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APPLICATIONS OF PARALLEL PROCESSING IN VISION

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# Parallel and Serial Connections Between Human Color Mechanisms

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Introduction

The concept of a discrete number of independent mechanisms functioning in parallel was first used in human vision by Young (1802) as an explanation for the trivariance of color vision. Young's idea has proven to be correct for the first stage of color processing by the visual system. The current picture of the color system consists of a series of stages, each with a number of mechanisms functioning in parallel. Successive stages are composed of mechanisms that combine the outputs of the previous stage. The first few stages of color processing are simple and understood better than any other sensory system. Analogies from color mechanisms have been used in models for spatial frequency discrimination, motion perception and adaptation. However, a number of color phenomena are extremely complex (Woodworth, 1938; Albers, 1963) and cannot be satisfactorily explained in terms of known mechanisms. Based on accumulated knowledge and technological advances in stimulus generation, it has now become possible to study the functional properties of color mechanisms at higher levels. If mechanistic explanations of complex color phenomena are successful, they will provide general insights into the processing of complex information by other parts of the nervous system. This essay presents a historical and formal examination of color vision mechanisms with an emphasis on the theoretical and empirical reasoning used to identify independent parallel mechanisms and their interactions at successive stages of a serial system. The intention is to give an extended discussion of basic concepts and details of a small number of experiments instead of providing an exhaustive survey. More complete references can be found in a number of books including LeGrand (1957), Graham (1965), Brindley (1970), Rodieck (1973), Evans (1974), Boynton (1979), Pokorny et al. (1979), Wyszecki and Stiles (1982), and Nassau (1983). Some important historical papers have been collected by MacAdam (1970).

Trichromatic representation of lights

Two lights may appear of identical color to a human observer, yet be distinguishable when passed through a simple prism. For observers with normal color vision, given any four spectrally distinct lights, it is always possible to place two in one half of a visual field and two in the other, or three in one half and one in the other, and by adjusting the radiances of three of the four lights to make the two halves of the field appear identical. This property of human vision, where the adjustment of three independent controls makes an exact color match possible, whereas two are generally not enough, is called trichromacy. Newton (1675) was the first to note that when sunlight is dispersed by means of a prism, the color of different rays corresponds to their physical properties. In modern terms, visible light is a small section of the electromagnetic spectrum and lights of different wavelengths correspond to different perceived colors, from violet at the short wavelength end of the visible spectrum (400nm) to red at long (700nm) (Figure 1). Newton (1704) showed that the different rays of the spectrum can be combined to form a single beam of uniform color and the result of combining arbitrary proportions of different colors can be represented in a diagram (Figure 2). This diagram shows that the domain of colors is more restricted than the domain of lights, and would have demonstrated trichromacy if it had been exactly correct.
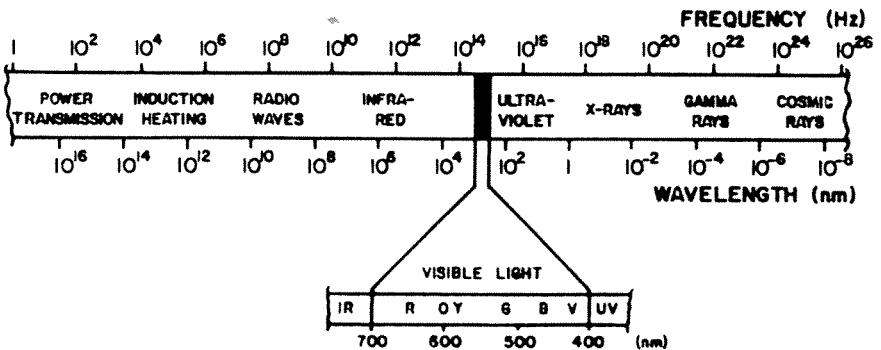
Figure 1. Visible wavelengths of the electro-magnetic spectrum with associated colors.

Based on Newton's work, Maxwell (1860) deduced that the result of any mixture of colors, however complicated, can be defined by its relation to three suitably chosen colors: any color which has the same relation to the standard colors will be identical in appearance, though its physical composition may be different. In modern terminology, the standard colors are called primaries, the numbers that relate the unit amount of a color to unit amounts of each of the primary colors are called tri-stimulus values, and the set of tri-stimulus values for monochromatic lights is called the set of color-matching functions. Maxwell (1860) measured color matching functions by using a colorimeter that was

essentially a reverse spectroscope enabling sunlight to be matched to a mixture of three spectral colors. The primaries were 456.9, 528.1, and 630.2 nm and tri-stimulus values were expressed in terms of the slit widths of the instrument. The color-matching procedure is diagrammed in Figure 3a. First, a mixture of the three primaries I_i, I_j, and I_k was matched to W, a unit amount of a standard white:

$$a_i I_i + a_j I_j + a_k I_k = W \tag{1}$$

In Equation 1, "=" refers to a color match between the two sides of the equation, "+" is summation of energy over each wavelength, and the coefficients are the energy of each primary in the match. To measure the tri-stimulus values of a spectral light of wavelength λ, a match was made to the standard white after replacing the appropriate primary with the test wavelength:

$$b_\lambda \lambda + b_j I_j + b_k I_k = W \tag{2}$$

By equating the left sides of equations 1 and 2 and solving for λ, the tri-stimulus values for λ were derived algebraically as the coefficients of the primaries in Equation 3:

$$\lambda = \left(\frac{a_i}{b_\lambda}\right) I_i + \left(\frac{a_j - b_j}{b_\lambda}\right) I_j + \left(\frac{a_k - b_k}{b_\lambda}\right) I_k \tag{3}$$

Maxwell's work provided the first empirical evidence for trichromacy and has been replicated by a number of later studies with more precise control over the stimuli (Konig and Dieterici, 1886; Abney, 1906; Wright, 1929; Guild, 1931; Stiles and Burch, 1955, and others). Stiles and Burch (1955) used the "maximum saturation" procedure devised by Guild (1931) to measure tri-stimulus values in a particularly direct way. As shown in Figure 3b, a mixture of the test light and the appropriate primary was matched to a mixture of the other two primaries:

$$C_\lambda \lambda + c_i I_i = c_j I_j + C_k I_k \tag{4}$$

where the coefficients were the measured radiances of the monochromatic lights. The tri-stimulus values were derived directly by solving Equation 4 for λ:

$$\lambda = -\left(\frac{c_i}{c_\lambda}\right) I_i + \left(\frac{c_j}{c_\lambda}\right) I_j + \left(\frac{c_k}{c_\lambda}\right) I_k \tag{5}$$

A standardized set of color matching functions (CIE, 1931) for a 2° foveal field is shown in Figure 4. A two dimensional representation similar to Newton's, the CIE (1931) chromaticity diagram is shown in Figure 5.

The derivations that lead to Equations 3 and 5 assume that the physical operations in Equations 1, 2, and 4 can be treated as mathematical operations: a color match like equality, W, λ, and the I's like unit vectors, the wavelength-by-wavelength sum like vector addition, and the coefficients like scalar multipliers of the unit vectors

that represent the primaries and the test wavelength. This isomorphism between experimental and mathematical operations was implicit in Newton's work. For a mixture of known amounts of primary colors, Newton determined the color of the compound by a center of gravity principle that was "accurate enough for practice, though not mathematically accurate." Grassman (1853) showed that the center of gravity rule, which was mathematically equivalent to vector addition, was justified if the "impression" of colors obeyed three propositions: three-dimensionality, continuity and additivity. In modern mathematical terminology, Grassman's propositions are satisfied if a color match is an equivalence relation and if the space of all color matches is a positive cone in a three-dimensional linear vector space (Schrodinger, 1920; Resnikoff, 1974; Krantz, 1975):

An equivalence relation in a set X, is a relation $x\#y$ between certain pairs of elements of X, satisfying the following conditions (Lang, 1966):

(i)   Identity: $x\#x$ for all x in X.
(ii) Commutativity: If $x\#y$ then $y\#x$.
(iii) Transitivity: If $x\#y$ and $y\#z$, then $x\#z$.

A linear vector space V is a set of objects that satisfy the following propositions (Lang, 1966):

(i)   Superposition: If v and w are elements of V, their sum $v + w$ is an element of V.
(ii) Scalar multiplication: If v is an element of V and c is a number, then cv is an element of V.
(iii) Null element There is an element of V, denoted by O, such that $O + v = v + O = v$.

Further, if $v_1, \ldots, v_n$, are elements of V, and $a_1, \ldots, a_n$, are real numbers, then a linear combination of $v_1, \ldots, v_n$, is written as:

$$a_1 v_1 + \ldots + a_n v_n \qquad\qquad (6)$$

$v_1, \ldots, v_n$, are called linearly independent if

$$a_1 v_1 + \ldots + a_n v_n = 0 \qquad\qquad (7)$$

only happens for all $a_1, \ldots, a_n$, equal to zero, i.e. no v_i can be written as a linear combination of the others. If every element of V can be written as the linear combination of a set of linearly independent elements $v_1, \ldots, v_n$, then $v_1, \ldots, v_n$, are called a basis of the vector space. Every basis of a vector space has the same number of elements and this number is called the dimension of this vector space. A vector u written as a linear combination of one basis $v_1, \ldots, v_n$, can be easily written as the linear combination of $w_1, \ldots, w_n$. Each w_i can be written as the linear combination of $v_1, \ldots, v_n$; therefore, by solving a system of n simultaneous linear equations, each v_i can be written as the linear combination of $w_1, \ldots, w_n$. Simple substitution then gives the required expression for u.

A color match requires only the judgement of identity without the extraction of any subjective quality, and should satisfy the requirements of an equivalence relation. The identity and commutativity conditions should be satisfied by the precision of the equipment and procedure used in the experiment. The transitivity condition is limited

by the finiteness of color discrimination. A number of experiments have shown that unless the luminance is high enough to significantly alter the optical density of the visual photopigments, or low enough to allow rods to intrude, foveal color matches satisfy the requirements for a three dimensional linear vector space: a) Any color can be expressed as a linear combination of three colors (Maxwell, 1860; and others). b) Brightening or dimming of all constituents by a constant factor (scalar multiplication) does not disturb a color match (von Kries, 1896; Trezona, 1954). Stiles (1955), in a single experiment on a 20 field (581.4 nm plus 445 nm matched to 526 nm plus 649 nm), found a small breakdown, but one that could well be within experimental error. c) Trezona (1953, 1954) did a number of experiments to test the invariance to superposition of color matches, i.e. if A matches B and C matches D, will A plus C match B plus D ? The deviations measured were generally smaller than a just discriminable difference. Von Kries (1878) investigated matches of sunlight against mixtures of pairs of complementary spectral lights before and after adaptation to various colored lights, and failed to detect any alteration in the amounts or wavelengths of the complementaries required. Additionally when color matching functions measured in two different primary systems are transformed to a common primary system, the two sets of color matching functions are similar. For example, Smith, Pokorny and Zaidi (1983) showed that the average of the color matching functions measured by Wright and Guild were similar to the average of the color matching functions measured by Stiles and Burch corrected for differences in pre-receptoral filters. These sets of evidence justify the representation of any color as a vector in a three-dimensional linear space. The mixture of two colors can be represented by the vector sum of the two colors.

Figure 2. Newton's (1704) color mixture diagram. The circumference represents colors in the Sun's spectrum. The mixture of any two colors lies on the straight line joining their locations in the diagram.

In a color matching experiment, the only formal condition that limits the choice of primaries is that it should not be possible to match any one of them by any combination of the other two. Color matches can be represented in a space with any three primaries as orthogonal axes. Moreover, the scale in which a primary is measured is independent of the scales for the other primaries. Consequently, angles and distances are arbitrary in a color matching space. However, ratios of segments along any line and the parallelism of lines are well defined. Transformation of a color matching space to another trio of primaries must preserve these last two properties, i.e. belong to the class of affine transformations (Schrodinger, 1920).
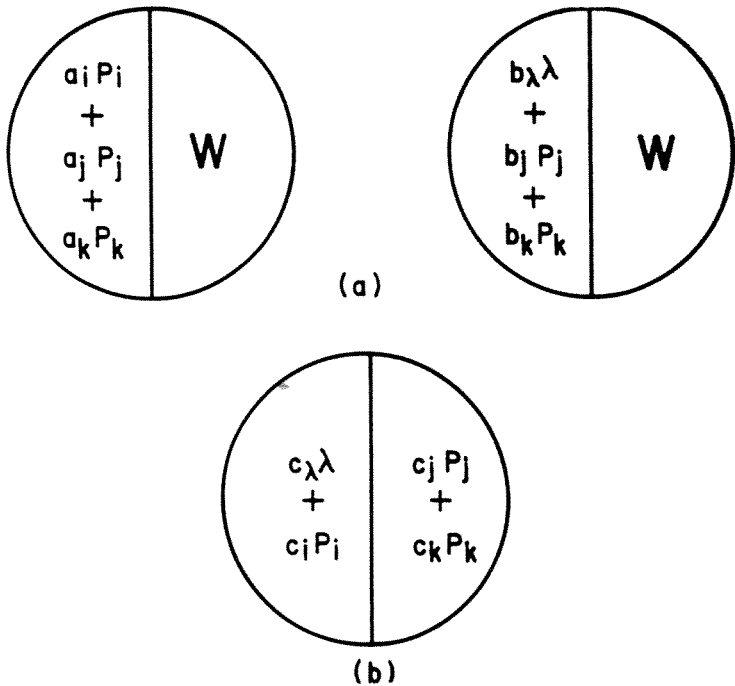
Figure 3. (a) Maxwell's method for measuring color matching functions. (b) Maximum saturation method for measuring color matching functions.

Mechanisms underlying trichromacy

A three-dimensional linear representation is compatible with many different mechanistic substrates. It is simplest to assume that the visual system is at some stage restricted to three independent wavelength sensitive linear channels, and that the information carried by each channel at a given instant and for a given point on the retina is expressible as the value of one continuous variable. The other stages of

the visual system cannot contain fewer than three independent channels, otherwise color discrimination would be mono- or dichromatic. They may, however, contain more than three independent channels peripheral to the critical stage, and as a result of interactions, more than three non-independent channels central to it. The first clear mechanistic explanation of trichomacy was given by Young (1802), who suggested that there was a continuous series of kinds of light, but only three kinds of sensitive particles in the retina, each preferentially but not exclusively sensitive to light from one part of the spectrum. The essential property of Young's mechanisms was explicated by Maxwell (1857): "Each nerve acts, not as some have thought, by conveying to the mind the knowledge of the length of an undulation of light, or of its periodic time, but simply by being more or less affected by the rays which fall on it. The sensation of each elementary nerve is capable only of increase or diminution, and no other change." This statement was given the physical interpretation that a photopigment can signal the number but not the wavelength of the quanta caught, and called the Principle of Univariance by Naka and Rushton (1960). The postulate generally used to link the response of mechanisms to empirical facts about color matches is Von Kries' (1878) implicit assumption that a match is established between two spectrally distinct lights, if and only if, the matched lights are alike in their effects on all three mechanisms. Brindley (1957, 1960) showed that the assumption is justified if the underlying mechanisms possess the following properties: a) Unidimensionality: For a receptor, given two distinct lights A and B there is always a number n such that nB provokes the same response as A; b) Substitutability: If a receptor x gives the same response to a light A as to a light B, then for any light C, $(A+C)$ has the same effect as $(B+C)$ and reciprocally, if $(A+C)$ and $(B+C)$ have equal effects, then so do A and B .

A mathematically more elegant way to build a mechanistic scheme is to represent the mechanisms as three linearly independent linear functionals (also see Resnikoff, 1974; Krantz, 1975). Let S be the infinite-dimensional linear vector space generated by the infinite basis $I_{400}, \ldots, I_{700}$. For all real numbers between 400 and 700, each I_λ is equal to one at wavelength λ and zero for all other wavelengths from 400 nm to 700 nm, i.e. S is the set of all visible spectral energy distributions. Then each mechanism can be regarded as a bounded linear functional F that assigns a real number to every vector (light) in S: If I_x and I_y are two elements of S, and a and b are real numbers, then a linear functional is defined by the property that the scalar assigned to a linear combination of vectors is equal to the linear combination of the scalars assigned to the individual vectors (Friedman, 1956):

$$F(aI_x + bI_y) = aF(I_x) + bF(I_y) \qquad (8)$$

A functional is bounded if there exists a constant m such that for all I_x in S:

$$\left| F(I_x) \right| < m \left| I_x \right| \qquad (9)$$

It can be shown that a linear functional is continuous if and only if it is bounded. Moreover, if $F(I_x)$ is a continuous linear functional on S, there

exists a vector F such that

$$F(I_x) = <F,I_x> \tag{10}$$

where $<F,I_x>$ is the scalar product of the vectors F and I_x. Therefore, the functional can be characterized by one vector. The characteristic vector expressed in the basis $I_{400}, \ldots, I_{700}$ is the spectral sensitivity of the mechanism, with each $<F,I_x>$ equal to the response to a unit amount of monochromatic light of wavelength λ. In the continuous case, the scalar product is equal to $\int F(\lambda) I(\lambda) \, d\lambda$.

The response of each mechanism is a scalar product, so no information about the constituents of the incident light is present in the response, consistent with the Principle of Univariance. A continuous linear functional satisfies both of Brindley's postulates: If the receptor has a non-zero response to both A and B, unidimensionality is satisfied if n is taken equal to $<F,A>/<F,B>$; substitutability is a direct consequence of Equation 8. Consequently, these mechanisms will also satisfy Von Kries' assumption.

Three linearly independent continuous linear functionals F_1, F_2, and F_3 generate a three-dimensional linear vector space. A set of linear functionals is linearly independent if F_i are linearly independent vectors. Addition and scalar multiplication of linear functionals is defined as follows:

$$(F_i + F_j)(I) = F_i(I) + F_j(I) \tag{11}$$

$$(cF_i)(I) = cF_i(I) \tag{12}$$

The null functional is the functional $F_i(I) = 0$ for all I in S, i.e. $F_i = (0, \ldots, 0)$. Every light I in S can be represented as a three dimensional point $(F_1(I), F_2(I), F_3(I))$ in this vector space.

It is straightforward to prove that three functional mechanisms are consistent with the tri-variance and linearity of color matches. A corollary is the proof of Konig and Dieterici's (1886) assumption that, in trichromatic vision, the spectral sensitivities of the three channels determining trichromacy must be linear functions of the tri-stimulus values, with coefficients independent of test wavelength. The proof begins by assuming that given a system consisting of three independent linear functionals F_1, F_2, and F_3, the number of primaries required for a color match is n. A color match for test wavelength λ and primaries $I_1, \ldots, I_n$, is defined as before:

$$I_\lambda = a_{\lambda 1} I_1 + \cdots + a_{\lambda n} I_n \tag{13}$$

By Von Kries' assumption, the response of each color mechanism should be equal for the two sides of the match. Therefore for each mechanism F_i:

$$F_i(\lambda) = F_i(a_{\lambda 1} I_1 + \cdots + a_{\lambda n} I_n) \tag{14}$$

Because the three mechanisms are linear, responses to a mixture can be separated into responses to each primary:

$$F_1(\lambda) = a_{\lambda 1 F_1}(I_1) + \cdots + a_{\lambda n}F_1(I_n)$$

$$F_2(\lambda) = a_{\lambda 1}F_2(I_1) + \cdots + a_{\lambda n}F_2(I_n) \quad (15)$$

$$F_3(\lambda) = a_{\lambda 1}F_3(I_1) + \cdots + a_{\lambda n}F_3(I_n)$$

The linearity of color matches is simply due to the linearity of all three underlying mechanisms. For each mechanism, if $F(I_w)=F(I_x)$ and $F(I_y)=F(I_z)$, then:

$$F(I_w + I_y) = F(I_x + I_z) \quad (16)$$

Therefore, if I_w matches I_x and I_y matches I_z then $(I_w + I_y)$ will match $(I_x + I_z)$.
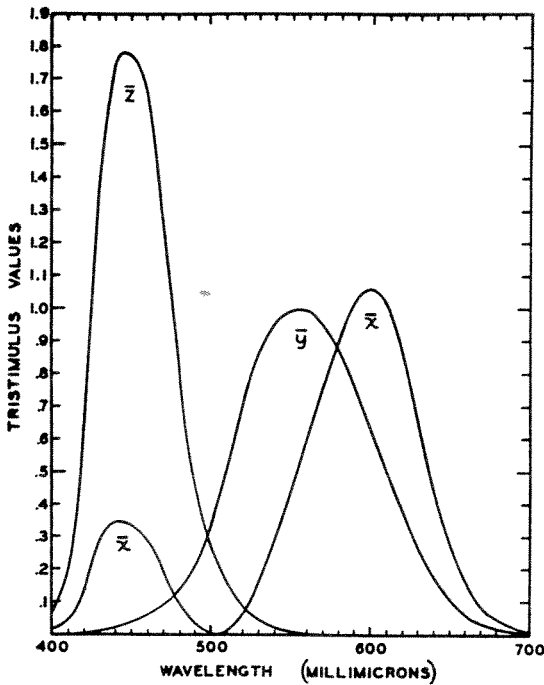
Figure 4. Tristimulus values for spectral lights. The values x, y, and z are the amounts of the three CE (1931) primaries required to color match a unit amount of energy having the indicated wavelength.

To see that trichromacy can be derived from the proposed scheme, consider solving the three simultaneous linear equations (Equation 15) for unknowns $a_{\lambda j}$ as a function of the different numbers of primaries in the match. If for a wavelength λ only one primary I_1 is needed for a color match, then either two of the mechanisms have zero response for λ and I_1, or $F_i(\lambda)/F_i(I_1)$ is equal for all three mechanisms.

If for a test wavelength λ only two primaries are needed, then either one of the mechanisms has zero response for λ, I_1, and I_2, or the response of one mechanism is the same linear combination of the responses of the other two for λ, I_1, and I_2. If three primaries are used in the match, the set of equations will have a unique solution expressing the $a_{\lambda j}$ as linear combinations of $F_i(\lambda)$. If four or more primaries are used, there will be an infinite number of solutions with all the extra primaries expressed as linear combinations of three primaries. Therefore, this set of mechanisms form a sufficient substrate for trichromatic matches. Furthermore, given a three primary match, for any wavelength λ, the spectral sensitivities of each of the three mechanisms $F_i(\lambda)$ are expressed in Equation 15 as linear combinations of the tri-stimulus values $a_{\lambda j}$, with coefficients $F_i(I_j)$ independent of wavelength λ.
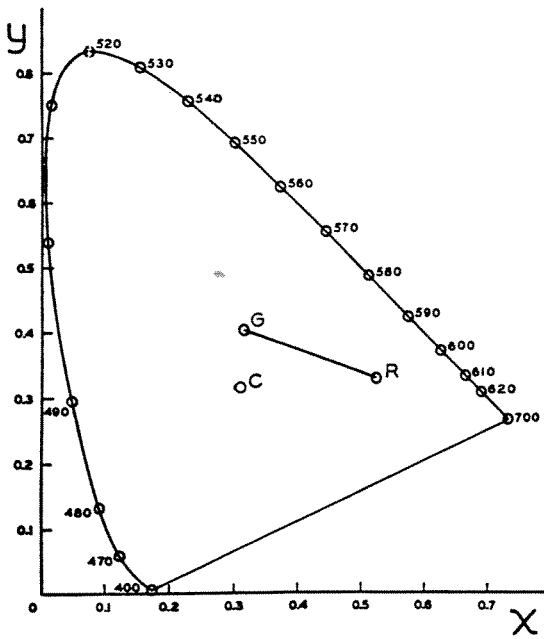
Figure 5. CIE (1931) chromaticity diagram showing the curved locus of spectral colors. The straight line joining 400 to 700 nm is the line of purples. All additive mixtures of the colors R and G lie on the line RG. Similarly, all real colors, i.e. all mixtures of the spectral colors, lie within the solid boundary.

Derivation of photopigment spectral sensitivities

Light absorption by photopigments has linear properties similar to those attributed to the three color mechanisms above, and there is evidence from microspectrophotometry and electrophysiology that

there are three classes of cone photopigment in the human fovea (Dartnall et al., 1983; Schnapf et al., 1987). Therefore, it is generally assumed that trichromacy is determined by the quantum catch of three cone photopigments S, M and L (short, middle and long wavelength sensitive). The derivation of the spectral sensitivities of these photopigments as unique linear combinations of color matching functions, requires additional information to pick from among the infinite number of possible combinations. A number of derivations have been based on Konig's hypothesis that congenital dichromats have reduced forms of trichromatic vision, i.e. dichromats accept all color matches made by normal trichromats but not vice versa (*e.g.* Konig and Dieterici, 1893; Thomson and Wright, 1953; Vos and Walraven, 1971; Smith and Pokorny, 1975; Vos et al., 1990). In a three-dimensional representation of trichromatic vision, due to the linearity of dichromatic color matches (Nagy, 1984), color confusions of dichromats form a simple picture and the derivation of cone spectra is easy to intuit. Since almost all published derivations represent colors in a two-dimensional projection plane (Vos and Walraven, 1971; Wyszecki and Stiles, 1982), a simpler three-dimensional derivation based on Maxwell's suggestions is presented in this section.

For notational convenience, the three mechanisms determining trichromacy are assumed to be L, M, and S cones. The characteristic vector, or spectral sensitivity of each of the cone types is given by:

$$L = (l_{400}, \ldots, l_{700}) \tag{17}$$

$$M = (m_{400}, \ldots, m_{700}) \tag{18}$$

$$S = (s_{400}, \ldots, s_{700}) \tag{19}$$

Each element in a vector represents the relative proportion of quanta absorbed by a class of cones from light of the subscripted wavelength. For example:

$$l_{520} = <L, I_{520}> \tag{20}$$

Because of the linearity of the mechanisms, the quanta absorbed by a class of cones from a heterochromatic light I is simply the sum of the quanta absorbed from each of the monochromatic constituents of I, i.e.

$$l_I = <L, I> \tag{21}$$

It would be easy to measure the spectral sensitivity of each cone type if three lights P, D, and T could be found such that each of them excited one type of cone only. If:

$$l_P = 1, \quad m_P = 0, \quad s_P = 0; \tag{22}$$

$$l_D = 1, \quad m_D = 0, \quad s_D = 0; \tag{23}$$

$$l_T = 1, \quad m_T = 0, \quad s_T = 0; \tag{24}$$

then all three spectral sensitivities could be measured directly by an

experiment in which a normal trichromat matched a unit amount of monochromatic light of each wavelength to a mixture of the three primaries P, D and T. Each match would yield an equation:

$$I_\lambda = p_\lambda P + d_\lambda D + t_\lambda T \tag{25}$$

From Equations 20 and 22-24, it is obvious that $l_\lambda = p_\lambda$, $m_\lambda = d_\lambda$, and $s_\lambda = t_\lambda$, therefore Equation 25 can be rewritten so that the coefficients in the match are the cone spectral sensitivities for λ:

$$I_\lambda = l_\lambda P + m_\lambda D + s_\lambda T \tag{26}$$

However, this trio of real lights P, D and T does not exist, therefore the derivation will resort to a method suggested by Maxwell(1860) and revived by Nuberg and Yustova (1955) and Judd (1964). For a trio of arbitrary real primaries R, G, and B, if the color match for any monochromatic light I_λ can be written as:

$$I_\lambda = r_\lambda R + g_\lambda G + b_\lambda B \tag{27}$$

Then the complete set of color matching functions can be depicted as:

$$R = (r_{400}, \ldots, r_{700}) \tag{28}$$

$$G = (g_{400}, \ldots, g_{700}) \tag{29}$$

$$B = (b_{400}, \ldots, b_{700}) \tag{30}$$

Maxwell's method requires assuming that spectral distributions (but not necessarily real lights) P, D and T exist, and can be matched to the three real primaries R, G and B, such that:

$$P = r_P R + g_P G + b_P B \tag{31}$$

$$D = r_D R + g_D G + b_D B \tag{32}$$

$$T = r_T R + g_T G + b_T B \tag{33}$$

Substituting Equations 31, 32, and 33 into 26:

$$I_\lambda = l_\lambda r_P R + l_\lambda g_P G + l_\lambda b_P B$$
$$+ m_\lambda r_D R + m_\lambda g_D G + m_\lambda b_D B \tag{34}$$
$$+ s_\lambda r_T R + s_\lambda g_T G + s_\lambda b_T B$$

Equating the amounts of R, G and B in Equations 27 and 34:

$$r_\lambda = l_\lambda r_P + m_\lambda r_D + s_\lambda r_T \tag{35}$$

$$g_\lambda = l_\lambda g_P + m_\lambda g_D + s_\lambda g_T \tag{36}$$

$$b_\lambda = l_\lambda b_P + m_\lambda b_D + s_\lambda b_T \tag{37}$$

This triplet of simultaneous linear equations can be solved for l_λ, m_λ, and s_λ by any of the traditional methods. A particularly convenient method is to represent Equations 35-37 in matrix notation:

$$\begin{pmatrix} r_\lambda \\ g_\lambda \\ b_\lambda \end{pmatrix} = \begin{pmatrix} r_P & r_D & r_T \\ g_P & g_D & g_T \\ b_P & b_D & b_T \end{pmatrix} \begin{pmatrix} l_\lambda \\ m_\lambda \\ s_\lambda \end{pmatrix} \tag{38}$$

The solution requires pre-multiplying both sides by the inverse of the matrix of coefficients:

$$\begin{pmatrix} l_\lambda \\ m_\lambda \\ s_\lambda \end{pmatrix} = \begin{pmatrix} r_P & r_D & r_T \\ g_P & g_D & g_T \\ b_P & b_D & b_T \end{pmatrix}^{-1} \begin{pmatrix} r_\lambda \\ g_\lambda \\ b_\lambda \end{pmatrix} \tag{39}$$

Therefore, the spectral sensitivities of the three cone types l_λ, m_λ, and s_λ can be derived for any wavelength λ, from a color match of l_λ. with any three real lights R, G and B, if the nine coefficients of the matrix can be determined.

These coefficients can be obtained from color matches made by congenital dichromats using the same primaries R, G and B. Congenital dichromats accept the matches made by trichromats, but also match some pairs of colors that are distinct to a trichromat, therefore, their color vision is a reduced form of trichromatic vision. It is assumed that protanopes lack L cones, deuteranopes M and tritanopes S . For example, a protanope may match two lights J and K that are distinct to a trichromat, i.e., $J=K$ for a protanope but $J \neq K$ for a trichromat. This can only be true if $m_J = m_K$ and $s_J = s_K$ but $l_J \neq l_K$. According to Maxwell's method, if $P = J\text{-}K$, then P will satisfy the requirements of Equation 22. Notice that even though J and K are real lights, P may be a spectral distribution with negative entries and hence not a physically realizable light. P is important only as a mathematical entity. Because cone absorptions are linear operations, the M cone absorption from P is equal to the M cone absorption from J minus the M cone absorption from K, i.e. zero:

$$m_p = <M,P> = <M,(J - K)> = <M,J> - <M,K> = m_j - m_k = 0 \tag{40}$$

Similarly $s_P = 0$ but $l_P \neq 0$, i.e. P excites only L cones. Since P is just the difference between two colors, the three coefficients of the matrix that correspond to P in Equation 39 can be derived from the tri-stimulus values for J and K. If for normal trichromats the color matches for J and K are represented by Equations 41 and 42:

$$J = r_j R + g_j G + b_j B \tag{41}$$

$$K = r_k R + g_k G + b_k B \tag{42}$$

then, because of the linearity of dichromatic color matches, the

coefficients for P in Equation 31 are simply the difference between the coefficients for the pair of confusion colors J and K:

$$r_P = (r_J - r_K)$$ (43)

$$g_P = (g_J - g_K)$$ (44)

$$b_P = (b_J - b_K)$$ (45)

It is worth noting that the difference between all pairs of protanopic confusion colors will give an estimate of the same nP where n is some constant. Similarly the coefficients corresponding to D and T can be derived by finding pairs of confusion colors for congenital deuteranopes and tritanopes. Then the spectral sensitivities L, M and S (Equations 17-19) for the three cone types can be derived from empirical color matching functions R, G, and B (Equations 28-30), by rewriting Equation 39 so that each row of variables is an array instead of a single wavelength:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} r_P & r_D & r_T \\ g_P & g_D & g_T \\ b_P & b_D & b_T \end{pmatrix}^{-1} \begin{pmatrix} R \\ G \\ B \end{pmatrix}$$ (46)

This algebraic derivation can also be pictured geometrically. Each I can be represented as a vector in the three-dimensional space formed by R, G, and B as axes. The three vectors P, D, and T are the vector differences of pairs of colors confused by congenital protanopes, deuteranopes and tritanopes respectively. Another way to visualize the confusion vectors is as follows: For any color E and any scalar n, let $F = E + nP$. Then using Equation 22 to add cone excitations from nP to excitations from E, $m_E = m_F$ and $S_E = S_F$, but $l_E \neq l_F$, i.e. E and F can be distinguished by a trichromat but not by a protanope. So for any color vector in RGB space, adding a vector parallel to P results in a confusion pair for protanopes. Similarly, adding a vector parallel to D or T results in con fusion pairs for deuteranopes and tritanopes respectively. Reciprocally, the difference vectors between pairs of confusion colors for an individual dichromat are all parallel. If the space is transformed to P, D, and T as axes, then each I will be represented in a cone-excitation space. Because color spaces are affine, the relative heights of the cone sensitivities cannot be ascertained from color matching data.

In practice there are a number of problems with the derivation of Konig fundamentals. The first problem is a logistic one. Generally, dichromatic color confusions were measured in chromaticity co-ordinates (Pitt, 1935; Wright, 1952) because colorimetric procedures were more accurate than available radiometric instruments. Since accurate instruments to measure tri-stimulus values are now available, it would be preferable to measure difference vectors, since in tri-stimulus values, every pair of confusion colors for a dichromat would provide an independent estimate of the same confusion vector and lead to greater numerical precision. In a chromaticity diagram, P, D, and T
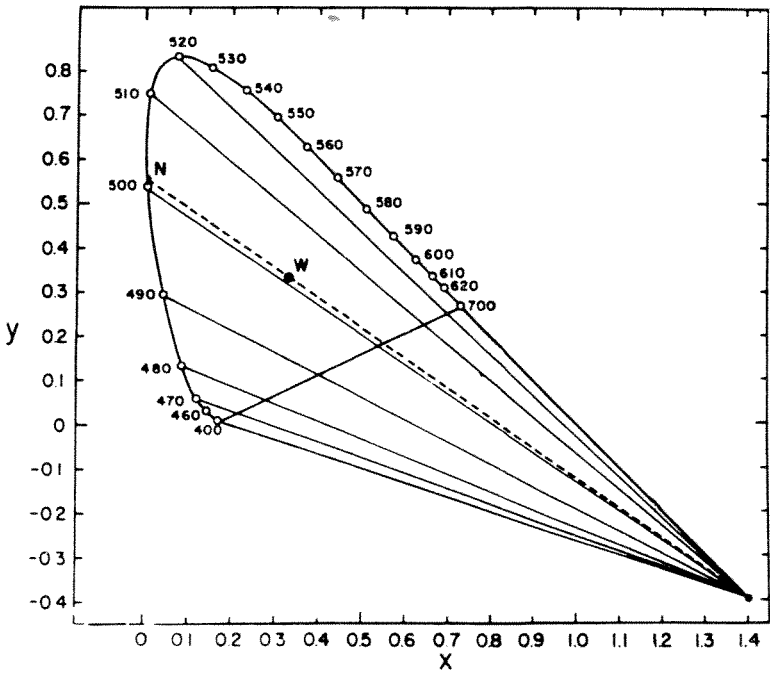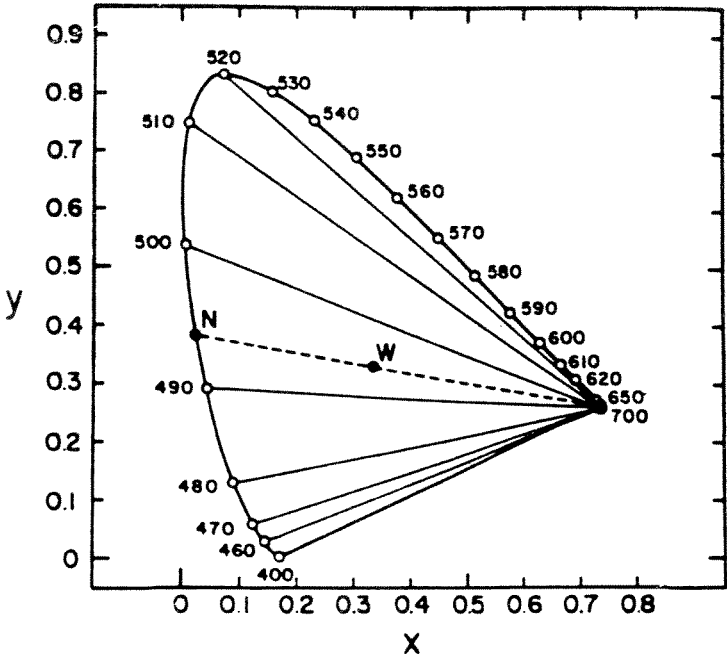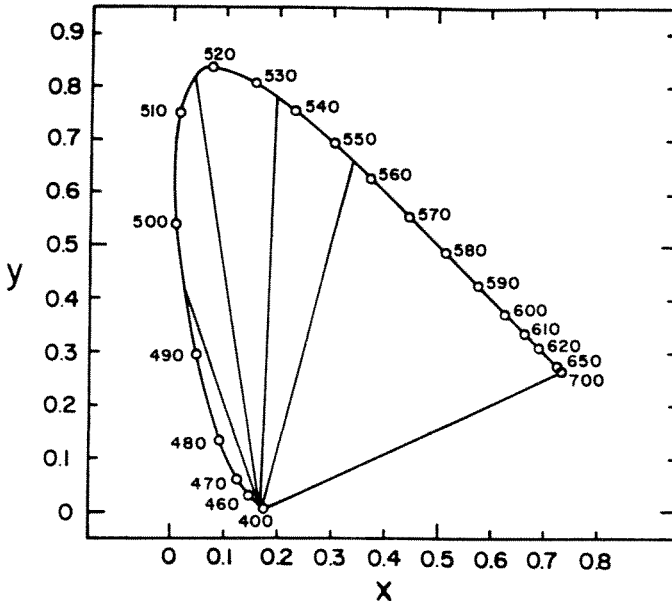
Figure 6. Dichromatic color confusions converging to single points in the CIE chromaticity diagram for (**a**) (top panel, preceding page) protanope, (**b**) (bottom, preceding page) deuteranope, and (**c**) tritanope.

each project to a single point called the convergence point for that class of dichromat (Figure 6), unless the plane of projection is parallel to one of the confusion vectors. The three pairs of dichromatic convergence coordinates only provide six of the coefficients needed in Equation 46, so auxiliary assumptions and data are needed for the remaining three. A usual strategy is to assume particular weights for the contributions of the three cone types to the luminosity function (Vos and Walraven, 1971; Smith and Pokorny, 1975; Vos et al., 1990). The second problem is that even if observers possess photopigments of identical spectral sensitivity, their color matching functions will be different due to differences in the amount of lens and macular pigments and in the optical density of the photopigments. A set of average color matching functions for a particular class of observer then depends on the characteristics of the sample of observers measured (Zaidi et al., 1989). More importantly, it is not possible to test Konig's reduction hypothesis by direct confrontation of trichromatic and dichromatic matches (Alpern and Pugh, 1977; Pokorny and Smith, 1977). A reduction system can be tested for an individual dichromat by testing that the differences between pairs of confusion colors are all parallel in *RGB* space, or equivalently, that in a chromaticity space the lines joining confusion colors converge to a single point. This problem has been dealt with by either using WDW normalization (Wright, 1928-1929) or using published estimates to correct to an average observer (Smith and Pokorny, 1975). A third problem is the potential of relying too heavily

on the precision of measurement of the dichromatic convergence points (Nimeroff, 1970; Walraven, 1974). Historically, the empirical estimates of convergence points have been adjusted iteratively so that the derived cone sensitivities are consistent with pigment nomograms and can predict not only color mixture data, but also a variety of types of other measurements on dichromats and monochromats, including spectral sensitivity and luminosity (Smith and Pokorny, 1972, 1975). A fourth problem is that whereas protanopes and deuteranopes have been shown to lack one of the normal pigments in the long wave part of the spectrum (Rushton, 1972), tritanopes with complete absence of S cone pigment may not exist (Pokorny, Smith and Went, 1981). Despite all these problems, estimates of cone sensitivities, derived from color mixture and other methods, converge to a set very close to that shown in Figure 7 (Stockman, 1989). This set (Smith and Pokorny, 1975) is based on the following transformation from Judd's (1951a) modification of the CE (1931) color matching functions:

$$
\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} .15514 & .54312 & -.03286 \\ -.15514 & .45684 & .03286 \\ 0 & 0 & .01608 \end{pmatrix} \begin{pmatrix} \bar{x} \\ \bar{y} \\ \bar{z} \end{pmatrix} \tag{47}
$$

Recently, additional support for the theory explicated above has come from electrophysiological recordings from single cones of the human retina (Schnapf et al., 1987). Four facts about the electrophysiological measurements are particularly germane. First, the response of a cone is the same for equal quanta caught from lights of different wavelengths, consistent with the Principle of Univariance. Second, the measured spectral sensitivities cluster into three discrete classes with minimal variability within each class. Third, the measured sensitivities provide a good fit to human color matching functions on the assumption that for a color match the quantal catch for each class of cone is identical for both sides of the match, and with adjustments for optical density of photo pigments and pre-retinal absorption. Fourth, within the freedom provided by these adjustments, the action spectra of the cones, that is the reciprocal of the amount of light of each wavelength required to produce a constant response, closely resemble the Smith-Pokorny fundamentals.

Cone interactions and opponent mechanisms

Because the output of cones of different classes are combined very early in the retina, it is difficult to find other psychophysical tasks besides color matching where each class of cones functions independently. One notable exception is dark adaptation after intense bleaches, where sensitivity as measured by a method of revived afterimages seems to be regulated within each cone class independently (Williams and MacLeod, 1979). Another possible case is the detection of small, brief pulses of light (Krauskopf and Srebro, 1965). In most color experiments, the results indicate some degree of interaction between different classes of cones. For example, Stiles' (1939, 1959) two color increment threshold technique identified seven foveal π-mechanisms, some of which are now thought to involve post-receptoral interactions

(*e.g.* Pugh and Mollon, 1979). Wright (1946) examined the possibility of parallel independent adaptation processes in the three cone systems by testing the assumption of superposition (additivity) for binocular color matches. With the two eyes in different states of adaptation, an observer matched stimulus s_1 in one eye by the mixture (r_1, g_1, b_1) in the other eye and stimulus s_2 by (r_2, g_2, b_2). However, s_3 equal to $s_1 + s_2$, was matched by (r_3, g_3, b_3) some of whose components were considerably less than the sum predicted by the assumption of additivity, e.g., $r_3 <<$ $r_1 + r_2$. This failure of additivity was consistent with inhibition between different classes of cone, and indicated a breakdown of the Von Kries (1905) coefficient rule of independent cone adaptations. Additional violations of the Von Kries rule have been described by a number of authors, including Brewer (1954), Hurvich and Jameson (1958) and Shevell (1978). Failures of additivity have also been used by Boynton et al (1964), Guth et al. (1969), Pugh (1976), Mollon and Polden (1977), and others to demonstrate cone interactions in increment threshold measurements.
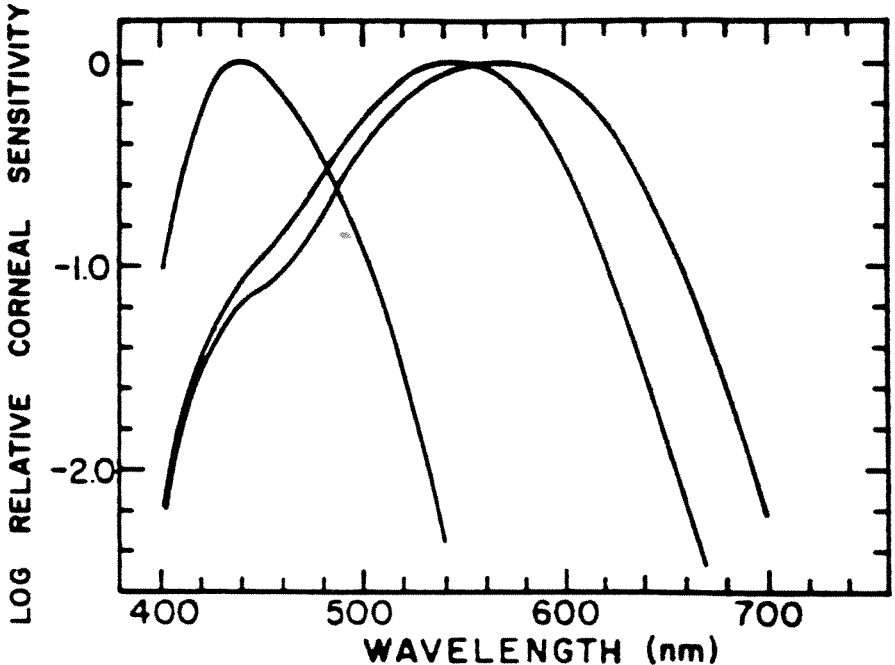
Figure 7.   Log of the spectral sensitivities of the visual pigments hypothesized to be active in foveal color matches of normal trichromats.

Identification of the chromatic properties of the mechanisms formed by interactions between cones had its beginning in Hering's (1878) phenomenal observation that any color can be described in terms of six basic sensations: red, green, yellow, blue, white and black

(English translation in Abney, 1895). Red-green and yellow-blue are opponent sensations along a single dimension, because only one sensation of each pair can be elicited by a uniform color. The two pairs function in parallel, so that red can be seen simultaneously with yellow or blue and the same is true of green. Instead of tri-stimulus color matching functions, Hering proposed a trio of "valence" curves (Figure 8). For each monochromatic light, the red-green valence curve
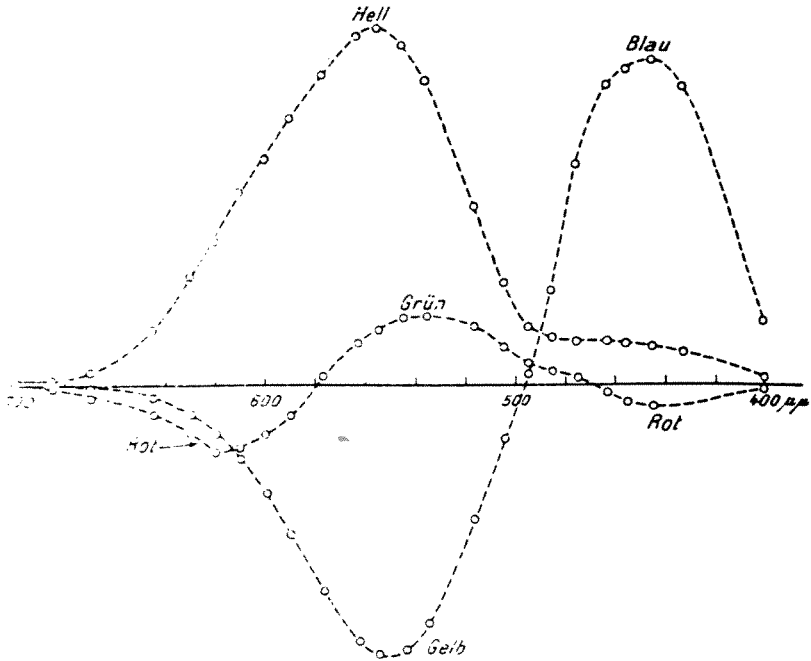
Figure 8. Hering's valence curves derived from Konig fundamentals (Schrodinger, 1925).

indicates the amount of redness or greenness and the yellow-blue curve the amount of yellowness or blueness. The third valence curve indicates lightness or darkness. The red-green valence curve has three lobes, red in the long and short wavelengths and green in the middle; the yellowblue curve has two lobes, yellow in the long and blue in the short wavelengths; the lightness curve has a peak in the middle wavelengths and tapers off to both sides. Hering was noncommittal about a peripheral or central locus for opponent color mechanisms, but other investigators incorporated opponent mechanisms into stage theories (Donders, 1881; Von Kries, 1905). In stage theories, a peripheral stage consists of three types of cones with sensitivities given by Konig fundamentals; a more central stage consists of mechanisms that linearly combine the outputs of the first stage into two subtractive chromatic mechanisms and one additive achromatic mechanism. Other versions of

these theories include those of Adams (1923, 1942), Muller (1924, 1930), Judd (1949, 1951b), Jameson and Hurvich (1955), Hurvich and Jameson (1958), Guth and Lodge (1973), and Ingling (1977).

Schrodinger (1925) showed that Hering type valence curves are equivalent to straight lines through white in a chromaticity diagram. The essential insight was that color matching functions are a linear transform of cone spectral sensitivities. If valence curves could be identified with linear combinations of cone spectra as proposed by Von Kries (1905), then valences should be a linear transform of color matching functions too. The explicit derivation is easy to describe in matrix notation. If RG, YB, and LD, the red-green, yellow-blue and light-dark valence associated with a spectral light l, are independent linear combinations of the quanta caught by L, M, and S cones, then:

$$\begin{pmatrix} RG \\ YB \\ LD \end{pmatrix} = \begin{pmatrix} l_{RG} & m_{RG} & s_{RG} \\ l_{YB} & m_{YB} & s_{YB} \\ l_{LD} & m_{LD} & s_{LD} \end{pmatrix} \begin{pmatrix} L \\ M \\ S \end{pmatrix} \tag{48}$$

Substituting the values of L, M, and S from Equation 46 into 48, the valences can be described as linear combinations of color matching functions:

$$\begin{pmatrix} RG \\ YB \\ LD \end{pmatrix} = \begin{pmatrix} r_{RG} & g_{RG} & b_{RG} \\ r_{YB} & g_{YB} & b_{YB} \\ r_{LD} & g_{LD} & b_{LD} \end{pmatrix} \begin{pmatrix} R \\ G \\ B \end{pmatrix} \tag{49}$$

where:

$$\begin{pmatrix} r_{RG} & g_{RG} & b_{RG} \\ r_{YB} & g_{YB} & b_{YB} \\ r_{LD} & g_{LD} & b_{LD} \end{pmatrix} = \begin{pmatrix} l_{RG} & m_{RG} & s_{RG} \\ l_{YB} & m_{YB} & s_{YB} \\ l_{LD} & m_{LD} & s_{LD} \end{pmatrix} \begin{pmatrix} r_P & r_D & r_T \\ g_P & g_D & g_T \\ b_P & b_D & b_T \end{pmatrix}^{-1} \tag{50}$$

In three-dimensional RGB space, lights with zero RG valence are described by Equation 51, which defines the null RG plane:

$$RG = r_{RG} R + g_{RG} G + b_{RG} B = 0 \tag{51}$$

In a two dimensional chromaticity space plotted in barycentric coordinates r, g, and b given by Equation 52:

$$r = \frac{R}{R + G + B}; \quad g = 1 - r - b; \quad b = \frac{R}{R + G + B} \tag{52}$$

The null plane projects to a straight line given by Equation 53:

$$b = \left(\frac{g_{RG}}{g_{RG} - b_{RG}} \right) + \left(\frac{r_{RG} - g_{RG}}{g_{RG} - b_{RG}} \right) r \tag{53}$$

Similar derivations lead to straight null lines in chromaticity space for YB and LD.

Schrodinger derived the coefficients for RG and YB in Equation 49 by using the chromaticity coordinates of psychologically unique hues (Figure 9). Unique blue and unique yellow are hues that are neither reddish nor greenish, and unique red and green are neither yellowish nor bluish. The line passing through unique yellow, achromatic white and unique blue was taken as the null line for RG and the coefficients derived from an equation similar to Equation 53. Similarly, the line passing through unique red, achromatic white and unique green was used to derive the coefficients for YB The coefficients for LD were derived from a new kind of line, the alychne, representing the null of Exner's luminosity function. The three valences derived using Konig and Dieterici's chromaticity diagram, when plotted on a wavelength axis, resembled Hering's qualitative valence curves (Figure 8).
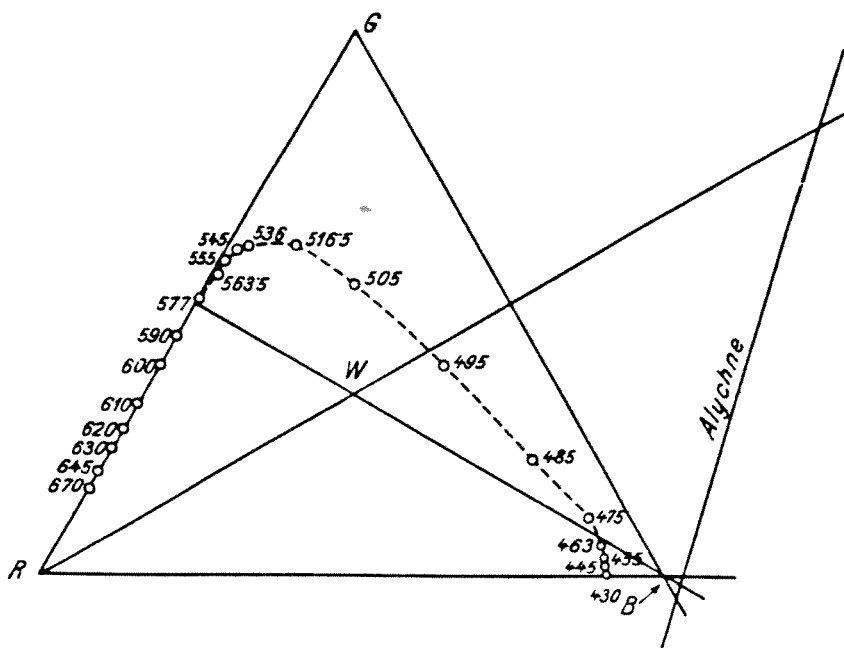
Figure 9.   Konig's color triangle with the alychne and null lines for opponent mechanisms passing through white (Schrodinger, 1925).

Schrodinger's procedure provides a method for critically testing the efficacy of Hering type hue judgments to reveal the properties of second stage mechanisms. Dimmick and Hubbard (1939a) measured the spectral locations of the unique hues; 477, 515 and 583nm for blue, green, and yellow respectively. The line joining unique blue and yellow

passed through the reddish side of white. The chromatic location of unique red was ascertained by mixing unique blue to a spectral red to get a color that was neither "yellowish" nor "bluish" (Dimmick and Hubbard, 1939b). Unique red was complementary to 493.6 nm and not to unique green, implying that the line joining unique red to achromatic white is not collinear with the line joining achromatic white to unique green. Consequently, the yellow-blue hue system is not a linear combination of cone inputs. Burns et al. (1984) measured the loci of constant unique hues at equal luminance. Their data plotted on a chromaticity diagram do not fall on straight null lines as required to generate hue valence curves. Jameson and Hurvich (1955) attempted to measure valence curves directly by extending the Dimmick and Hubbard type of hue cancellation technique to all four unique hues. For each of the unique hues, hue-cancellation results in colors of a constant hue but varying saturation. In a chromaticity diagram, these points are just a subset of constant hue data like that of Abney (1910), Burns et al. (1984), and others. Further work with the hue-cancellation technique, *e.g.* Larimer, Krantz and Cicerone (1975), Ikeda and Ayama (1980) and Pokorny et al. (1981), has provided more evidence that hue judgments do not satisfy assumptions of linearity.

The spectral sensitivity or valence of a post-receptoral mechanism enables the response of the mechanism to a compound light I to be predicted from its response to monochromatic lights I_λ. Nonlinear post-receptor mechanisms cannot be said to have a spectral sensitivity or a valence in the usual sense. A post-receptor mechanism whose response is a function H of the quantum catches of L, M, and S cones, has a response $H(<L,I>,<M,I>,<S,I>)$ to light I. The response of this mechanism can be written as a function of the spectral distribution of the light I: $<H(L,M,S),I>$, if and only if H is a linear function. The sensitivity of a nonlinear mechanism can be described only as a function of quanta caught by the three classes of cones.

A related issue is the independence of hue judgments across the three Hering dimensions. It was recognized by Purdy (1931), that this issue could be tested by measuring the perceived change in hue with changes in radiance (Bezold-Brucke effect) and by the perceived change in saturated hues due to addition of an achromatic white (Abney effect). Purdy showed that hues that were invariant to changes in radiance or saturation were not the same as the psychologically unique hues, contradicting the independence of Hering's hue mechanisms. Measurements of the Bezold-Brucke and Abney effects for an extensive set of wavelengths (Nagy, 1980; Burns et al., 1984) cannot be explained by simple response non-linearities in independent hue mechanisms, but require interactions across hue dimensions. Judgments based on the appearance of colors are probably the result of higher level processing of cone signals and not a suitable method to isolate the properties of an early opponent stage.

Schrodinger's mathematical analysis of second stage mechanisms need not be restricted to hue judgments alone. Linear post-receptoral mechanisms can be identified with straight null lines in chromaticity space as a general rule. In addition, hue judgments are not the only data on which second stage mechanisms have to be based. Steps in this direction were taken by Guth and Lodge (1973) and Guth, Massof and Benzchawel (1980), who based their model on a variety of

threshold measurements and hue judgments. A different approach to second-stage mechanisms was taken by Krauskopf et al. (1982) who directly searched for three linear second-stage mechanisms defined with reference to cone signals rather than unique hues.

The experiments that follow are more easily described if colors are represented on a set of axes defined using estimates of cone spectra. The space is depicted in three planes in Figure 10 (a three-dimensional picture of a subset of this space can be found in Derrington et al., 1984). To derive this space, the Smith-Pokorny cone excitations, L, M, and S (Equation 47) are converted to luminance units l, m, and s for each light:

$$l = \frac{L}{L + M} \; ; \quad m = 1 - l \; ; \quad s = \frac{S}{L + M} \qquad (54)$$

l and m are defined relative to one another, whereas s can be independently multiplied by any constant. The MacLeod and Boynton (1978) chromaticity diagram uses s and l (or m) as axes and depicts colors on a plane of unit luminance. Similar transformations were used previously by LeGrand (1949) and Rodieck (1973). The three axes are called rg, yu and ld So that their names can function as mnemonics based on the approximate colors, red, green, yellow, violet, light, dark, at the ends of the axes. In the space depicted in Figure 10, the transformation from the units of Equation 54 to the axes is:

$$\begin{pmatrix} ld \\ rg \\ yv \end{pmatrix} = \begin{pmatrix} 1 & 1 & 0 \\ 5.68 & -11.27 & 0 \\ -1.235 & -1.235 & 58.82 \end{pmatrix} \begin{pmatrix} l \\ m \\ s \end{pmatrix} - \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \qquad (55)$$

The reverse transform is easy to see in the figure:

$$\begin{pmatrix} l \\ m \\ s \end{pmatrix} = \begin{pmatrix} .665 & .059 & 0 \\ .335 & -.059 & 0 \\ .021 & 0 & .017 \end{pmatrix} \begin{pmatrix} ld \\ rg \\ yv \end{pmatrix} + \begin{pmatrix} .665 \\ .335 \\ .021 \end{pmatrix} \qquad (56)$$

A number of properties of this space are apparent on examining the figure: a) The origin of the space is at a white of mid-radiance; b) along the rg axis, s is constant and l and m change in opposite directions so as to keep their sum, i.e. luminance, constant; c) along the yv axis, l and m are constant and only s varies. d) along the ld axis, the cone excitations increase proportionally from zero keeping the ratios equal to the ratios of excitation at white.

In the Krauskopf et al. (1982) experiments, two lines in color space were taken to be mutually independent, if color discriminations along each line were not affected by prolonged exposure to a field temporally modulated along the other line. First, the isoluminant plane shown in Figure 10a was examined. With the observer adapted to the mid-white, thresholds were measured for pure chromatic changes towards different test directions. The field was then sinusoidally modulated in time symmetrically around white along one of the test directions. After habituation, the chromatic discrimination thresholds
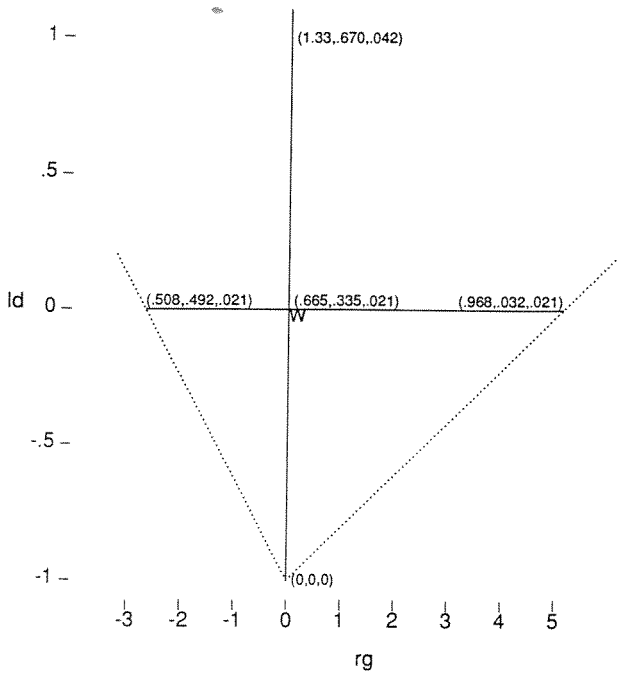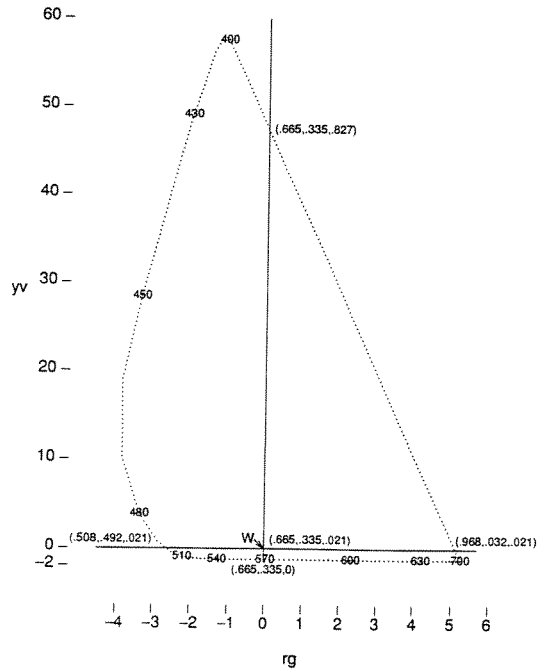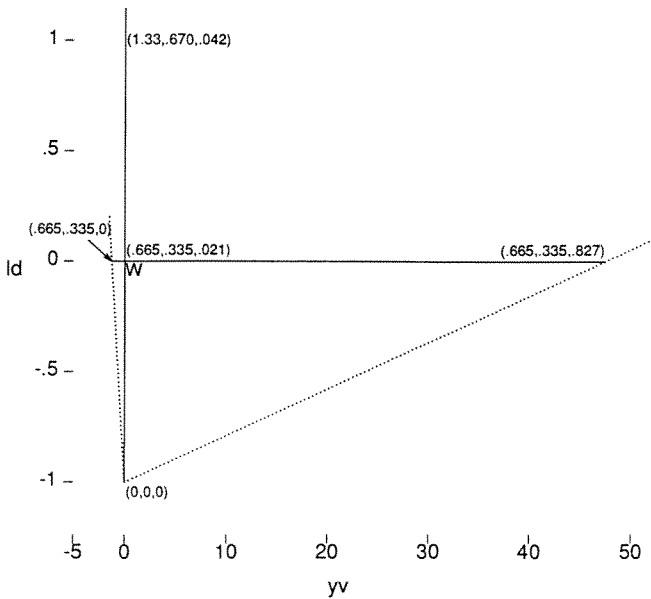
Figure 10. Three planes depicting a three-dimensional color space in cardinal axes. (**a**) (top panel, preceding page) *rg* vs *y v* on the isoluminant plane, cone excitations from MacLeod and Boynton (1978); (**b**) (bottom panel, preceding page) *rg* vs *ld*; (**c**) *yv* vs *ld* . The axes are solid lines; the dotted lines depict the boundary of real lights. The units of the main axes are given on the left and bottom; the triplets in parentheses are (*l,m,s*) excitations; the numbers on the curved boundary are wavelengths of spectral lights.

were remeasured, and the log of the ratio of the post to pre thresholds taken as an index of desensitization. The main result was that for *rg* and *yv* axes, thresholds were raised in the direction of habituation but virtually unchanged in the orthogonal direction. Habituation along one of the intermediate directions, however, elevated thresholds fairly uniformly around the plane, including in the orthogonal direction. There were thus only two independent or cardinal directions in the isoluminant plane as defined by selective habituation. By a similar procedure, the *ld* axis was found to be the third independent or cardinal axis of color space. As is clear from Figure 10, modulations along *ld* lead to the maximum modulation of cone signals. Since this modulation had negligible effects on discriminations along chromatic axes, the desensitizing effect of chromatic modulation must occur after cone interactions. The results of this experiment would obviously be consistent with the existence at some stage, of three linear post-receptoral mechanisms with cone weights given by the 3 x 3 matrix of coefficients in Equation 55. Two questions could be raised about the cardinal directions experiment: 1) Can independent directions be found using lines joining unique hues a la Schrodinger (1925)? The

answer was given in the negative by Krauskopf et al. (1982). 2) Are linear cardinal mechanisms approximations to underlying nonlinear mechanisms like those revealed by hue judgments? If the habituating mechanisms are non-linear combinations of cone signals, then modulating along any straight line will excite more than one mechanism and, therefore, reduce the selectiveness of the desensitization. To the extent that the independence of the directions is almost perfect, the probability of underlying nonlinear mechanisms is low.

What stage of the visual system is being isolated by the habituation procedure? Additional evidence that selective habituation isolates mechanisms past the first stage comes from an experiment designed to search for static response non-linearities in the visual system (Zaidi and Hood, 1988). Thresholds were measured for probe increments on brief flashes superimposed on a steady white background. Both probes and flashes were changes along the cardinal directions. The threshold results showed the presence of post-opponent response compression along both *rg* and *yv* axes, and independence between the two chromatic cardinal directions. However, thresholds for probes along *rg* or *yv* were raised by *ld* flashes, consistent with pre-opponent response compression. Unlike increment threshold measurements, the habituation procedure seems not to be affected by first stage nonlinearities. Evidence from electrophysiology, however, indicates that the site of habituation may not be an early opponent stage. Since the work of DeValois et al. (1966) and Wiesel and Hubel (1966), it has been known that chromatic signals from the retina to the cortex pass mainly through P-cells of primate lateral geniculate nucleus. Derrington, Krauskopf and Lennie (1984) studied macaque LGN cells using modulations around white in cardinal color space. Based on their chromatic properties, P-cells clustered into two classes corresponding closely to the two chromatic cardinal mechanisms. They found, however, as had Wiesel and Hubel (1966), that the structure of the receptive fields of P-cells enabled them to carry luminance as well as chromatic signals (see also Ingling and Martinez-Uriegas, 1983). Luminance and chromatic signals are not separated until the striate cortex (D'Zmura and Lennie, 1986), making the retina or the LGN an unlikely site for cardinal mechanisms. Additionally, at least in anesthetized macaques, the response of P-cells is not reduced by prolonged exposure to temporal modulation. It is probable that habituation occurs at a later stage, but that the desensitization data reflect signals arriving from a stage consisting of independent cardinal mechanisms. This scheme would also be consistent with results on the effect of color direction on the perception of coherent motion. Krauskopf and Farell (1990) found that drifting gratings modulated along different cardinal directions appear to slip past one another, whereas when the directions of the modulation are rotated by 45° in color space, the gratings cohere. This task isolates the properties of motion-selective mechanisms, but seems to reflect the independence of chromatic signals from an earlier stage.

Higher order interactions

At present, one of the most interesting questions in color vision is the identification of mechanisms beyond the linear opponent stage. A

reanalysis of the data of Krauskopf et al. (1982) showed that the desensitizing effect of isoluminant chromatic modulation along lines intermediate to the two cardinal directions was greatest in the same direction as the habituating modulation. An explanation of this effect required the desensitization of not only second stage mechanisms but also of higher level mechanisms maximally sensitive to different isoluminant colors distributed about the color circle. These higher level mechanisms were also consistent with the transient elevation of thresholds after changes in adaptation state, and with data on the detection and discrimination of isoluminant changes in color (Krauskopf et al., 1986). Another clue to the properties of higher level mechanisms was provided by experiments on pure chromatic induction using a modulation nulling technique (Krauskopf, Zaidi, and Mandler, 1986). When average adaptation was kept constant, induced colors were in the direction complementary to the inducing color with respect to the test color. However, the functions relating nulling to inducing amplitude were different for the three cardinal directions. Therefore, simultaneous chromatic contrast in different directions along the color circle could not be predicted by the lateral interaction of either like receptors, or like second-stage opponent mechanisms and was a consequence of lateral interaction within higher-level chromatic mechanisms. Similar multiple mechanisms have been invoked to explain changes in perceived color following habituation to temporal modulation (Webster and Mollon, 1990), and for contrast detection in luminance and chromatic noise (Gegenfurtner and Kiper, 1990). In addition to these psychophysical results, cells in the striate cortex do not cluster into two chromatic classes as in the LGN, but seem to be tuned to many different directions in color space (Lennie et al., 1990). A different sort of property was revealed by the desensitizing effect of sawtooth chromatic modulation. Prolonged viewing of sawtooth modulation along a color line raised thresholds more for step changes in color when they were in the same direction as the slow phase of the habituation stimulus than when they were in the opposite direction (Krauskopf et al., 1982). When the sawtooth modulation in the test area was induced by surround modulation, the relation between the sign of the sawtooth and the magnitude of threshold elevation was reversed (Krauskopf and Zaidi, 1986). These results could be explained by color mechanisms that respond to change in one color direction but not its complement. Similar mechanisms have been revealed by an experiment that involved the detection of purely temporal step changes in color on a background that was modulated chromatically in time around circles in an iso-luminant color plane (Zaidi and Halevy, 1990).

Higher order color mechanisms could reflect linear, nonlinear, temporal, and spatial interactions between second stage mechanisms. Questions about the number and function of higher order mechanisms and the rules of combination of second-stage mechanisms remain unresolved. What could be the functional reason to have multiple mechanisms at one stage of a system that was restricted to just three at a prior stage? Part of the answer could be that inhibition and excitation within narrow bands of color space may serve some purpose. Part of the answer may have to wait for a better understanding of the functional role of color in a visual system. Knowledge of the rules that govern color appearance in real scenes is very incomplete. It is sometimes stated

without explicit evidence that the appearance of all colors can be described in a three dimensional system. The tri-variance of color *matches* is well established when both the test and the match color are seen with the same adaptation. However, if the test and the match color are seen with widely different adaptations, it may be impossible to match the test not only with a combination of three primaries, but also with a light of any spectral composition (Hunt, 1953; Bartleson, 1978). When considering the dimensions of color signals, the dimensions of space and time, i.e. the effect of spatial configuration and temporal sequence, should be added to the dimensions provided by the three independent classes of cones (see also Judd, 1961). It is likely that the manifold of *apparent* colors has more than three dimensions.

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