PHYSIOLOGICALLY-BASED COLOUR MATCHING FUNCTIONS

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ABSTRACT

Since the establishment of the trichromatic theory of colour perception [e.g., 6-8], a central goal of vision science has been the accurate determination of the spectral sensitivities of the long-, middle- and short-wavelength-sensitive (L, M and S) cones, $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$, the physiological bases of trichromacy. These are also known as the fundamental colour matching functions (CMFs). Like most previous estimates, the cone fundamentals of Stockman and Sharpe [1], which are to be recommended by the CIE Technical Committee 1-36 as an international standard for colorimetry, rely on measurements made in both normal trichromats and colour deficient blind observers. The Stockman and Sharpe $\bar{l}(\lambda)$ and $\bar{m}(\lambda)$ cone fundamentals were initially derived from measurements made in deuteranopes and protanopes (dichromats who lack the M- and L-cones, respectively) of known genotype [3]. Their $\bar{s}(\lambda)$ cone fundamental was initially derived [11] both from: (i) spectral sensitivity measurements made in S-cone monochromats, who lack functioning M- and L-cones, and in normal trichromats under intense long-wavelength adaptation; and (ii) a direct analysis of the 10-deg CMF data of Stiles & Burch [5]. The final cone fundamental estimates are linear transformations of the 10-deg CMF data guided mainly by the cone spectral sensitivity data and proposed for 2- or 10-deg viewing conditions.

Keywords: Colour matching, colour matching functions, cone fundamentals, colorimetry, photometry, trichromacy, univariance, scotopic, photopic, mesopic, rods, cones, cone spectral sensitivities, chromaticity diagrams, colour, CIE, macular pigment, lens pigment.

1. INTRODUCTION

Colour vision depends ultimately on the transduction properties of the light-sensitive cone photoreceptors in the eye; in particular, on the spectral absorbances of their photopigments. A knowledge of the cone spectral sensitivities is important not only for the understanding and modelling of visual function, but also for practical applications of colour matching and colour measurement.

Here we describe the relationship between colour matching and cone spectral sensitivities and then explain the derivation of the "physiologically-relevant" Stockman and Sharpe [1] cone fundamentals.

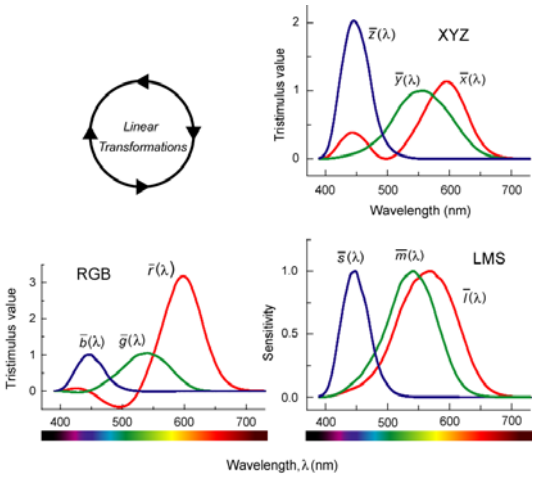

Figure 1 CMFs can be linearly transformed from one set of primaries to another. Shown here are 10 deg CMFs for *real,* spectral RGB primaries, *imaginary* XYZ primaries and *physiologically-relevant* LMS cone fundamental primaries [1, 5].

2. TRICHROMACY

Because normal human photopic vision is trichromatic, the colour of a light can be defined by just three variables: the intensities of three specially chosen primary lights that match it. The lower left 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 two will match 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 all-positive **X**, **Y** and **Z** primaries favoured by the CIE to define international lighting standards, or to the **L**, **M** and **S** cone *fundamental* primaries, which are the physiologically important photoreceptor spectral sensitivities. 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 $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$, 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 (like those shown in Fig. 2).

3. PREVIOUS CONE SPECTRAL SENSITIVITY MEASUREMENTS

Studies of human cone spectral sensitivity have encompassed many fields of inquiry, including fundus reflectometry [e.g., 12], microspectrophotometry [e.g., 13], suction electrode recordings [e.g., 14, 15], electroretinography [e.g., 16] and absorption spectroscopy [17-20]. Our method of choice is a technique of visual psychophysics, known as heterochromatic flicker photometry (HFP), which provides extensive and accurate *in vivo* spectral sensitivity data.

Most psychophysical estimates of the cone spectral sensitivities depend on the use of dichromats or monochromats and the assumption—known as the "loss", "reduction" or "König" hypothesis—that their remaining cone classes are normal [10, 21]. This approach now has a much firmer foundation, since it is possible to use molecular genetics to select those dichromats who truly conform to the reduction hypothesis [22, 23]. Appropriate selection is important, because some dichromats have hybrid cone photopigments with a spectrally-shifted or altered spectral sensitivity [4]. Moreover, a common polymorphic variation in the spectral sensitivity of the L-cone photopigment, which depends upon a single amino acid substitution of alanine (ala^{180}) for serine (ser^{180}) at position 180 in the photopigment gene, affects the spectral sensitivity of the L-cones in both dichromat (deuteranope) and normal observers. The λ_{max} of the L(ala^{180}) variant is shifted ~2.5 nm to shorter wavelengths than the λ_{max} of the L(ser^{180}) variant [3] and most be taken into account when deriving a mean L-cone function.

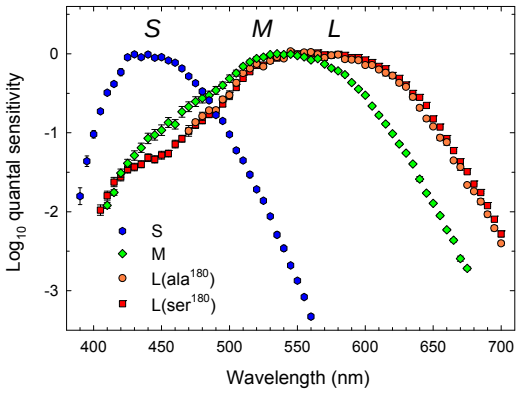

Figure 2 Mean cone spectral sensitivity data. L-cone data from 17 L(ser^{180}, red squares) and 5 L(ala^{180}, orange circles) deuteranopes measured by Sharpe *et al*. [3]; M-cone data from 9 protanopes (green diamonds) measured by Sharpe *et al.* [3]; and S-cone data from 5 normals and 3 blue-cone monochromats (blue hexagons) measured by Stockman, Sharpe & Fach [11].

Arguably, the first plausible psychophysical estimates of $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ and $\bar{s}(\lambda)$ were obtained by König & Dieterici [10] (see Fig. 5, below). Since then, many other estimates have been made, notably by Bouma [24], Judd [25, 26], Wyszecki & Stiles [27], Vos & Walraven [28], Vos [29], Estévez [30], Vos, Estévez & Walraven [31], and Stockman, MacLeod & Johnson [32]. These have been discussed elsewhere [e.g. 33-36]. Until recently, the estimates by Smith & Pokorny [37] were widely used in science and research as a *de facto* standard. But now the estimates by Stockman & Sharpe [1] are being proposed as a new CIE standard for "physiologically-relevant" fundamental primaries.

4. STOCKMAN & SHARPE CONE 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 (red squares), from 5 single-gene L(ala^{180}) deuteranopes with alanine at position 180 (orange circles),

and from 9 protanopes (green diamonds) [for further details, see 1, 3]. An overall L-cone mean was also derived (not shown) to reflect the proportions of the two polymorphic variants in the population [1].

In defining a mean S-cone spectral sensitivity, Stockman, Sharpe & Fach [11] measured S-cone spectral sensitivities in three blue-cone monochromats [38-44], 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. 3 (blue hexagons).

5. STOCKMAN & SHARPE (2000) CONE FUNDAMENTALS

Although the cone fundamentals could be defined by the direct spectral sensitivity measurements shown in Fig. 2, it is customary to define them in terms of linear combinations of a set of CMFs, which are—in principle—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 cone spectral sensitivity, $\bar{l}(\lambda)$, $\bar{m}(\lambda)$ 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 (these factors are age- and race-dependent and highly variable between individuals) and to account for differences in retinal area (because the pre-retinal filtering densities change with retinal eccentricity) [see, for discussion, 36].

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:

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

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

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

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.

5.1 Choice of CMFs

Of critical importance in the derivation 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 [45], are probably the least secure. They are based on the *relative* colour matching data of Wright [46] and Guild [47]. The CIE attempted to reconstruct the *absolute* matching information required for defining three CMFs by assuming that the linear combination of the colour matches must equal the 1924 CIE *V(λ)* function [48, 45]. Aside from uncertainties about the validity of this assumption [e.g., 49], the CIE *V(λ)* curve is far too insensitive at short wavelengths (see Fig. 6, below). Moreover, the assumption that *V(λ)* 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 [9] 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.

By far the most secure and comprehensive set of directly measured colour matching data are the large-field, centrally-

viewed 10-deg CMFs of Stiles & Burch [5]. 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 [5], were compromised by the inclusion of the Speranskaya [50] 10-deg data, and by several adjustments carried out by the CIE [see 1]. 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 relatively straightforward once the spectral sensitivities are known [for details and formulae, see 36]. For these reasons, the 10-deg CMFs of Stiles & Burch, were chosen as the basis for defining the "physiologically relevant" Stockman and Sharpe [1] cone fundamentals.

5.2 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 [9] 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 (red diamonds), L(ala^{180}) deuteranope data (orange and white squares), and L1M2/L2M3 protanope data (green circles) 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 1].

Having defined the mean L- and M-cone fundamentals in terms of the 2-deg CMFs, we next defined them in terms of linear combinations of Stiles & Burch [5] 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

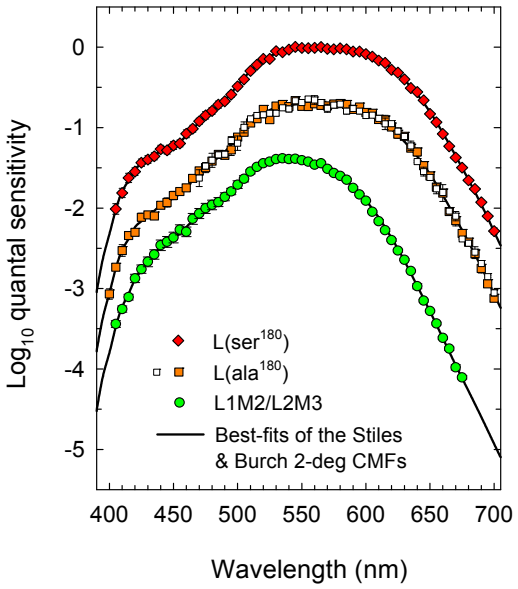

Figure 3 Fits of the 2-deg CMFs to mean L1M2 & L2M3 protanope data (red circles, n=9), and L(ala^{180}) (orange squares, n=2; white squares n=3) and L(ser^{180}) (red diamonds, n=17) deuteranope data from Sharpe *et al.* [4] and the linear combinations of the Stiles & Burch 2-deg CMFs [9] (continuous 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 [1]

weights of the blue CMF were fine-tuned for consistency with tritanopic colour matching data [51], from which the S-cones are excluded [for further details, see 1]. This adjustment is important because of the inevitable uncertainties that arise at short-wavelengths owing to individual differences in pre-retinal filtering.

5.3 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. Figure 4 shows the mean central S-cone spectral sensitivities (blue circles) measured by Stockman, Sharpe & Fach [11], 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.

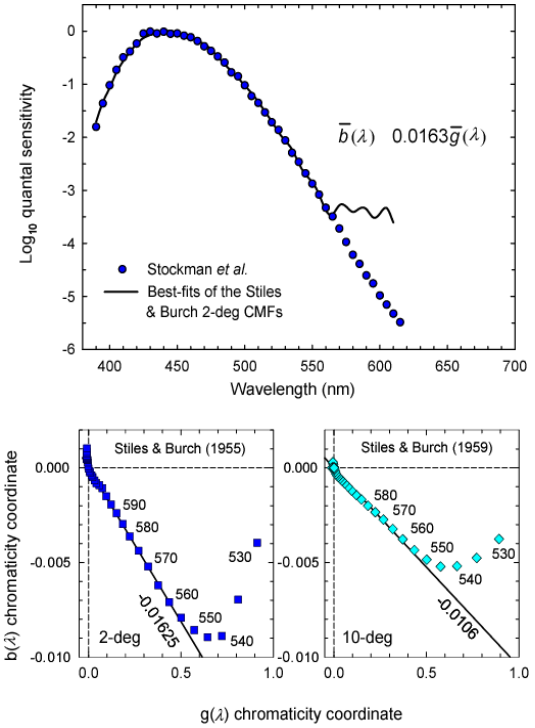

Figure 4 Top: Mean S-cone data of Stockman, Sharpe & Fach (1999), and linear combination of the Stiles & Burch 2-deg CMFs that best fits them (≤565 nm), after applying lens and macular pigment density adjustments. Bottom left: Stiles & Burch green and blue 2-deg chromaticity coordinates. The best-fitting 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.

Using the method explained in Stockman, MacLeod & Johnson [32], the unknown value, $\bar{s}_G/\bar{s}_B$, can be derived directly from the colour matching data [52]. 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 [9] 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 [5] green, $g(\lambda)$, and blue, $b(\lambda)$, 10-deg, 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 [5] 10-deg space. The small difference between the 2-deg (left panel) and 10-deg (right panel) coefficients accord with the predicted changes in preretinal filtering and in photopigment optical density with eccentricity.

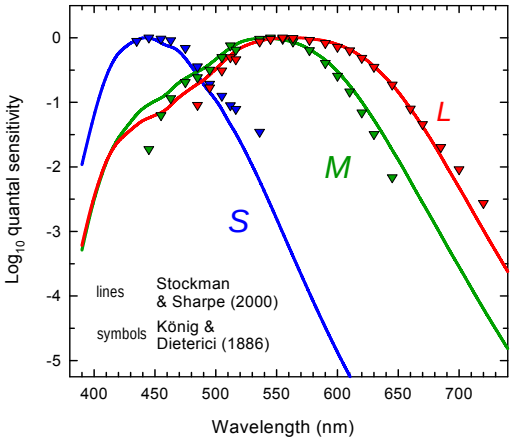

Figure 5 S-, M- and L-cone 2-deg spectral sensitivity estimates of Stockman & Sharpe [1] (coloured lines), based on linear transformations of the Stiles & Burch 10-deg RGB CMFs [5], using the mean spectral sensitivity data shown in Fig. 3 as a guide. They are compared with the historical estimates of König & Dieterici [10] (coloured triangles).

5.4 Transformation matrix

The transformation matrix for the Stiles and Burch [5] 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 [11] and in Stockman & Sharpe [1].

Figure 5 shows the 2-deg estimates of Stockman & Sharpe [1] (coloured lines) compared with the much earlier estimates obtained by König & Dieterici [10] (coloured triangles). Given the large technological advancements over the last 120 years, the agreement is remarkable.

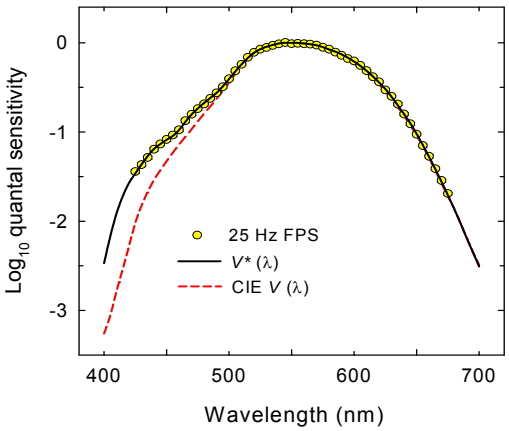

Figure 6 The new, photopic luminous efficiency function, *V**(λ), (black line) proposed by Sharpe *et al.* [2] and the mean lens- and macular-density adjusted 25-Hz HFP data from 40 color normals upon which it is based (yellow circles). The CIE 1924 photopic *V(λ)* function (red dashed line), which seriously underestimates sensitivity at short wavelengths, is also shown.

6. A COMPATIBLE LUMINOUS EFFICIENCY FUNCTION

The standard CIE photopic 1924 *V*(λ) function is a speculative hybrid function, artificially smoothed, and dubiously constructed from divergent data measured under very different procedures at several laboratories [53]. The CIE *V*(λ) function shown in Fig. 6 as the dashed red line substantially underestimates luminous efficiency at short wavelengths.

Recently, Sharpe e*t al.* [2] have proposed a new luminous efficiency function, *V**(λ), which is based on experimentally-determined 25-Hz, 2-deg diameter, HFP data from 40 observers of known genotype, taking into account the polymorphism of the L-cone photopigment. *V**(λ) defines luminance for a reproducible, phase of natural daylight (CIE standard illuminant D_{65} adaptation), while being a linear combination of the Stockman & Sharpe [1] M- and L-cone fundamentals. (The S-cone fundamental has only a small or negligible contribution to luminous efficiency defined by such procedures [2].) The *V*(λ)* function (black line) and the mean luminous efficiency data upon which it is based (yellow circles) are shown in Fig. 6. In terms of the Stockman & Sharpe [1] M- and L-cone *quantal* fundamentals normalized to unity peak, the *quantal* function is:

$$V^*(\lambda) = [1.55\bar{l}(\lambda) + \bar{m}(\lambda)]/2.476985; \quad (5)$$

whereas, in terms of the Stockman & Sharpe [1] M- and L-cone *energy* fundamentals normalized to unity peak, the *energy-based* function is :

$$V^*(\lambda) = [1.624340\bar{l}(\lambda) + \bar{m}(\lambda)]/2.525598. \quad (6)$$

Most of the functions described here can be downloaded from:

http://www.cvrl.org

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