

## COLOR AND CONE FUNDAMENTALS

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### Abstract

*We propose a scaling for the S-cone fundamental which is approximately one eleventh of the respective L-cone scaling, and about one sixth of the M-cone scaling. We review supporting evidence and discuss some consequences for representing perceived colors. We find that our metric color space is locally isotropic around a certain white point close to CIE-D<sub>65</sub>.*

The input signals into color vision are provided by the excitations of three cone types sensitive to wide, overlapping ranges of short (S), middle (M) and long (L) wavelengths of the visible light. The results of many physiological experiments carried out in primate cones (Schnapf et al 1999) closely correspond to those of psychophysical experiments that describe the receptor mechanisms. Cones count quanta: the more quanta they receive, the higher is the amplitude of their electrical signals. For a given level of adaptation and within about 2 orders of magnitude changes in light flux are coded in proportional changes of cone voltage.

The spectral sensitivities of cone types, also called cone fundamentals, are very well known since quite a while (see the page [www.cvrl.org](http://www.cvrl.org) by Stockman & Sharpe). Hence cone excitations are used to quantitatively characterize colors: each color is a point in three-dimensional cone space with the axes L, M and S representing excitations of respective cone types (MacLeod & Boynton 1973). Cone space provides a physiologically plausible representation of color that is also used by physiologists (review: Dacey 1999).

Cone excitations are combined into at least three postreceptor mechanisms relevant for color vision. The important property of these mechanisms is that they compute differences between cone signals. To illustrate this they are called red-green, blue-yellow, and achromatic opponent. These signals are often expressed in the respective contrasts. The correlation between properties of retinal ganglion cells found by physiologists and those of postreceptor mechanisms found by psychophysicists is not as strong as that seen for receptor mechanisms and cones (Valberg 2001). Even though cones do not signal contrasts, their functional properties are often described using cone contrast to have a convenient frame work for both receptor and postreceptor mechanisms.

It is known that a surface can take on virtually any color depending on surround conditions, observer's adaptation due to illumination, and reflected spectral distribution. For the sake of the arguments presented we assume that colors are imbedded into a surround of uniform well defined white.

The value of any color on one of the axes in color space is obtained by integrating the spectral radiance of the stimulus over the spectral sensitivity of the respective cone type. Thus cone excitations depend on the absolute amplitudes of the spectral sensitivities of the cone types, or cone fundamentals. But only the shapes of cone fundamentals are known.

When the maximum values of all three cone fundamentals is scaled to 1 (Kaiser & Boynton 1996), colors of equal angular increments around a white point within an isoluminant plane are dominated by reddish or greenish hues, corresponding to activation of the red-green opponent pathway. Smith & Pokorny (1975) scaled cone fundamentals to maximum values of  $S=0.013$ ,

$M=0.392$  and  $L=0.637$ . Here the hues of equal angular increments within the isoluminant plane cluster around the blue-yellow opponent pathway (appearing mostly bluish or yellowish). In other words both these scales define a metric for three-dimensional color space that does not necessarily correspond with isotropy of perceived colors. Earlier color spaces like the 1931 CIE-xy space or the color space of Stiles & Burch (1955)(see Wysecki & Stiles 1982) share the disadvantage that equal distances in space do not correspond to steps of equal perceptual saliency (MacAdam 1942). De Valois et al. (1997) used the maximum excursion along the cardinal axis that was possible with their monitor as unit length to specify vector length and angles of intermediate color vectors.

From a perceptual point of view a color space in which isoluminance, detectability and discriminability of colors are intuitively accounted for in the geometry of this space seems desirable. A way to achieve such a scaling was mentioned before (Kaiser & Boynton 1996). It consists in attenuating the strength of the postreceptoral mechanisms such that detection thresholds of equal amplitude are obtained along the cardinal directions of color space (Krauskopf et al. 1982). This procedure is a generalization of earlier approaches (Webster & Mollon 1994, Knoblauch et al. 1995) who also used detection thresholds as unit lengths for radial distance and calculated the angles of the stimuli from the cone contrasts of the detection thresholds along the cardinal axes. Here we rescale the cone fundamentals such that detection ellipses are transformed into circles (Teufel & Wehrhahn 2000). This takes three successive steps.

### **Determining the isoluminant plane**

First, a range of isoluminant chromatic stimuli with respect to the white surround is established in each observer. Why do we need to do that? It's obvious that the probability of finding isoluminant colors in the real world is close to zero. But if we want to study chromatic mechanisms in isolation, we have to have as little luminance influence as possible. Isoluminant colors are thus model stimuli for real world colors allowing us to study specific properties that are otherwise masked by luminance. This is only one step in the analysis of color vision. Understanding real world colors requires analysis of the influence of luminance components on color perception (Wachtler et al 2001).

Isoluminance of a color is achieved by using flicker fusion photometry (Kelly & van Norren, 1977). It exploits the fact that the luminance mechanism exhibits a higher temporal resolution than the chromatic mechanisms. In a flicker photometric experiment, two light patches, one colored and the other white, are modulated in time. If the modulation frequency exceeds the resolution limit of the chromatic pathways, the sensation of color attributed to the stimuli fuses into a steady color sensation while luminance differences are still transmitted by the luminance mechanism. In some cases the perceived flicker frequency is just reduced. Flicker reappears if the radiance is increased or decreased.

Here the luminance of the grey surround is the condition we want the luminance of our colors be matched to. Thus the color stimulus is a square of 2 deg side length that is flickered against a grey square, identical in size and position to the color stimulus, and of identical color as the background. Points of isoluminance are measured for at least 32 colors in five observers. The data of each subject are numerically fitted to a plane in cone space by minimizing the sum of squared distances of all flicker points to achieve the best fit.

The data of all subjects fit well to a plane in cone space (for details of experiments and plane fit see Teufel & Wehrhahn 2000). Thus the individual plane of isoluminance is established in each observer.

### **Detecting isoluminant chromatic contrast**

In the second step a range of colors from each observer's plane of isoluminance is chosen to serve as stimuli in detection experiments. Chromatic differences reliably indicate surface edges

(Mollon 1989). Small rectangular chromatic and isoluminant stimuli are flashed (one at a time) on a grey surround equal to the one used in the flicker experiments. They appear for 200 msec either to the right or left of the fixation point. Observers indicate the side on which they see the stimulus by pressing a mouse button. In this way detection thresholds are measured for the 5 observers. Detection experiments are carried out using the 2AFC procedure and the method of constant stimuli. Parameter of the experiment is the distance in cone space along the lines originating from the grey  $D_{65}$ , the white point within the isoluminant plane of each observer. Results are plotted in a plane that was the average of the subjective planes of isoluminance in cone space for the observers tested (MacLeod & Boynton 1973). Not surprisingly thresholds are found to form ellipses. Even though broad band stimuli generated on a color monitor are used in these experiments, the absolute sensitivity of the observers and the orientations of the flanks of the detection contours are consistent with those found in earlier detection experiments carried out with narrow band stimuli and using a Maxwellian view system for stimulation (Chaparro et al 1993, Cole et al 1993).

### Rescaling cone fundamentals

Finally in the third step the elliptical detection contour resulting from averaged thresholds of five observers can be fitted into a circle in cone space. This is achieved by setting the scaling of cone fundamentals to  $S = .0596$ ,  $M = .3699$  and  $L = .6301$ . While relative values for L- and M-cone fundamentals are similar to those proposed by Smith and Pokorny (1975), the S-cone fundamental is almost five times larger. One consequence of this is that contributions of S-cone to flicker brightness have a stronger effect on the angle by which the plane of isoluminance is tilted with respect to the plane spanned by L- and M-cone excitations. This can be seen by inspecting Fig 1.

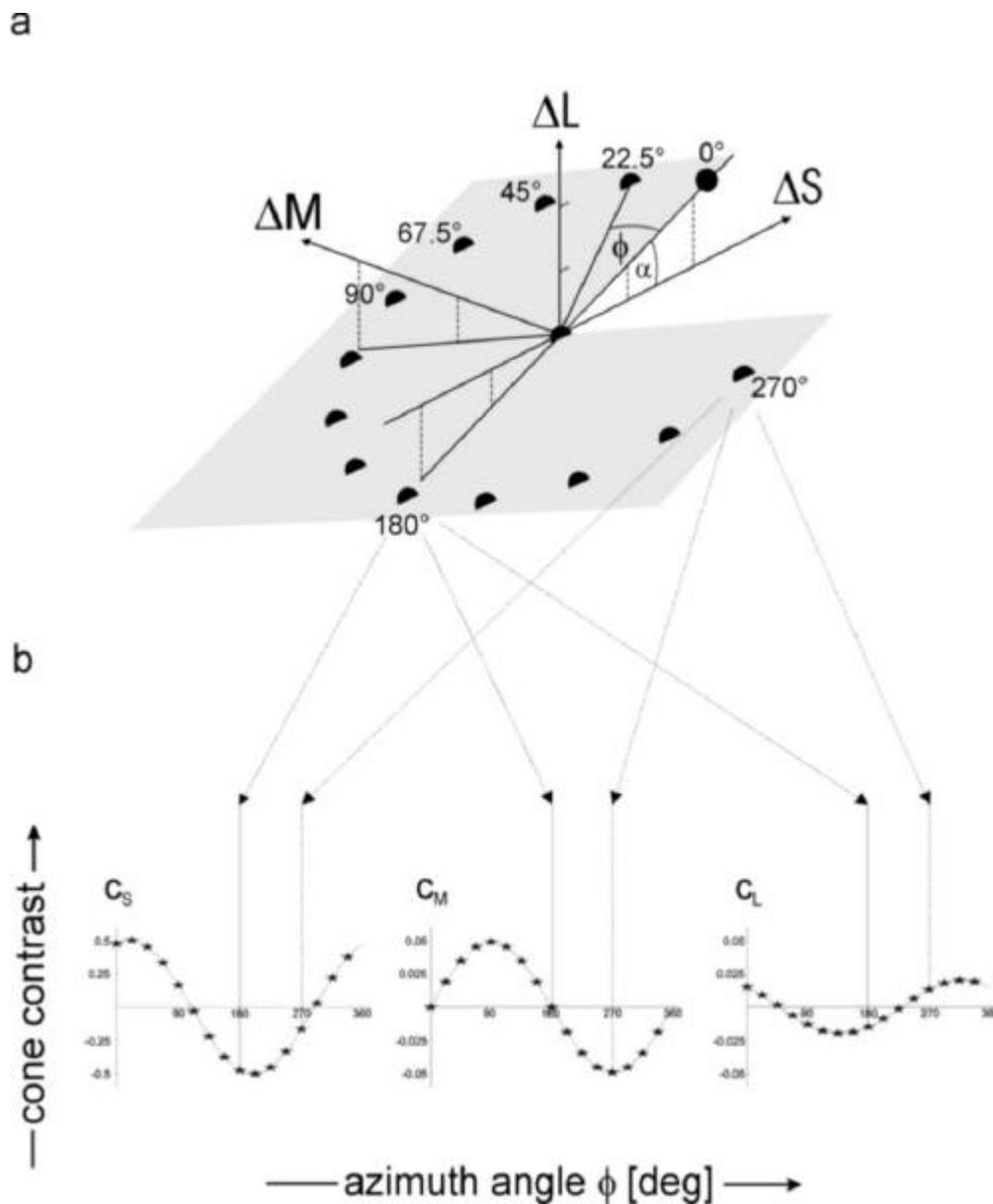
The other, more important difference is that the 16 colors have a well balanced occurrence of colors from the red-green as well as from the blue-yellow range. An approximate appearance of these colors can be seen in the web: [www.kyb.tuebingen.mpg.de/~wehrhahn](http://www.kyb.tuebingen.mpg.de/~wehrhahn). Nevertheless the basic features of cone space are unchanged (MacLeod & Boynton 1973). The centre of the circle formed by the equally detectable colors represents the white background surrounding detection stimuli.

Figure 1 is plotted in cone difference space choosing cone excitations as base vectors and shifting the origin to the location of the grey background. Phase and amplitude of the cone contrast functions depicted in b. are given by:  $c_S = 0.1006 \sin(\phi - 289.1)$ ,  $c_M = 0.0098 \sin(\phi)$ ,  $c_L = 0.0040 \sin(\phi - 48.8)$ . The azimuthal angle  $\phi$  begins when M-cone contrast vanishes ( $\phi = 0$ ) and increases going counterclockwise. The 16 colors on the circle are generated from each other through equal increments of azimuthal angle  $\phi$ . Thus the 16 colors are equidistant.

Obviously we need to vary just one parameter to go through all possible isoluminant colors of equal detectability: starting at any point on the circle and increasing the azimuthal angle  $\phi$  is equivalent to going counterclockwise around the circle, and to passing through all chromatic isoluminant stimuli available at threshold. We emphasize that that this isotropy of color space is a local phenomenon around the white point chosen for the experiments. Global isotropy of color space may be achieved by nonlinear transformations as used in the CIE-Lab color space.

Figure 1.

a. The circle formed by the equally detectable colors is schematically depicted in cone difference space, where the origin coincides with the white forming the centre of the plane of isoluminance. The plane is tilted to the three axes of cone difference space since there is a small, but significant contribution of S-cones to flicker brightness. Equal increments of azimuthal angle  $\phi$  define 16 colors of equal distance in cone difference space. Modified from Teufel & Wehrhahn (2000).



b. Projection onto the three axes of cone contrast  $c_S$ ,  $c_M$  and  $c_L$  of the circle shown in a. Plotted as a function of the azimuthal angle  $\phi$  the cone contrasts the three sinusoids show differences in phase angle characterizing differences in S-cone excitation.

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## References

- Boynton, R.M. (1996). History and current status of a physiologically based system of photometry and colorimetry. *J. Opt. Soc. Am. A* 13:1609-1621.
- Chaparro, A., Stromeyer, C. F., Huang, E. P., Kronauer, R. E., Eskew, R. T. (1993). Colour is what the eye sees best. *Nature (London)* 361: 348-350.
- Chaparro, A., Stromeyer, E. P., Kronauer, R. E., Eskew, R. T. (1994). Separable red-green and luminance detectors for small flashes. *Vision Res.* 34: 751-762.
- Cole, G. R., Hine, T., McIlhagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space," *J. Opt. Soc. Am. A* 10: 38-51.
- Dacey, D. M. (2000). Parallel pathways for spectral coding in primate retina. *Annu. Rev. Neurosci.* 23: 743-775 .
- De Valois, R. L., De Valois, K. K., Switkes, E., Mahon, L. (1997). Hue scaling of isoluminant and cone-specific lights. *Vision Res.* 37: 885-897.
- Kaiser, K.K., Boynton, R.M. (1996). *Human Color Vision* 2nd edition. Optical Society of America, Washington, DC.
- Kelly, D. H., van Norren, D. (1977). Two-band model of hetero-chromatic Flicker. *J. Opt. Soc. Am.* 67: 1081-1091.
- Knoblauch, K. K. (1995). Dual bases in dichromatic color space. In: *Colour Vision Deficiencies XII*. Drum B, Ed. Kluwer Academic, Dordrecht, The Netherlands, pp. 165-176.
- Krauskopf, J., Williams, D. R., Heeley, D. W. (1982) Cardinal directions of color space. *Vision Res.* 22: 1123-1131.
- MacAdam, D. L. (1942) Visual sensitivities to color differences in daylight. *J. Opt. Soc. Am.* 32: 247-274.
- MacLeod, D.I.A., Boynton, R.M. (1973). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *J. Opt. Soc. Am* 69:1183-1186.
- Mollon, J. D. (1989). "Tho' she kneel'd in that Place where they Grew". *J. exp. Biol.* 146: 21-38.
- Smith, V.C., Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Res.* 15: 161-171.
- Schnapf, J. L., Scheeweis, D. M. (1999) Electrophysiology of primate cone photoreceptors. In: *Color Vision: From Genes to Perception*. Eds. Sharpe, L., Gegenfurtner, K. Cambridge University Press, Cambridge, U. K.
- Stockman, A., MacLeod, D.I.A., Johnson, D. (1993). Spectral sensitivities of the human cones. *J. Opt. Soc. Am. A* 10: 2491-2521.
- Stockman, A., MacLeod, D.I.A., Vivien, J.A. (1993). Isolation of the middle- and long-wavelength- selective cones in normal trichromats. *J. Opt. Soc. Am. A* 10: 2471-2490.
- Teufel, H.J., Wehrhahn, C. (2000). Evidence for the contribution of S-cones to the detection of flicker brightness and red-green. *J. Opt. Soc. Am. A* 17: 994-1006.
- Valberg A. (2001). Unique hues: an old problem for a new generation. *Vision Res.* 41: 1645-1657.
- Wachtler, T., Lee, T. W., Sejnowski, T. J. (2001). Chromatic structure of natural scenes. *J. Opt. Soc. Am. A* 18(1): 65-77.
- Webster, M.A., Mollon, J.D. (1994). The influence of contrast adaptation on color appearance. *Vision Res.* 34: 1993-2020.
- Wyszecky, G., Stiles, W.S. (1982). *Color Science: Concepts and methods, quantitative data and formulae*, second edition. New York: John Wiley & Sons.