Computation of cone contrasts for color vision research

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Cone-contrast coordinates have proved useful for representing transient test stimuli used in color vision experiments. These representations automatically take into account the spectral absorption of cones and any Weberian adaptation to steady fields of light. Under these conditions, they also can be interpreted as being an approximation to the incremental cone response. A detailed methodology is presented for making appropriate measurements and calculations of cone contrasts for any light source, especially color monitors.

In studying the basic mechanisms of human color vision, many researchers are concerned with the detection of transient test stimuli presented on steady background fields of light. It has proved to be convenient to represent these stimuli in terms of their *cone contrast* within each of the three classes of cones (Clavdetscher, Brown, Ankrum, & Teller, 1988; King-Smith, Vingrys, & Benes, 1987; Lee, Martin, & Valberg, 1989; McIlhagga, Hine, Cole, & Snyder, 1990; Noorlander, Heuts, & Koenderink, 1981; Stromeyer, Kronauer, & Cole, 1983). There are a number of reasons for using cone-contrast coordinates. Within one class of cones, the contrast of a stimulus is the estimated quantal catch rate of absorption of the test stimulus relative to the absorption due to the background field. Thus, cone contrasts automatically take into account the first stage of color processing: absorption of light by cones as a function of wavelength. Second, physiological evidence suggests that above a certain background level, equal-contrast stimuli produce equal-threshold cone signals (Weber's law; see Shapley & Enroth-Cugell, 1984). Finally, since a cone contrast is a ratio, any particular scaling constant used in a given set of cone fundamentals is canceled out.

However, the representation of test stimuli in terms of cone contrasts does not imply that all or any of the adaptation occurs within the cones themselves. Nor does it imply any lack of cone interactions. On the contrary, because the representation takes into account both the quantal absorption process and any cone-specific Weberian adaptation, results presented in terms of cone contrasts automatically highlight any non-Weberian adaptation and interactions among cone signals (Stromeyer et al., 1983).

For these reasons, cone contrasts have clear advantages over other systems of representing visual stimuli. For ex-

ample, simply to represent stimuli in terms of the spectral content or phosphor modulation of a color monitor has no physiological basis. In fact, modulation of just one phosphor can excite all three cone types simultaneously in a normal subject. From the point of view of understanding the underlying physiological mechanisms of color vision, Boynton (1986) and MacLeod and Boynton (1979) have discussed at length the theoretical and practical reasons for expressing stimuli in terms of cone excitation rather than the CIE system of stimulus specification. Brief coverage of a cone-excitation space is provided in the texts by Cornsweet (1970) and Rodieck (1973).

The present paper constitutes a tutorial for the reader interested in color vision but not familiar with the technical details of calculating cone excitations and contrasts for a particular set of light sources. Described below are the details of the calculations, with their concomitant simplifications, that are necessary for the computation of cone-contrast coordinates. We have included an explicit calculation of these coordinates for stimuli produced with a color monitor. This should be useful, because more and more researchers are using such monitors.

METHOD

Cone Excitation

There is now a general acceptance of psychophysically derived cone fundamentals (e.g., Smith & Pokorny, 1975; Vos, Estevez, & Walraven, 1990; Vos & Walraven, 1971), as a result of their good agreement with microspectrophotometric measurements (Bowmaker & Dartnall, 1980; Dartnall, Bowmaker, & Mollon, 1983) and electrical recordings (Schnapf, Kraft, & Baylor, 1987) of human cones. This has enabled vision researchers (Boynton, 1986; MacLeod & Boynton, 1979) to confidently represent stimuli in terms of their quantal catch rates of absorption within the different classes of cones, or *cone excitations* (ϵ_i), which are defined as follows:

$$\epsilon_i = \int_{\lambda} Q_i(\lambda) N(\lambda) d\lambda, \quad (1)$$

where $i = L, M, S$ represents each class of cones, which

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qualitatively have their peak sensitivities in the long, medium, or short wavelength regions of the spectrum, respectively. $Q_i(\lambda)$, the quantal sensitivity, represents the probability of absorption of a quantum of light of wavelength λ by the L, M, or S class of cones, respectively. $N(\lambda)$ is the quantal flux (quanta/second) of the light stimulus as a function of wavelength. The univariance principle states (Rushton, 1972) that, independently of wavelength, each absorbed photon produces exactly the same neural effect. Thus, the wavelength affects only the probability of absorption. This is precisely why cone excitation is the effective stimulus.

Since the energy per quanta is inversely proportional to wavelength (Wysecki & Stiles, 1982), the radiant power of a light stimulus $P(\lambda)$ (i.e., power per unit wavelength: watts/nanometer) is proportional to $N(\lambda)/\lambda$, and so an "energy-based" sensitivity $S_i(\lambda)$ is proportional to $Q_i(\lambda)\lambda$. Given that most spectral power measurements are in "energy units," as are most tabulated cone fundamentals (Smith & Pokorny, 1975; Vos et al., 1990; Vos & Walraven, 1971), it is more convenient to compute cone excitations by using the following version of Equation 1:

$$\epsilon_i = \int_{\lambda} S_i(\lambda) P(\lambda) d\lambda. \quad (2)$$

Normally, measurements are available only at a series of discrete wavelengths, and hence the integrations are approximated in the usual way by finite sums. Note that all published human cone sensitivities are only relative and have different scalings, independent of their specific shapes (Wysecki & Stiles, 1982). For example, Smith and Pokorny's (1975) data are convenient because the L and M cone fundamentals are scaled in such a way that their sum is equal to the photopic luminosity function, V_{λ} . Therefore, the sum of the L and M cone excitations is proportional to the luminance and troland value of the stimulus. This relative nature of the sensitivities—and thus of the cone excitations—is of no consequence here, because cone contrasts are simply ratios of cone excitations within the same cone class.

In terms of its effect on the visual system, any light can be described by three numbers: the L, M, and S cone excitations (ϵ_L , ϵ_M , ϵ_S). It is therefore convenient to represent that light as a vector in the three-dimensional space of L, M, and S cone excitations. This is shown schematically in Figure 1, where only the L and M cone excitations are considered (it is a straightforward extension to all three cone classes and a three-dimensional diagram). There are physical limits on the possible representations of lights. First, excitations are non-negative quantities. Second, there is overlap of the cone sensitivities, corresponding to a normal trichromat (Smith & Pokorny, 1975), and therefore there are regions in the space that do not correspond to any physical light. In particular, the considerable overlap of the L and M cone sensitivities makes it impossible to generate any light that uniquely "excites" the M class of cones without also exciting the L class. In Figure 1, the hatched regions correspond to

Figure 1. Schematic of L and M cone excitations corresponding to a steady adapting field of light and a transiently presented test stimulus. For didactic purposes, the adapting field and test stimulus are both shown to be a superposition of red and green stimulus components (see text for details).

these physically impossible lights. On the other hand, it is possible for a transient test that is superimposed on a steady light to uniquely stimulate a single cone type with either an increment or a decrement.

It follows from both the definition of cone excitations above and the additivity of light that the total cone excitation in each class of cones (ϵ_L , ϵ_M , ϵ_S) due to the physical superposition of many lights is equal to the sum of the individual L, M, and S cone excitations for each light. Additionally, cone excitations scale in direct proportion with the intensity of a light whose spectral power distribution or "shape" does not change (see below for details). Geometrically, the vectors corresponding to each light are added vectorally to yield a sum corresponding to the net stimulus (Figure 1), where the length of the vector is proportional to the net intensity.

Measurements of Lights

To compute cone excitations, it is necessary to know the spectral power distribution of all the light stimuli. This measurement is often the most difficult aspect of performing cone-contrast calculations. When stimuli are known to be monochromatic (e.g., generated from a narrow-band interference filter or monochromator), the spectral power distribution can usually be approximated by a narrow Gaussian centered on the appropriate wavelength and having a width as specified in the technical data of the device. Broad-band stimuli (e.g., the phosphors of a color monitor), however, should ideally be measured with a spectroradiometer. Failing this, manufacturers' specifications or data from similar equipment in other laboratories could be used. Note that when one is using color monitors, the relationship between electron gun input voltage and corresponding output light intensity (gamma correction) must be measured. Also, one should be aware of the possibility of interactions between phosphors: the brightening of one phosphor may cause a slight brightening or dimming

of another phosphor. These points and related issues are addressed by Brainard (1989).

Many lights used in the laboratory as visual stimuli in color vision experiments have spectral power distributions with intensity-independent shapes: for example, any light controlled with a neutral density wedge with transmittance as nearly flat as possible across the visible spectrum. The phosphors of a color monitor behave in this way to a good approximation (Brainard, 1989). The absolute spectral power distribution of any such light $P(\lambda)$ is conveniently written as the product of two terms:

$$P(\lambda) = P \cdot p(\lambda), \quad (3)$$

where $P = \int P(\lambda) d\lambda$ is the total power (watts) of the light stimulus (i.e., the intensity of the light in the nontechnical sense), and $p(\lambda)$ is the relative power distribution when the total power is 1 W. Thus, $p(\lambda)$ is the intensity-independent shape. Applying Equation 3 to Equation 2 for each cone class yields the L, M, and S cone excitations for this light:

$$\begin{aligned} \epsilon_L &= P \cdot \langle S_L \rangle, \\ \epsilon_M &= P \cdot \langle S_M \rangle, \\ \epsilon_S &= P \cdot \langle S_S \rangle, \end{aligned} \quad (4)$$

where $\langle S_L \rangle$, $\langle S_M \rangle$, and $\langle S_S \rangle$ are simply three numbers that are the average cone excitations produced by the light having a spectral power distribution $P(\lambda)$. The symbol $\langle \rangle$ is a shorthand to indicate that for any given function of wavelength $F(\lambda)$, $\langle F \rangle$ is computed with the following formula:

$$\langle F \rangle = \int_{\lambda} F(\lambda) p(\lambda) d\lambda. \quad (5)$$

Therefore, any light that has an intensity-independent shape may be represented as a vector in the L, M, and S cone-excitation space, the direction of which is fixed ($\langle S_L \rangle \langle S_M \rangle \langle S_S \rangle$), but which has a length that scales in direct proportion with the total power P of the light. This is a useful simplification in the computation of cone excitations, because both the spectral power distribution of the light and the average L, M, and S cone excitations need only be computed the one time.

To compute the overall cone excitation of the light, one must measure the total power (P) of the light. This may be done as follows. Consider a standard radiometer with a detector (e.g., a PIN photodiode) having a linear response and a spectral responsivity $R(\lambda)$ (amp. watts⁻¹). The meter readout M (proportional to the electrical current from the detector) is described by the following formula (Taylor, 1987):

$$M = k \cdot \int_{\lambda} R(\lambda) P(\lambda) d\lambda, \quad (6)$$

where k is the proportionality constant (specific to a radiometer and detector combination) having units amp⁻¹, rendering M a dimensionless quantity. By using Equations 3 and 5, Equation 6 may be rewritten in the following format for the computation of the total power P :

$$P = \frac{M}{k \cdot \langle R \rangle}, \quad (7)$$

where $\langle R \rangle$ is the average responsivity of the radiometer to the light according to Equation 5. For each light described by Equation 3, $\langle R \rangle$ need only be computed once, independently of the intensity of the light.

The only complication is the radiometric nature of the quantity being measured by the specific radiometer or power meter. For example, suppose the radiometer measures the radiant flux, which is the total power of the light (in watts) incident upon the detector. Provided the light stimulus incident on the detector underfills its surface, the total power of the light can be computed directly with the equation above. On the other hand, if the same light spills over the edge of the detector, the quantity computed with the equation above is no longer the total power but is implicitly the power per unit area of the detector surface—the irradiance. In fact, for the free-viewing situation, irradiance can be used instead of total power without loss of generality in all subsequent computations of cone contrasts. Furthermore, the appropriate measurement is also dependent on the geometry of the viewing situation. For most cases in visual experimentation, the intensity of light impinging on the retina is paramount but impossible to measure directly. By convention, we specify the light incident upon the cornea in terms of the radiant flux per unit of visual solid angle per unit area of the pupil (radiance). These specific issues are addressed elsewhere (Westheimer, 1966; Wyszecki & Stiles, 1982).

Conversion from CIE Coordinates

Alternatively, if the spectral power distribution of a stimulus is not known, it is still possible to obtain the cone excitations of a stimulus given its CIE x and y chromaticities and the photopic luminance Y (Wyszecki & Stiles, 1982; pp. 139, 615). When one uses Smith and Pokorny (1975) fundamentals, the formula is as follows:

$$\begin{aligned} \epsilon_L &= Y \cdot [0.15514x/y + 0.54312 - 0.03286(1-x-y)/y], \\ \epsilon_M &= Y \cdot [-0.15514x/y + 0.45684 + 0.03286(1-x-y)/y], \\ \epsilon_S &= Y \cdot [0.00801(1-x-y)/y]. \end{aligned} \quad (8)$$

Note that this formula has the same form as Equation 4, with the cone excitations being directly proportional to the luminance of the stimulus, which in turn is proportional to the total power P of the stimulus. Equation 8 is useful for researchers using color monitors with CIE coordinates for each of the phosphors provided by the supplier.

Cone Contrasts

Given the presentation of a transient test stimulus relative to a steady background field of light, the cone contrast for a particular cone class can be defined as the ratio of the cone excitation due to the test stimulus relative to that due to the background field. This contrast can be either positive or negative. More explicitly, if ($\epsilon_L \epsilon_M \epsilon_S$)

are the cone excitations due to the steady adapting field, and if $(\Delta\epsilon_L \Delta\epsilon_M \Delta\epsilon_S)$ are the changes in cone excitation due to the transient test stimulus alone, the cone-contrast coordinates of the test can be defined as:

$$\begin{aligned} C_L &= \Delta\epsilon_L/\epsilon_L, \\ C_M &= \Delta\epsilon_M/\epsilon_M, \\ C_S &= \Delta\epsilon_S/\epsilon_S. \end{aligned} \quad (9)$$

Each contrast component is a measure of the effective test-stimulus contrast in that particular class of cones. With respect to Figure 1, the transformation from cone excitations to cone contrasts corresponds geometrically to a translation of the origin to the end of the steady-field vector, with each axis then scaled by the size of the translation in that direction.

EXAMPLE CALCULATIONS

To illustrate the preceding rationale, we shall now proceed step-by-step through the explicit calculation of cone contrasts for stimuli produced with our experimental apparatus. All test stimuli are produced by transient modulations in the red, green, and blue phosphors of a color monitor (Tektronix 690SR), relative to an invariant "white" field. To provide a sufficiently intense adapting field, this monitor field is optically superimposed on two additional steady adapting fields of monochromatic light (455.8 and 570.0 nm). These particular wavelengths were chosen so that their combination would match the hue of the white of the color monitor. Note that the presence of the additional monochromatic lights only changes the details of computation of cone contrasts compared with their computation for a monitor alone. The additional adapting fields constituted a two-channel Maxwellian view system (Westheimer, 1966), with an artificial pupil smaller than the natural pupil. The monitor was optically incorporated into a third channel in a plane conjugate with the observer's retina.

The spectral power distributions of each of the phosphors of the color monitor were measured with a spectroradiometer (Powell, 1989). These distributions were almost identical to those given in Arend and Reeves (1986). In our case, these distributions were modified appropriately to take into account the optical transmittance of the lenses in our optical system. The two monochromatic

components were represented by two Gaussian spectral distributions centered at the appropriate wavelengths and with bandwidths given in the technical data.

With a numerical integration computer program, the average cone sensitivities $(\langle S_L \rangle \langle S_M \rangle \langle S_S \rangle)$ were computed by using Equation 5. In this case, $F(\lambda)$ is each of the Smith and Pokorny cone fundamentals (L, M, and S) tabulated in Wyszecki and Stiles (1982, p. 614). However, to facilitate the computation of L, M, and S trolands (Boynton, 1986), the S cone fundamental from this table has been multiplied by 124.8.² The relative spectral power distribution of each of the stimulus components is $p(\lambda)$. Similarly, the average responsivity $(\langle R \rangle)$ of each component was computed by using the manufacturer's supplied spectral responsivity of our radiometer (United Detector Technology Model 371, PIN Model 260). The results of all these calculations, which are shown in the first four columns of Table 1, are fixed quantities independent of the intensities of the lights. The meter readings (M) obtained at the exit pupil of the optical system for each stimulus component is presented in the next column. Finally, the total power (P), computed according to Equation 7, constitutes the final column.³

Application of Equation 4 to the results in Table 1 yields the cone excitations of each stimulus component as shown in Table 2. However, since we are using Smith and Pokorny cone sensitivities, it is convenient to scale these so that the L, M, and S cone excitations are the L, M, and S trolands of Boynton (1986).⁴ This scaling has no effect on the calculations of cone contrasts.

The test stimulus consists of a simultaneous perturbation of the red, green, and blue phosphors from their steady-state values of P_R , P_G , and P_B as specified in Table 1, by the amounts ΔP_R , ΔP_G , and ΔP_B , respectively. According to Equation 4—and summing the effects within each class of cones due to each transient change—the changes in the cone excitations due to the test are given by:

$$\begin{aligned} \Delta\epsilon_L &= \Delta P_R \langle S_{LR} \rangle + \Delta P_G \langle S_{LG} \rangle + \Delta P_B \langle S_{LB} \rangle, \\ \Delta\epsilon_M &= \Delta P_R \langle S_{MR} \rangle + \Delta P_G \langle S_{MG} \rangle + \Delta P_B \langle S_{MB} \rangle, \\ \Delta\epsilon_S &= \Delta P_R \langle S_{SR} \rangle + \Delta P_G \langle S_{SG} \rangle + \Delta P_B \langle S_{SB} \rangle, \end{aligned} \quad (10)$$

where $\langle S_{ij} \rangle$ is the average sensitivity of the i th cone class (L, M, or S) to the j th phosphor (R, G, or B) as specified in the first three rows and columns of Table 1. By representing the transient test perturbations in terms of phosphor

Table 1
Average Cone Sensitivities and Radiometer Measures
of Each Adapting Field Component

Light	$\langle S_L \rangle$	$\langle S_M \rangle$	$\langle S_S \rangle$	$\langle R \rangle (AW^{-1})$	M	$P(nW)$
Phosphor						
Red (P_R)	0.270	0.059	0.024	0.379	20.0	11.3
Green (P_G)	0.442	0.271	0.114	0.319	21.7	14.6
Blue (P_B)	0.0686	0.0582	1.085	0.232	11.8	10.9
Monochromatic						
455.8 nm	0.0342	0.0374	1.292	0.229	9.55	8.91
570.0 nm	0.632	0.314	0.002	0.343	21.0	13.1

Table 2
Cone Excitations and Troland Value of Each
Adapting Field Component

Light	ϵ_L	ϵ_M	ϵ_S	Troland Value (Td)
Phosphor				
P_R	110.1	24.2	9.7	134.3
P_G	232.0	142.4	59.8	374.4
P_B	26.9	22.8	425.3	49.7
Monochromatic				
455.8 nm	11.0	12.0	415.0	23.0
570.0 nm	299.2	148.7	1.0	447.9
Total	679.2	350.1	910.8	1029.3

contrasts (C_j) (i.e., the ratio of phosphor increment to background level) and making use of Equation 4 or 8, Equation 10 becomes:

$$\begin{aligned}\Delta\epsilon_L &= C_R\epsilon_{LR} + C_G\epsilon_{LG} + C_B\epsilon_{LB}, \\ \Delta\epsilon_M &= C_R\epsilon_{MR} + C_G\epsilon_{MG} + C_B\epsilon_{MB}, \\ \Delta\epsilon_S &= C_R\epsilon_{SR} + C_G\epsilon_{SG} + C_B\epsilon_{SB},\end{aligned}\quad (11)$$

where ϵ_{ij} is the cone excitation of the i th cone class (L, M, or S) due to the j th phosphor (R, G, or B) as specified in the first three rows and columns of Table 2. C_j is the fractional change in the light stimulus relative to the steady value, whether measured as a ratio of powers ($\Delta P_j/P_j$) or luminances ($\Delta Y_j/Y_j$). Finally, with the use of Equations 9 and 11, the L, M, and S cone contrasts can be given by:

$$\begin{aligned}C_L &= [C_R\epsilon_{LR} + C_G\epsilon_{LG} + C_B\epsilon_{LB}]/\epsilon_L, \\ C_M &= [C_R\epsilon_{MR} + C_G\epsilon_{MG} + C_B\epsilon_{MB}]/\epsilon_M, \\ C_S &= [C_R\epsilon_{SR} + C_G\epsilon_{SG} + C_B\epsilon_{SB}]/\epsilon_S,\end{aligned}\quad (12)$$

where ϵ_L , ϵ_M , and ϵ_S are the total L, M, and S cone excitations of the entire adapting field condition as specified in the very bottom row of Table 2. If this equation is re-written in the convenient form of a product between a 3×3 matrix and a vector, and if we substitute the explicit values for our experimental situation, we have

$$\begin{bmatrix} C_L \\ C_M \\ C_S \end{bmatrix} = \begin{bmatrix} 0.162 & 0.342 & 0.039 \\ 0.069 & 0.407 & 0.065 \\ 0.011 & 0.066 & 0.467 \end{bmatrix} \begin{bmatrix} C_R \\ C_G \\ C_B \end{bmatrix}. \quad (13)$$

DISCUSSION

The matrix in Equation 13 "describes" the adaptation condition for our experimental set-up and is constant throughout a series of experiments. Equation 13 is simple and hence easy to program. In fact, many modern hand-held calculators and programming languages directly provide for matrix and vector multiplication. To reiterate, this equation gives the L, M, and S cone contrasts of a test stimulus, given the red, green, and blue phosphor contrasts. For example, a 10% green phosphor con-

trast (0.0, 0.1, 0.0) produces the cone contrasts of 0.034, 0.041, 0.007. As an aside, it is often more convenient to represent cone contrasts in spherical coordinates (i.e., as a length and direction in cone-contrast space). The length is then a physiologically based measure of the contrast of the stimulus independent of the direction of the stimulus. Luminance and chromatic contrasts can then be directly compared.

Inverting Equation 13 yields the phosphor contrasts required to produce a given cone-contrast stimulus. For example, if it is desired to produce a 10% modulation of the M cones alone (0.0, 0.1, 0.0), this requires red, green, and blue phosphor contrasts of -0.813, 0.389, and -0.036 relative to their steady-state values. In fact, we are able to achieve about seven times more contrast in the white-black direction on our standard color monitor than in the "red-green" chromatic direction.

Finally, we have found it convenient to record all experimental results in terms of phosphor contrasts and then plot these results by using the transformation matrix in Equation 13. This allows us to easily perform a "sensitivity" analysis (in the engineering sense) on the data. That is, we examine the robustness to changes in a subject's results as a function of slight perturbations of the adapting conditions and/or cone fundamentals. These perturbations simply correspond to appropriate changes of the transformation matrix.

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NOTES

1. Very brief, high-intensity "flashes" on a television monitor can readily saturate photodetectors and their associated amplifying electronics, causing the response to be nonlinear. For safety, the detector should sample large areas of the screen to avoid this type of overload.
2. This scaling renders the sum of the areas under the L and M cone fundamentals equal to the area under the S cone fundamental.
3. For our radiometer and detector combination, $k = 4.664 \text{ nA}^{-1}$.
4. The L, M, and S trolands are given by $[P \cdot \langle S_i \rangle] \cdot [2.242 \times 10^{12} / FA]$, where $i = (L, M, \text{ and } S)$ and FA is the field area (62.2 deg^2 in our case). This formula is derived from Wyszecki and Stiles (1982, p. 103); the definition of cone trolands is from Boynton (1986, p. 248), which takes into account the scaling used in Table 1.

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