# A luminous efficiency function, $V^*(\lambda)$, for daylight adaptation

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We propose a new luminosity function, $V^*(\lambda)$, that improves upon the original CIE 1924 $V(\lambda)$ function and its modification by D. B. Judd (1951) and J. J. Vos (1978), while being consistent with a linear combination of the A. Stockman & L. T. Sharpe (2000) long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cone fundamentals. It is based on experimentally determined 25 Hz, 2° diameter, heterochromatic (minimum) flicker photometric data obtained from 40 observers (35 males, 5 females) of known genotype, 22 with the serine variant L(ser180), 16 with the alanine L(ala180) variant, and 2 with both variants of the L-cone photopigment. The matches, from 425 to 675 nm in 5-nm steps, were made on a 3 log troland xenon white (correlated color temperature of 5586 K but tritanopically metameric with CIE $D_{65}$ standard daylight for the Stockman and Sharpe L- and M-cone fundamentals in quantal units) adapting field of 16° angular subtense, relative to a 560-nm standard. Both the reference standard and test lights were kept near flicker threshold so that, in the region of the targets, the total retinal illuminance averaged 3.19 log trolands. The advantages of the new function are as follows: it forms a consistent set with the new proposed CIE cone fundamentals (which are the Stockman & Sharpe 2000 cone fundamentals); it is based solely on flicker photometry, which is the standard method for defining luminance; it corresponds to a central 2° viewing field, for which the basic laws of brightness matching are valid for flicker photometry; its composition of the serine/alanine L-cone pigment polymorphism (58:42) closely matches the reported incidence in the normal population (56:44; Stockman & Sharpe, 1999); and it specifies luminance for a reproducible, standard daylight condition. $V^*(\lambda)$ is defined as $1.55\mathrm{L}(\lambda) + \mathrm{M}(\lambda)$, where $\mathrm{L}(\lambda)$ and $\mathrm{M}(\lambda)$ are the Stockman & Sharpe L- & M-cone (quantal) fundamentals. It is extrapolated to wavelengths shorter than 425 nm and longer than 675 nm using the Stockman & Sharpe cone fundamentals.

Keywords: CIE standards, cone fundamentals, heterochromatic flicker photometry, L-cone polymorphism, luminous efficiency, minimum flicker

## Introduction

Luminous efficiency or luminosity is the measure of the effectiveness of lights of different wavelengths defined for specific matching tasks. The term was introduced by the International Lighting Commission (Commission Internationale de l'Eclairage or CIE) to provide a psychophysical or perceptual analog of radiance, called luminance. Any definition of luminous efficiency, however, is complicated by the fact that there are considerable differences between the luminous efficiency functions obtained by different measurement procedures and criteria, which include heterochromatic flicker photometry (HFP) or minimum flicker, a version of minimum flicker called heterochromatic modulation photometry (HMP), direct heterochromatic brightness matching, step-by-step brightness matching, minimally distinct border (MDB), minimum motion, color matching, absolute threshold, increment threshold, visual acuity, and critical flicker frequency (for reviews, see Lennie, Pokorny, & Smith, 1993; Stockman & Sharpe, 1999, 2000; Wagner & Boynton, 1972; Wyszecki & Stiles, 1982). Moreover, as measured by any one of these criteria, there are large differences between the luminous efficiency functions of individual normal trichromats. An important source of variability is the differing contributions of the long-wavelength-sensitive (L), middle-wavelength-sensitive (M), and short-wavelength-sensitive (S) cones and their retinal pathways to the different types of luminosity task. These contributions are strongly adaptation dependent and complicated by differences in relative cone numbers and by a polymorphism in the L-cones that shifts L-cone sensitivity by 2–4 nm (for reviews, see Sharpe, Stockman, Jägle, &

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Nathans, 1999; Stockman, Sharpe, Merbs, & Nathans, 2000). Such differences put severe constraints on the validity of the basic principle of photometry and luminous efficiency. Moreover, of the common methods used in the past to define luminous efficiency, only a few adequately satisfy the most fundamental law of photometry: the linear additivity of spectral lights, or Abney's Law (Abney, 1913; Abney & Festing, 1886). These include variants of HFP, in which two lights of different wavelength that are alternated in opposite phase are matched in luminance to minimize the perception of flicker, and MDB, in which the relative intensities of the two half fields are set so that the border between them appears "minimally distinct" (e.g., Boynton & Kaiser, 1968; Dresler, 1953; Guth, Donley, & Marrocco, 1969; LeGrand, 1972). Without additivity, the luminances of spectrally broadband lights, whether natural or artificial, cannot be predicted from those of the narrowband spectral lights used to define luminous efficiency functions.

In 1924, the CIE (1926) adopted a standard photopic luminous efficiency function for 2° angular subtense photopic viewing conditions, CIE 1924 $V(\lambda)$, which is still used today to define luminance. Unfortunately, $V(\lambda)$ is a speculative hybrid function, originally proposed by Gibson & Tyndall (1923), artificially smoothed and symmetrized from very divergent data measured under very different procedures at several laboratories (see Figure 1, continuous line). In fact, the final result was not even an average of the experimental data, but a weighted assembly of different sets of data (Wyszecki & Stiles, 1982); some of which were not the optimal choice. The wide discrepancy in the data can be easily seen by comparing the divergent data sets shown in Figure 1. From 400 to 490 nm, the $V(\lambda)$ curve represents roughly the direct brightness matching results of Hyde, Forsythe, & Cady (1918); from 490 to 540 nm, the minimum flicker results of Coblentz & Emerson (1918; open circles); from 540 to 650 nm, the step-by-step matching results of Gibson & Tyndall (1923; filled squares); and above 650 nm, the minimum flicker results of Coblentz & Emerson (1918; open circles). In these experiments, the size of the test field varied among 2° (Coblentz & Emerson, 1918; Ives, 1912; Nutting, 1914), 3° (Gibson & Tyndall, 1923), and 7° (Hyde, Forsythe, & Cady, 1918). Moreover, a surround field was not always present or of constant luminance. The 1924 $V(\lambda)$ function deviates from typical luminosity data (Figure 1, filled squares, open circles) by a factor of nearly a log unit in the violet. In hindsight, it is now clear that Gibson & Tyndall (1923) and the CIE (1926) made a patently wrong choice of direct brightness matching to represent luminous efficiency at short wavelengths. Moreover, their mixing of data obtained by very different methods, some of which do not obey the law of additivity, has subsequently plagued the effectiveness of the $V(\lambda)$ function even as a mere contrivance as opposed to a valid representation of the performance of the visual system under specific photometric conditions. Even at middle and long wavelengths, the $V(\lambda)$ luminous efficiency values have been neither fully tested nor validated. Its subsequent use to guide the construction of the CIE (1931) color matching functions (CIE, 1932) also corrupted the international colorimetric standard (see Stockman & Sharpe, 1999, 2000).

Judd (1951) proposed a substantial modification of the $V(\lambda)$ function to overcome the discrepancies at short wavelengths, by increasing the sensitivities at wavelengths shorter than 460 nm. Unfortunately, while improving the $V(\lambda)$ function in the violet part of the spectrum, this adjustment artificially created an average observer with implausibly high macular pigment density for a 2° field (Stiles, 1955; see also p. 1727 of Stockman & Sharpe, 2000). This error arises mainly because of the insensitivity of the Judd-modified CIE 1924 $V(\lambda)$ function near 460 nm, where the original value was left unadjusted. Vos (1978) subsequently made minor adjustments to the Judd-modified CIE $V(\lambda)$ function below 410 nm to produce the Judd–Vos-modified CIE $V(\lambda)$ or $V_M(\lambda)$ function (Figure 1, dashed line). The function, however, like Judd's, yields a "standard observer" with an artificially high macular pigment density. Despite its advantages over the 1931 function, $V_M(\lambda)$ has been little used outside human vision research laboratories.

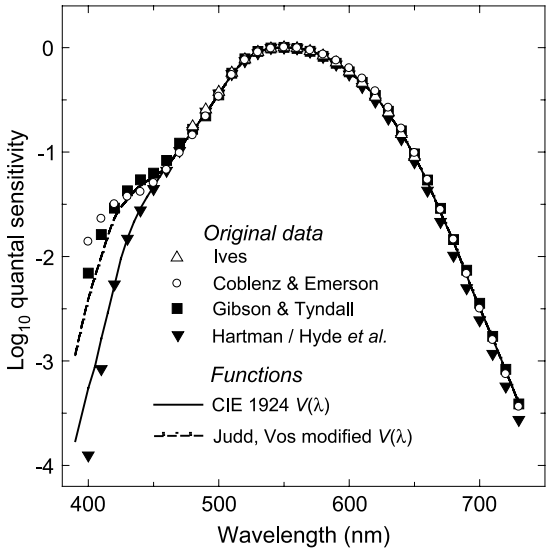


Figure 1. The original luminosity measurements by Ives (1912) (open triangles), Coblentz & Emerson (1918) (open circles), Gibson & Tyndall (1923) (filled squares), and Hartman/Hyde, Forsythe, & Cady (1918) (filled inverted triangles), which were used in part to derive the CIE 1924 $V(\lambda)$ function (continuous line), and the Judd–Vos modification to the CIE 1924 $V(\lambda)$ function or $V_M(\lambda)$ (dashed line).

The limitations of the CIE $V(\lambda)$ function, and its difficulties, have in part been ignored because, as pointed out by Wyszecki & Stiles (1982), "any minor improvement at this stage would be outweighed by the very considerable practical inconvenience of a change in the basic function on which all photopic photometry has been based for more than 50 years" (p. 258). However, such practical considerations have been greatly assuaged by present computer capabilities; and the availability of relatively inexpensive photodiode-array spectroradiometers, which are a much more flexible way of measuring luminance than conventional photometers that rely upon photopic correction filters. In addition, the CIE is now presently engaged with recommending a standard set of the cone fundamentals (i.e., the L-, M-, and S-cone spectral sensitivities), which is based on the Stiles & Burch (1959) 10° CMFs as well as new measurements in dichromats (Stockman & Sharpe, 1999, 2000) and which, importantly and quite correctly, is not constrained to agree with the erroneous $V(\lambda)$. Thus, it is of considerable practicable interest to define a reliable luminosity function that is consistent with them.

Instead of $V(\lambda)$, the CIE 1964 estimate of the luminosity function for 10° vision $[\bar{y}_{10}(\lambda)]$, which we refer to as $V_{10}(\lambda)$, adjusted to 2° could be used, which is based in part on the Stiles & Burch (1959) 10° CMFs data from the same subjects. This function, however, is "synthetic" because it was constructed from luminosity measurements made at only four wavelengths in only 26 of the 49 observers used by Stiles & Burch (1959), and it may not be appropriate for a 2° field of view.

As a more appropriate solution, we previously proposed a preliminary version of $V^*(\lambda)$ (Stockman & Sharpe, 1999, 2000) based on HFP measurements in 22 males of known genotype with respect to the L-cone serine/alanine (ser/ala or S/A) polymorphism at codon 180 [13 L(ser180) and 9 L(ala180)]. Now we provide a more exact and refined version of $V^*(\lambda)$, based on HFP in 40 observers of known genotype, and publish the underlying data for the first time.

The new function incorporates a number of advantages, not shared by other luminosity functions:

- It is consistent with a linear combination of the Stockman & Sharpe (2000) L- and M-cone spectral sensitivities, which are currently being proposed to the CIE as the recommended standard for "physiologically relevant" cone fundamentals.
- It is based solely on the minimum flicker (HFP) technique, which together with the MDB and HMP techniques yields the most reliable and consistent photometric results. Both tasks minimize contributions from the S-cones and produce nearly additive results (e.g., Ives, 1912; Wagner & Boynton, 1972).
- It is guided by the minimum flicker data from 40 normal trichromats, who have been genotyped for the L-cone ser/ala polymorphism.
- Its composition of the L-cone ser/ala polymorphism (58:42) almost exactly matches the incidence in the normal population (56:44; Stockman & Sharpe, 1999; Table 1.2).
- It provides an excellent—much better than the CIE Judd–Vos $V(\lambda)$ function—fit to the Stiles & Burch (1959) 2° flicker photometry measurements made at four wavelengths as part of the Stiles & Burch (1959) 10° color matching study (see Figure 10).
- It is based on a field of 2° angular subtense, for which the basic photometric law of additivity is valid over a wide intensity range for HFP (see Lennie, Pokorny, & Smith, 1993; Stockman & Sharpe, 1999, 2000; Wagner & Boynton, 1972; Wyszecki & Stiles, 1982).
- It corresponds to a representative young population of mean age 33.08 ± 6.15 (±1 *SD*) years. This is important because there is a gradual change in luminous efficiency, whether measured by flicker photometry or direct brightness matching, with age (Kraft & Werner, 1994; Sagawa & Takahashi, 2001; Verriest, 1970); in part because of the age-related increase of the optical density of eye lens at short wavelengths and a reduced chromatic contribution to brightness at long wavelengths.
- It is measured under moderate (3.0 log photopic trolands or 3.39 log scotopic trolands) xenon white adaptation and with the flickering lights set close to flicker (intensity) threshold (i.e., elevated by only 0.2 log unit). These conditions were chosen to eliminate rod intrusion and to prevent the targets themselves acting as adapting fields and thereby causing a breakdown in additivity (De Vries, 1948).
- The chosen xenon white adapting field exactly corresponds, in terms of the relative L- and M-cone excitations, to CIE standard illuminant $D_{65}$, which represents a phase of natural daylight and is a widely used and well-defined adapting condition in industry and in research.

## Choice of background

The use of targets without an adapting field, which intuitively might seem the best way to avoid any selective chromatic adaptation of the cones, is impracticable at the high flicker frequencies required to avoid intrusions from the rods, S-cones, and the chromatic pathways. Indeed, presented alone, 25-Hz flickering targets, even when adjusted to be near flicker threshold, selectively adapt the L- or M-cones at most target wavelengths, artefactually narrowing the luminosity function by reducing the contribution of the more sensitive cone (see Jägle, Knau, & Sharpe, 2005). Some type of background is therefore desirable, but deciding which one is optimal is compli-

cated. Ideally, the background should (i) produce equal first-site adaptation in both the M- and the L-cones (so that there is no selective adaptation with increasing adaptation levels); (ii) yield neutral second-site adaptation at L–M opponent stages [because chromatic adaptation also alters the $V(\lambda)$ spectral sensitivity; e.g., Eisner & MacLeod, 1981; Stockman, MacLeod, & Vivien, 1993]; and (iii) be representative of standard and/or natural viewing conditions. Unfortunately, however, such a background is not necessarily physically realizable.

An adapting background equivalent in its effects on the L- and M-cones to a monochromatic one of 549 nm (which, given the assumption that those cones have equivalent peak sensitivities, would produce equal first-site M- and L-cone adaptation; Stockman & Sharpe, 2000) will be neither neutral at the second site nor representative of standard viewing conditions. An adapting background more likely to be neutral at a chromatically opponent L–M site typically found in the retina or LGN, such as a "unique" yellow background for a foveal 2° field of c. 575 nm (e.g., Nerger, Volbrecht, & Ayde, 1995), is likely to adapt selectively the L-cones at the first site and will also be unrepresentative of standard viewing conditions. We therefore chose a background intermediate between these extremes in its effects on the L- and M-cones that corresponded to a standard, natural white (CIE standard illuminant $D_{65}$). Our white, similar to illuminant $D_{65}$, produces a 1.16 times greater adaptation of the L- than of the M-cones (given again equal peak M- and L-cone sensitivities) and is thus equivalent in its effects on the L- and M-cones to a monochromatic adapting light of 566 nm (Stockman & Sharpe, 2000). Importantly, this wavelength is close to 568 nm, which is the field wavelength at which the relative sensitivities of Stiles' $\pi_4$ and $\pi_5$ remain invariant with field intensity (Stiles, 1978). A white background that maintains the relative sensitivities of the underlying cone mechanisms with luminance, even below the Weber region, is the optimal choice for defining a luminous efficiency function that is not specific to the luminance at which it was measured. (Once Weber's Law holds for both mechanisms, their sensitivity losses will be proportional to the background intensity and their relative sensitivities will be maintained.)

We note that although our white was a tritanopic metamer of $D_{65}$, in that it produces the same relative absorptions in the Stockman & Sharpe (2000) L- and M-cone fundamentals, its CIE (1931) *x*-*y* chromaticity coordinates were 0.3301 and 0.3844. Thus, its correlated color temperature was 5586 K, instead of 6500 K (as $D_{65}$). However, because luminous efficiency is dependent on the excitations of the L- and M-cones, the tritanopic equivalence of our background to a white $D_{65}$ is more relevant in this context that its similarity to a white of 5586 K.

The particular intensity of the white that we used (3.0 log trolands) was bright enough to be representative of photopic light levels, without substantially bleaching the L- or M-cones (Rushton & Henry, 1968), and bright enough so that, near flicker threshold, the superimposed 25-Hz flickering targets were no longer significant adapting stimuli. Were the targets not presented on a background, distortions of the HFP spectral sensitivity would be expected (De Vries, 1948; Ingling et al., 1978). It was also bright enough (3.39 log scotopic trolands) to fully saturate the rods (Aguilar & Stiles, 1954). By keeping the test and reference lights near threshold, we were able to keep the entire retinal illuminance in the retinal region where the flicker nulls were determined at 3.19 log trolands in a surrounding background of 3.0 log trolands.

Because we superimpose our reference and target on a neutral background and because our reference stimulus is close to threshold, our HFP method differs from classical applications of HFP in which only the reference and target were flickered. Given that any combined reference and target that exceeds 50 trolands causes a breakdown of additivity in HFP (De Vries, 1948), the only way of using HFP to measure luminous efficiency at higher temporal frequencies or at more representative luminance levels is to superimpose the targets upon a background field, the effect of which is to reduce the adaptation caused by the targets. Backgrounds have been used before (e.g., Eisner & MacLeod, 1981).

# Methods

## Subjects

Forty observers (35 males, 5 females) with normal visual acuity were recruited. All had normal trichromatic color vision as defined by standard tests, including their Rayleigh match on a standard Nagel Type I anomaloscope. They were genotyped according to the ser/ala photopigment polymorphism at amino acid position 180 in the L-cone photopigment gene: 22 with the ser variant L(ser180), 16 with the ala L(ala180) variant, and 2 (females) with both variants of the L-cone photopigment. Their age ranged between 18 and 48 years, with a mean of 33.08 ± 6.15 (±*SD*) years (see Table 1).

### *Genotyping*

The classification of photopigment genes is complicated by polymorphisms in the normal population, the most common of which is the frequent replacement of serine by alanine at codon 180 in exon 3 of the X-chromosome-linked opsin gene. Approximately 56% of a large sample of 304 Caucasian males with normal and deutan color vision have the ser variant [identified as L(ser180)] and 44% the

| ID | Gender | Age | L-cone polymorphism (codon 180) | *a* (L:M cone ratio) | *SE* | $k_{lens}$ | *SE* | $k_{mac}$ | *SE* | RMS |
|---|---|---|---|---|---|---|---|---|---|---|
| AN | m | 18 | Ala | 2.52 | 0.36 | 0.32 | 0.07 | −0.05 | 0.07 | 0.04 |
| CF | m | 40 | Ala | 0.47 | 0.03 | 0.09 | 0.06 | −0.81 | 0.06 | 0.03 |
| CH | f | 32 | Ala | 5.76 | 0.61 | 0.09 | 0.03 | 0.15 | 0.03 | 0.01 |
| CP | m | 33 | Ala | 1.51 | 0.10 | 0.14 | 0.04 | −0.07 | 0.04 | 0.02 |
| FG | m | 30 | Ala | 2.55 | 0.20 | 0.03 | 0.04 | 0.49 | 0.04 | 0.02 |
| HJ | m | 39 | Ala | 0.93 | 0.09 | −0.06 | 0.07 | −0.82 | 0.07 | 0.04 |
| HM | m | 32 | Ala | 1.59 | 0.17 | −0.05 | 0.07 | 0.38 | 0.07 | 0.04 |
| HS | m | 30 | Ala | 7.97 | 3.80 | 0.01 | 0.09 | 0.33 | 0.10 | 0.05 |
| JK | m | 40 | Ala | 1.33 | 0.10 | 0.08 | 0.05 | −0.05 | 0.05 | 0.03 |
| MJ | m | 27 | Ala | 1.44 | 0.07 | 0.07 | 0.03 | 0.17 | 0.03 | 0.02 |
| MS | m | 37 | Ala | 2.04 | 0.38 | −0.03 | 0.10 | −0.20 | 0.10 | 0.05 |
| OB | m | 28 | Ala | 1.27 | 0.10 | −0.10 | 0.06 | −0.14 | 0.06 | 0.03 |
| RL | m | 32 | Ala | 2.03 | 0.28 | 0.17 | 0.07 | 0.41 | 0.08 | 0.04 |
| RT | m | 42 | Ala | 1.26 | 0.23 | 0.09 | 0.12 | 0.04 | 0.12 | 0.06 |
| SK | m | 31 | Ala | 1.28 | 0.12 | 0.19 | 0.07 | −0.45 | 0.07 | 0.03 |
| SW | m | 34 | Ala | 1.29 | 0.16 | −0.30 | 0.08 | −0.43 | 0.08 | 0.04 |
| ED | f | 38 | Ala/Ser | 0.84 | 0.07 | 0.41 | 0.07 | −0.25 | 0.06 | 0.03 |
| SWI | f | 27 | Ala/Ser | 1.79 | 0.23 | 0.40 | 0.10 | −0.07 | 0.08 | 0.04 |
| AC | m | 30 | Ser | 1.17 | 0.15 | 0.06 | 0.10 | 0.26 | 0.10 | 0.05 |
| AS | m | 44 | Ser | 1.67 | 0.17 | 0.01 | 0.07 | 0.07 | 0.07 | 0.03 |
| AT | m | 31 | Ser | 1.32 | 0.12 | −0.06 | 0.07 | −0.54 | 0.07 | 0.03 |
| CFR | m | 31 | Ser | 2.75 | 0.29 | −0.01 | 0.05 | −0.15 | 0.05 | 0.03 |
| CK | m | 36 | Ser | 1.54 | 0.18 | 0.44 | 0.08 | 0.32 | 0.08 | 0.04 |
| DR | m | 26 | Ser | 2.08 | 0.24 | 0.10 | 0.06 | 0.52 | 0.07 | 0.03 |
| EA | m | 39 | Ser | 1.30 | 0.11 | −0.12 | 0.06 | −0.54 | 0.06 | 0.03 |
| HJS | m | 29 | Ser | 1.81 | 0.19 | 0.00 | 0.06 | 0.31 | 0.07 | 0.03 |
| HK | m | 35 | Ser | 1.12 | 0.07 | 0.34 | 0.05 | 0.35 | 0.05 | 0.03 |
| HSC | m | 32 | Ser | 15.82 | 12.3 | 0.18 | 0.08 | 0.22 | 0.10 | 0.04 |
| JA | m | 33 | Ser | 1.65 | 0.14 | 0.03 | 0.05 | 0.01 | 0.06 | 0.03 |
| KK | m | 47 | Ser | 1.71 | 0.19 | 0.08 | 0.07 | 0.49 | 0.07 | 0.04 |
| LS | m | 29 | Ser | 1.89 | 0.15 | 0.29 | 0.05 | −0.08 | 0.05 | 0.02 |
| LTS | m | 48 | Ser | 1.45 | 0.09 | −0.09 | 0.04 | −0.45 | 0.04 | 0.02 |
| MK | f | 27 | Ser | 1.99 | 0.34 | 0.77 | 0.16 | 0.17 | 0.10 | 0.04 |
| MR | m | 33 | Ser | 1.01 | 0.12 | −0.21 | 0.09 | 0.08 | 0.09 | 0.05 |
| TB | f | 29 | Ser | 1.34 | 0.10 | 0.32 | 0.05 | 0.27 | 0.06 | 0.03 |
| TD | m | 38 | Ser | 0.48 | 0.05 | 0.08 | 0.17 | −0.77 | 0.10 | 0.04 |
| TE | m | 25 | Ser | 1.93 | 0.23 | 0.26 | 0.07 | −0.16 | 0.07 | 0.04 |
| UW | m | 31 | Ser | 1.36 | 0.12 | 0.04 | 0.06 | −0.20 | 0.06 | 0.03 |
| WJ | m | 33 | Ser | 4.89 | 1.01 | −0.02 | 0.06 | 0.03 | 0.07 | 0.03 |
| WL | m | 27 | Ser | 2.05 | 0.36 | 0.14 | 0.10 | −0.02 | 0.10 | 0.05 |

Table 1. Age, gender, and L-cone polymorphism of the 40 observers of known genotype [L(ser180) or L(ala180)], whose 25-Hz HFP sensitivities, measured on a white (xenon) 3.0 log trolands adapting field, were best-fitted by a linear combination (Equation 1) of the Stockman & Sharpe (2000) L- and M-cone fundamentals: *a* (L-cone weighting factor), $k_{lens}$ (lens pigment density weighting factor) and $k_{mac}$ (macular pigment density weighting factor). The best-fitting parameters are shown for the spectral range 425–675 nm. Standard errors (*SE*) for each fitting parameter are given as well as the root mean square error (RMS) of the entire fit.

ala variant [identified as L(ala180)] for their L-cone gene (summarized in Table 1 of Stockman & Sharpe, 2000). In contrast, in the M-cone pigment, the ala/ser polymorphism is much less frequent, 93–94% of males having the ala variant (Neitz & Neitz, 1998; Winderickx, Battisti, Hibiya, Motulsky, & Deeb, 1993). Therefore, we only identified the genotype with respect to the ser/ala polymorphism in the first (L-cone) photopigment gene in the array of our observers (see Table 1).

The genotype was first determined by amplification, using total genomic DNA, of exon 3 followed by digestion with *F*nu4H as previously described by (Deeb,

Hayashi, Winderickx, & Yamaguchi, 2000). If both the ser and ala alleles were detected, the genotype of the first gene of the array was determined using long-range (LR) PCR product of the first gene (diluted 1:1000) as template for a second round of amplification of the exon 3 fragment, followed by digestion with *F*nu4H.

When one considers all 45 X-chromosomes (35*1 per male and 5*2 per female) in our population, the incidence of the L-cone photopigment polymorphism [i.e., the allele frequency of the L(ser) and L(ala) variants] is 57.8:42.2. Alternatively, when one considers the genotypes contributing to the final luminosity function, in which case all individuals, whether male or female, contribute a single mean curve, the polymorphic ratio is 57.5:42.5. The small difference compared with the allele frequency is negligible. This proportion almost exactly matches the estimated incidence in the normal population: 56:44 (Stockman & Sharpe, 1999).

## Apparatus

Full details of the design and calibration of the four-channel Maxwellian-view optical system, used to measure the HFP sensitivities, are provided in Sharpe et al. (1998). They will be only briefly summarized here. A Maxwellian-view optical system produced the flickering test stimuli and the steady adapting field. All optical channels originated from a 75-W xenon arc lamp (Osram, Berlin, Germany) run at constant current. Two channels provided the 2° (diameter) flickering test and reference lights, which were alternated at 25 Hz in opposite phase. A frequency of 25 Hz was chosen to obviate signals from the rods and S-cone pathways and because it was the same as that used to measure the flicker data guiding the derivation of the Stockman & Sharpe (2000) L- and M-cone fundamentals. Wavelengths were selected by grating monochromators (Model CM110, CVI Spectral Products, Putnam, USA), with 0.6-mm entrance and exit slits, that generated triangular profiles having a full bandwidth at half-maximum (FWHM) of <5 nm. The wavelength of the reference light was always set to 560 nm, whereas that of the test light was varied from 400 to 690 nm in 5-nm steps (but only data from 425 to 675 nm was used). At wavelengths longer than 560 nm, a glass cutoff filter (Schott OG550, Mainz, Germany), which blocked short wavelengths but transmitted wavelengths higher than 550 nm, was inserted after the exit slit of both monochromators. This filter reduces the skirt of shorter wavelength stray light. The third channel provided the 16° diameter (neutral white) adapting field, which was 3.0 log photopic trolands. The CIE (1931) *x-y* chromaticity coordinates, measured *in situ* after passing through UV and infrared filtering glass chosen to prevent retinal damage to the observers, were 0.3301 and 0.3844.

Infrared radiation was eliminated by heat-absorbing glass (Schott, Mainz, Germany) placed early in each beam. The images of the xenon arc were 1.5 mm in diameter at the plane of the observer's pupil. Circular field stops placed in collimated portions of each beam defined the test and adapting fields as seen by the observer. Mechanical shutters driven by a computer-controlled square-wave generator were positioned in each channel near focal points of the xenon arc. The optical waveforms so produced were monitored periodically with a Pin-10 diode (United Detector Technology, Santa Monica, CA) and oscilloscope. Fine control over the luminance of the stimuli was achieved by variable 2.0-log unit linear (LINOS Photonics GmbH & Co. KG, formerly, Spindler and Hoyer) or 4.0-log unit circular (Rolyn Optics, Covina, California, USA) neutral density wedges positioned exactly at focal points of the xenon arc lamp and by insertion of fixed neutral density filters in parallel portions of the beams. The position of the observer's head was maintained by a rigidly mounted dental wax impression.

## Calibration

During the experiments, the radiant fluxes of the test and adapting fields were measured *in situ* at the plane of the observer's pupil with a silicon photodiode (Model SS0-PD50-6-BNC, Gigahertz-Optics, München, Germany), which was calibrated against the German National Standard and a picoammeter (Model 486, Keithley, Germering, Germany). The fixed and variable neutral density filters were calibrated *in situ* for all test and field wavelengths. Particular care was taken in calibrating the monochromators and interference filters: a spectroradiometer (Compact Array Spectrometer CAS-140, Instrument Systems GmbH, München, Germany) with a spectral resolution better than 0.2 nm was used to measure the center wavelength and the bandpass (full-width at half-maximum, FWHM) at each wavelength. The absolute wavelength accuracy was better than 0.2 nm, whereas the resolution of the wavelength settings was better than 0.15 nm (Sharpe et al., 1998). The wavelengths of the two CVI monochromators were additionally calibrated against a low-pressure mercury source (Model 6035, L.O.T.-Oriel GmbH & Co. KG, Darmstadt, Germany). Because of the critical importance of radiometric calibrations when proposing a standard relative luminosity function, we performed an additional control. Radiometric measurements were carried out successively with three calibrated devices at the plane of the observer's pupil: two calibrated radiometers (Model 80X Optometer, United Detector Technology) as well as the calibrated Pin-10 diode connected to the picoammeter. The calibrated radiometers had been calibrated by the manufacturers against standards traceable to the National Bureau of Standards, USA, whereas the diode and picometer were checked against a photodiode that was calibrated against the German

national standard (Braunschweig). In relative quantal flux density, we found that the three devices agreed to within 0.01 log unit as a function of wavelength from 400 to 700 nm. Given that the two radiometers and the calibrated diode had different origins, ages, and amounts of usage, and given that we define $V^*(\lambda)$ in relative terms, this agreement was very satisfying.

## 25-Hz HFP measurements

Corneal spectral sensitivities were measured by HFP. The measurements were confined to the central 2° of the fovea. The reference light (560 nm) was alternated at a rate of 25 Hz, in opposite phase with a superimposed test light (see Figure 2). The flickering stimuli were superimposed on a 16° diameter white adapting field (xenon arc white) with an intensity of 3.0 log trolands, which was sufficiently luminous to saturate the rod response. The HFP task was easily explained to the subjects who were experienced and well trained. None expressed any difficulties with the technique. We chose not to use HMP, a version of HFP in which the task is reduced to the detection of flicker rather than setting the flicker minimum. Although HMP is easier to use with inexperienced subjects, infants, and animals, with experienced subjects HFP is an inherently faster and more efficient method. As noted by the originators of the HMP method, "whereas well-trained observers do give reliable and reproducible [HFP] data, the task is hard to explain to naive observers, and a training period is needed" (Pokorny, Smith, & Lutze, 1989, p. 1618).

HMP has some advantages over HFP, but it also has some serious disadvantages. The main advantage of HMP is that luminance matches between any two lights can be made without varying the chromaticity. This advantage is to some extent lost, however, when a series of spectral lights are matched against each other or against a fixed wavelength standard (i.e., as in any determination of spectral sensitivity). As with HFP and other methods, the state of chromatic adaptation will vary as the wavelength of the spectral light is varied. The main disadvantage of HMP is that it is a threshold measure. In HFP, two flickering lights are matched to produce a steady or nulled target: flicker can be seen both above and below the null intensity. In HMP, in contrast, the modulations of both lights are varied together to find the threshold for detecting flicker. HFP is a matching method. HMP is a threshold method. Because it is a threshold measure, HMP can be influenced by "nonluminance" flicker signals, such as chromatic flicker signals, which arguably do not influence flicker nulls (e.g., Eisner & MacLeod, 1980; 1981). The only safeguard against such effects is obedience to a theoretical HMP template. A more practical disadvantage of HMP is that it is slow. In its initial variant (Pokorny et al., 1989), HMP requires 15 detection threshold settings for a single luminance match. We estimate that a single luminous efficiency function with 60 wavelengths as measured in our experiment would take about 15 hr.

At the start of the spectral sensitivity experiment, the subject adjusted the intensity of the 560-nm reference flickering light until satisfied that the flicker was just at threshold. After five settings had been made, the mean threshold setting was calculated and the reference light was set 0.2 log unit above this value. Then the test light was added to the reference light in counterphase. The subject adjusted the intensity of the test light until the flicker percept of the combined test and reference disappeared or was minimized. This procedure was repeated five times at each wavelength. After each setting, the intensity of the flickering test light was randomly reset to a higher or lower intensity so that the subject had to readjust the intensity to find the best setting. The target wavelength was varied randomly in 5-nm steps from 400 to 690 nm (but data were only retained from 425 to 675 nm). Two to six complete runs were performed by each subject. Thus, each data point represents between 10 and 30 threshold settings.

Because the intensity of the reference light was determined independently for each subject by measuring 25-Hz flicker thresholds at 560 nm, the reference and matching intensities vary slightly between subjects. At the flicker null, the reference, averaged over the 40 subjects, had a mean quantal flux density of 8.55 ± 0.04 (*SEM*) log quanta ($\lambda$ = 560nm) $s^{-1}$ $deg^2$ or 2.45 log photopic trolands. Assuming that the matching light at the null had the same luminous efficiency as the reference, in the region of the targets the combined stimulus intensity at the flicker null, including the white background, was, on average, 3.19 log trolands.

## Curve fitting and statistics

All curve fitting was carried out with the standard Marquardt–Levenberg algorithm implemented in SigmaPlot (SPSS Inc., Chicago), which was used to find the coefficients (parameters) of the independent variable or variables that gave the "best fit" between our model and the data. This algorithm seeks the values of the parameters that minimize the sum of the squared differences between the values of the observed and predicted values of the dependent variable or variables. Fits were made to log quantal spectral sensitivity data. It is important to note that fits made on a quantal and on an energy basis differ (see below).

Statistical evaluations were performed using JMP Version 5.0.1.2 (SAS Institute Inc., Cary, USA). A Shapiro–Wilk test for normality was performed before applying a *t* test to compare group data. If the data sets were distributed normally, a paired *t* test was used. Otherwise, a nonparametric Wilcoxon signed-rank test was used to determine if the mean of the difference was zero.

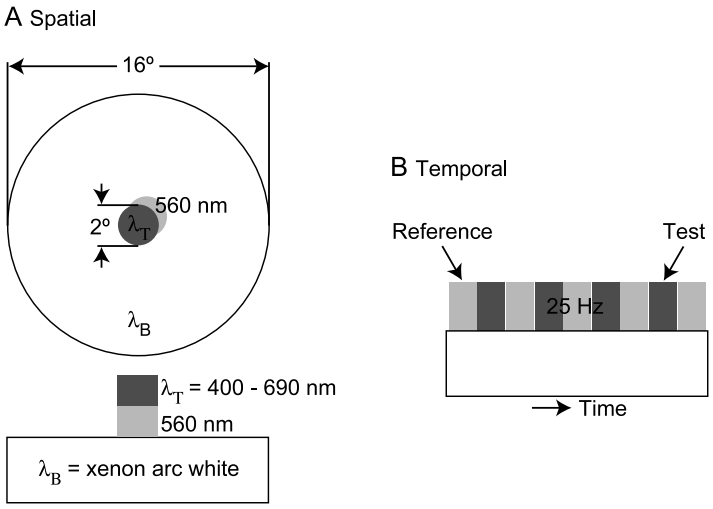


Figure 2. Stimulus configuration for the heterochromatic flicker photometry (HFP) measurements. (A) The test target $\lambda_T$ of variable wavelength ($\lambda$), from 400 to 690 nm in 5-nm steps, was matched to the standard wavelength reference (560 nm) target by adjusting its intensity. The two 2° diameter targets were alternated at 25 Hz in counterphase, while superimposed upon a 16° diameter xenon arc white (c. 5586 K) adapting field of 3.0 log trolands $\lambda_B$, which is a tritanopic metamer of CIE standard illuminant $D_{65}$, in terms of the Stockman & Sharpe (2000) L- and M-cone absorptions. (B) The time course of the flickering test and reference targets.

## Analysis of the 25-Hz HFP data

Measurements were made in trained subjects. Although a majority of the measurements were acceptable, a small minority were of doubtful quality. To avoid distorting the flicker photometric estimates, we adopted a standard method for eliminating doubtful data points from the analysis. Because each data point was averaged from five individual settings, its quality could be judged from the standard deviation. To eliminate the most doubtful data, we rejected points for which the standard deviation of the five settings was 0.15 log unit. In terms of the frequency distribution, this cutoff is 2 *SD* higher than the mean. In the range 425–675 nm, the total number of data points from individual runs that were rejected on this basis was 123 out of a total of 7089 points (1.7%). Sixty-four of those were due to only 5 of the 40 observers. The data used in the analysis were restricted to the range 425–675 nm. Outside this range, the data for some subjects were biased towards higher sensitivities. This bias occurred at the spectral extremes, we believe, because the range of adjustment was skewed towards lower efficiencies as the available light ran out.

Each subject's mean flicker photometric curve was assumed to be a linear combination of the quantized Stockman & Sharpe (2000) L- and M-cone spectral sensitivities. The white adapting field was calculated to bleach the L- and M-cones by approximately 4.8%, given a half-bleaching constant of 4.3 log trolands for the combined L (Rushton, 1965)- and M (Rushton & Henry, 1968)-cones. Assuming an estimated full photopigment optical density of 0.50 for both the L- and M-cones in the unbleached state (see Stockman & Sharpe, 2000), this amount of bleaching would reduce the effective optical density to 0.48, which would imply a very small change in the shape of the L- and M-cone-fitting templates that we decided to ignore.

The fit of the L- and M-cone photopigment templates to the individual 25-Hz HFP data was carried out in the single fitting procedure defined by Equation 1:

$$\log_{10}[V(\lambda)] = \log_{10}[a\bar{l}(\lambda) + \bar{m}(\lambda)] + k_{\text{lens}}d_{\text{lens}}(\lambda) + k_{\text{mac}}d_{\text{mac}}(\lambda) + c \quad (1)$$

where $V(\lambda)$ is the luminous efficiency function, $\bar{l}(\lambda)$ is either the L(ser180), the L(ala180), or the combined (mean) L template variant of the Stockman & Sharpe (2000) quantized L-cone spectral sensitivity, $\bar{m}(\lambda)$ is the Stockman & Sharpe quantized M-cone spectral sensitivity, $d_{\text{lens}}(\lambda)$ is the lens pigment density spectrum of van Norren & Vos (1974), slightly modified by Stockman et al. (1993) & Stockman & Sharpe (1999, 2000), and $d_{\text{mac}}(\lambda)$ is the macular pigment density spectrum of Stockman & Sharpe (1999, 2000) based on the Vos (1972) estimate. The lens $d_{\text{lens}}(\lambda)$ and macular $d_{\text{mac}}(\lambda)$ pigment spectra are mean population density spectra determined by Stockman & Sharpe and used to calculate their cone fundamentals; thus, $d_{\text{lens}}(\lambda)$ is 1.48 at 400 nm and $d_{\text{mac}}(\lambda)$ is 0.37 at peak. All of the functions in Equation 1 can be downloaded from the Web site http://www.cvrl.org. The lens density multiplier or weight $k_{\text{lens}}$ applied to $d_{\text{lens}}(\lambda)$, the macular pigment density multiplier $k_{\text{mac}}$ applied to $d_{\text{mac}}(\lambda)$, and the L-cone template

weight $a$ and the vertical shift component $c$ are all best-fitting values determined by the fit of the model defined for each observer's mean data. It is essential to use the appropriate L(ser180) or L(ala180) cone template rather than the mean L-cone template in Equation 1 to obtain accurate fits. This is because the spectral peaks of the L(ser180) and L(ala180) cone spectral sensitivities are shifted by 2.8 nm relative to one another (Sharpe, Stockman, Jägle, & Nathans, 1999). Even such small shifts produce large differences in L:M cone ratio estimates (for a discussion, see Jägle et al., 2005; see also Bieber, Kraft, & Werner, 1998).

The appropriate L(ser180) and L(ala180) cone templates are based on the Stockman & Sharpe (2000) L-cone fundamental calculated back to an absorbance spectrum (see their Table 2, Column 9), and then shifted along a logarithmic wavelength scale by −1.51 nm at $\lambda_{max}$ for L(ala180) or by +1.19 nm for L(ser180) in accordance with the 2.7-nm spectral shift between the L(ala180) and L(ser180) spectral sensitivities and the 56:44 L(ser180):L(ala180) ratio found in the population. The two shifted spectra were then corrected back to corneal spectral sensitivities to generate the corneal templates used in the fits. For further details, see Stockman and Sharpe (2000).

# Results

## Individual 25-Hz flicker photometry data

The individual 25-Hz HFP matches measured in the 22 L(ser180) observers, in the 16 L(ala180) observers, and in the 2 female observers with both variants of the L-cone photopigment, for the spectral range 425–675 nm, are presented in Figure 3, panels A–C. The fits of the model, using the appropriate L(ser180), L(ala180), or mean L-cone template, are shown by the continuous lines; the relative L:M cone ratios of the fitted Stockman & Sharpe (2000) spectral sensitivities (i.e., the weighting coefficient applied to the L-cones, $a$, in Equation 1) are shown above each curve (see also Table 1). The overall quality of the data is very good. The standard deviations within an observer were small and independent of test wavelength.

In Figures 4A and 5A, the individual L(ser180) and L(ala180) data, respectively, have been vertically aligned (using the best least-squares fit) with the logarithmic mean for each group. The variance in the L(ser180) and L(ala180) data sets can be estimated from inspecting the residual differences shown in the accompanying panels (Figures 4B and 5B, respectively). As expected, in both data sets, the greatest discrepancies are at short wavelengths. This is because the individual differences in macular and lens pigment densities cause individual spectral sensitivity data to appear highly discrepant even if they are determined by the same underlying L- and M-cone photopigments. There are also discrepancies at longer wavelengths caused by the changing cone weights, but these are exaggerated in the figures by the vertical alignments to the mean at short wavelengths. The data from two females who have an L(ser180) and an L(ala180) opsin gene on one of each of their two X-chromosomes are not included in this analysis (but are included in the combined analysis, see Table 1 and below).

## Individual estimates of lens and macular densities and of L:M cone ratio contributions

For each individual set of 25-Hz HFP matches, simultaneous estimates were made of the observer's lens and macular pigment density weighting factors and of the relative contribution of the Stockman & Sharpe (2000) L- and M-cone fundamentals to the curve (see Equation 1). Depending upon the L-cone polymorphism present in the observer, the appropriate L(ser180) or L(ala180) template was used in the fits (see above and Stockman & Sharpe, 2000). These parameters (see Equation 1), as well as the standard errors of each fitted parameter and the corresponding estimate of the goodness or root mean square error of the fit (RMS), are listed in Table 1. The macular pigment density scaling estimates correspond to the amount the macular pigment density spectrum template $[d_{mac}(\lambda)]$ of Stockman & Sharpe (1999, 2000) has to be weighted to adjust to the observer's own macular pigment density. The lens pigment density scaling estimates correspond to the amount the lens pigment density spectrum template $[d_{lens}(\lambda)]$ of van Norren & Vos (1974), slightly modified by Stockman et al. (1993) and Stockman & Sharpe (1999), has to be weighted to adjust to the observer's own lens pigment density. The lens and macular pigment optical density estimates for all observers fall within the normal range of values.

The individually determined L:M cone ratios (the L-cone weighting factor, $a$, in Equation 1) are illustrated in the scatterplots in Figure 6 for the L(ser180) and L(ala180) and mixed [L(ser180)/L(ala180)] observers. For the L(ser180) population of 22 observers, the ratios range from 0.48 (M-cone dominated) to 15.82 (strongly L-cone dominated). For the L(ala180) populations of 16 observers, the ratios range from 0.47 to 7.97. When all the data are considered together (40 observers), the ratios range from 0.47 to 15.82.

Notice that high standard errors are associated with large ratios (see also Figure 7A, below). This is an important point to consider when calculating mean L:M cone ratios to prevent skewing or distortions, because the larger ratios are poorly constrained by these fits.

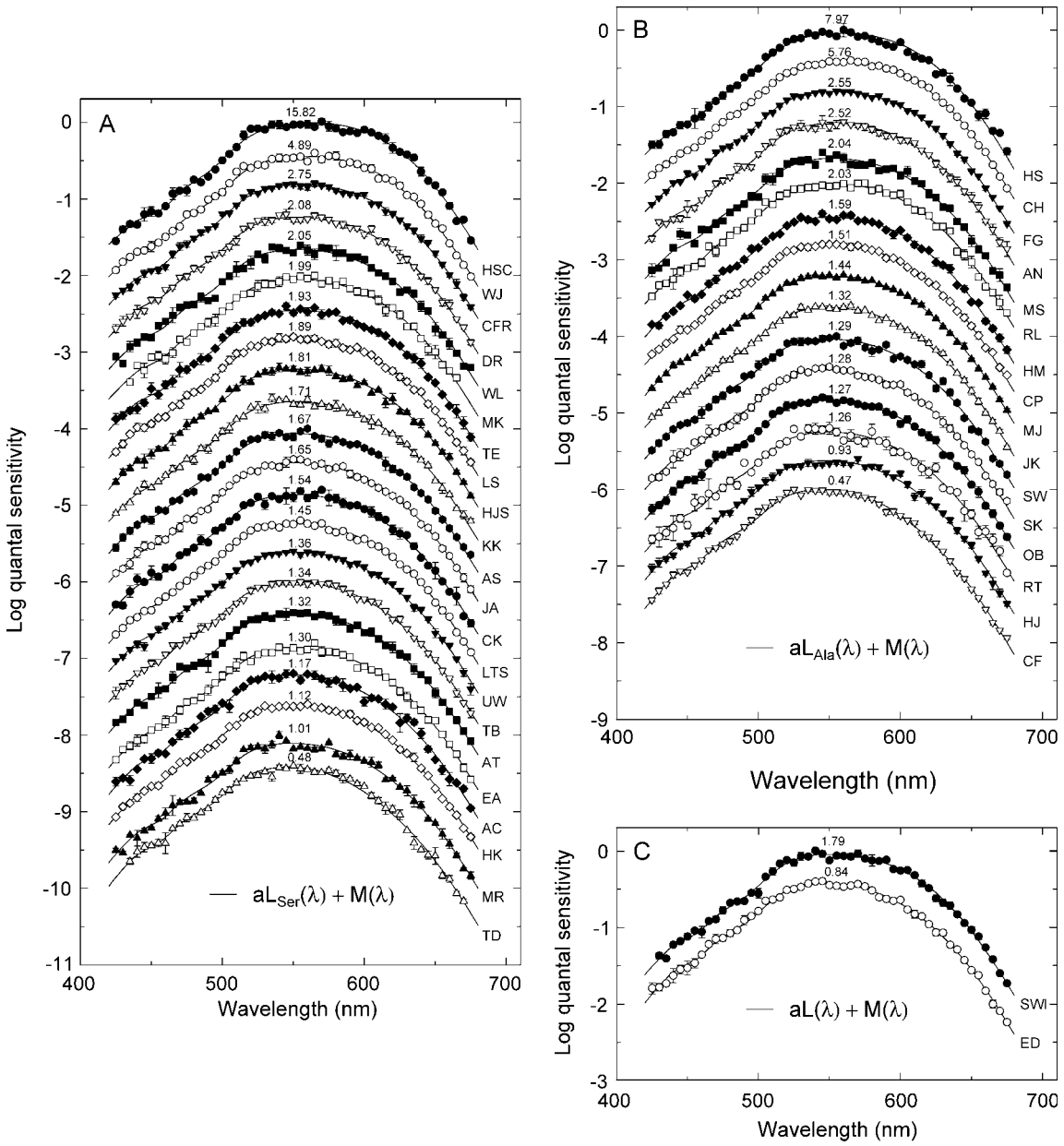


Figure 3. Individual mean 25-Hz HFP data, plus standard errors of the mean, measured for the 22 L(ser180) observers (panel A), for the 16 L(ala180) observers (panel B), and for the 2 female observers with both variants of the L-cone photopigment (panel C). The fits of the full-spectrum model, from 425 to 675 nm (see text), using the appropriate L(ser180), L(ala180), or mean L-cone template together with the M(ala180) template, are shown by the continuous lines; the estimated relative L:M cone ratios (i.e., the weighting coefficient *a* in Equation 1 applied to the L-cones) of the fitted Stockman & Sharpe (2000) spectral sensitivities are shown above each curve. The uppermost curve in each panel is in the correct position; the other curves have been shifted downwards, successively, by 0.4 log unit.

## Mean L:M cone ratios determined by averaging individual L:M cone ratio estimates

The mean L:M cone weights for the population of 16 L(ala) observers is 2.20, for the 22 L(ser) observers 2.38, and for all 40 observers 2.26. L:M cone weights, however, do not lend themselves to simple averaging because the ratios are not symmetric around a unity value of the weighting coefficient *a* in Equation 1, when L = M = 1.0. As the L-cone weight exceeds the M-cone weight *a* tends to ∞; whereas as the M-cone weight exceeds the L-cone weight *a* tends to 0.

Other measures of central tendency yield different values. The median value for the L(ala) subjects is 1.47, for the 22 L(ser) subjects 1.66, and for all subjects 1.57. On the other hand, the geometric mean for the L(ala) subjects is 1.73, for the L(ser) subjects 1.76, and for all

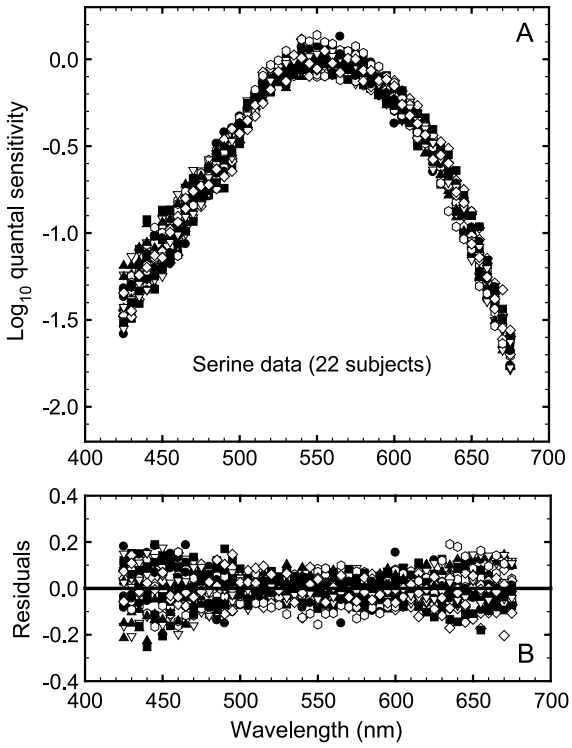


Figure 4. (A) Raw individual 2° diameter, 25-Hz HFP measurements, over the spectral range from 425 to 675 nm, from the 22 L(ser180) observers vertically aligned with the mean. (B) Differences between each data set and the mean.

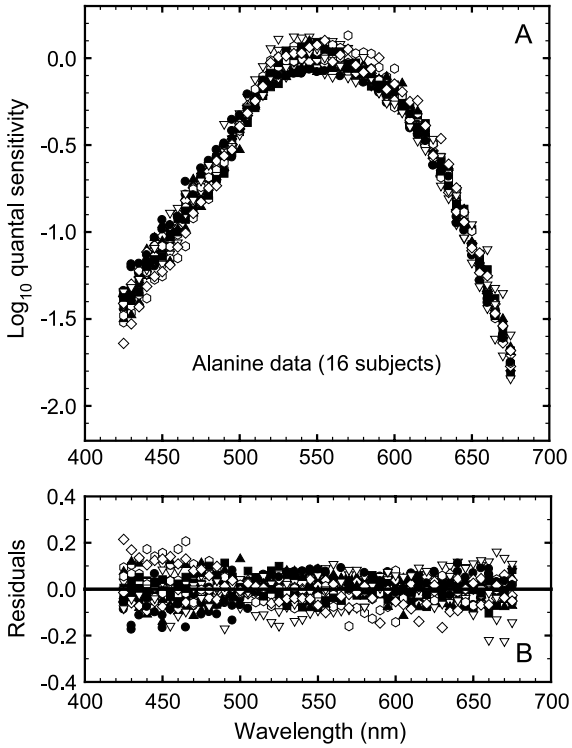


Figure 5. (A) Raw individual 25-Hz HFP measurements, over the spectral range from 425 to 675 nm, from the 16 L(ala180) observers vertically aligned with the mean. (B) Differences between each data set and the mean.

subjects 1.72. These are lower values than the arithmetic means.

A more serious problem is that as the weighting factor $a$ increases, so too does its standard error (see Figure 6 and Table 1). This increase is illustrated in Figure 7A, in which the fitted L:M cone weights and their standard errors are plotted on double logarithmic coordinates. The points are well described by a straight line (with a slope of 1.57), which in linear coordinates is a power function. As the weighting factor, $a$, increases (and the fit becomes dominated by the L-cones), the standard error increases by $a^{1.57}$. This nonlinear increase is due mainly to the relationship between $a$ and spectral sensitivity, which is illustrated in Figure 7B. The solid line in Figure 7B is the relative sensitivity loss at 675 nm (calculated using Equation 2, below, and the Stockman & Sharpe, 2000, fundamentals) plotted as a function of the logarithm of $a$. Up to an $a$ of about 2, the function is approximately a straight line, which is consistent with Figure 7A. As the L:M cone weight increases, a given change in weight has a proportionally smaller effect on spectral sensitivity, but a disproportionably larger influence on the mean L:M cone weight.

Estimates of L:M cone weight determined from electroretinographic or psychophysical measures of luminous efficiency are sometimes quoted without an estimate of error. As Figures 6 and 7 illustrate well, this could be potentially misleading, particularly for larger values of $a$. The dependence of spectral sensitivity on $a$ can be highlighted using our estimate of the mean L:M cone weight of 1.55 (see Figure 9, below): to decrease the weight by 0.1 to 1.45 would require a change in spectral sensitivity equivalent to a decrease of only 0.011 log unit at 675 nm, whereas to increase it by 0.1–1.65 would require a increase equivalent to only 0.010 log unit. These are very small changes in the experimental variable.

We tried several strategies to overcome the bias introduced by high L:M weights with high standard errors. One strategy was to transform the space in which the weighting factor $a$ was averaged so that its standard errors were roughly constant. Another strategy was to average the logarithmic L:M cone weights inversely weighted by the linear standard error estimated by the fitted regression line (see Figure 7A). So weighted and averaged, the mean logarithmic weight was 0.1985 (in log units), corresponding to a mean L:M weight of 1.58 (in arithmetic units). While this ratio is pleasingly close to the weight obtained from fits to the mean luminous efficiency function of 1.55 (see below), none of the strategies seemed particularly convincing or well justified.

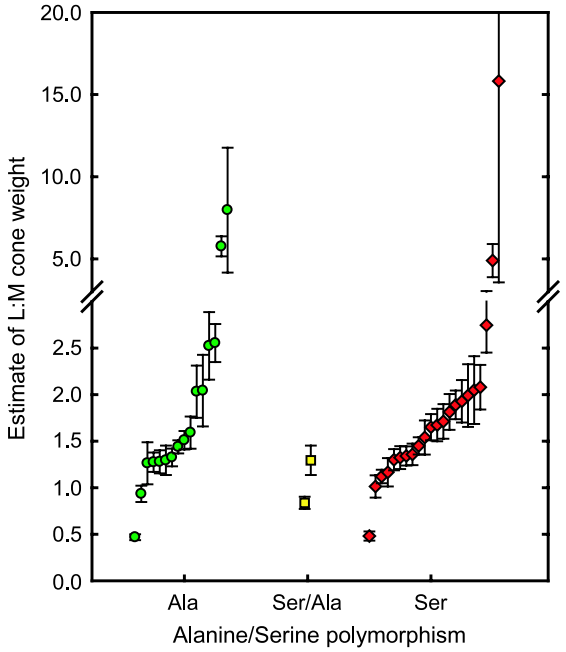


Figure 6. Scatter plot of L:M cone ratios (i.e., the L-cone weighting factor, *a*, in Equation 1) determined from fitting the individual mean 25-Hz HFP measurements of the 40 observers with a linear combination of the Stockman & Sharpe (2000) L- and M- cone fundamentals (see Table 1 for values and Equation 1). L(ser180) observers: red diamonds; L(ala180) observers: green circles; mixed L(ser180)/L(ala180) observers: yellow squares. Note for clarity and to accommodate all the values, the scaling along the ordinate has been broken at an L:M cone ratio of 3.

### Mean L:M cone ratio determined by fitting the mean 25-Hz flicker data

The alternative and our preferred method of estimating the mean L:M cone ratios is to fit Equation 1 to the mean logarithmic quantal sensitivity data. The fits and the residual errors of the L:M cone ratio estimates (i.e., L-cone weighting factor, *a*) are shown in Figure 8 for the 22 L(ser180) observers (panel A) and for the 16 L(ala180) observers (panel B). The best-fitting L:M cone ratios are as follows: 1.60 ± 0.04 for the 22 L(ser180) observers when fitted with the L(ser180) template; 1.56 ± 0.06 for the 16 L(ala180) observer when fitted with the L(ala180) template; and 1.55 ± 0.05 for the 40 combined observers when fitted with the combined L-cone template [two females could not be included in either the L(ser180) or L(ala180) template fits because they had both alanine and serine on one of each of their two X-chromosomes, but they could be included in the total fit, which relies on a mean L-cone template, see Figure 9].

The mean 25-Hz HFP measurements of the 40 observers are shown in Figure 9 in quantal units (panel A), fitted with a linear combination of the quantized Stockman & Sharpe (2000; CIE 2005) L- and M-cone fundamentals. The best-fitting L:M cone ratio estimate is 1.55 ± 0.05. It should be noted that were this fit to be carried out in energy units, which given the quantal nature of phototransduction is less appropriate, the fit would be 1.63 ± 0.04. Surprisingly, this dependence of the cone weights on the units used is seldom mentioned or taken into account, despite the alleged importance of such weights in estimating the ratio of L-cone to M-cones in the human eye. Indeed, the different weights reflect mainly the fact that the quantal- and energy-based L- and M-cone fundamentals have different $\lambda_{max}$ values and therefore different unity peak normalizations (see Equations 4 and 5).

Because it might be argued that the mean fit is being influenced by average differences in the lens and macular pigment densities between the values found for our populations and those used to derive the Stockman & Sharpe (2000) cone fundamentals and/or contributions in the S-cones, the mean fit shown in Figure 9 was repeated for the partial spectral region 555–675 nm. In this spectral region, lens and macular pigment absorptions can safely be assumed to be negligible and the S-cones, especially for 25-Hz flickering targets, can be considered as being functionally in abeyance. The best-fitting L-cone weighting factor (L:M cone weights) is 1.54 ± 0.05. This is not shown in Figure 9 because it is visually indistinguishable from the full spectrum fit. This result confirms that the full spectrum mean fit is not artefactually altered by differences in subject lens and macular pigment densities nor by contributions of the S-cones.

The values of the best-fitting linear combination to the HFP data, which define $V^*(\lambda)$, are tabulated in logarithmic quantal units in Table 2 and in linear energy units in Table 3. These functions can be downloaded from http://www.cvrl.org. The lens and macular pigment densities values for the average observer represented by Tables 2 and 3 are the same as those assumed to apply for the Stockman & Sharpe (2000) 2° M- and L-cone fundamentals. Those density values can be obtained from Table 2 of Stockman & Sharpe or http://www.cvrl.org. They correspond to a peak macular density of 0.35 at 460 nm and a lens density of 1.76 at 400 nm.

## Discussion

We propose a modified $V(\lambda)$ function for 2° observing conditions, which we refer to as $V^*(\lambda)$ that retains some of the properties of the original CIE $V(\lambda)$, but is consistent with the Stockman & Sharpe (2000) cone fundamentals. The consistency with the Stockman & Sharpe cone fundamentals guarantees that the average lens and macular pigment densities for $V^*(\lambda)$, which are large sources of individual variation, are the same as those for the new cone fundamentals. Other advantages of $V^*(\lambda)$ are that it is solely based on flicker photometry,

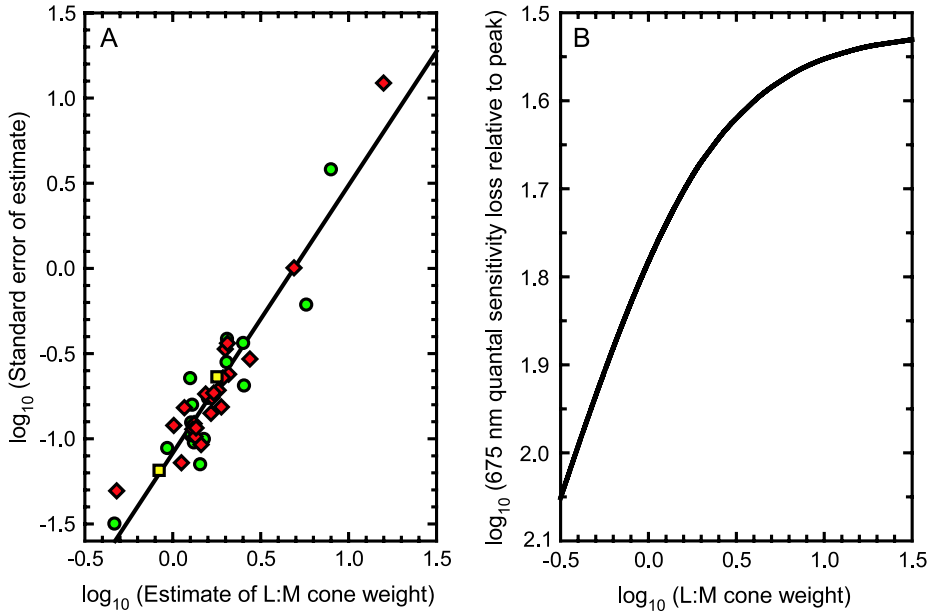


Figure 7. (A) The fitted L:M cone weighting coefficients (*a*) plotted against the standard error for each fitted coefficient on double logarithmic coordinates. The solid line is the best-fitting regression line (with a slope of 1.57 and intercept of −1.08). Symbols as Figure 6. (B) The logarithmic L:M cone weight plotted against the logarithmic sensitivity loss at 675 nm relative to the peak sensitivity.

which is the standard method for defining luminance; it corresponds to a central 2° viewing field, for which the basic laws of brightness matching are valid for flicker photometry (Wyszecki & Stiles, 1982); its composition of the ser/ala L-cone pigment polymorphism (58:42) closely matches the estimated incidence in the normal population (56:44; Stockman & Sharpe, 1999; Tables 1 and 2); and it defines luminance for conditions similar to CIE standard illuminant $D_{65}$ adaptation.

## Cone spectral sensitivities and the luminosity function

In order for a luminous efficiency function to be additive and for it to correspond to the assumed properties of the traditional model of the luminance channel, its measurement conditions must discriminate against contributions from the S-cone pathways or from L- and M-cone chromatic pathways (Lennie, Pokorny, & Smith,

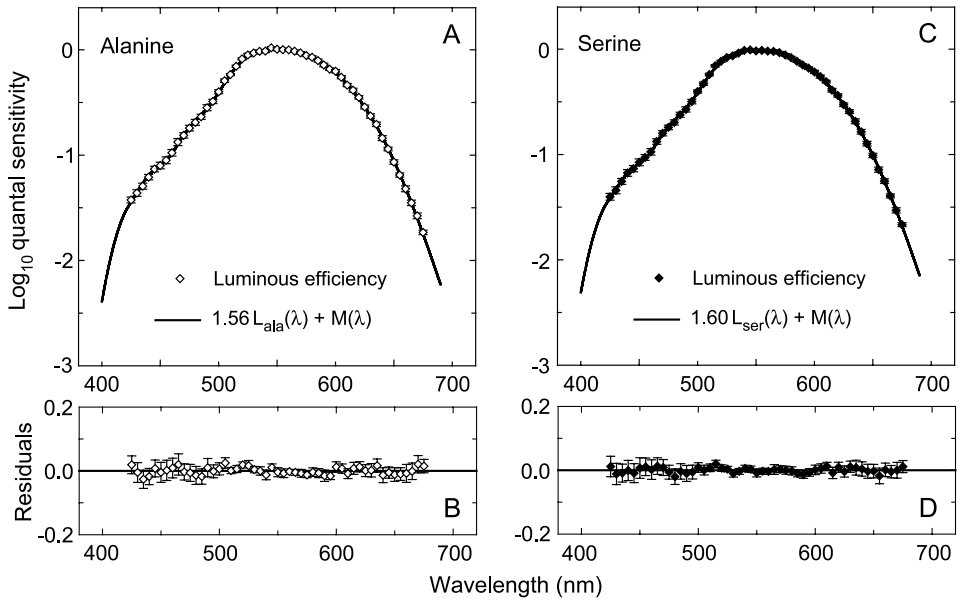


Figure 8. The mean L(ala180) cone (panel A) and mean L(ser180) cone (panel C) 25-Hz HFP (luminous efficiency) measurements. The error bars correspond to the standard error of the mean. The subpanels B and D show the residuals between the mean data and the final fit. The weighting coefficient applied to the appropriate L-cone template, *a*, is given for each fit (Equation 1).

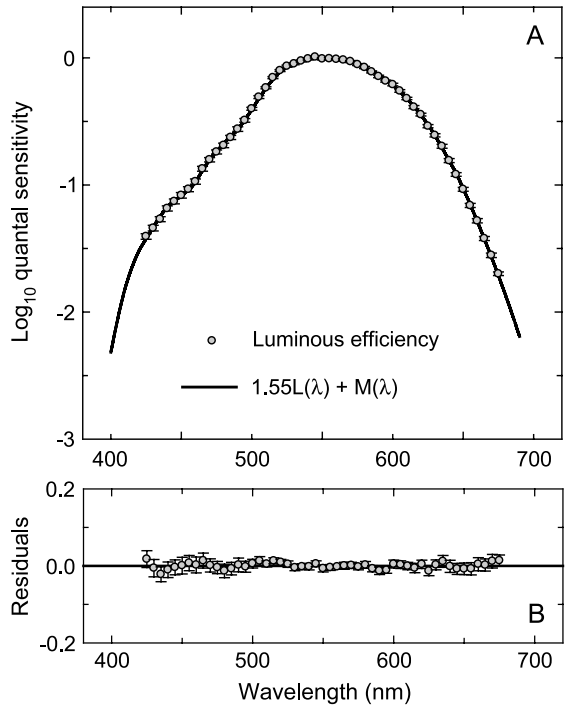


Figure 9. (A) The mean 25-Hz HFP measurements of the 40 observers, in quantal units, fitted with a linear combination of the quantized Stockman & Sharpe (2000) L- and M-cone fundamentals. The weighting coefficient applied to the L-cones, *a*, is shown. (B) Residuals of the fit.

1993). Such conditions are favored by the use of high temporal frequencies. Having used such conditions (25 Hz) to measure the HFP data that guided our derivation of $V^*(\lambda)$, we are confident that the M- and L-cones contribute predominantly or exclusively to it and that the contribution of the S-cones and its pathways can be practically treated as negligible or null. Thus, the final luminance efficiency function, $V^*(\lambda)$, has the convenient property that it is a linear combination of the signals from the L- and M-cones; namely, that (Equation 2):

$$V^*(\lambda) = a\bar{l}(\lambda) + \bar{m}(\lambda), \quad (2)$$

where $a$ is the L-cone scaling constant. When we originally applied this procedure to the 22 observers used in the preliminary version of $V^*(\lambda)$, we obtained a value of 1.5 for $a$ (Stockman & Sharpe, 2000). However, based on the fit to all 40 observers and curtailing the analysis at short wavelengths to be ≥425 nm (to avoid flicker matches made at the short wavelength spectral extremes where some observers ran out of light), the value of $a$ is now 1.55 ± 0.05, and the final definition of $V^*(\lambda)$ is therefore (Equation 3):

$$V^*(\lambda) = 1.55\bar{l}(\lambda) + \bar{m}(\lambda), \quad (3)$$

where $\bar{l}(\lambda)$ and $\bar{m}(\lambda)$ have the same (normalized) peak sensitivities. Importantly, given that the L(ser180): L(ala180) ratio of 0.58:0.42 for our 40 subjects is so similar to the 0.56:0.44 ratio assumed by Stockman & Sharpe (2000) in deriving their cone sensitivities, we did not need to weight the L(ala180) and L(ser180) data before averaging them, as we did in the preliminary version (Stockman & Sharpe, 2000).

Interestingly, a quantal weighting factor of 1.55 is identical to the L:M cone energy weight of 1.62 implied by the relationship of the Smith–Pokorny L- and M-cone fundamentals to the Judd–Vos $V(\lambda)$. However, if the Judd–Vos $V(\lambda)$ function is fitted with the Stockman & Sharpe (2000) cone fundamentals, the weighting factor is only 1.29. A value of 1.55 accords with a greater dominance of L- than M-cones in the retina, as first inferred quantitatively by Walraven (1974). It is supported by psychophysical (e.g., Cicerone & Nerger, 1989; Vimal, Smith, Pokorny, & Shevell, 1989), electroretinographic (e.g., Albrecht, Jägle, Hood, & Sharpe, 2002; Kremers, Usui, Scholl, & Sharpe, 1999; Kremers et al., 2000), microspectrophotometric (Bowmaker, Parry, & Mollon, 2003), and retinal densitometric (e.g., Kremers et al., 2000) measurements in different groups of observers and psychophysical, electroretinographic, and retinal densitometric measurements made in the same group of observers (Kremers et al., 2000). However, even given the doubtful assumption that the relative cone numbers in the standard or average retina can be directly derived from luminosity functions, the value of 1.55 used to define $V^*(\lambda)$ for the white adapting field condition is likely to underestimate the relative proportions of the L- and M-cones. This is because the white adapting field selectively desensitizes the L-cones relative to the M-cones by a factor of 1.16 (thus a value of 1.80 may more closely reflect the relative L- to M-cone proportions).

We chose the white adapting field, rather than one that equally desensitizes the L- and M-cones for two practical reasons. First, the relative desensitization factor of 1.16 is the same as would be achieved with a standard CIE $D_{65}$ illuminant. Moreover, it is less than or similar to the selective adaptation that obtains with other relative spectral radiant power distributions of daylight of different correlated color temperatures, such as 5,000 K (1.2249); 5,500 K (1.2015); 6,000 K (1.1827); or 7,000 K (1.1547). Only at very high correlated color temperatures is the factor slightly reduced: 7,500 K (1.1440); 8,000 K (1.1348); 10,000 K (1.1088); 15,000 K (1.0775); and 20,000 K (1.0635). In contrast, an equal energy spectrum yields a selective adaptation of the L-cones by a factor of 1.23; and the CIE standard illuminant A, corresponding to incandescent light, yields a selective adaptation of the L-cones by a factor of 1.45. Second, to produce equal M- and L-cone excitations, given similar peak M- and L-cone sensitivities, an adapting wavelength of 549.1 nm must be used (this wavelength is the

cross-over point or intersection of the Stockman & Sharpe, 2000, L- and M-cone sensitivities normalized to unity peaks). However, this adapting wavelength is not representative of natural conditions, does not necessarily produce equal adaptation of the M- and L-cone mechanisms (see above, and Stiles, 1978), and is not neutral at a typical chromatically opponent L–M site.

## S-cones and the luminosity function

The question of whether the S-cones contribute to luminance has been somewhat contentious, but it now seems clear that the S-cones can make a small contribution when the S-cone response is enhanced (relative to the responses of the L- and M-cones) by intense long wavelength adaptation (Lee & Stromeyer, 1989; Stockman & MacLeod, 1987; Stockman, MacLeod, & DePriest, 1991). Under such conditions, the S-cone contribution to luminance is negative, but substantially delayed, so that at moderate frequencies (15–25 Hz, depending on the S-cone adapting level) the S-cone flicker adds to luminance (Stockman et al., 1991). As far as we are aware, there is as yet no strong evidence of a significant S-cone input under conditions of neutral chromatic adaptation. The suggestion by Vos, Estévez, and Walraven (1990) of a small negative S-cone contribution to luminance was based on a comparison between data obtained from distinctly different populations using distinctly different methods, one set of which is highly selected and arbitrary. Attributing small deviations between such disparate data sets to a small negative S-cone contribution is at best speculative.

Given that any S-cone contribution to luminance is small, and that its contribution is strongly frequency and adaptation dependent, it is of practical convenience to assume that the S-cone contribution to $V^*(\lambda)$ is zero. For this reason, we chose a frequency for our HFP measurements that is slightly above the conventional S-cone CFF (Brindley, Du Croz, & Rushton, 1966; Green, 1969; Marks & Bornstein, 1974; but see Stockman, MacLeod, & Lebrun, 1993), thus ensuring that any S-cone contribution to our measurements would be small.

Like Vos et al. (1990), we can compare the luminous efficiency data with linear combinations of the cone fundamentals to determine if there is a significant S-cone contribution (by adding an S-cone component to Equation 1 and repeating the fit). When we carried out the fit, we also found a small negative S-cone contribution, but of only −0.35% of the total cone contributions (relative to unity peak). Moreover, the S-cone weight was not significantly different from zero.

The finding that the S-cone weight is statistically insignificant under the conditions of our experiment is remarkable given the very large S-cone modulations that are produced by the short wavelength stimuli on our white background (which excites the S-cones less than a standard $D_{65}$ background).

For both practical and empirical reasons, therefore, we assume that there is no significant S-cone contribution to the HFP data and to the $V^*(\lambda)$ function as so defined and measured. We do not assume that there is no S-cone contribution to luminance under all conditions. Under conditions for which a contribution is found, $V^*(\lambda)$ should be modified appropriately using the Stockman & Sharpe (2000) S-cone fundamental.

## Final $V^*(\lambda)$ function

The HFP data, which are defined over the spectral range of 425–675 nm, were used to guide the fits of the previously defined Stockman & Sharpe (2000) L- and M-cone spectral sensitivities, which are defined over the spectral range of 390–830 nm, after the data were adjusted to correspond to the same average lens and macular pigment absorption spectra. Although $V^*(\lambda)$ is completely defined by the appropriate weighting of the Stockman and Sharpe cone fundamentals in Equation 3, for convenience it is also tabulated in quantal units in Table 2 and in energy units in Table 3. Both versions can also be downloaded in 0.1-, 1-, or 5-nm steps from http://www.cvrl.org.

In Figure 10A, the final version of the quantized $V^*(\lambda)$ luminosity function (continuous line) is compared with original data—the mean 25-Hz HFP measurements from the 40 color normals (yellow diamonds) used to guide the choice of $V^*(\lambda)$ and the flicker photometric sensitivity measurements by Stiles & Burch (1959) (red dotted circles)—and with the Judd–Vos-modified $V(\lambda)$ or $V_M(\lambda)$ (dashed line). The differences between $V^*(\lambda)$ and the other functions are shown in Figure 10B. The Judd–Vos-modified $V(\lambda)$ mainly differs from $V^*(\lambda)$ in the short wavelength region of the spectrum below 520 nm where it is known to be erroneous, but also at long wavelengths greater than 680 nm where it is too sensitive. The 2° flicker photometric sensitivity measurements made at four wavelengths in 26 of the 49 observers of the Stiles & Burch (1959) 10° color matching study are closer to $V^*(\lambda)$ than to the Judd–Vos $V(\lambda)$, as are the mean 25-Hz HFP measurements that we used to guide the choice of $V^*(\lambda)$.

As noted in the legends of Tables 2 and 3, the $\lambda_{mac}$ of $V^*(\lambda)$ is 555.5 nm in energy units, yet is 545.6 nm in quantal units. These values compare with $\lambda_{max}$'s of 555.0 and 550.2 nm for energy and quantal units, respectively, for both the CIE 1931 $V(\lambda)$ and the Judd–Vos-modified $V_M(\lambda)$ functions. The greater shift in peak of the $V^*(\lambda)$ function with the change from energy to quantal units simply results from the fact that it has a slightly flatter top than the artificially smoothed CIE $V(\lambda)$ and $V_M(\lambda)$ functions. Parenthetically, the large shifts of $\lambda_{max}$ caused by the change of unit emphasize that conclusions based on such values are capricious and should always be qualified.

The quantal $V^*(\lambda)$ curve in Equation 4 is defined relative to the quantal cone fundamentals $\bar{l}(\lambda)$ and $\bar{m}(\lambda)$, having unity peak sensitivities. The factor 2.476985 renormalizes the $V^*(\lambda)$

| λ [nm] | log *V**(λ) | λ [nm] | log *V**(λ) | λ [nm] | log *V**(λ) |
|---|---|---|---|---|---|
| 390 | *−3.2329* | | | | |
| 395 | *−2.8304* | | | | |
| 400 | *−2.4708* | 600 | −0.2104 | 800 | *−5.5627* |
| 405 | *−2.1687* | 605 | −0.2587 | 805 | *−5.6975* |
| 410 | *−1.9117* | 610 | −0.3144 | 810 | *−5.8331* |
| 415 | *−1.7184* | 615 | −0.3766 | 815 | *−5.9662* |
| 420 | *−1.5702* | 620 | −0.4450 | 820 | *−6.0962* |
| 425 | −1.4634 | 625 | −0.5187 | 825 | *−6.2259* |
| 430 | −1.3627 | 630 | −0.6061 | 830 | *−6.3542* |
| 435 | −1.2681 | 635 | −0.7014 | | |
| 440 | −1.1888 | 640 | −0.8003 | | |
| 445 | −1.1354 | 645 | −0.9033 | | |
| 450 | −1.0877 | 650 | −1.0199 | | |
| 455 | −1.0435 | 655 | −1.1470 | | |
| 460 | −0.9775 | 660 | −1.2797 | | |
| 465 | −0.8870 | 665 | −1.4173 | | |
| 470 | −0.8037 | 670 | −1.5594 | | |
| 475 | −0.7363 | 675 | −1.7070 | | |
| 480 | −0.6752 | 680 | *−1.8603* | | |
| 485 | −0.6178 | 685 | *−2.0198* | | |
| 490 | −0.5614 | 690 | *−2.1864* | | |
| 495 | −0.4880 | 695 | *−2.3469* | | |
| 500 | −0.4060 | 700 | *−2.5074* | | |
| 505 | −0.3218 | 705 | *−2.6693* | | |
| 510 | −0.2416 | 710 | *−2.8363* | | |
| 515 | −0.1701 | 715 | *−3.0036* | | |
| 520 | −0.1116 | 720 | *−3.1671* | | |
| 525 | −0.0725 | 725 | *−3.3300* | | |
| 530 | −0.0442 | 730 | *−3.4897* | | |
| 535 | −0.0246 | 735 | *−3.6488* | | |
| 540 | −0.0073 | 740 | *−3.8083* | | |
| 545 | −0.0001 | 745 | *−3.9623* | | |
| 550 | −0.0015 | 750 | *−4.1169* | | |
| 555 | −0.0019 | 755 | *−4.2690* | | |
| 560 | −0.0081 | 760 | *−4.4189* | | |
| 565 | −0.0160 | 765 | *−4.5681* | | |
| 570 | −0.0288 | 770 | *−4.7146* | | |
| 575 | −0.0481 | 775 | *−4.8617* | | |
| 580 | −0.0754 | 780 | *−5.0041* | | |
| 585 | −0.0997 | 785 | *−5.1457* | | |
| 590 | −0.1298 | 790 | *−5.2862* | | |
| 595 | −0.1671 | 795 | *−5.4258* | | |

Table 2. Quantal 2° luminosity function *V**(λ), tabulated in 5-nm steps from 390 to 830 nm. *V**(λ) is scaled to unity peak, which is at 545.6 nm (not tabulated). The data contained in this table are available in 0.1-, 1-, and 5-nm steps here and at the Web site: http://www.cvrl.org. The data given in italics are extrapolated using the Stockman & Sharpe (2000) cone fundamentals.

function so that it also peaks at unity at its $\lambda_{max}$ (545.6 nm). The function is tabulated in Table 2:

$$V^*(\lambda) = [1.55\ \bar{l}(\lambda) + \bar{m}(\lambda)]/2.476985. \quad (4)$$

Likewise, the energy based function, $V_e^*(\lambda)$ in Equation 5 is defined relative to the *energy based* cone fundamentals $\bar{l}_e(\lambda)$ and $\bar{m}_e(\lambda)$, having unity peak sensitivities. The factor 2.525598 renormalizes the $V_e^*(\lambda)$ function so that it also

| (λ) nm | V*(λ) | (λ) nm | V*(λ) | (λ) nm | V*(λ) |
|---|---|---|---|---|---|
| 390 | *4.1276E−04* | | | | |
| 395 | *1.0561E−03* | | | | |
| 400 | *2.4477E−03* | 600 | 6.6879E−01 | 800 | *3.9620E−06* |
| 405 | *4.9696E−03* | 605 | 6.0338E−01 | 805 | *2.9231E−06* |
| 410 | *9.0909E−03* | 610 | 5.3516E−01 | 810 | *2.1522E−06* |
| 415 | *1.4360E−02* | 615 | 4.6755E−01 | 815 | *1.5939E−06* |
| 420 | *2.0443E−02* | 620 | 4.0263E−01 | 820 | *1.1888E−06* |
| 425 | 2.6457E−02 | 625 | 3.4256E−01 | 825 | *8.8734E−07* |
| 430 | 3.3752E−02 | 630 | 2.8231E−01 | 830 | *6.6438E−07* |
| 435 | 4.2453E−02 | 635 | 2.2848E−01 | | |
| 440 | 5.1540E−02 | 640 | 1.8338E−01 | | |
| 445 | 5.8947E−02 | 645 | 1.4581E−01 | | |
| 450 | 6.6538E−02 | 650 | 1.1233E−01 | | |
| 455 | 7.4472E−02 | 655 | 8.4474E−02 | | |
| 460 | 8.7660E−02 | 660 | 6.2710E−02 | | |
| 465 | 1.0913E−01 | 665 | 4.6031E−02 | | |
| 470 | 1.3362E−01 | 670 | 3.3432E−02 | | |
| 475 | 1.5773E−01 | 675 | 2.3981E−02 | | |
| 480 | 1.8348E−01 | 680 | *1.6971E−02* | | |
| 485 | 2.1158E−01 | 685 | *1.1841E−02* | | |
| 490 | 2.4342E−01 | 690 | *8.1286E−03* | | |
| 495 | 2.9118E−01 | 695 | *5.6566E−03* | | |
| 500 | 3.5522E−01 | 700 | *3.9376E−03* | | |
| 505 | 4.3550E−01 | 705 | *2.7317E−03* | | |
| 510 | 5.2907E−01 | 710 | *1.8727E−03* | | |
| 515 | 6.2979E−01 | 715 | *1.2830E−03* | | |
| 520 | 7.2759E−01 | 720 | *8.8670E−04* | | |
| 525 | 8.0387E−01 | 725 | *6.1360E−04* | | |
| 530 | 8.6611E−01 | 730 | *4.2769E−04* | | |
| 535 | 9.1467E−01 | 735 | *2.9852E−04* | | |
| 540 | 9.6067E−01 | 740 | *2.0821E−04* | | |
| 545 | 9.8593E−01 | 745 | *1.4702E−04* | | |
| 550 | 9.9160E−01 | 750 | *1.0368E−04* | | |
| 555 | 9.9987E−01 | 755 | *7.3527E−05* | | |
| 560 | 9.9460E−01 | 760 | *5.2413E−05* | | |
| 565 | 9.8535E−01 | 765 | *3.7415E−05* | | |
| 570 | 9.6525E−01 | 770 | *2.6879E−05* | | |
| 575 | 9.3132E−01 | 775 | *1.9280E−05* | | |
| 580 | 8.8215E−01 | 780 | *1.3981E−05* | | |
| 585 | 8.4131E−01 | 785 | *1.0154E−05* | | |
| 590 | 7.9168E−01 | 790 | *7.3951E−06* | | |
| 595 | 7.3264E−01 | 795 | *5.3959E−06* | | |

Table 3. Energy-based version of the 2° luminosity function $V^*(\lambda)$, tabulated in 5-nm steps from 390 to 830 nm. $V^*(\lambda)$ is scaled to unity peak, which is at 555.6 nm (not tabulated). The data contained in this table are available in 0.1-, 1-, and 5-nm steps in linear and logarithmic versions on the Web site: http://www.cvrl.org. The data given in italics, ≤425 and ≥675 nm, are extrapolated using the Stockman & Sharpe (2000) cone fundamentals.

peaks at unity at its $\lambda_{max}$ (555.5 nm). The function is tabulated in Table 3:

$$V_e^*(\lambda) = [1.624340\,\bar{l}_e(\lambda) + \bar{m}_e(\lambda)]/2.525598. \quad (5)$$

The L-cone weight differs in the two equations, even though the functions are the same except for an energy to quanta conversion, because the underlying quantal and energy fundamentals have different $\lambda_{max}$s and therefore different unity normalizations.

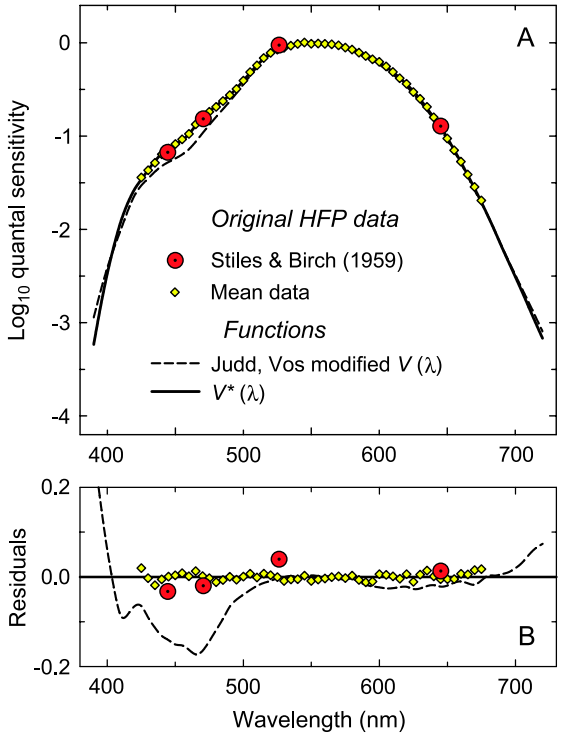


Figure 10. (A) The final version of $V^*(\lambda)$ (continuous line), the mean macular and lens adjusted 25-Hz HFP measurements from the 40 color normals (yellow diamonds) used to guide the choice of $V^*(\lambda)$, the Judd–Vos-modified $V(\lambda)$ or $V_M(\lambda)$ (dashed line), and the flicker photometric sensitivity measurements by Stiles & Burch (1959) (red dotted circles). (B) Differences between the $V^*(\lambda)$ and the other functions are shown in panel A.

## Applications of the $V^*(\lambda)$ function

A standard photopic luminosity function should define luminosity over a wide range of conditions that differ in luminance and chromaticity, but this requirement is inherently impossible for a single function. Strictly, the $V^*(\lambda)$ function defines luminance only for the conditions under which it was measured and is not simply generalizable to other conditions of adaptation or viewing. Unlike cone spectral sensitivities, the shape of the luminosity function changes with chromatic adaptation (e.g., De Vries, 1948; Eisner & MacLeod, 1981) and is highly dependent on the observing conditions (e.g., size, retinal eccentricity, duration and intensity of the viewing field) and the measurement criterion. Different methods or viewing conditions can bring about changes in the state of chromatic adaptation or, potentially, tap into different postreceptoral mechanisms. In fact, in terms of luminance sensitivity, the visual system behaves linearly (and additively), as explicitly required for luminous efficiency and photometry, only under rather narrow circumstances (Lennie, Pokorny, & Smith, 1993; Wyszecki & Stiles, 1982). Therefore, the significance of the $V^*(\lambda)$ function, *per se,* for vision research is limited, although it improves upon the presently established standards for photometry—the CIE $V(\lambda)$ function and its modification $V_M(\lambda)$—in its construction, derivation, and the conditions under which it was measured. Moreover, there are large individual differences and luminous efficiency functions such as $V^*(\lambda)$, which is based on additive 25-Hz HFP data, represent averages of data rather than the sensitivity of any given observer. For example, one of the individual normal observer HFP functions upon which it is based is fit by an L:M cone ratio of 0.48; another by a ratio of 14.0.

Nevertheless, given that the choice of the adapting field is inevitably arbitrary, it is arguably best and most consistent to choose one that represents a natural daylight condition measured under internationally recognized and standardized conditions. Accordingly, the function we present here is representative of real-life or natural conditions and corresponds to a natural phase of daylight. Indeed, one of the added benefits of defining $V^*(\lambda)$ initially for a phase of natural daylight may be in its relevance to studying and modeling the effects of natural images.

Moreover, because our definition of luminous efficiency is directly linked to the Stockman & Sharpe (2000) cone fundamentals, it is possible to derive values of the L-cone weighting factor, $a$ that are representative of other states of adaptation. Indeed, a more general definition of luminance would be one in which the relative cone weight, $a$ is defined for a variety of different conditions that might include natural daylights, artificial lighting conditions, and various chromaticities, all as a function of overall luminance. In an accompanying paper, we have determined the changes in weighting factor $a$ (Equation 3) in a subset of our subjects for adapting backgrounds that vary in spectral content and in luminance away from the standard $D_{65}$ white used here. This additional refinement will enable $V^*(\lambda)$ to be modified appropriately for other adapting conditions (Stockman, Jägle, Pirzer, & Sharpe, 2005).

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