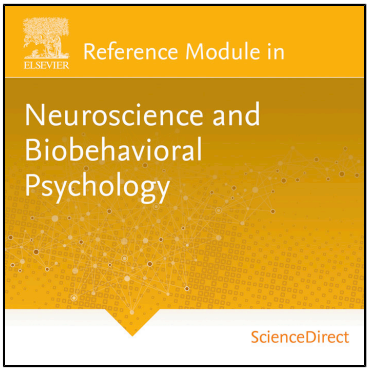

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Chromatic Function of the Cones☆

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Glossary

CIE, Commission Internationale de l'Eclairage The CIE is an independent, nonprofit organization responsible for the international coordination of lighting-related technical standards, including colorimetry standards.

Color-matching functions Functions of wavelength λ that describe the amounts of three fixed primary lights which, when mixed, match a monochromatic light of wavelength λ of constant radiant power. The amounts may be negative. The color-matching functions obtained with any two different sets of primaries are related by a linear transformation. Particular sets of color-matching functions have been standardized by the CIE.

Fundamental spectral sensitivities The color-matching functions corresponding to the spectral sensitivities of the three cone types, measured at the cornea. The spectral sensitivities may be normalized so that the maximum is unity or according to the nominal population densities of the cone types.

Heterochromatic flicker photometry The adjustment of the radiant power of one of two spatially coextensive lights presented in alternating sequence at a temporal frequency such that there is a unique value of the radiant power where the sensation of flicker is minimum; ie, with a higher or lower radiant power, the sensation of flicker becomes greater.

Luminous efficiency function V_λ The inverse of the radiant power of a monochromatic stimulus of wavelength λ that produces a luminous sensation equivalent to that of a monochromatic stimulus of fixed wavelength λ_0. The units and λ_0 may be chosen so that the maximum of this function is unity. It is also known as the relative luminous efficiency or relative luminosity function.

Optical density Absorbance; see spectral absorbance.

Radiant power and quantum units Radiant power is measured in watts but it is sometimes more appropriate to measure it in quanta per second. Sensitivities may be expressed as the logarithm to the base 10 of the reciprocal of the radiant power required to reach a criterion level of performance.

Spectral absorbance $A(\lambda)$ Logarithm to the base 10 of the reciprocal of the spectral transmittance, $\tau(\lambda)$; ie, $A(\lambda) = -\log_{10}\tau(\lambda)$. It depends on the path length. If l is the path length and $a(\lambda)$ is the spectral absorptivity, then, for a homogeneous isotropic absorbing medium, $A(\lambda) = la(\lambda)$ (Lambert's law).

Spectral absorptance $\alpha(\lambda)$ Ratio of the spectral radiant flux absorbed by a layer to the spectral radiant flux entering the layer. If $\tau(\lambda)$ is the spectral transmittance, then $\alpha(\lambda) = 1 - \tau(\lambda)$. The value of $\alpha(\lambda)$ depends on the length or thickness of the layer. For a homogeneous isotropic absorbing medium, $\alpha(\lambda) = 1 - \tau(\lambda) = 1 - 10^{-la(\lambda)}$, where l is the path length and $a(\lambda)$ is the spectral absorptivity. Changes in the concentration of a photopigment have the same effect as changes in path length.

Spectral absorptivity $a(\lambda)$ Spectral absorbance of a layer of unit thickness. Absorptivity is a characteristic of the medium, ie, the photopigment. Its numerical value depends on the unit of length.

☆*Change History:* August 2015. DH Foster made a minor correction to the title.

Spectral sensitivity The inverse of the radiant power of a monochromatic stimulus of wavelength λ that produces a criterion response equal to that of a monochromatic stimulus of fixed wavelength λ_0. The units and λ_0 may be chosen so that the maximum of this function is unity. In specifications by the CIE, the lower limit of the wavelength range is generally 360–400 nm and the upper limit is generally 760–830 nm, but smaller ranges may be used. The spectral sensitivity of a cone is essentially the normalized spectral absorptance of its photopigment (discounting any geometrical factors, eg, cone waveguide properties).

Spectral transmittance $\tau(\lambda)$ Ratio of the spectral radiant flux leaving a layer to the spectral radiant flux entering the layer. The value of $\tau(\lambda)$ depends on the path length.

Unique hues Hues that are judged to be unmixed. They form mutually exclusive pairs, so that no light can appear to contain both red and green or both blue and yellow.

Wavenumber The reciprocal of wavelength, usually in cm^{-1}.

Introduction

Normal human color vision is governed by three types of retinal cone photoreceptors sensitive to light over different, but overlapping, regions of the spectrum and conventionally designated long-, medium-, and short-wavelength-sensitive (L, M, and S). Because the intensity and spectral properties of light cannot be distinguished once it has been absorbed (the principle of univariance), chromatic information is obtained by comparing the outputs of these different cone types. Signals from L, M, and S cones converge via excitatory and inhibitory pathways onto subsets of anatomically distinct ganglion-cell populations, which then project to the lateral geniculate nucleus, and thence to the higher cortical areas. The aim of this article is to provide an overview of how the cones contribute to chromatic function and how that contribution is modified by prereceptoral filtering and postreceptoral processing within the eye.

Photopigments and Phototransduction

The photopigment in the outer segment of the cone consists of two covalently linked parts, a protein called opsin and a chromophore based on retinal, an aldehyde of vitamin A. It is the latter that provides light sensitivity by isomerizing from *11-cis* to all-*trans* forms. This leads to the activation of a guanine nucleotide-binding protein (G-protein), transducin, and a cascade of molecular events that result in a change in the rate of neurotransmitter release from the receptor to other neurons in the retina. In the course of the cascade, the signal provided by photon absorption is greatly amplified.

The wavelength λ_{max} of maximum absorption of the pigment (see the section: Cone Spectral Sensitivities) depends on the particular amino acid sequence of the opsin and its relationship to the chromophore. The L and M pigments are members of an ancestral medium/long-wavelength-sensitive class of vertebrate pigments. These two pigments have a high degree of homology, and the majority of the difference in λ_{max} arises at just a few amino acid sites. A common polymorphism of the L and M pigments, in which alanine is substituted for serine at codon 180, can create shifts in λ_{max} of several nanometers.

The S pigment is a member of a distinct ancestral ultravoilet (UV)-sensitive class of vertebrate pigments. Its spectral tuning is different from that of the L and M pigments, and the shift in λ_{max} from UV to the violet of normal human S cones arises from amino acid replacements at multiple tuning sites.

Fundamental Spectral Sensitivities

The spectral sensitivities of the cones, in vivo, have been estimated by many different methods. Historically, the most important method is based on psychophysical color-matching, in which a mixture of three fixed primary lights is matched against a monochromatic light of variable wavelength and constant radiant power. These data form the basis of the system of colorimetry standardized by the Commission Internationale de l'Eclairage (CIE). In the normal trichromatic eye, such color-matching functions yield a family of spectral sensitivities that are a linear transformation of the unknown cone spectral sensitivities. This transformation is not unique in that it varies with the choice of primaries, but data obtained from dichromatic and sometimes monochromatic observers, who have, respectively, only two and one of the three normal cone types, provide good estimates of these so-called fundamental spectral sensitivities.

Fig. 1 shows one set of normalized L-, M-, and S-cone fundamental spectra, with wavelengths λ_{max} of maximum sensitivity of c. 570, 543, and 442 nm. These estimates represent corneal cone spectral sensitivities, as color matching necessarily involves the spectral transmission properties of the ocular media (see the section: Prereceptoral Attenuation). Several such sets of fundamentals have been derived, based on different sets of color-matching functions and different assumptions about cone sensitivity and pre-receptoral absorption.

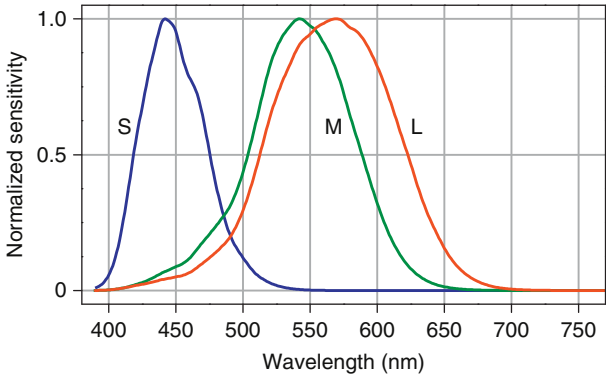

Figure 1 Fundamental spectral sensitivities of the long-, medium-, and short-wavelength-sensitive (L, M, and S) cones. Data are normalized to a maximum of unity on a radiance scale and *are based on the 2 degrees data of Table 2 of Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737*; *Modified from the mean 10 degrees color-matching functions of Stiles, W.S., Burch, J.M., 1959. N.P.L. colour-matching investigation: final report (1958). Optica Acta 6, 1–26.*

Other psychophysical methods of estimation involve selectively chromatically adapting the three cone types by a background light and measuring the spectral sensitivity of the most sensitive color mechanism at or near its threshold level of response, a technique associated primarily with W. S. Stiles (see the subsection: Isolating Cone Responses: Selective Chromatic Adaptation). Psychophysical methods have the advantage that sensitivity can be determined over a range of two to five decades (ie, two to five log units), although with normal trichromats, chromatic adaptation cannot generally isolate the response of a single cone type throughout the spectrum.

Nonpsychophysical but noninvasive methods of in vivo estimation include retinal densitometry (ie, fundus spectral reflectometry) and electroretinography. In retinal densitometry, differences in reflectance of the fundus are measured, at various wavelengths, before and after selectively bleaching the cone pigments. The method is limited by its low signal-to-noise ratio and the need to distinguish between signals from L and M cones. It is also difficult to obtain signals reliably from S cones. In electroretinography, the summed electrical response of the retina to a flickering light is measured with a corneal electrode. This method provides a much larger dynamic range, of several log units, along with a good signal-to- noise ratio, but, as with retinal densitometry, signals from L and M cones need to be separated. Both techniques are best applied to well-characterized dichromats.

Prereceptoral Attenuation

The spectrum of the incident light reaching the cones is modified by two prereceptoral filters. The first is the lens (and cornea). In the young eye, the lens appears colorless, but, with increasing age, it becomes yellow, partly as a result of light scatter and absorption, which produce large transmission losses at short wavelengths (Fig. 2). Even within the same age group, however, the size of the loss at 400 nm may vary over one log unit. Another important factor in the changing appearance of the lens is the accumulation of a particular fluorogen, which leads to increased lens fluorescence.

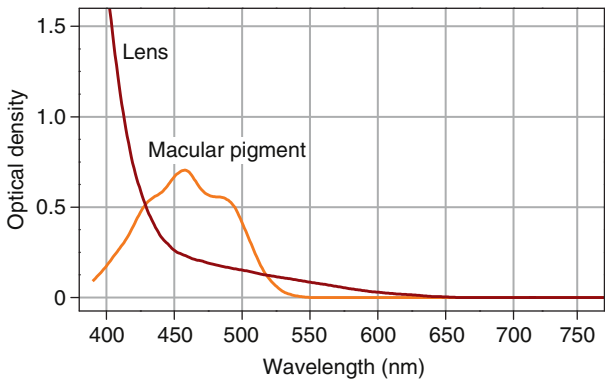

Figure 2 Variation of the optical density of the lens and of the macular pigment with wavelength. *Data are from Table 2 of Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737; Based on van Norren, D., Vos, J.J., 1974. Spectral transmission of human ocular media. Vis. Res. 14, 1237–1244; and on Bone, R.A., Landrum, J.T., Cains, A., 1992. Optical density spectra of the macular pigment in vivo and in vitro. Vis. Res. 32, 105–110.* Plotted values are means over observers. Macular-pigment densities have been doubled for clarity.

The second prereceptoral filter is a nonphotosensitive yellow pigment, usually referred to as the macular pigment. Its maximum absorption is at c. 460 nm (Fig. 2). It is a carotenoid consisting of two xanthophylls, lutein and zeaxanthin, whose densities decline with increasing eccentricity, with zeaxanthin concentrated only in the fovea.

The optical density of macular pigment can be quantified, in vivo, by heterochromatic flicker photometry and by Raman spectroscopy, in which argon laser light is used to excite the xanthophylls. Values of the optical density at the fovea vary markedly across individuals, from >1.0 to almost zero, with a mean of c. 0.6. Some of the hypothesized benefits of the macular pigment include protection from the damaging effects of short-wavelength light, reducing the effects of longitudinal chromatic aberration and glare, and protection against reactive oxygen species.

In addition to the lens and macular pigment, there is another important factor modifying the effective spectral sensitivity of the cones, namely, self-screening by the photopigment, which acts to broaden its absorption spectrum. If at wavelength λ the spectral absorptivity is $a(\lambda)$ and the path length is l, then the spectral absorptance $\alpha(\lambda)$ is given by $1-10^{-la(\lambda)}$. Therefore, increasing l (or equivalently the concentration of the pigment) has a proportionally larger effect at values of λ where $\alpha(\lambda)$ is small than at values where it is large.

Cone Spectral Sensitivities

Estimates of cone spectral sensitivities can be obtained from corneal spectral sensitivities, ie, the fundamental spectra of Fig. 1, by eliminating the estimated effects of prereceptoral losses (see the section: Prereceptoral Attenuation). Fig. 3 shows the results. The normalized L-, M-, and S-cone spectral sensitivities have wavelengths λ_{max} of maximum sensitivity of c. 559, 530, and 421 nm, respectively. Comparing these spectra with corneal spectra (Fig. 1) reveals the influence of prereceptoral filtering in shifting λ_{max} toward longer wavelengths, especially for S cones, where the increase in λ_{max} is c. 20 nm.

In vitro methods of estimating cone spectral sensitivities include recording from single cone outer segments with a suction microelectrode, direct microspectrophotometry of intact receptor outer segments, and differential spectrophotometry of recombinant cone pigments produced in tissue-culture cells. Microelectrode recordings take advantage of the amplification of the signal provided by the phototransduction cascade and so can provide sensitivities over five to six log units, but spectrophotometry, as with in vivo reflectance measurements, is limited by its low signal-to-noise ratio, providing sensitivities over only one or one to two log units. All in vitro methods are constrained by the nonphysiological nature of the illumination (and sometimes by the method of specimen preparation and recording). Notwithstanding the differences in experimental methodology and analysis, there is broad agreement in the values of λ_{max} (Table 1).

Template for Cone Spectral Sensitivity

The response of a cone is determined by the number of photons it absorbs: the spectral sensitivity describes the probability of that absorption at each frequency ν, which is invariant of the medium, unlike wavelength λ. The main absorption band of mammalian visual pigments is the α band (the β and other bands at progressively shorter wavelengths have less influence because of absorption in the ocular media). Despite the differences in λ_{max} of the L, M, and S pigments, plotting cone spectral sensitivity or spectral absorbance against the normalized frequency, ie, ν/ν_{max}, where ν_{max} is the frequency of maximum sensitivity, yields closely similar dependencies, as illustrated by the data in Fig. 4 for suction microelectrode recordings from monkey cones (symbols).

These dependencies may be fitted empirically by a polynomial or other smooth function of normalized frequency (Fig. 4, curve). This function may then be used as a template or nomogram and applied to sample data that are noisy or of limited range, allowing, eg, more accurate estimates of λ_{max}, as was done with the entries in Table 1. Templates are best obtained separately for sensitivities

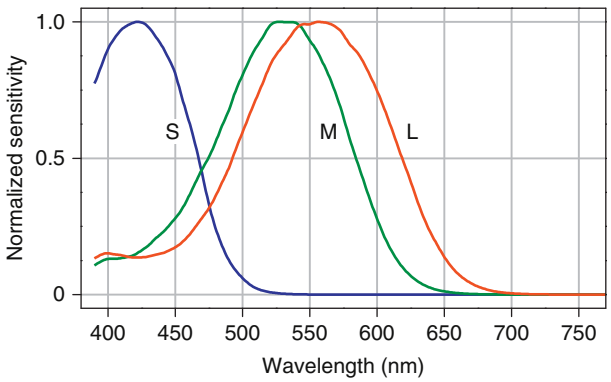

Figure 3 Spectral sensitivities of the long-, medium-, and short-wavelength-sensitive (L, M, and S) cones derived from mean L-, M-, and S-cone fundamental spectra (Fig. 1). Data are normalized to a maximum of unity on a radiance scale and *are based on Table 2 of Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737.*

Table 1 Estimated wavelengths λ_{max} of maximum sensitivity of long-, medium-, and short-wavelength-sensitive cones and cone pigments from in vivo and in vitro measurements in humans and primates

	λ_{max} (nm)		
Method	*L*	*M*	*S*
Psychophysics[a]	559	530	421
Suction microelectrode recording from primate cones[b]	561	531	430
Microspectrophotometry of excised human cones[c]	558	531	419
Recombinant human cone pigments[d]	558	530	425

[a]Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737.
[b]Baylor, D.A., Nunn, B.J., Schnapf, J.L., 1987. Spectral sensitivity of cones of the monkey *Macaca fascicularis*. J. Physiol. Lond. 390, 145–160.
[c]Dartnall, H.J.A., Bowmaker, J.K., Mollon, J.D., 1983. Human visual pigments: microspectrophotometric results from the eyes of seven persons. Proc. R. Soc. Lond. Ser. B Biol. Sci. 220, 115–130.
[d]Merbs, S.L., Nathans, J., 1992. Absorption spectra of human cone pigments. Nature 356, 433–435; Oprian, D.D., Asenjo, A.B., Lee, N., Pelletier, S.L., 1991. Design, chemical synthesis, and expression of genes for the three human color vision pigments. Biochemistry 30, 11367–11372.

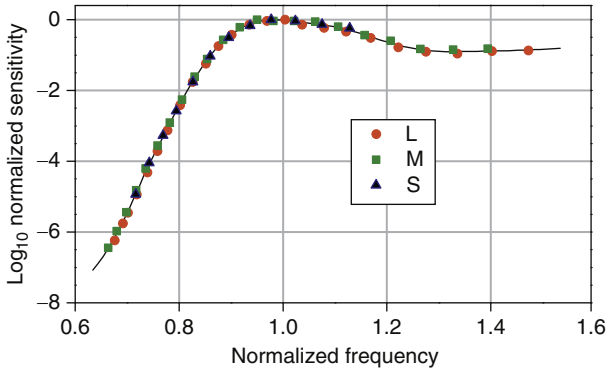

Figure 4 Spectral sensitivities of long-, medium-, and short-wavelength-sensitive (L, M, and S) monkey cones measured by suction microelectrode. Log mean absorbance, normalized to a maximum of zero (ie, unity on a linear scale), is plotted against normalized frequency ν/ν_{max} for each cone type. Data are from Table 1 of Baylor, D.A., Nunn, B.J., Schnapf, J.L., 1987. Spectral sensitivity of cones of the monkey *Macaca fascicularis*. J. Physiol. Lond. 390, 145–160. The smooth curve is a locally weighted polynomial regression.

on logarithmic and linear ordinates, for the weighting of the fits is different and the templates are therefore not exact logarithmic transforms of each other (the data in Table 1 were based on both kinds of templates).

Cone Gains and von Kries Scaling

The chromatic function of the cones is determined by not only their spectral sensitivities but also their relative gains. The effect of the spectrum of the prevailing light on those gains is summarized by the coefficient rule of von Kries, which refers to the idea that the sensitivity of each cone type depends only on activity in that cone type. Thus, if the radiant power in the light is biased toward long wavelengths, then the gain of the L cones is reduced in proportion to that bias. In fact, the evidence from microelectrode recordings in the retina of primates suggests that although substantial and independent chromatic adaptation does takes place among the three cone types, it is not complete. Adaptation also takes place at postreceptoral levels (see the section: Postreceptoral Spectra). Even so, to a first-order approximation, von Kries scaling achieves a normalization of cone responses over a wide range of illumination conditions before bleaching dominates.

Isolating Cone Responses

The experimental investigation of chromatic function sometimes requires the selective stimulation of a particular cone type. There are two general methods for achieving this in vivo: one employs selective adaptation either by a steady or temporally modulated background field so that only the chosen cone type mediates detection; the other constrains changes in the stimulus so that they are invisible to all but the chosen cone type.

Selective Chromatic Adaptation

The two-color threshold method of Stiles is based on the properties of the increment-threshold function. The minimum detectable radiance (the increment threshold) of a small test flash of wavelength λ is measured as a function of the radiance of a large steady background field of wavelength μ. The resulting monotonically increasing, threshold-versus-radiance (t.v.r.) curve may have more than one branch, but, over a limited range, each branch typically retains its shape while undergoing a vertical displacement with a change in λ (yielding a test spectral sensitivity) or a horizontal displacement with a change in μ (yielding a background-field spectral sensitivity). Provided certain assumptions hold, the test spectral sensitivity should coincide with the background-field spectral sensitivity, where both are defined. The assumptions are that the mechanisms underlying the t.v.r. curves – Stiles' π mechanisms – act independently of each other; that the observed t.v.r. curve depends only on the smallest increment threshold ofthe mechanisms available; and that each mechanism has a well-defined spectral sensitivity.

Fig. 5 shows background-field spectral sensitivities for three mechanisms, π_3, π_4, and π_5 (symbols) superimposed on the corresponding S-, M-, and L-cone fundamental spectra (curves) (see the section: Fundamental Spectral Sensitivities).

The π mechanisms cannot represent individual cone activity, for there are too many of them: three S mechanisms (π_1 π_2, and π_3), two M mechanisms (π_4 and π_4'), and two L mechanisms (π_5 and π_5'), depending on the conditions of measurement. In addition to their multiplicity, there is evidence of nonadditivity, ie, the effect of a background field consisting of two monochromatic lights is different from the sum of the effects of the two lights alone. Yet, as Fig. 5 shows, π_3, π_4, and π_5 approach quite closely the corresponding cone fundamentals.

The mechanisms defined by the t.v.r. curves depend, of course, on where in the visual pathway the threshold for detection is determined. With an appropriate choice of the spatial and temporal properties of the test flash and the background field, it is possible to obtain both test and background-field spectra that appear to mainly represent not cone responses but opponent combinations of cone responses (see the subsection: Postreceptoral Spectra: Cone Opponency).

Silent Substitution

The principle of silent substitution is illustrated in Fig. 6. At a particular criterion response level, here 0.9 of maximum (other levels might be chosen), there are two wavelengths, 543 and 594 nm, at which the L-cone sensitivities are equal (red crosses). The alternation of two monochromatic, equal-radiance lights at these two wavelengths is therefore invisible to L cones but visible to M cones, for the M-cone sensitivity at 543 nm is more than twice that at 594 nm (green crosses). At these two wavelengths, the S-cone sensitivity is vanishingly small and can be ignored. The same technique may be applied to M and S cones.

Unlike selective chromatic adaptation, the isolation achieved by silent substitution is a second-order one: it is not the stimulus but its alternation ie, silent. Nevertheless, the method may be used to determine the spectral sensitivity of the isolated cone class (here the M cones); and even when the spectral sensitivity of the silenced class (the L cones) is known only approximately, it may still, in principle, be applied in an iterative way.

Rod Intrusion

The rod photoreceptors of the retina are not normally associated with chromatic function. But with large stimulus fields of low-to-moderate luminance, color vision can be influenced by rod activity, which biases the apparent hue and diminishes the saturation of

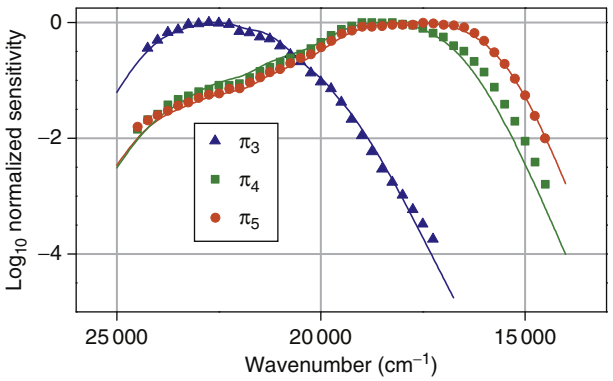

Figure 5 Stiles' background-field spectral sensitivities of the mechanisms π_3, π_4, and π_5 (symbols). Log mean sensitivity, normalized to a maximum of zero on a log quantum scale (ie, unity on a linear scale), is plotted against wavenumber (proportional to frequency). The corresponding mean S-, M-, and L-cone fundamental spectral sensitivities, in the same units, are also shown (curves). Data are based on Table 2 (7.4.3) of Wyszecki, G., Stiles, W.S., 1982. Color Science: Concepts and Methods, Quantitative Data and Formulae. John Wiley & Sons, New York and on Table 2 of Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737.

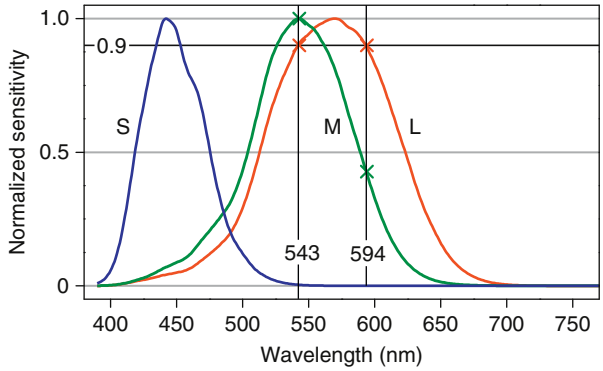

Figure 6 Silent substitution. Responses at 543 and 594 nm are the same for L cones (red crosses) but different for M cones (green crosses). Data are normalized cone fundamental spectra (Fig. 1).

extrafoveal stimuli. Even for foveal stimuli of just 1 degree visual angle, some rod involvement may be detected. Under daylight conditions, however, rod intrusion in color matches is small and is likely to be negligible above 100 cd m^{-2}.

Spatial Densities

The numbers of the three cone types are neither constant over individuals nor uniform across the retina. These variations have different implications for chromatic and luminance function.

Individual Variations

The relative frequencies of the different cone types, as proportions of the total number of cones, have been estimated across individuals by indirect psychophysical methods and by more direct methods, both in vivo and in vitro. The most important psychophysical method models the photopic luminous efficiency function obtained by heterochromatic flicker photometry as a linear sum of signals from L and M cones, under the working assumptions that the contribution of each is weighted by its numerosity and that the spectral sensitivity of each is known. Direct in vivo methods include retinal densitometry, electroretinographic flicker photometry, and high-resolution adaptive-optics imaging combined with retinal densitometry. Results from flicker photometry correlate with those from electroretinographic methods. In vitro methods include microspectrophometry with single cones, immunocytochemical labeling of small retinal patches, and analysis of L and M opsin messenger RNA in homogenized retinal patches.

It is clear that the relative frequency of S cones is fairly constant over individuals, c. 5–6% for a patch of retina at 1 degree eccentricity. For L and M cones, it is their ratio ie, normally specified, and, although a working value of 1.5:1 or 2:1 is often assumed in modeling their contributions to the luminous efficiency function, the actual ratio varies greatly from individual to individual, from c. 0.7:1 to 12:1, by direct measurement, and over a somewhat larger range by indirect measurement. This variation may reflect the different evolutionary and developmental histories of the S-cone and L- and M-cone pathways.

Retinal Distributions

That the three cone types have different distributions across the retina has been long known from psychophysical measurements of, eg, increment threshold and grating acuity with cone-specific stimuli. These findings have been confirmed and extended by some of the techniques mentioned in the preceding subsection.

The spatial density of L and M cones is greatest in the central fovea and it declines steadily with increasing retinal eccentricity. By contrast, the spatial density of S cones is zero in the central c. 20 arcmin of the fovea (0.1 mm); it increases to a maximum at c. 1 degree eccentricity, and then declines again. Because the decrease in S-cone density is less rapid than that of the other cone types, the relative frequency of S cones, as a proportion of the total number of cones at each eccentricity, increases slowly with eccentricity and levels off at c. 5 degrees or a little more.

In the fovea, there seems to be little evidence for other than a random distribution of S cones and L and M cones, although occasional departures in the direction of a more regular S-cone distribution and some clumping of L and M cones have been observed. In the periphery, there are more systematic departures from randomness in the distributions of both S cones and L and M cones. The purpose of the cone-rich rim of the ora serrata is unknown.

Eccentricity and Chromatic Function

The absence of S cones in the center of the fovea accounts for the perceptual phenomenon of small-field tritanopia: for sufficiently small fields, color vision is dichromatic, so that just two fixed primary lights are needed to match an arbitrary test light (see the section: Fundamental Spectral Sensitivities). The size of the tritanopic zone varies across individuals, and it may be absent in some.

The consequences of individual variation in L:M cone ratios are largely confined to luminance function. For chromatic function, the variation may be counterbalanced by changes in gain associated with excitatory and inhibitory inputs. In judgments of a perceptually unique yellow, in which the wavelength of a monochromatic light is adjusted so that it appears neither red nor green and which might be expected to reveal an imbalance between L and M cone inputs, the variation in the selected wavelength seems not to be attributable to ratio differences. One factor contributing to the stability of unique hues may be a form of chromatic adaptation to the spectrum of the environment.

For the individual eye, there are marked variations in chromatic function with retinal eccentricity. Thus, in general terms, color-matching performance with a small field, of the order of 1 degree extent, diminishes with increasing distance from the fovea, tending to dichromacy at 25–30 degrees and to monochromacy at 40–50 degrees. More specific changes are revealed by psychophysical measurements of hue and saturation and of chromatic contrast sensitivity with eccentricity. The latter is quantified by the detectability of a stimulus modulated along a red-green or blue-yellow color axis, defined with respect to stimuli specific for L, M, or S cones (ie, an L vs. M axis and an S vs. L + M axis). The size of the stimulus is usually increased with eccentricity for optimum response. For red-green modulation, contrast sensitivity is high at the fovea and then declines rapidly with eccentricity, falling to zero at 25–30 degrees, whereas for blue-yellow modulation, contrast sensitivity is much flatter and declines only slowly with eccentricity, and at a rate similar to that for luminance modulation. Since luminance contrast sensitivity is determined by the same cone signals as red-green contrast sensitivity, the decline in the latter with eccentricity is presumably due to changes in chromatic coding rather than in L and M cone densities (see the subsection: Postreceptoral Spectra: Cone Opponency).

Postreceptoral Spectra

Cone Opponency

Spectral sensitivity at postreceptoral levels is modified by antagonistic interactions between signals from the different cone types. This cone opponency—also occasionally called color opponency—is not the same as the red-green and blue-yellow color opponency identified in some perceptual experiments where the poles of the reference axes correspond to the unique hues, red, green, blue, and yellow.

The detailed organization of cone opponency has been difficult to characterize unambiguously, and retinal connectivity is not as specific as has sometimes been assumed. Thus, there is anatomical evidence of random, nonselective connectivity of L and M cones to ganglion-cell receptive fields, and physiological evidence of both randomness and selectivity. Nevertheless, because the response of a ganglion cell is determined by a weighted sum of its excitatory and inhibitory inputs, the nature of the connectivity has less effect on the spectral characteristics of cone-opponent responses than the weights associated with the inputs. Fig. 7 shows theoretical cone-opponent spectra (curves) from simple linear combinations of cone signals of the form S – k(M + L) in the left panel, M – kL in the middle panel, and L – kM in the right panel, where the amount of inhibition is indicated by the weight constant k (the assumption of linearity is not essential).

With $k = 0.4$, the wavelength λ_{max} of maximum sensitivity for the L – kM spectrum shifts from 570 to 589 nm, a difference of 19 nm, whereas for the M – kL spectrum, λ_{max} shifts from 543 to 539 nm, ie, just 4 nm, and for the S – k(M + L) spectrum, there is

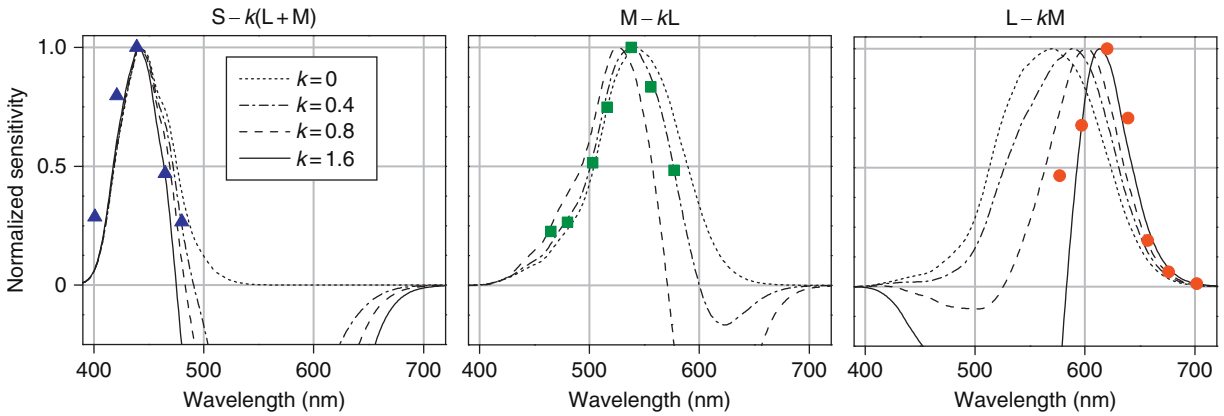

Figure 7 Theoretical and observed cone-opponent spectral sensitivities. Each set of curves represents spectra of the form S – k(M + L) (left panel), M – kL (middle panel), and L – kM (right panel), normalized to a maximum of unity on a radiance scale, with values of the weight constant k indicated (for $k = 1.6$, the function M – kL is mainly negative). *Normalized L-, M-, and S-cone fundamental spectra were taken from Table 2 of Stockman, A., Sharpe, L.T., 2000. The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vis. Res. 40, 1711–1737.* The symbols show psychophysical background-field spectra obtained under conditions intended to isolate cone-opponent function, and *are means calculated from Fig. 1A–C of Foster, D.H., Snelgar, R.S., 1983. Test and field spectral sensitivities of colour mechanisms obtained on small white backgrounds: Action of unitary opponent-colour processes? Vis. Res. 23, 787–797.*

no shift at all. With larger k, both L – kM and M – kL spectra become more narrowed. Combined with a shift in λ_{max}, the effect is sometimes described as spectral sharpening.

These changes in spectral shape are similar to those observed in microelectrode recordings in primate retina and psychophysically in both test and background-field spectral sensitivities (see the subsection: Isolating Cone Responses: Selective Chromatic Adaptation) obtained under conditions designed to isolate cone-opponent activity. Examples of background-field cone-opponent spectra are also shown in **Fig. 7** (symbols). Notice that the asymmetries in the shifts of λ_{max} do not themselves require asymmetric weighting of cone signals nor do they imply asymmetric L – kM and M – kL responses.

As already observed (see the subsection: Spatial Densities: Eccentricity and Chromatic Function), red-green and blue-yellow contrast sensitivity varies with retinal eccentricity, but there is evidence that the opponent weights revealed in those measurements remain constant with retinal location up to *c*. 10 degrees eccentricity. Beyond that, differences emerge in the L versus M and M versus L responses.

It is at present unclear how these kinds of cone-opponent activity relate to the perceptual color opponency of unique hues.

Advantages of Cone Opponency

Along with providing information about the spectral content of a stimulus, cone opponency has two other advantages. First, it reduces information redundancy. Because of the close overlap in the L- and M-cone spectral sensitivities, their responses are highly correlated. But spectrally sharpened L – kM and M – kL combinations provide greater independence and more efficient coding for neural transmission. Second, with chromatic adaptation at a cone-opponent level and not just at a receptoral level (see the subsection: Cone Spectral Sensitivities: Cone Gains and von Kries Scaling), it is possible to compensate more completely for any bias in the spectrum of the prevailing light. This may be achieved by von Kries scaling, but of cone-opponent responses rather than cone responses.

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