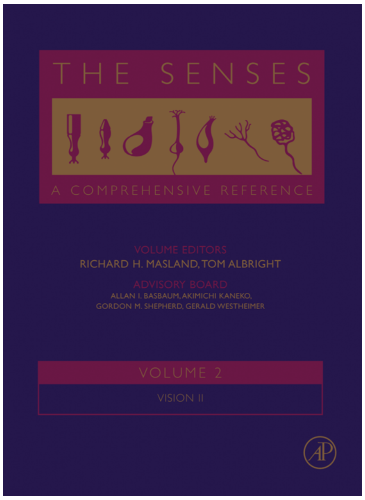

A Stockman and L T Sharpe, Spectral Sensitivity. In: Allan I. Basbaum, Akimichi Kaneko, Gordon M. Shepherd and Gerald Westheimer, editors The Senses: A Comprehensive Reference, Vol 2, Vision II, Thomas D. Albright and Richard Masland. San Diego: Academic Press; 2008. p. 87-100.

2.06 Spectral Sensitivity

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Glossary

achromatic Perceptually, devoid of hue or colorless. The nonchromatic dimension of a visual stimulus; including neutral grays, white, and black.

anomalous trichromacy A type of color blindness, in which one of the three cone pigments is altered in its spectral sensitivity, but trichromacy is not fully impaired.

chromatic Perceived as having hue or being colored (blue, green, yellow, red, purple, etc.). The hue and saturation dimensions of a visual stimulus.

color match A perceptual match between pairs or mixtures of lights with different spectral power distributions (which are therefore metamers).

***color matching function* (*CMF*)** $\bar{x}(\lambda), \bar{y}(\lambda)$, and $\bar{z}(\lambda)$. Tristimulus values, usually defined for an equal-energy spectrum locus.

***Commission Internationale de l'Éclairage* (*CIE; or International Commission on Illumination*)** An organization that recommends international standards of color and lighting.

cone fundamentals Cone spectral sensitivities: $\bar{l}(\lambda), \bar{m}(\lambda),$ and $\bar{s}(\lambda)$ in color matching function (CMF) notation. These are the CMFs that would result if imaginary primaries could be used that uniquely stimulated the three cones.

dichromacy A type of color blindness in which one of the three normal cone pigments is missing and color vision is reduced to two dimensions, so that any test light can be matched with a mixture of only two independent primary lights. There are three kinds of dichromacy: protanopia (lacking the L-cones), deuteranopia (lacking the M-cones), and tritanopia (lacking the S-cones).

large-field or 10-deg matches Color matches for centrally viewed, circular fields subtending 10-deg diameter of visual angle.

mesopic Light levels at which both rods and cones operate.

monochromacy A type of color blindness, in which two or all three of the cone pigments are missing and color and lightness vision is reduced to a single dimension, so that any test light can be matched with a single primary light. At night, when only the rods are functioning, normal observers are monochromats.

photometry The measurement and quantification of the luminous efficiency of lights. It is intended to be independent of color.

photopic Light levels at which only cones operate.

photopic luminous efficiency function Photometric measure of the efficiency or effectiveness as a function of wavelength under photopic, rod-free conditions: $V(\lambda)$ or $\bar{y}(\lambda)$.

photoreceptors The light-sensitive receptors, lying on the rear surface of the eye or retina, which transduce photons into electrical signals. Morphologically and physiologically, they can be distinguished as either rods, responsible for our achromatic night vision, or cones, responsible for our chromatic daytime vision.

primary lights R, G, B. The three independent primaries (real or imaginary) to which the test light is matched (actually or hypothetically), when defining color-matching functions. They must be independent in the sense that no combination of any two can match the third.

scotopic Light levels at which only rods operate.

small-field or 2-deg matches Color matches for centrally viewed, circular fields subtending 2-deg diameter of visual angle.

trichromacy The ability of normal observers to match test lights with a mixture of three independent primary lights, one of which may have to be added to the test light to complete the match.

tristimulus values R, G, B, the amounts of the three primaries required to match a given stimulus.

univariance The output of a photoreceptor varies unidimensionally according only to the rate of photon absorption.

visual angle The angle subtended by an object in the external field at the effective optical center of the eye: $\theta = 2\tan^{-1}([x/2]/d)$ where x is the dimension of the object that is of interest (e.g., height, width, or diameter) and d is the distance of the object from the eye.

2.06.1 Introduction

Vision is initially limited by the transduction properties of the light-sensitive photoreceptors in the eye, and in particular by their spectral sensitivities. In most observers with normal color vision, there are four photoreceptor classes: three types of cone photoreceptors, which are referred to as long-, middle-, and short-wavelength-sensitive (L, M, and S), according to the part of the visible spectrum in which they are most sensitive, and a single type of rod photoreceptor. A knowledge of the spectral sensitivities of these photoreceptors is essential for the understanding and modeling of visual function. Rods, which are more sensitive than cones, mediate vision at night when photons are relatively scarce, whereas cones mediate color vision during the day when photons are abundant. Those conditions under which the rods and the cones operate alone are known as scotopic and photopic, respectively, while those under which they operate jointly are known as mesopic (see Figure 1).

2.06.1.1 Univariance and Trichromacy

Photoreceptors are essentially sophisticated photon counters, the outputs of which vary according to the number of photons that they absorb (e.g., Stiles, W. S., 1948; Mitchell, D. E. and Rushton, W. A. H., 1971). Although the probability that a photon is absorbed by a photoreceptor varies substantially with wavelength (defining its spectral sensitivity), the effect of an absorbed photon is independent of wavelength. Thus, it is impossible to tell whether a change in the output of a single photoreceptor is due to a change in light intensity, or due to a change in wavelength. Color and intensity are confounded, so that the output of an individual photoreceptor is effectively color blind or monochromatic. By extension, normal photopic human vision, which depends on the outputs of three different classes of photoreceptor, is a trichromatic or trivariant system. A behavioral consequence of trichromacy is that observers can match a test light of any spectral composition to a mixture of just three primary lights, as illustrated in Figure 2.

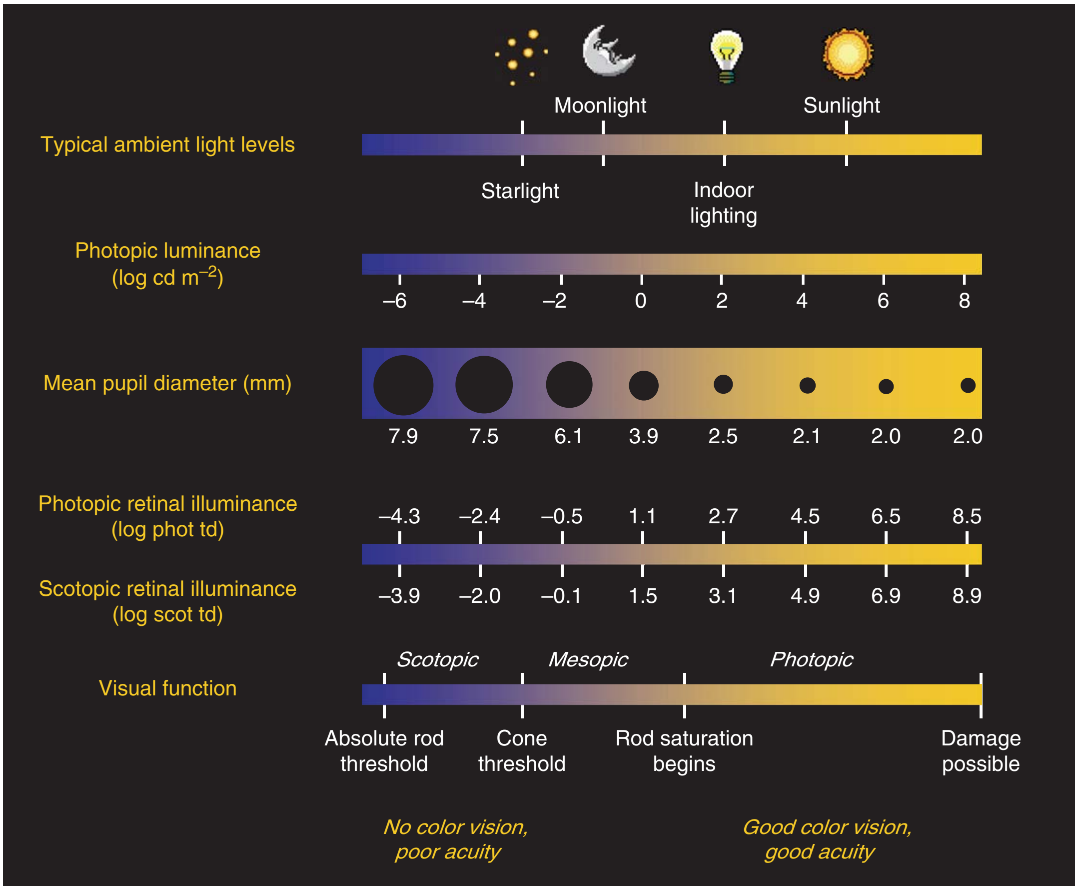

Figure 1 Illumination levels. Typical ambient light levels are compared with photopic luminance (log cd. m^{-2}), mean pupil diameter (mm), photopic and scotopic retinal illuminance (log photopic and scotopic tds, respectively), and visual function. The scotopic, mesopic, and photopic regions are defined according to whether rods alone, rods and cones, or cones alone operate. The conversion from photopic to scotopic values assumes a white standard CIE D_{65} illumination. Figure based in part on the design of Hood, D. C. and Finkelstein, M. A. 1986. Sensitivity to Light. In: Handbook of Perception and Human Performance (*eds*. K. Boff, L. Kaufman, and J. Thomas), pp. 5–1–5–66. Wiley.

2.06.1.2 Color Matching Functions

Because normal human photopic vision is trichromatic, the color of a light can be defined by just three variables: the intensities of three specially chosen primary lights that match it. Figure 2 shows examples of the $\bar{r}(\lambda), \bar{g}(\lambda)$, and $\bar{b}(\lambda)$ color matching functions (CMFs) for red–green–blue (RGB) 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 Figure 2, to imaginary primary lights, such as the all-positive X, Y, and Z primaries favored by the CIE to define international lighting standards, or to the L, M and S cone fundamental primaries, which are physiologically relevant. The three cone 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 $\bar{s}(\lambda)$, or the L-, M-, and S-cone spectral sensitivity functions. For convenience and precision, cone spectral sensitivities are usually defined in terms of transformed CMFs (see Section 2.06.2.3), rather than as raw sensitivity measurements (like those shown in Figure 3, below). Notice that for the R, G, and B primaries, one of the CMFs is negative over the region of the spectrum where three primaries are required, which indicates that

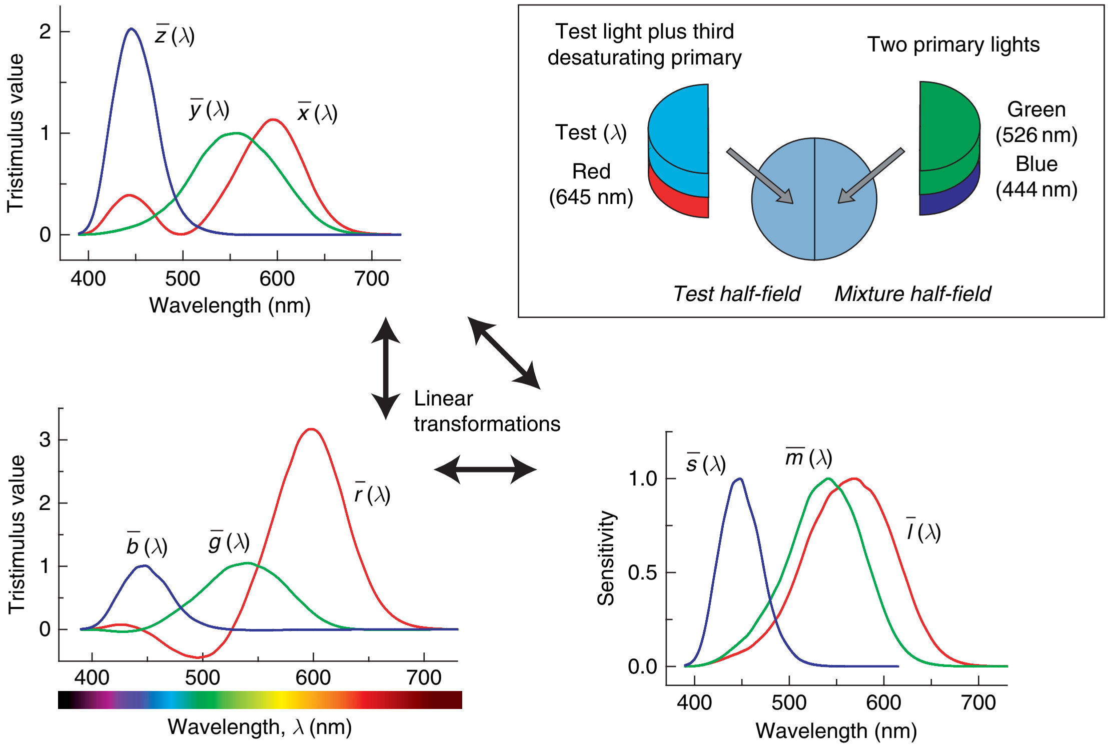

Figure 2 Upper right inset: Maximum saturation method of color matching using spectral lights. A monochromatic test field of wavelength, λ, is matched to a mixture of red (645 nm), green (526 nm), and blue (444 nm) monochromatic primary lights, one of which, as in this example, may have to be added to the test field to complete the match. The amounts of each of the three primaries required to match monochromatic lights spanning the visible spectrum are known as the red, $\bar{r}(\lambda)$, green, $\bar{g}(\lambda)$, and blue, $\bar{b}(\lambda)$ color matching function (CMFs; red, green, and blue lines, respectively) shown in the lower left panel. A negative sign means that that primary must be added to the target to complete the match. CMFs can be linearly transformed from one set of primaries to another. Also illustrated here are CMFs for the imaginary X, Y, and Z primaries (top left) and the cone fundamental L, M, and S primaries (bottom right). The CMFs are transformations of the Stiles W. S. and Burch J. M. (1959) 10-deg CMFs. The fundamentals are the 10-deg cone fundamentals of Stockman A. and Sharpe L. T. (2000).

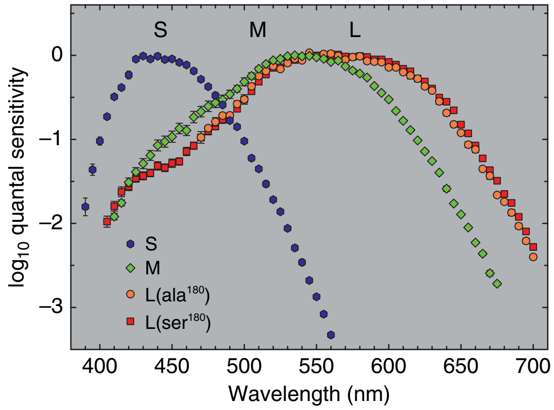

Figure 3 Mean spectral sensitivity data. L-cone data from 17 L(ser^{180}) subjects (red squares), five L(ala^{180}) subjects (orange circles), and M-cone data from nine L1M2/L2M3 protanopes (green diamonds) measured by Sharpe L. T. *et al.* (1998); and S-cone data from five normals and three blue-cone monochromats (blue hexagons) measured by Stockman A. *et al.* (1999).

the primary in question has to be added to the test light in order to complete the match. This does not violate the trichromatic principle, but simply reflects the fact that real primaries excite more than one cone type (see Figures 3 and 4), with the result that no triad of such primaries can completely enclose the three-dimensional space of physically realizable colors. For a further discussion about colorimetry, and its link to the cone fundamentals, see Stockman A. and Sharpe L. T. (1999) and Stockman A. (2003).

2.06.1.3 Dichromacy and Monochromacy

Some people have reduced forms of normal trichromat color vision. Dichromats, who lack one of the three cone photoreceptor types and can therefore match test lights to a mixture of just two primary lights, fall into three classes: protanopes, deuteranopes, and tritanopes, who lack the L-, M-, and S-cones,

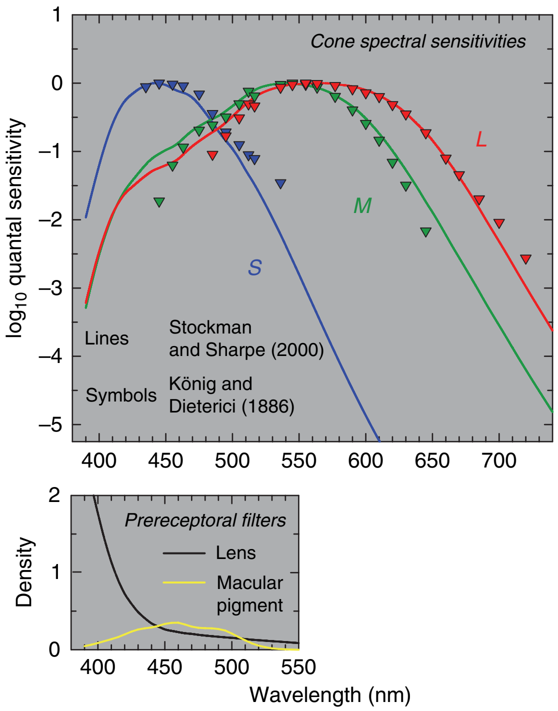

Figure 4 S-, M-, and L-cone 2-deg spectral sensitivity estimates of Stockman A. and Sharpe L. T. (2000), based on linear transformations of the Stiles W. S. and Burch J. M. (1959) 10-deg RGB color matching function (CMFs), determined by the mean spectral sensitivity data shown in Figure 3 as a guide, (colored lines) compared with the historical estimates of König A. and Dieterici C. (1886) (colored triangle). The lower inset shows the mean macular density spectrum for a 2-deg field (yellow line) based on measurements by Bone R A. *et al.* (1992), and the mean lens density spectrum of van Norren D. and Vos J. J. (1974) slightly adjusted by Stockman A. *et al* (1999) (black line).

respectively. Most estimates of the cone spectral sensitivities (see below) depend on the use of dichromats and the assumption – known as the loss, reduction, or König hypothesis – that their remaining cone classes are normal (Maxwell, J. C., 1860; König, A. and Dieterici, C., 1886). 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 (Nathans, J. *et al.*, 1986a; 1986b). Appropriate selection is important, because some red–green or X-linked dichromats have an LM-hybrid cone photopigment with a spectrally shifted spectral sensitivity, while others have multiple cone photopigments (LM-hybrid plus normal) with slightly different spectral sensitivities. If an individual has an LM-hybrid and a normal photopigment that differ sufficiently from one another, that person will usually retain some (reduced) trichromacy and be classed as an anomalous trichromat (see Section 2.06.4.1).

Monochromats can match test lights to just one primary light. In principle, they can lack two of the three cone types (S-, M-, and L-cone monochromats) or all three of them (rod monochromats, or complete achromats). S-cone (or blue-cone) monochromats (Blackwell, H. R. and Blackwell, O. M., 1957; 1961) are particularly useful for measuring S-cone spectral sensitivity (see Section 2.06.2.2). For an extended discussion of color deficiencies and their molecular origins, see Sharpe L. T. *et al.* (1999).

2.06.2 Cone Spectral Sensitivities

Since the establishment of trichromatic color theory (e.g., Young, T., 1802; von Helmholtz, H. L. F., 1852; Maxwell, J. C., 1855), a central goal of color science has been the accurate determination of the three cone spectral sensitivities, $\bar{l}(\lambda), \bar{m}(\lambda)$, and $\bar{s}(\lambda)$. Studies of human cone spectral sensitivity have encompassed many fields of inquiry, including fundus reflectometry (e.g., Rushton, W. A. H., 1965), microspectrophotometry (e.g., Dartnall, H. J. *et al.*, 1983), suction electrode recordings (e.g., Schnapf, J. L. *et al.*, 1987; Kraft, T. W. *et al.*, 1998), electroretinography (e.g., Neitz, J. *et al.*, 1995), and absorption spectroscopy (Oprian, D. D. *et al.*, 1991; Merbs, S. L. and Nathans, J., 1992a; 1992b; Asenjo, A. B. *et al.*, 1994). Our primary focus will be visual psychophysics, which provides the most extensive and accurate *in vivo* spectral sensitivity data.

2.06.2.1 Historical Overview

Arguably, the first plausible psychophysical estimates of $\bar{l}(\lambda), \bar{m}(\lambda)$, and $\bar{s}(\lambda)$ were obtained by König A. and Dieterici C. (1886; see Figure 4). Since then, many other estimates have been made, notably those by Bouma P. J. (1942), Judd D. B. (1945; 1949), Wyszecki G. and Stiles W. S. (1967), Vos J. J. and Walraven P. L. (1971), Vos J. J. (1978), Estévez O. (1979), Vos J. J. *et al.* (1990), and Stockman A. *et al.* (1993a). These have been discussed elsewhere (e.g., Parsons, J. H., 1924; Boring, E. G., 1942; Le Grand, Y., 1968; Stockman, A. and Sharpe, L. T., 1999). Until recently, the estimates by Smith V. C. and Pokorny J. (1975) have been widely used in science and research as a *de facto* standard. Newer estimates by Stockman A.

and Sharpe L. T. (2000) have been proposed as a new CIE standard for physiologically relevant fundamental primaries.

2.06.2.2 Cone Spectral Sensitivity Measurements

Although the cone fundamentals can be estimated by comparing dichromatic and normal color matches (Maxwell, J. C., 1855; 1856), the most straightforward method is to measure the cone spectral sensitivities directly. Because the three cone types peak in sensitivity in different parts of the spectrum, and their spectral sensitivities overlap extensively, spectral sensitivity measurements reflect the activity of more than one cone type. The isolation of the response of a single cone type over substantial regions of the spectrum requires special procedures to favor the wanted cone type and disfavor the two unwanted ones; or it requires the use of dichromats or monochromats, who lack one or two of the cone types. A now classical approach is to use selective chromatic adaptation (e.g., Stiles, W. S., 1939; 1978) and to present a target of variable wavelength on a larger adapting or background field of a second wavelength (or mixture of wavelengths) that selectively suppresses the sensitivities of the two unwanted cone types. However, cone isolation in normal observers becomes increasingly difficult as the wavelength of the target approaches the wavelength of the background, because any advantage gained by the background's selective suppression of the unwanted cone types is offset by the target selectively favoring detection by the unwanted cone types. Complete isolation can be achieved, but only if the selective sensitivity losses due to adaptation by the background exceed the selective effect of the target (e.g., King-Smith, P. E. and Webb, J. R., 1974; Eisner, A. and MacLeod, D. I. A., 1981; Stockman, A. and Mollon, J. D., 1986; Stockman, A. *et al.*, 1993a). Data obtained in normals can be effectively used to complement and verify much more easily isolated cone spectral sensitivity data measured in monochromats and dichromats who lack one or two of the three normal cone types (for such comparisons, see figures 3–5 of Stockman, A. and Sharpe, L. T., 2000). Now that the approach of using data from color deficient observers to model normal color vision has a firm molecular genetic foundation, it is in many ways the more preferable approach.

With the S-cones disadvantaged or suppressed, L- and M-cone spectral sensitivities can be directly measured in deuteranopes who lack M-cone function and in protanopes without L-cone function. Figure 3 shows the mean spectral sensitivity data obtained from seventeen single-gene L(ser^{180}) deuteranopes with serine at position 180 of their L-cone photopigment opsin gene (red squares), from five single-gene L(ala^{180}) deuteranopes with alanine at position 180 (orange circles), and from nine L1M2/L2M3 protanopes (green diamonds). For further details, see Sharpe, L. T. *et al.*, 1998; Stockman, A. and Sharpe, L. T., 2000. The two mean L-cone functions, which are separated by ~2.7 nm in $\lambda_{\max}$ (Sharpe, L. T. *et al.*, 1998), reflect the two commonly occurring L-cone photopigment polymorphisms (see Section 2.06.4.1). An overall L-cone mean was also derived (not shown) to reflect the proportions of the two polymorphic variants in the population (Stockman, A. and Sharpe, L. T., 2000). This was used to determine the mean L-cone fundamentals (see Section 2.06.2.3).

S-cone spectral sensitivity is most easily measured throughout the spectrum in S-cone monochromats (e.g., Blackwell, H. R. and Blackwell, O. M., 1961; Grützner, P., 1964; Alpern, A. *et al.*, 1965; Alpern, M. *et al.*, 1971; Daw, N. W. and Enoch, J. M., 1973; Smith, V. C. *et al.*, 1983; Hess, R. F. *et al.*, 1989). In defining a mean S-cone spectral sensitivity, Stockman A. *et al.* (1999) measured S-cone spectral sensitivities in three blue-cone monochromats 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 Figure 3 (blue hexagons).

2.06.2.3 From Cone Spectral Sensitivities to Color Matching Functions

Although the cone spectral sensitivities could be defined as the direct sensitivity measurements shown in Figure 3, it is customary to define them in terms of linear combinations of a set of CMFs, which are – in principle at least – 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 fits each cone spectral sensitivity, as defined above, allowing adjustments in the densities of prereceptoral 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 filtering densities change with retinal eccentricity; see Section 2.06.4).

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

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

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 M- and S-cone sensitivities. Since the S-cones are insensitive in the red, 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:

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

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:

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

where the absolute values of $k_l\left(1/\bar{l}_B\right)$, $k_m(1/\bar{m}_B)$, 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. The five unknowns in Eqn. (3), $\bar{l}_R/\bar{l}_B, \bar{l}_G/\bar{l}_B, \bar{m}_R/\bar{m}_B$, $\bar{m}_G/\bar{m}_B$, and $\bar{s}_G/\bar{s}_B$, can then be estimated by directly fitting CMFs to the Stockman A. and Sharpe L. T. (1999) cone spectral sensitivity data shown in Figure 3. The transformation matrix for the Stiles W. S. and Burch J. M. (1959) 10-deg RGB CMFs, on which the Stockman A. and Sharpe L. T. (2000) cone fundamentals are based, is:

$$\begin{pmatrix}2.846201 & 11.092490 & 1\\ 0.168926 & 8.265895 & 1\\ 0 & 0.010600 & 1\end{pmatrix}\qquad[4]$$

This transformation is illustrated in Figure 2. The transformation matrix given in eqn [4] multiplied by the CMFs (which are in energy units) yields cone fundamentals in energy units. To convert to quantal units 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 A. *et al.* (1999) and in Stockman A. and Sharpe L. T. (2000).

Figure 4 shows the current 2-deg estimates of Stockman A. and Sharpe L. T. (2000) (colored lines) compared with the much earlier estimates obtained 120 years ago by König A. and Dieterici C. (1886) (colored triangles). The Stockman A. and Sharpe L. T. 2-deg estimates are based on a transformation of the Stiles W. S. and Burch J. M. (1959) 10-deg CMFs given by eqn [4] adjusted to 2-deg by correcting for changes in photopigment optical density and macular pigment density (for details, see Stockman, A., and Sharpe, L. T., 2000). These 10-deg CMFs, which were measured in 49 subjects from approximately 390 to 730 nm (and in nine subjects from 730 to 830 nm), were chosen as the basis of the 2-deg cone fundamentals because they are the most secure set of existing color matching data, and are available as individual as well as mean data.

2.06.2.4 Rod Spectral Sensitivity Measurements

Because there is only a single type of rod photoreceptor, rod spectral sensitivity is achromatic and univariant and may be measured by any method that excludes detection being mediated by the less sensitive cones (e.g., scotopic luminance levels should be used). It is identical with scotopic luminous efficiency (see Section 2.06.3.1.1 and Figure 5).

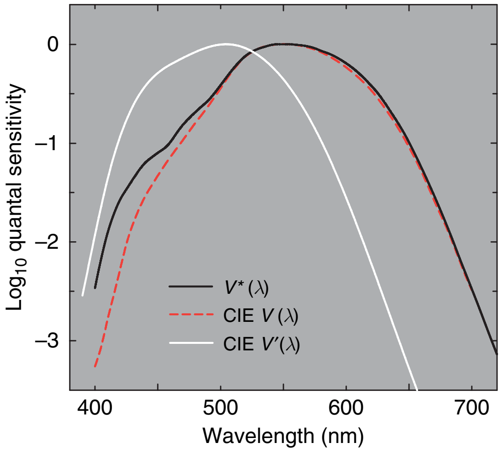

Figure 5 The Commission Internationale de l'Eclairage (CIE) scotoptic $V'(\lambda)$ (white line) and 1924 photopic $V(\lambda)$ (red dashed line) functions. The recent, photopic luminous efficiency function, $V*(\lambda)$, proposed by Sharpe L. T. *et al.* (2005) is shown by the black line.

2.06.3 Achromatic and Chromatic Spectral Sensitivity

When spectral sensitivity is measured under most practical conditions, it will inevitably involve detection by more than one photoreceptor type. Such spectral sensitivities are potentially complex, since they typically reflect interactions that occur between photoreceptor signals in different postreceptoral channels. One simplification has been to measure the spectral sensitivity of achromatic or luminance mechanisms (or luminous efficiency) separately from those of chromatic ones.

2.06.3.1 Achromatic Luminous Efficiency

Luminous efficiency is a measure of spectral sensitivity that might be described as a measure of apparent intensity. It is actually defined as the effectiveness of lights of different wavelength in specific matching or detection tasks. The term was introduced by the International Lighting Commission (CIE) to provide a psychophysical or perceptual analog of radiance, called luminance. Luminous efficiency has been defined for scotopic, photopic, and mesopic illumination levels.

2.06.3.1.1 Scotopic luminous efficiency

Scotopic luminous efficiency is comparatively straightforward, since it depends on the activity of a single univariant photoreceptor type, the rods. Thanks to univariance, scotopic luminous efficiency fulfils the basic requirement of any system of photometry that the luminous efficiency of any mixture of lights is the sum of the efficiencies of the components of the mixture; otherwise known as Abney's Law (Abney, W. d. W. and Festing, E. R., 1886; Abney, W. d. W., 1913). Figure 5 shows the scotopic CIE 1951 $V'(\lambda)$ function (white line), which is based on original data from Crawford B. H. (1949) and Wald G. (1945).

2.06.3.1.2 Photopic Luminous Efficiency

Photopic luminous efficiency, $V(\lambda)$, is complicated by the fact that there are considerable differences between the 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 Wagner, G. and Boynton, R. M., 1972; Wyszecki, G. and Stiles, W. S., 1982; Lennie, P. *et al.*, 1993; Stockman, A. and Sharpe, L. T., 1999).

Although $V(\lambda)$ is often treated as if it were comparable to the spectral sensitivity of a univariant photoreceptor, it is not: it depends on the activity of more than one photoreceptor type. Thus, unlike $V'(\lambda)$, additivity is not inevitable, but requires the adoption of special tasks, the performance of which is supposed to depend on an additive luminance mechanism. Such tasks include HFP, in which continuously alternating lights of different wavelength are matched in luminance to minimize the perception of flicker, and MDB, in which the relative intensities of the two half fields is set so that the border between them appears minimally distinct (e.g., Sperling, H. G., 1958; Wagner, G. and Boynton, R. M., 1972). The generality of such luminous efficiency functions are severely limited, however, since their spectral sensitivities are strongly dependent on chromatic adaptation (e.g., De Vries, H., 1948; Eisner, A. and MacLeod, D. I. A., 1981; Stockman, A. *et al.*, 1993b). In other words, the shapes of measured luminous efficiency functions vary with the adapting condition, even though functions like $V(\lambda)$ and $V^*(\lambda)$ (see below) have a fixed shape.

Nevertheless, a luminous efficiency function is of practical use in many applications, especially for conditions that are similar to those under which the function was defined (e.g., neutral adaptation). Unfortunately, however, the standard CIE photopic 1924 $V(\lambda)$ function is seriously in error. It is a speculative hybrid function, artificially smoothed, and dubiously constructed from divergent data measured under very different procedures at several laboratories (Wyszecki, G. and Stiles, W. S., 1982). The CIE $V(\lambda)$ function shown in Figure 5 as the dashed red line substantially underestimates luminous efficiency at short wavelengths. Attempts to improve it (Judd, D. B., 1951; Vos, J. J., 1978) have been less than satisfactory (Stockman, A. and Sharpe, L. T., 1999; 2000), and have been little used outside vision science laboratories.

Recently, Sharpe L. T. *et al.* (2005) have proposed a new luminous efficiency function, $V^*(\lambda)$, 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. $V^*(\lambda)$ defines luminance for a reproducible, phase of natural daylight (CIE standard illuminant D_{65} adaptation), while being a linear combination of the Stockman A. and Sharpe L. T. (2000) M- and L-cone fundamentals. The $V^*(\lambda)$ function (black line) is shown in Figure 5. In terms of the Stockman A. and Sharpe L. T. (2000) M- and L-cone quantal fundamentals normalized to unity peak, the quantal $V^*(\lambda) = [1.891\bar{l}(\lambda) + \bar{m}(\lambda)]/2.80361$; whereas, in terms of the Stockman A. and Sharpe L. T. (2000) M- and L-cone energy fundamentals normalized to unity peak, the energy-based $V^*(\lambda) = \left[1.98065\bar{l}_e(\lambda) + \bar{m}_e(\lambda)\right]/2.87091$. The different weights and scaling factors simply reflect the different unity normalizations in quantal and energy units. Note that these constants define $V^*(\lambda)$, which was determined for adaptation to the D_{65} daylight standard; different adaptation conditions would lead to different constants and different efficiency functions.

2.06.3.1.3 *Mesopic Luminous Efficiency*

Mesopic luminous efficiency has been measured in several laboratories using a variety of methods (e.g., Walters, H. V. and Wright, W. D., 1943; Kinney, J. A. S., 1958; Palmer, D. A., 1968; Kokoschka, S., 1972; Yaguchi, H. and Ikeda, M., 1984; Nakano, Y. and Ikeda, M., 1986; Sagawa, K. and Takeichi, K., 1986; Viénot, F. and Chiron, F., 1992; He, Y. *et al.*, 1998). The main challenge of mesopic photometry is to characterize how the luminous efficiency changes between the scotopic and photopic levels. The modeling, however, has proven to be difficult, since the relationship between mesopic luminous efficiency and $V(\lambda)$ and $V'(\lambda)$ is complex and nonlinear. Such complexities are inevitable because of the substantial and often rapid changes in the spatial and temporal properties of the visual system that accompany the transition from scotopic to photopic vision. These are caused not only by the change from rod to cone photoreceptors, but also by changes between the different postreceptoral pathways through which the rod and cone signals are transmitted. For a recent review, see Stockman A. and Sharpe L. T., 2006.

2.06.3.2 Chromatic Spectral Sensitivity

Spectral sensitivities measured under conditions that are not specially chosen to yield additive data typically reflect the interaction of complex processes. Generally the shape of the sensitivity curve becomes broader and has pronounced notches and humps (e.g., Stiles, W. S. and Crawford, B. H., 1933; Sperling, H. G. and Harwerth, R. S., 1971; King-Smith, P. E. and Carden, D., 1976; Kranda, K. and King-Smith, P. E., 1979; Thornton, J. E. and Pugh, E. N., Jr., 1983; Kalloniatis, M. and Sperling, H. G., 1990). These characteristics can be accounted for by detection being mediated by chromatic, cone-opponent mechanisms in addition to achromatic ones. Thus, the so-called Sloan's notch (Sloan, L. L., 1928) occurs at target wavelengths at which the target produces the same chromatic signal as the background, so that it cannot be detected by the chromatic mechanism, and is instead detected by a less sensitive achromatic one; by contrast, the humps correspond to target wavelengths at which the target produces a large chromatic signal with respect to the background (e.g., Ingling, C. R., Jr., 1969; Sperling, H. G. and Harwerth, R. S., 1971; King-Smith, P. E. and Carden, D., 1976; Kranda, K. and King-Smith, P. E., 1979; Thornton, J. E. and Pugh, E. N., Jr., 1983; Kalloniatis, M. and Sperling, H. G., 1990; Calkins, D. J. *et al.*, 1992).

Chromatic detection is treated further in Chapter Chromatic Detection and Discrimination. By replotting these types of spectral sensitivity data in cone contrast space, the importance of detection by chromatic and luminance mechanisms becomes much clearer (e.g., Stromeyer, C. F., III *et al.*, 1985; Kalloniatis, M. and Sperling, H. G., 1990; Chaparro, A. *et al.*, 1995; Eskew, R. T. *et al.*, 1999). Spectral sensitivity measurements are now of little value in studying chromatic mechanisms, which are better studied using more complex stimuli that produce chromatic modulations (e.g., modulations of opposite signs in the M- and L-cones). It should be noted, however, that the production of these complex stimuli is still critically dependent on a precise knowledge of the underlying cone spectral sensitivities.

2.06.4 Other Factors that Influence Spectral Sensitivity

Several other factors influence spectral sensitivities and color matches. The most important ones arise from individual differences among observers, and so should be taken into account when trying to predict the spectral sensitivities of an individual from standard or mean functions. Some of them vary with retinal position, and so should be considered when trying to predict the spectral sensitivities for retinal areas or retinal positions that differ from the centrally viewed 2-deg or 10-deg areas used to obtain the standard functions.

2.06.4.1 Photopigment Variability and Anomalous Trichromacy

There is now clear molecular genetic, psychophysical, and electroretinographic evidence that the M- and L-cone photopigments can vary in spectral position between observers (for a review, see Sharpe, L. T. *et al.*, 1999), thus confirming earlier evidence for such shifts (e.g., Alpern, M. and Pugh, E. N., Jr., 1977; Dartnall, H. J. A. *et al.*, 1983; MacLeod, D. I. A. and Webster, M. A., 1983; Alpern, M., 1987; Webster, M. A. and MacLeod, D. I. A., 1988). These shifts are caused by the inheritance of hybrid LM or ML cone photopigment opsin genes, which are fusion genes produced by intragenic crossing over, containing the coding sequences of both L- and M-cone pigment genes. Both *in vitro* and *in vivo* measurements of the absorbance spectrum peaks of the hybrid pigments reveal a wide range of possible anomalous pigments lying between the normal L- and M-cone pigments. Rather than a continuous distribution, there is a clustering of LM hybrid pigments having their peak absorbances within about 8 nm of the peak absorbance of the normal M-cone pigment and a clustering of ML hybrid pigments having their peak absorbances within about 12 nm of the peak absorbance of the normal L-cone pigment (see table 1 of Stockman, A. *et al.*, 2000). Smaller shifts occur within the normal population, because of different polymorphisms (commonly occurring allelic differences) of the M- and L-cone photopigment opsin genes. The two common polymorphic variants of the L-cone photopigment (which have either alanine or serine at position 180 of the L photopigment opsin gene) differ in spectral position by 2.7 nm or more. The same polymorphic variation occurs in the M-cone photopigment, with a similar shift in spectral sensitivity, but the serine variant is rather rare (see Sharpe, L. T. *et al.*, 1999).

Hybrid LM and ML pigments in people with otherwise normal photopigments result in anomalous trichromacy. Individuals with a hybrid LM pigment replacing one of the two polymorphic variants of the normal L cone pigment are known as protanomalous trichromats; whereas those with a hybrid ML pigment replacing one of the two polymorphic variants of the normal M cone pigment are known as deuteranomalous trichromats. The color vision deficits of anomalous trichromats are usually less severe than those of dichromats, but there is considerable variability among individuals. In general, the smaller the separation between the spectral sensitivities of the normal and anomalous hybrid pigments, the poorer the anomalous trichromat's color discrimination (for more details, see Sharpe, L. T. *et al.*, 1999). Anomalous trichromacy can sometimes arise in individuals lacking either the normal L- or M-cone photopigment because of photopigment optical density differences between photoreceptors containing ostensibly the same remaining L- or M-cone photopigment (Neitz, J. *et al.*, 1999).

2.06.4.2 Lens Pigment

Light is brought into focus on the retina by the cornea and the pigmented crystalline lens. The pigment in the lens absorbs light mainly of short wavelengths (see lower inset of Figure 4, black line). Individual differences in lens pigment density can be large with a range of approximately ±25% of the mean density in young observers (<30 years old; see van Norren, D. and Vos, J. J., 1974). Since lens density increases with the age of the observer (e.g., Crawford, B. H., 1949; Said, F. S. and Weale, R. A., 1959; Pokorny, J. *et al.*, 1988), the variability in the general population is even larger. A two-factor model has been proposed to account for changes in lens density spectrum with age (Pokorny, J. *et al.*, 1988; Xu, J. *et al.*, 1997). Stockman, A. *et al.* (1999) have proposed a slightly adjusted version of the mean lens density spectrum of van Norren D. and Vos J. J. (1974) that is consistent with the Stockman A. and Sharpe L. T. (2000) cone fundamentals.

2.06.4.3 Macular Pigment

Before reaching the photoreceptor, light must pass through the ocular media, including, at the fovea, the macula lutea, which contains macular pigment. This pigment also absorbs light mainly of short wavelengths (see lower inset of Figure 4, yellow line). Individual differences in its density can also be large with a range of peak density from 0.0 to *c.* 1.2 at 460 nm (Wald, G., 1945; Bone, R. A. and Sparrock, J. M. B., 1971; Pease, P. L. *et al.*, 1987). The density of the pigment changes with retinal location; tending to become more transparent with eccentricity. It is wholly or largely absent by a retinal eccentricity of 10 deg (e.g., Bone, R. A. *et al.*, 1988). Stockman A. and Sharpe L. T. (2000) have proposed a mean macular density spectrum based on measurements by Bone R. A. *et al.* (1992) that is consistent with their cone fundamentals.

2.06.4.4 Photopigment Optical Density

The axial optical density of the photopigment in the receptor outer segment varies between individuals. Estimates of photopigment optical density vary considerably depending to a large extent on the method used to estimate them, but all estimates show sizeable individual differences (e.g., Terstiege, H., 1967; Miller, S. S., 1972; King-Smith, P. E., 1973b, 1973a; Smith, V. C. and Pokorny, J., 1973; Alpern, M., 1979; Burns, S. A. and Elsner, A. E., 1993; Berendschot, T. T. J. M. *et al.*, 1996). Decreases in photopigment optical density result in a narrowing of cone spectral sensitivity curves, which cause corresponding changes to their linear transformations, the CMFs. Any corrections are most easily applied to the cone fundamentals rather than the CMFs. For further details and the relevant equations, see Stockman A. and Sharpe L. T. (1999), eqns [9]–[12].

2.06.4.5 Changes with Eccentricity

Macular pigment and photopigment optical density both decline with eccentricity. Consequently, cone spectral sensitivities, which are defined for centrally viewed 2- or 10-deg diameter fields, must be adjusted in order to predict accurately color matches for other viewing conditions – either for different field sizes or for different viewing angles.

One additional complication is that the S-cones are absent in approximately the central 25 min diameter of vision, so that in that region color matches become tritanopic (e.g., König, A., 1894; Thomson, L. C. and Wright, W. D., 1947; Willmer, E. N., 1950; Williams, D. R. *et al.*, 1981). The small-field tritanopic effect may also occur with steady fixation of parafoveal fields (Hartridge, H., 1945; Thomson, L. C. and Wright, W. D., 1947). The exclusion of the S-cones from the very central fovea is usually attributed to the need to counteract the deleterious effects of light scattering and axial chromatic aberration on spatial resolution, which cause blurring and/or defocus particularly at short wavelengths (but see McClellan, J. S. *et al.*, 2002). For most practical purposes, small field tritanopia can be largely ignored, however, because its influence on color matching and discrimination is mitigated by the blur introduced by the optics of the eye and constant microsaccades (Bedford, R. E. and Wyszecki, G., 1958; McCree, K. J., 1960).

2.06.5 Conclusions

A precise knowledge of the spectral sensitivity of the human rod and cone photoreceptors is central to our understanding and modeling of vision and visual function in normals and individuals with color vision deficiencies. For the rods, spectral sensitivity and luminous efficiency are identical and both are defined by the CIE 1951 $V'(\lambda)$ function. For the cones, the 2-deg and 10-deg cone fundamentals, and the associated lens and macular pigment and photopigment templates, of Stockman A. and Sharpe L. T. (2000), and the photopic luminous efficiency functions of Sharpe L. T. *et al.* (2005) provide a consistent set of standard functions with which to model human vision. These functions, and others, can be downloaded from the Color and Vision Research Laboratories' website.

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