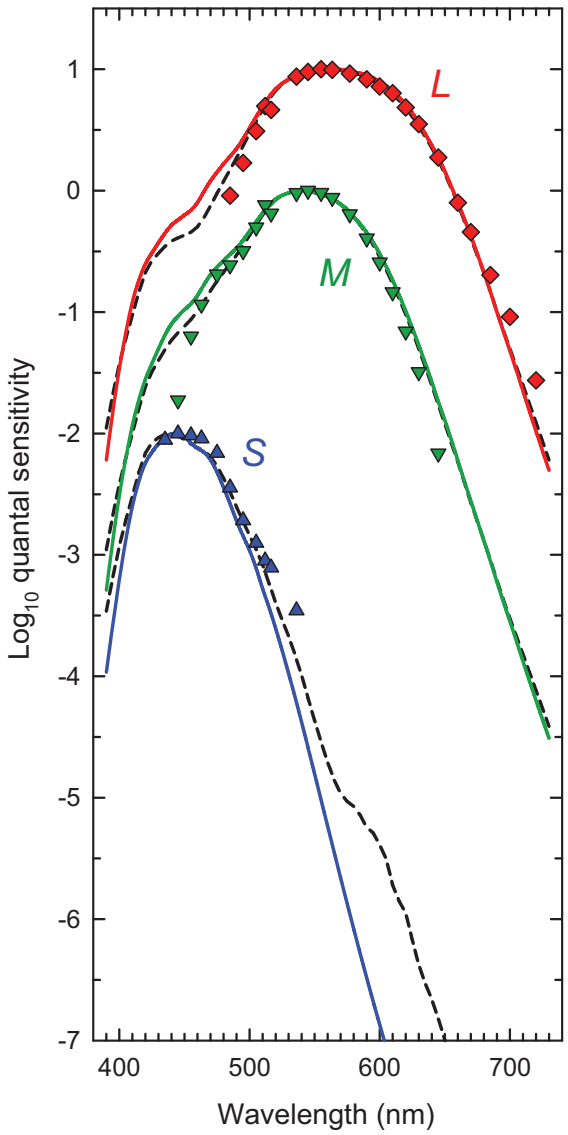

Figure 5 *S-, M- and L-cone 2-deg spectral sensitivity estimates of Stockman & Sharpe [2] (solid lines), based on linear transformations of the Stiles & Burch 10-deg RGB CMFs [1], using the mean spectral sensitivity data shown in Figs 3 and 4 as a guide. They are compared with the estimates of Smith & Pokorny [9] (dashed line) and König & Dieterici [11] (symbols).*

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Author Biography

Andrew Stockman received his B.A. from the University of Oxford and his Ph.D. from the University of Cambridge. He spent the next seventeen years at the University of California at San Diego first as a NATO Postdoctoral Fellow and finally as a Senior Research Scientist. Since 2001, he has been the Steers Chair of Investigative Eye Research at the Institute of Ophthalmology, University College London.