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Trichromacy, opponent colours coding and optimum colour information transmission in the retina

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This paper presents a systematic analysis of the role of opponent type processing in colour vision and the relation between opponent type colour transformations and the initial three colour mechanisms. It is shown that efficient information transmission is achieved by a transformation of the initial three colour mechanisms into an achromatic and two opponent chromatic channels. The derivation of the transformation is dependent solely on criteria from information theory. Thus it provides a logical rationale reconciling opponent type processing as an optimal necessary step after the initial three colour mechanisms, unifying respectively the Hering and Young–Helmholtz approaches to colour vision. The effects of chromatic adaptation on the spectral response of the achromatic and two chromatic channels are discussed from the point of view of information theory. It is argued that adaptation serves as a dynamic readjustment of these responses, necessary to meet criteria of efficient colour information transmission. The results are confronted with empirical observations to test the principles of the theory and the relation to other theories is discussed. Within the same framework the issue of trichromacy is discussed. It is argued that a broad class of typical colour spectra can effectively be represented by three significant degrees of freedom that make up a trichromatic system.

1. INTRODUCTION

The development of colour vision theory has progressed for over a century along two lines. One is the Young–Helmholtz (Young 1802; von Helmholtz 1866) geometrical trichromatic approach. A basic premise behind the simple geometrical colour theories is that the limitations on the performance of the visual system in simple colour discrimination experiments are set by the shape and response dynamics of the initial three colour mechanisms. However, the simple Young–Helmholtz trichromatic approach, as reflected later in the various line–element theories (von Helmholtz 1866; Schrödinger 1920; Stiles 1946; Koenderink *et al.* 1972; Vos & Walraven 1972*a, b*), did not account for colour appearance attributes as such. This is because they were designed to account for discrimination performance only. In an earlier treatment of colour discrimination that applied signal detection theory (Buchsbaum & Goldstein 1979*a, b*; Buchsbaum 1981) it is shown that for simple colour discrimination, performance is essentially limited by the spectral response of the colour mechanisms and by the type of noise in the

visual system. The failure of a simple geometrical colour space to account for colour sensation phenomena beyond those explained by simple colour mixing led Hering (1920) to develop another theoretical line. The Hering theory is based on the measurement of the equilibria of two sets of combinations of the initial three colour mechanisms that each control the response of a chromatic channel in the visual system.

This ambivalent nature of visual system modelling has persisted since the beginning of quantified colour vision theory in the 19th century. On one side is the Young–Helmholtz trichromatic approach; physically oriented, compatible with the science of colorimetry, very good for accounting for phenomena where the limiting factors are in the initial receptor stage. On the other side is the opponent approach based mainly on colour sensation and good at accounting for phenomena where the physiological implementation of the visual system sets the boundary conditions for perception. Many theoretical bridges have been built between the trichromatic and opponent approaches. These include von Kries' coefficient law (1905) that describes operations on the initial mechanisms as the first attempt to reconcile the two approaches. Hurvich & Jameson (1955) and Jameson & Hurvich (1955, 1956, 1968), in their opponent colour theory, consider combinations of the initial colour mechanisms to account for discrimination data and for many experiments dealing with hue cancellation and chromatic adaptation. Other theories include the Walraven (1962) zone theory, as later elaborated by Vos & Walraven (1971, 1972*a, b*) and by Vos (1979), the Guth vector model (Guth 1972; Guth *et al.* 1980), and many more (Boynton 1979, which also includes a review; Massof & Bird 1978; Werner & Wooten 1979; Krantz 1975*a, b*; Deutsch 1967; Koenderink *et al.* 1972).

This paper investigates the purpose of opponent type processing in the visual system and the principles that necessitate it. An early general discussion is presented by Guild (1932), and more recently in other studies (Barlow 1981; Fukurotani 1982). The questions investigated in this study are: given the trichromatic nature of initial colour processing, why should combinations of the initial colour mechanisms be taken and which of the infinite number of possible combinations should be taken at a given adaptation condition? In other words the question is: *opponent processing, why?* The paper considers systematically the opponent colour transformation and develops a deductive rationale for its existence by viewing the visual system as an information processing network. We find that opponent coding and major effects of chromatic adaptation can be viewed to serve as information compression and redundancy-reducing mechanisms for the perceived colour information. These ideas in similar contexts have a long history (Attneave 1954; Barlow 1961, 1980, 1981) that goes back to the last century (reviewed in Barlow 1961).

The analysis also becomes relevant in identifying possible cause for trichromacy. Barlow (1982) established a relation between the Fourier properties of the colour mechanisms and the number of possible independent samples the cones can provide, and found it to be about three. We complement this finding here and argue that typical colour spectra in themselves are well represented by three significant degrees of freedom and have Fourier properties that are matched by those of the cone responses.

2. FORMULATION OF THE THEORY

Efficient information transmission can be defined mathematically in terms of minimizing the channel capacity required to transmit the information at a given level of reliability. By analogy to the visual system, consider the stages beyond the retina as an integrated information channel, that comprises many nerve fibres that themselves are information channels. The optic nerve has a finite number of fibres of finite dynamic range and thus limited information transmission capacity (channel capacity); therefore good design will preserve this limited resource and optimize its use.

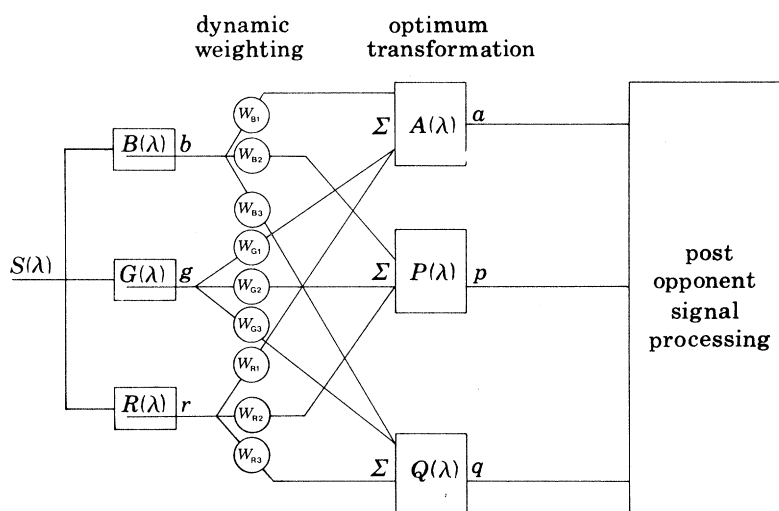


FIGURE 1. Schematic diagram of colour processing in the visual system. The three initial colour mechanisms $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ are converted via opponent type processing into the three channels $A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$. This paper considers the issue of the optimal combination of the initial three mechanisms under the criterion of most efficient information transmission.

Given a set of primaries $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ and a class of signals, the theory defines a unique transformation that has the property of most efficiently transmitting the visual information to higher stages of perception. Figure 1 summarizes the central issue of this paper. $B(\lambda)$, $G(\lambda)$, $R(\lambda)$ and b , g , r represent the initial colour mechanisms and their outputs respectively. These are transformed into three channels $A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$, with respective outputs a , p , q . This can be explained by using an example from colour vision. Figure 2, representing the response of the Vos-Walraven primaries, shows that the 'red' and 'green' mechanisms overlap greatly and every spectrally broadband colour signal will excite both mechanisms together (we will refer to the colour mechanisms 'red', 'green' and 'blue' for convenience). Therefore, mainly (but not exclusively, as equation 8 later shows) because of this overlap, the 'red' and 'green' mechanisms will have outputs that are correlated. The transmission of the outputs of these mechanisms to higher stages of perception without first transforming them would result in inefficient use of available channel capacity.

It can be shown (Gallager 1968; Pratt 1971) that there exists a mathematically unique transformation that decorrelates the message components (b, g, r) and enables the best energy distribution (in information theory terms, energy compaction) among the transformed components a, p, q . If we order the transformed components a, p, q according to descending amount of message energy, then the above is equivalent to finding a transformation that decorrelates the initial

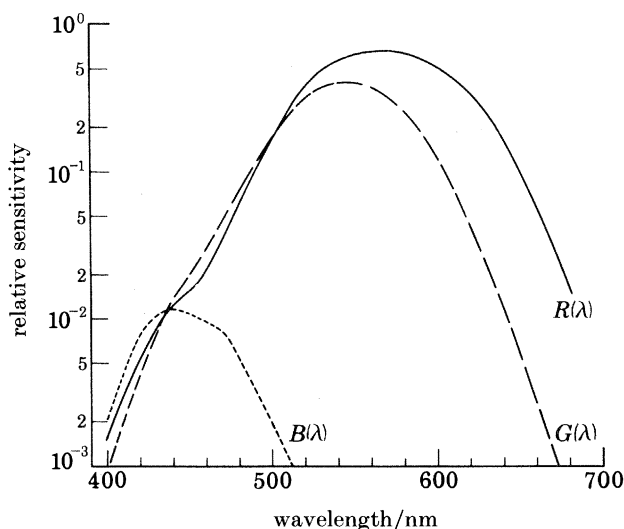


FIGURE 2. The Vos-Walraven primaries (*Vision Res.* **14**, 1974). These functions were used for computations of the eigenvector transformations.

variables b, g, r , and also maximizes the energy in the first transformed component and in the first two transformed components combined. The idea is that more resources will then be allocated in transmitting the message components that have most of the signal energy and less in transmitting those with little energy without much effect on the error in the received signal (Pratt 1971, 1978; Watanabe 1967; Limb *et al.* 1977). A word of caution concerning the term 'signal' (or message) energy. The visual system is concerned with estimating the spectral functional shape of the incoming colour stimulus. The signal energy is the integral of the square of this spectral shape scaled for desired units. It must not necessarily coincide with the actual light energy measured in terms of photon quantum energy (this is because the same amount of information can be carried by photons of different wavelengths which therefore have different physical energy).

Decorrelation of the message components and optimal information compaction (energy compaction) leading to error minimization of the signal, is achieved by what is known as the discrete Karhunen-Loeve expansion, eigenvector transformation or principal component transformation. The eigenvector transformation actually constitutes the most efficient tool of information compression for a collection of signals. Watanabe (1967) provides a rigorous mathematical proof of the properties of this transformation.

We now introduce some definitions. Let $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$, as earlier, be the response of the three colour mechanisms as function of wavelength, and let $\{S(\lambda)\}$ be the class of visual colour signals. We view each signal $S(\lambda)$ as a member of the set (ensemble) $\{S(\lambda)\}$. The responses of the three colour mechanisms to $S(\lambda)$ are b , g , r , i.e.

$$b = \int S(\lambda) B(\lambda) d\lambda, \quad g = \int S(\lambda) G(\lambda) d\lambda, \quad r = \int S(\lambda) R(\lambda) d\lambda. \quad (1)$$

The integration is over the visual spectrum. Since $S(\lambda)$ is an arbitrary member of $\{S(\lambda)\}$, b , g and r are random variables. In this context $\{S(\lambda)\}$ can also be considered a random process generating functions of wavelength.

We now define and form the covariance matrix C of b , g , r as follows (Van Trees 1968; Papoulis 1965):

$$C = \begin{bmatrix} C_{rr} & C_{rg} & C_{rb} \\ C_{rg} & C_{gg} & C_{gb} \\ C_{rb} & C_{gb} & C_{bb} \end{bmatrix}, \quad (2)$$

where

$$\left. \begin{aligned} C_{rr} &= E(r \cdot r) - (Er)^2, & C_{gg} &= E(g \cdot g) - (Eg)^2, & C_{bb} &= E(b \cdot b) - (Eb)^2, \\ C_{rg} &= E(r \cdot g) - EgEb, & C_{rb} &= E(r \cdot b) - ErEb, & C_{gb} &= E(g \cdot b) - EgEb, \end{aligned} \right\} \quad (3)$$

and E is the expectation operator.

We now proceed to derive the eigenvector transformation. Since $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ are linearly independent the covariance matrix C (equation 2) is non-singular. It has three real eigenvalues, say, Γ_1 , Γ_2 , and Γ_3 that are positive and three corresponding eigenvectors \mathbf{v}_1 , \mathbf{v}_2 and \mathbf{v}_3 , fulfilling $C\mathbf{v}_i = \Gamma_i\mathbf{v}_i$ ($i = 1, 2, 3$). In the case of real symmetric matrices the eigenvectors constitute an orthogonal set spanning the three dimensional space. We now form a 3×3 matrix W whose columns are the three eigenvectors (W is an orthogonal matrix, i.e. $WW' = I$, where W' is the transpose of W , and I is the identity matrix. W fulfils the relation

$$W'CW = \begin{bmatrix} \Gamma_1 & 0 & 0 \\ 0 & \Gamma_2 & 0 \\ 0 & 0 & \Gamma_3 \end{bmatrix}. \quad (4)$$

The eigenvector transformation of b , g and r is defined as follows:

$$\begin{bmatrix} a \\ p \\ q \end{bmatrix} = W' \begin{bmatrix} r \\ g \\ b \end{bmatrix}. \quad (5)$$

a , p , q (the response of the transformed channels $A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$) are uncorrelated and their covariance matrix is represented by equation (4). The two vectors in equation 5 are not necessarily parametrized by λ .

A property of positive matrices (like C) is that they have one and only one eigenvector whose entries are of like sign (Berman & Plemmons 1979). This means

that only one of the transformed channels generated by W' can be an all positive combination of b, g, r . A conclusion is that the optimum transformation must have two opponent antagonistic channels.

In order to find a relation between the last equation and the actual initial colour mechanisms $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ we must substitute these and the signal $S(\lambda)$ into the covariance matrix C . By substituting, equation (1) into equation (3) we get

$$\left. \begin{aligned} C_{rr} &= E[\int S(\lambda) R(\lambda) d\lambda \int S(\mu) R(\mu) d\mu] - E[\int S(\lambda) R(\lambda) d\lambda] E[\int S(\mu) R(\mu) d\mu] \\ C_{rg} &= E[\int S(\lambda) R(\lambda) d\lambda \int S(\mu) G(\mu) d\mu] - E[\int S(\lambda) R(\lambda) d\lambda] E[\int S(\mu) G(\mu) d\mu] \end{aligned} \right\} \quad (6)$$

and similarly for the other combinations. $E(S(\lambda))$ is the mean of the signal ensemble. A correlation function, \mathbf{R} , and a covariance function, \mathbf{K} , can be defined for this process as follows (Van Trees 1968, chapter 3; Papoulis 1965)

$$\mathbf{R}(\lambda, \mu) = E(S(\lambda) S(\mu)), \quad (7a)$$

$$\mathbf{K}(\lambda, \mu) = \mathbf{R}(\lambda, \mu) - E S(\lambda) E S(\mu). \quad (7b)$$

Substituting equation (7b) into equation (6) yields (Van Trees 1968, chapter 3)

$$\left. \begin{aligned} C_{rr} &= \iint \mathbf{K}(\lambda, \mu) R(\lambda) R(\mu) d\lambda d\mu, \\ C_{rg} &= \iint \mathbf{K}(\lambda, \mu) R(\lambda) G(\mu) d\lambda d\mu, \end{aligned} \right\} \quad (8)$$

and similarly for the other combinations.

Equation (8) shows that the entries in the covariance matrix C (equation 2) are a function of $\mathbf{K}(\lambda, \mu)$ and depend on both the properties of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ and the signal ensemble $\{S(\lambda)\}$. Prevalence of different wavelengths in the signal ensemble would be reflected in $\mathbf{K}(\lambda, \mu)$. Therefore the correlation between pairs of b, g, r does not depend only on the overlap of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$.

To proceed and determine $A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$, $\mathbf{K}(\lambda, \mu)$ in equation (8) must be specified. We select

$$\mathbf{K}(\lambda, \mu) = \delta(\lambda - \mu), \quad (9)$$

where δ is the Dirac delta function. Equation (9) models individual realizations of $\{S(\lambda)\}$ as being minimally correlated with respect to their energy at different wavelengths. Equation (9) is realized when the ensemble $\{S(\lambda)\}$ has a broadband (ideally uniform) Fourier frequency power spectrum (not to be confused with the wavelength spectrum). As implied by equation (8) the high frequency components of such a power spectrum will be filtered out by the low pass Fourier filtering properties of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ (Barlow 1982) and will not exceed the effective cut-off frequency of the latter. In §5 it is discussed how the Fourier properties of colour signals are essentially matched by those of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$. Equation (9) is satisfied exactly if $\{S(\lambda)\}$ is confined to combinations of monochromatic signals. This indicates that a similar covariance matrix will be derived for both classes of signals, broadband and monochromatic, generalizing results from visual experiments employing primarily monochromatic stimuli. Empirical observations from experiments with monochromatic stimuli underlie most actual discussions of

the properties of opponent processing. Substituting $\mathbf{K}(\lambda, \mu) = \delta(\lambda - \mu)$ into equation (8) yields

$$\left. \begin{aligned} C_{rr} &= \int R^2(\lambda) d\lambda, & C_{gg} &= \int G^2(\lambda) d\lambda, & C_{bb} &= \int B^2(\lambda) d\lambda, \\ C_{rg} &= \int R(\lambda) G(\lambda) d\lambda, & C_{rb} &= \int R(\lambda) B(\lambda) d\lambda, & C_{gb} &= \int G(\lambda) B(\lambda) d\lambda, \end{aligned} \right\} \quad (10)$$

as the elements of the covariance matrix C (equation 2). The covariance matrix thus generated reflects the functional correlation between pairs of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ (Van Trees 1968, chapter 3). The eigenvector transformation can be parametrized in terms of λ when the expected response of the channels for monochromatic signals is considered. The transformation (equation 5) becomes:

$$\begin{bmatrix} A(\lambda) \\ P(\lambda) \\ Q(\lambda) \end{bmatrix} = W' \begin{bmatrix} R(\lambda) \\ G(\lambda) \\ B(\lambda) \end{bmatrix}. \quad (11)$$

where W' was defined as the transpose of the matrix of eigenvectors of C .

3. FUNDAMENTAL RESULTS

(a) Properties of the eigenvector transformation

The eigenvector transformation of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ is unique, given the covariance matrix C (10), and has the following basic properties:

- (i) $A(\lambda)$, $P(\lambda)$, $Q(\lambda)$ are mathematically orthogonal, i.e.

$$\int A(\lambda) P(\lambda) d\lambda = \int A(\lambda) Q(\lambda) d\lambda = \int P(\lambda) Q(\lambda) d\lambda = 0.$$

Their outputs a , p , q are uncorrelated and have a diagonal covariance matrix given by equation (4).

- (ii) The expected monochromatic signal energy of the channels $A(\lambda)$, $P(\lambda)$, and $Q(\lambda)$ will have the ratio $\Gamma_1 : \Gamma_2 : \Gamma_3$ where $\Gamma_1, \geq \Gamma_2, \geq \Gamma_3$ are the eigenvalues of the covariance matrix C of the trichromatic responses, i.e.

$$\int A^2(\lambda) d\lambda : \int P^2(\lambda) d\lambda : \int Q^2(\lambda) d\lambda = \Gamma_1 : \Gamma_2 : \Gamma_3.$$

This eigenvalue ratio provides the optimum in signal energy compaction.

- (iii) We are assured mathematically that one, and only one, of the eigenvectors will have entries of like sign that we can choose to be positive, and that this eigenvector is associated with the largest eigenvalue Γ_1 (Berman & Plemmons 1979). This means that one (and only one) of the combinations generated by W' (equation 11) will be an all positive linear combination of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$, and that this channel, assigned $A(\lambda)$ for achromatic, has the largest share of the signal energy.

- (iv) The second largest eigenvalue Γ_2 will be associated with a channel with one zero crossing (of the wavelength axis). This may turn to be either a red-green type (r-g) channel, $P(\lambda)$, or a yellow-blue type (y-b) channel, $Q(\lambda)$, depending on the location of the maximal responses along the wavelength axis.

(v) The smallest eigenvalue Γ_3 will be associated with a channel with two zero crossings (of the wavelength axis).

The above properties of the transformation will hold for all $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$, which are all unimodal positive analytical and linearly independent functions. In the following sections we will investigate numerical examples of the optimum colour encoder and show that it has correlates in opponent processing in the visual system.

(b) Numerical results

(i) Colour vision in the unadapted state

A basic issue is which set of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ should be employed in the numerical stimulation. The question is twofold: (i) the functional spectral shape of the colour mechanisms and (ii) the relative sensitivity of the three colour mechanisms. Currently in use are two psychophysically developed sets of primaries, the Vos–Walraven primaries (Vos & Walraven 1971; Walraven 1974; Vos 1978) and the Smith–Pokorny primaries (Smith & Pokorny 1975). In the present context $R(\lambda)$ and $G(\lambda)$ are essentially the same in each set and $B(\lambda)$ is the same up to a multiplicative constant. We apply the eigenvector transformation to the Vos–Walraven primaries, presented in figure 2, and later discuss the sensitivity of this choice to the level of $B(\lambda)$. The transformation is applied using the primaries as numerical examples. It does not validate or embrace the various methods of their derivation (Vos & Walraven 1971; Smith & Pokorny 1975). The transformation for threshold is

$$\begin{bmatrix} A \\ P \\ Q \end{bmatrix} = \begin{bmatrix} 0.887 & 0.461 & 0.0009 \\ -0.46 & 0.88 & 0.01 \\ 0.004 & -0.01 & 0.99 \end{bmatrix} \begin{bmatrix} R \\ G \\ B \end{bmatrix}. \quad (12a)$$

$A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$ are mathematically orthogonal with eigenvalue ratio corresponding to their signal energy

$$\int A^2(\lambda) d\lambda : \int P^2(\lambda) d\lambda : \int Q^2(\lambda) d\lambda = \Gamma_1 : \Gamma_2 : \Gamma_3 = 97.2 : 2.78 : 0.015.$$

The meaning of this ratio is further discussed in §5.

Figure 3 shows the achromatic channel derived from the information theoretical considerations together with Judd's (1951) $V(\lambda)$ curve. The curves are similar, suggesting that $A(\lambda)$ is the major contributant to $V(\lambda)$. Expressed for comparison purposes, in terms of Judd's (1951) colour matching functions, the derived $A(\lambda)$ follows $0.095 \bar{x}'(\lambda) + 1.0 \bar{y}'(\lambda) + 0.027 \bar{z}'(\lambda)$ and differs from $V(\lambda)$, which, by convention, follows $\bar{y}'(\lambda)$. When adjusted for height the difference between the curves is marked in the blue end of the spectrum (figure 3).

To ascertain that the above result is insensitive to our choice of the level of $B(\lambda)$ (i.e. the choice of Vos–Walraven or Smith–Pokorny primaries), the eigenvector transformation was derived for various levels of $B(\lambda)$. We find that for an arbitrary constant $0 \leq \alpha \leq 10$ multiplying $B(\lambda)$ the corresponding transformation for $A(\lambda)$ in the unadapted state is

$$A(\lambda) \cong 0.887 R(\lambda) + 0.461 G(\lambda) + 0.0009 \alpha B(\lambda), \quad (12b)$$

with eigenvalue ratio

$$\Gamma_1:\Gamma_2:\Gamma_3 \cong 97:2.78:0.015\alpha^2.$$

This approximation becomes invalid as α further increases and under conditions of chromatic adaptation as discussed in following sections. The result in equation (12b) arises because of the high correlation between $R(\lambda)$ and $G(\lambda)$ relative to their respective correlation pairwise with $B(\lambda)$. The relative insensitivity of $B(\lambda)$ compared to $R(\lambda)$ and $G(\lambda)$ only accentuates these correlation disparities.

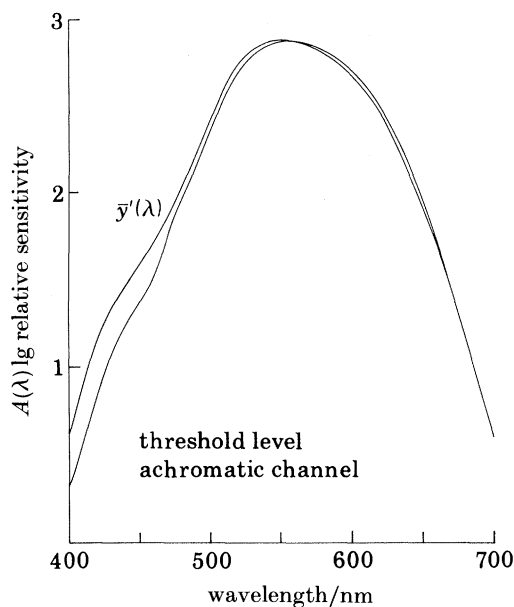


FIGURE 3. Achromatic channel derived by eigenvector transformation of the Vos-Walraven primaries. Also shown for comparison is the Judd 1951 $\bar{y}'(\lambda)$ curve. The curves are shifted vertically for comparison purposes.

The preceding sensitivity analysis suggests that at threshold the optimum achromatic channel is similar to $V(\lambda)$ and combines a negligible portion of the available output from the 'blue' mechanism. This issue as to whether there is any contribution from the 'blue' mechanism to an achromatic channel is debated in the literature (Guth *et al.* 1980; Smith & Pokorny 1975; Drum 1981; Eisner & MacLeod 1980; Marks 1974; Whittle 1974; Vos & Walraven 1971, 1972a, b; Boynton 1979) and is further discussed §4(b)(i).

Figures 4 and 5 show the result for the two opponent channels $P(\lambda)$ and $Q(\lambda)$. The derived r-g channel at threshold (figure 4) is bimodal, it is associated with the second largest eigenvalue and hence with the second largest share of the signal energy. The r-g channel presented by Guth *et al.* (1980) follows $-0.40 R(\lambda) + 0.88 G(\lambda)$ (adjusted for the level of primaries in equation (12) and figure 2). The model of Guth *et al.* (1980) assumes no contribution of $B(\lambda)$ to the r-g channel. Ingling & Tsou (1977, p. 1081) compute a r-g channel in terms of

Vos–Walraven primaries whose shape follows $-0.44 R(\lambda) + 0.88 G(\lambda)$. Both are very similar to equation (12a).

The y–b channel at threshold (figure 5) is trimodal, it is associated with the smallest eigenvalue (and smallest energy share). This result suggests that the y–b channel will be the least susceptible to direct sensitivity measurements. The studies

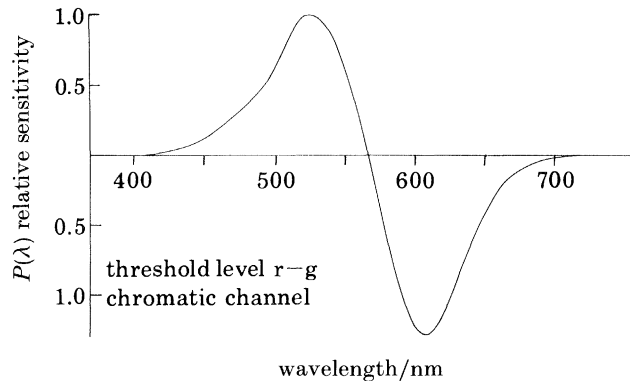


FIGURE 4. First chromatic channel derived by eigenvector transformation of threshold level Vos–Walraven primaries, corresponding to a r–g opponent channel.

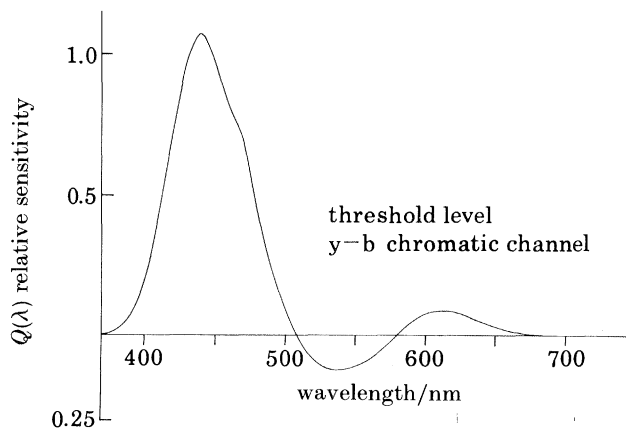


FIGURE 5. Second chromatic channel derived by eigenvector transformation of threshold level Vos–Walraven primaries. The spectral shape of this channel is discussed in the text.

of Guth *et al.* (1980) and Ingling & Tsou (1977) also exhibit a y–b channel that is much less sensitive than the other two. Equation (12a) and figure 5 indicate that in short wavelengths the y–b channel essentially follows $B(\lambda)$. In middle and long wavelengths the sensitivity of the y–b channel is very low and exhibits two modes. Psychophysical correlates of the middle and long wavelength response are not available. The corresponding channel in Guth *et al.* (1980) study (adjusted for the levels of the primaries in equation 12 and figure 2) follows $-0.0094 R(\lambda) + 0.99 B(\lambda)$. Because $G(\lambda)$ is non-contributory, a trimodal form is

unrealizable in their study. The shape of Ingling & Tsou's (1977) y - b channel follows $0.006 R(\lambda) + 0.004 G(\lambda) - 0.99 B(\lambda)$. At short wavelengths Guth *et al.*'s (1980) and Ingling & Tsou's (1977) channels also essentially follow $B(\lambda)$ but have only one mode in the middle and long wavelengths. The relations and transitions between bimodal and trimodal shapes under adaptation is discussed in §4(b)(ii).

There are many physiological correlates of opponent processing and a small capsule is reviewed here in the context of the model. De Valois *et al.* (1966) demonstrated the physiological correlates of opponent colour processing measuring opponent type responses in ganglion cells of primates. They have found monophasic cells and biphasic cells corresponding to an achromatic and two types of opponent chromatic channels. Indications for triphasic ganglion cells in primates, under certain chromatic adaptation conditions, is suggested by De Monasterio & Gouras (1975, figures 6, 12). Gielen *et al.* (1982) recently demonstrated that response contributions from different types of cones appear to add linearly in l.g.n. neurons of primates. Evidence for biphasic and triphasic cells in teleost fish species, believed to be trichromatic, was demonstrated by Svaetichin (1956), Svaetichin *et al.* (1961), Tomita (1963, figure 6), Mitarai *et al.* (1978); Hashimoto & Inokuchi (1981) and Fukurotani (1982). Comparison between teleost fish and primates and among the various teleost fish species may be difficult because of wide variations in distribution and wavelength spacing of cone pigments in the fish species (Levine & MacNichol 1979). Fukurotani (1982) also found that the wavelength responses at low light levels for three types of horizontal cell are orthogonal and suggests that the orthogonality serves for efficient coding of colour information. He proposed a physiological model based on the Gram-Schmidt orthogonalization algorithm to account for his observations. Because the Gram-Schmidt process is neither unique nor does it guarantee uncorrelated outputs (Van Trees 1968), Fukurotani (1982) suggested that the eigenvector (Karhunen-Loeve) transformation be used to understand the meaning of the transformation.

(ii) *Defective colour vision*

The analysis of defective colour vision in the context of efficient information processing raises an important biological issue. If we assume that the major classes of dichromatic vision, protanopia, deuteranopia and tritanopia, correspond to missing $R(\lambda)$, $G(\lambda)$, and $B(\lambda)$ respectively (Vos & Walraven 1971; Guth *et al.* 1980), there are two alternative representations. The first consists of applying the trichromatic transformation (equation 12) to a set of primaries suitably adjusted to reflect the different sensitivities of the dichromat. The second involves directly computing the optimal transformation for the dichromat. In the latter case, the correlation matrix has two, rather than three, dimensions. The eigenvector transformation will yield two orthogonal channels, one with no zero crossing of the wavelength axis (an achromatic channel, figure 6) and a single opponent channel with one zero crossing (figure 7). These results are consistent with known characteristics of dichromats (for example, Hurvich & Jameson 1955; Hurvich 1979, chapter 17), but are not sufficient to distinguish between the two alternative representations of dichromacy in the present theory. Being able to make this distinction would bear on the source of neural connectivity in dichromacy. That

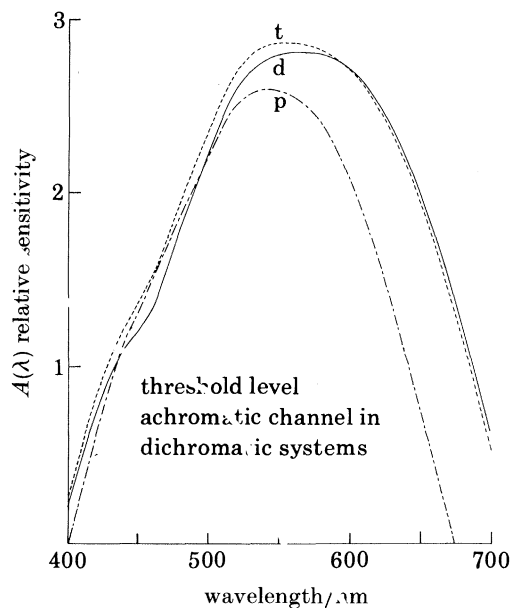


FIGURE 6. Achromatic channel corresponding to the three types of dichromatic vision. The calculations assume that protanopia (p), denteranopia (d) and tritanopia (t) correspond to missing of the 'red', 'green' and 'blue' mechanisms respectively. Vos-Walraven primaries were used.

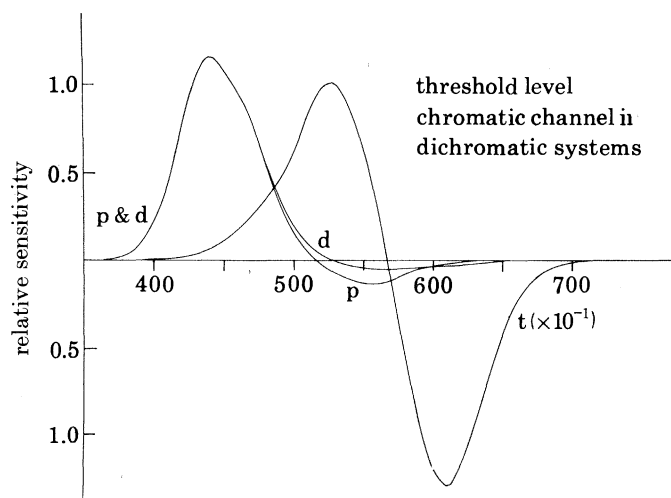


FIGURE 7. The single chromatic channel derived for each type of colour defective vision, under conditions as described in the caption to figure 6.

is, whether the neural network is preset genetically in the dichromat or has the capacity to organize according to some criteria.

4. CHROMATIC ADAPTATION

(a) *Mathematical formulation*

The basic problem is to define what effect adaptation will have on the covariance matrix C of the three initial colour mechanisms $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ (equation 2). The question of how to define the effect of chromatic adaptation on the response of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ is in itself not simple (Eisner & MacLeod 1981; Guth *et al.* 1980; Walraven 1981). We will employ a von Kries coefficient scheme that assigns a suppression coefficient k_B , k_G , and k_R to outputs of $B(\lambda)$, $G(\lambda)$, and $R(\lambda)$ respectively. When no adaptation conditions are present, k_B , k_G , and k_R equal 1 and are smaller than 1 when adaptation conditions are introduced. The suppression coefficients act upon the outputs of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ before they are transformed into a , p , q .

We define a matrix K such that

$$K = \begin{bmatrix} k_R & 0 & 0 \\ 0 & k_G & 0 \\ 0 & 0 & k_B \end{bmatrix}. \quad (13)$$

If C is the covariance matrix in the absence of adaptation conditions as defined in equation (2), then at an adaptation condition defined by a matrix K the resulting covariance matrix will be (Van Trees 1968),

$$KCK = \begin{bmatrix} k_R^2 C_{rr} & k_R k_G C_{rg} & k_R k_B C_{rb} \\ k_R k_G C_{rg} & k_G^2 C_{gg} & k_G k_B C_{gb} \\ k_R k_B C_{rb} & k_G k_B C_{gb} & k_B^2 C_{bb} \end{bmatrix}. \quad (14)$$

The eigenvalues and eigenvectors of KCK are not linearly related to those of C . Therefore the contribution of the suppressed $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ to the optimum channels $A(\lambda)$, $P(\lambda)$ and $Q(\lambda)$ will not vary linearly as function of the suppression coefficients and will be specified by the eigenvectors of KCK . For any given K the transformed channels are mathematically orthogonal.

The exact physiological implementation of the entire adaptation process is outside the scope of this paper. It is evident, however, that implementation would require two stages: the first associated with the suppression coefficients k_B , k_G , k_R ; the second stage would be associated with the realization of the mathematically defined eigenvector transformation. Realizations of the latter are well documented in the adaptive array literature (Monzingo & Miller 1980). Abundant psychophysical data requiring (at least) two sites of adaptation exist in the literature (Stiles 1978; Pugh 1976; Augenstein & Pugh 1977; Pugh & Mollon 1979; Mollon & Polden 1977; Walraven 1976, 1981; Werner & Walraven 1982; Krauskopf *et al.* 1982). One-to-one parallels between the mathematical principles underlying the optimum eigenvector transformation and two physiologically or psychophysically defined adaptation sites are difficult to draw. However, they appear to be congruous.

(b) Results

(i) The achromatic channel

Figure 8 presents the results of simulating the changes in the achromatic channel when the initial 'red' and 'green' mechanisms are suppressed by a factor $k_G = k_R$ respectively. The curves are marked a, b, c, etc., corresponding to values of k_G and k_R as shown in the table in figure 8. In certain combinations the achromatic

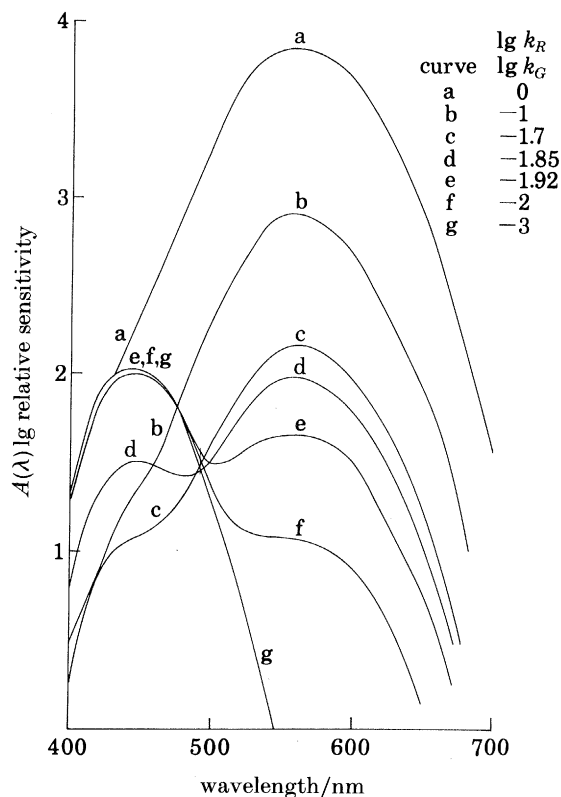


FIGURE 8. The effect of suppressing the response of the 'red' and 'green' mechanism by k_R and k_G on the achromatic channel is presented. The curves a-g correspond to the conditions listed in the figure.

channel may have two peaks. Eventually the achromatic channel will converge into the blue mechanism (figure 8, curve g). Simulation of suppression of $R(\lambda)$ and $G(\lambda)$ such that $k_G \gg k_R$ or $k_G \ll k_R$ resulted in $A(\lambda)$ converging into patterns following $G(\lambda)$ and $R(\lambda)$ respectively. The results are consistent with the idea of isolating one cone mechanism by strong suppression of the others (Wald 1964). For reasons already discussed suppression of $B(\lambda)$ negligibly affected $A(\lambda)$.

The response of the eye to blue light has exhibited enigmatic behaviour under many experimental conditions and the role of the blue mechanism in the transformed colour channels, particularly its contribution to detection threshold, is much debated in the literature (Whittle 1974; Eisner & MacLeod 1980; Marks

1974; Drum 1981; Vos 1978; Smith & Pokorny 1975; Vos & Walraven 1972*a, b*; Guth *et al.* 1980). In the present model the contribution of the 'blue' to the achromatic channel is set by the transformation as a dynamic adjustment to meet an optimum information transmission condition. It is not biased one way or the other concerning this issue. However, it appears that for threshold conditions (see equation 12) the combination is such that the 'blue' contribution is negligibly small. With changing adaptation conditions (suppression of $R(\lambda)$ and $G(\lambda)$, figure 8), this contribution increases until the achromatic channel converges into the blue mechanism.

(ii) *The chromatic channels*

The red-green opponent channel. Figure 9 (left) shows the changes in the r-g channel as function of equal suppression of the 'red' and 'green' mechanisms. When k_G and k_R equal 1 (i.e. no suppression) the r-g channel exhibits two modes (figure 9, top left). With decreasing k_G and k_R (i.e. increasing suppression of $G(\lambda)$ and $R(\lambda)$ figure 9*b*) some effect of the 'blue' mechanism is noted in the short wavelength lobe. Eventually, (figure 9*c-e*), the curve becomes trimodal. Implementation of the r-g channel under various adaptation conditions in terms of colour receptive fields is discussed by Ingling (1977) and Ingling & Tsou (1977). Ingling (1977) introduces a special receptive field operator to account for the change of the r-g channel from a bimodal to a trimodal curve with changing adaptation. A similar effect of the change of the r-g channel from a bimodal to trimodal shape is exhibited in the cases when the 'red' mechanism and 'green' mechanism are suppressed individually. The changes in the spectral shape of the r-g mechanism correspond to a readjustment of the optimum transformation as the 'blue' mechanism becomes more sensitive than either one or both of the 'red' and 'green' mechanisms when these are suppressed.

The yellow-blue opponent channel. Figure 9 (right) shows the corresponding effects of equal suppression of the 'red' and 'green' mechanisms on the y-b channel. Both bimodal and trimodal y-b channels are exhibited under the various suppression coefficients. By comparing the left and right side of figure 9, it can be seen that for any given level of suppression there is always a bimodal function with a corresponding trimodal one (see §3).

At threshold a trimodal y-b form prevails in concert with a bimodal r-g form. With increasing suppression of the 'red' and 'green' mechanisms the y-b function assumes a bimodal form as simultaneously the r-g function becomes trimodal. This mode reversal corresponds to a level of suppression of the 'red' and 'green' mechanisms where the y-b eigenvalue is greater than the r-g eigenvalue. The bimodal y-b curves have psychophysical correlates in hue cancellation experiments under adaptation (for example Hurvich & Jameson 1955; Jameson & Hurvich 1956). Psychophysical correlates for a trimodal y-b channel, which corresponds in this model to minimally adapted close to threshold conditions, are not available, particularly for middle and long wavelengths. It may be that such determination is impeded by the low sensitivity of the y-b channel which is overwhelmed by the response of the other channels, as is also reflected by the eigenvalue distribution.

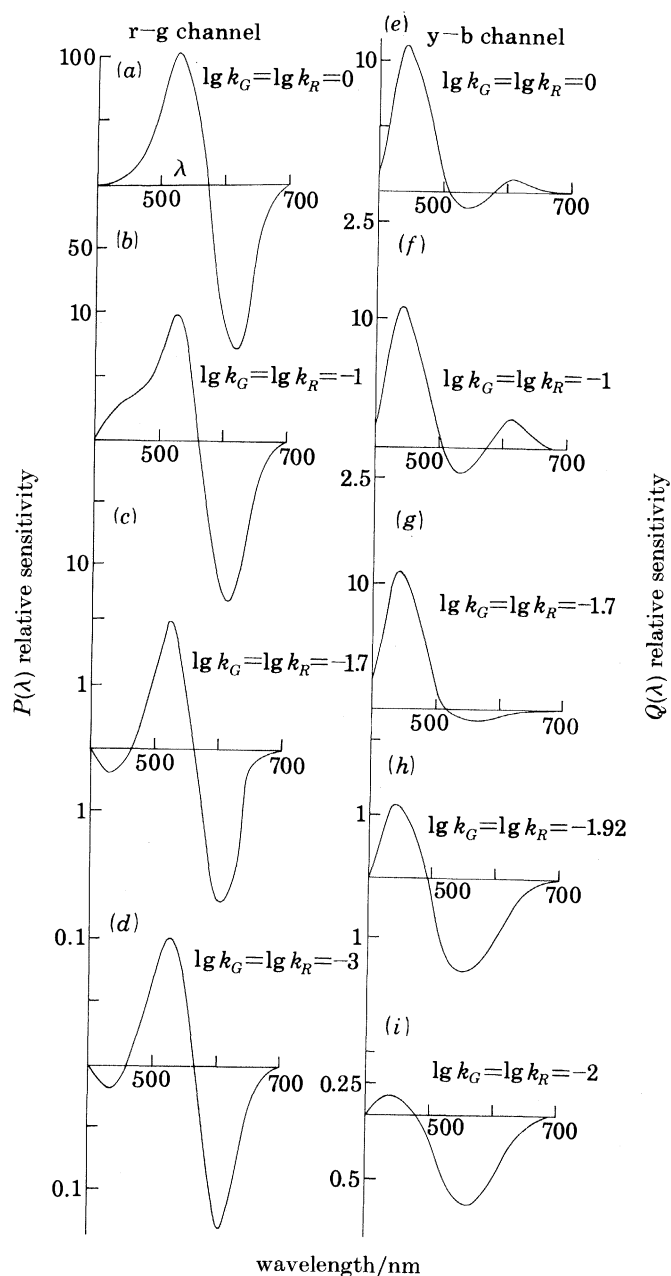


FIGURE 9. The effect of suppression of the 'red' and 'green' mechanisms on the two chromatic channels. The r-g channel (left) changes from a bimodal shape at threshold to a trimodal curve with increasing suppression of the 'red' and 'green' mechanisms. The corresponding effects on the y-b channel are drawn on the right hand side of the figure. The top subfigures correspond to unsuppressed colour mechanisms. Note the relative changes of sensitivity.

The low threshold sensitivity of the y–b channel is also reflected in the models used by Ingling & Tsou (1977) and Guth *et al.* (1980). Ingling (1977) also discusses the possibility that in certain threshold conditions the sensitivity of the y–b channel is affected by the contribution of rods, suggesting that the latter may mask the shape of the y–b channel at threshold. Possible physiological correlates of trimodal channels, under chromatic adaptation conditions, are reported by De Monasterio & Gouras (1975, compare figures 6, 12). A trimodal y–b channel in horizontal cells of trichromatic teleost fish was measured by Svaetichin *et al.* (1961), Tomita (1963), Fukurotani (1982) and by Hashimoto & Inokuchi (1981).

5. A DISCUSSION ON THE NUMBER OF COLOUR MECHANISMS IN THE RETINA

We have stressed in this paper the role of the eigenvalues of the covariance matrix as corresponding to the distribution of signal energy among the transformed channels (see §3). The number of significant eigenvalues and their ratio corresponds to the number of significant degrees of freedom of a class of signals of essentially limited frequency and extent (Van Trees 1968; Gallager 1968). The composition of the covariance matrix, and hence its eigenvalues, is determined by both the properties of the signal ensemble and the properties of the colour mechanisms as shown in equation (8). In this section we investigate whether typical colour signals can be sufficiently represented by only three degrees of freedom (eigenvalues), and discuss the relation between the Fourier properties of typical colour signals and those of the cone spectra. Barlow (1982) already demonstrated that the bandwidth of the three cone spectra in themselves can serve as a powerful constraint for the dimensionality of colour vision. We discuss how both of these results conjoin to understand possible causes for trichromacy.

We recall another result from information theory (Gallager 1968, chapter 8; Van Trees 1968, chapter 3) that states that the number of significant (in terms of their signal energy content) degrees of freedom, n , of a signal of essentially limited extent T and essentially limited frequency B corresponds to the number of significant eigenvalues (each associated with a band-limited basis eigenfunction) such that

$$n = [2BT] + 1, \quad (15)$$

the symbol $[a]$ corresponding to the highest integer number smaller than a . The term ‘essentially limited in extent and frequency’ is applied since ideal limitation in both extent and frequency are conflicting requirements. This result is more general than the well known uniform sampling theorem as it provides the required band-limited orthogonal sampling functions (eigenfunctions) to achieve representation in a minimum number of significant samples. Additional eigenvalues (above n as defined in equation 15) get increasingly smaller and represent channels with negligibly small signal energy compared with the first n eigenvalues. The constraints of equation (15) can be applied to the properties of the visual signal, T being the wavelength span of visual signals (400–700 nm) and B the Fourier transform frequency limits of the signals. For a trichromatic system $n = 3$ and equation (15) becomes

$$[2BT] + 1 = 3. \quad (16)$$

Equation (16) corresponds to a frequency limit for B of 0.005 sinewave cycles nm^{-1} . This means that all colour spectra that are essentially frequency-limited by 0.005 cycles nm^{-1} can be effectively represented by three frequency-limited channels. A frequency limit of 0.005 cycles nm^{-1} corresponds to a limit of 1.5 cycles for the entire visual spectrum. An implicit assumption made here is that the wavelength extent of interest actually is 400–700 nm. If this extent range is smaller, B will increase accordingly (see also Barlow 1982, p. 641).

The eigenvalue distribution of the covariance matrix of a, p, q (see §2) changes with different adaptation condition as expressed by the suppression matrix K , since the eigenvalues of KCK are different from those of C . Applying eigenvalue inequalities for symmetric matrices (Berman & Plemmons 1979, chapter 4), it can be shown that the smallest eigenvalue has an upper bound and its corresponding energy share is limited. The inequalities supported by the simulation show that the expected signal energy share of the smallest eigenvalue will not exceed 0.036 of the total energy output of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$, i.e. $\Gamma_3/(\Gamma_1 + \Gamma_2 + \Gamma_3) \leq 0.036$. This is valid for any combination of k_R, k_G, k_B and is a result of the energy compaction property of the eigenvector transformation. This distribution is reflected in the studies by Guth *et al.* (1980, figure 3) and Ingling & Tsou (1977), who present one channel that is much less sensitive than the other two. Though small, this channel constitutes an available degree of freedom necessary to represent adequately typical colour signals. A similar mathematical situation arises in the eigenvector analyses of Munsell colours (Cohen 1964) and of daylight (Judd *et al.* 1964) discussed below.

In what follows we discuss how the above considerations for the eigenvalues distribution and for frequency limitations are met by typical colour spectra. Cohen (1964) performed eigenvector analysis on a large number of actual spectral reflectances of Munsell chips. Cohen (1964) finds that for 150 randomly selected such reflectances three principal components are sufficient to extract over 0.99 of the variance in these spectra. The three components extract 0.927, 0.0453 and 0.0193 of the variability respectively and the eigenvalue distributions in the present study are in conformity with this finding. Cohen (1964, table 1) finds that the first three basis functions for Munsell colours have none, one and two zero crossings along the wavelength axis respectively in accordance with the mathematical fundamentals described in §3. This basis is orthogonal and will comply with the frequency limitations set by equations (15) and (16). Cohen (1964) argues for trichromacy on the basis of this account although such inference may be limited, because Munsell colours are spectrally smooth and have been designed to avoid sharp changes in appearance with illumination (Wyszecki & Stiles 1982).

Frequency domain results are provided by Stiles *et al.* (1977), showing that a collection of frequency limited functions can be applied to describe typical colour reflectance spectra for colour rendering purposes. Stiles *et al.* (1977) find that for most practical applications a frequency limit of about 0.01 cycles nm^{-1} may be appropriate to represent reflectances compared under different illuminants. Frequency limits lower than 0.01 cycles nm^{-1} were not investigated. Stiles *et al.* (1977) apply nonorthogonal frequency-limited reflectance functions with a prefixed shape of the form $\sin^2 \pi f \lambda / \pi \lambda^2$. Representation of signals employing these functions

does not conform with equation (15) and may require an arbitrarily larger number of significant samples.

A limitation of the current analyses is that practical colour surfaces act as combinations of diffuse (scattering) and of regular (nonscattering) reflecting materials making the colour signal reaching the eye a result of illuminant–reflectance interactions (Wyszecki & Stiles 1982). Judd *et al.* (1964) applied eigenvector analysis to the most common illuminant, daylight of various types. Their results indicate that over 0.997 of the expected signal energy of daylight is concentrated in a mean vector and one additional degree of freedom (Judd *et al.* 1964, table 1). Therefore, the colour signal emanating from an arbitrary natural surface need not, in general, exactly correspond to the spectrophotometric absorption properties of the natural surface material and may have a considerable contribution from the low-frequency illuminant.

The frequency limit of $0.005 \text{ cycles nm}^{-1}$ for typical colour signals, which is based on the number of available significant samples of a signal essentially limited in extent, sets a frequency limit on potential colour channels. The bandwidth limitations on visual colour channels are set by the Fourier properties of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$. An investigation shows that at $0.005 \text{ cycles nm}^{-1}$ the power spectrum of $G(\lambda)$ and $R(\lambda)$ reaches 0.25 of its maximum and that of $B(\lambda)$ reaches 0.4 of its maximum (the power spectrum is the square of the magnitude spectrum presented by Barlow (1982, figure 5)). This result demonstrates that $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$ are essentially band-limited. Barlow (1982), investigating the causes of trichromacy and tetrachromacy in some bird species, starts with the Fourier properties of the cone pigments. On the basis of the essential frequency band-limiting of $B(\lambda)$, $G(\lambda)$ and $R(\lambda)$, and considering the essentially limited signal extent, the number of possible independent samples of an arbitrary function projected on a basis comprising of cone pigments only is computed. Properties of typical colour signals are not considered in the calculation. The result is found to be about three, which indicates a cause for trichromacy whose source is the breadth (on the wavelength axis) of the visual cone pigments. The last result is complemented and extended here to show that there is a strong match between the Fourier filtering properties of the three colour mechanisms and Fourier properties of typical colour signals and that trichromacy can be attributed to the Fourier properties of either the cone photopigments (Barlow 1982) or typical physical colour spectra, and not necessarily to the fact that there are only three types of cone pigments in the retina.

6. DISCUSSION

Applications of information theory and related analytical techniques to vision and other sensory modalities have been discussed many times since the early days of information theory in the late 1940s and are not reviewed here. A fundamental philosophical difference sets this study apart from earlier ones. Earlier theories usually accounted for sensory discrimination and the perception of sensory attributes by using a model based on knowledge of the physiological implementation and noise properties of the sensory system in question; for example, in the auditory system, Siebert (1968, 1970), Goldstein (1973); in vision, early examples are given

by Barlow (1956) and Barlow & Levick (1962) and recently by Teich *et al.* (1982). Major characteristics of the sensory system implementation (such as the number of initial colour mechanisms and opponent processing in colour vision) were preset in these models, and the optimal processor was assigned or associated with the central nervous system. Here, rather than assessing colour discrimination and detection performance or the estimation of colour attributes, the theory accounts for and predicts certain concepts of colour signal encoding that are known to occur at the level of the retina. The inherent reason for this difference is that the present theory was concerned with efficient colour information transmission and not with the interpretation of this information. Srinivasan *et al.* (1982) have recently shown that similar considerations of information processing may also apply in the spatial and temporal domains. The principles underlying stimulus transformations in sensory systems, particularly the redundancy-reducing hypothesis, were discussed before (Attneave 1954; Barlow 1961, 1980, 1981). The present theory is a demonstration of this principle in colour encoding by the visual system.

Several theoretical and experimental issues were raised throughout this paper. Foremost is the relation of the present approach to visual physiology. While the model is successful in accounting for a number of well known features of colour vision, a limitation is that few clues can be given as to how the mathematically defined optimization process might be implemented in the visual system. Generally, in any optimization problem, the solution is as globally applicable as the initial set of constraints. For example, our analysis considers only the wavelength parameter of the stimulus domain. Clearly, all stimuli are also defined in space and time. Srinivasan *et al.* (1982) recently proposed that efficient information encoding takes place in the spatial and temporal domains. In particular, in the spatial domain, centre-surround organization of the ganglion cell receptive field is modelled as a method of removing redundant information arising from the high spatial correlation of natural scenes. Similar arguments are made for the temporal domain with respect to self-inhibitory neurons. In this context the centre-surround organization of colour receptive fields can be seen to subserve efficient coding of an entire natural scene rather than the colour of a limited stimulus exciting a single location on the retina. These limitations of the optimality constraints limit the discussion on possible physiological and psychophysical correlates of the optimum colour encoder. The living system may for the above considerations not reach the ultimate mathematical optimum but just approximate it.

Additionally, in the present analysis, the size, shape and location along the wavelength axis of the colour mechanisms is given and their selection is not part of the optimization process. A more comprehensive optimization might include the wavelength response of the colour mechanisms and perhaps their spatial distribution in the retina. However, indications exist that this distribution may be overwhelmed by constraint considerations other than information encoding or adequate representation of the colour signal. Wald (1967) suggests that the absence of the 'blue' mechanism from the fixation point is constrained by a need to minimize the effect of chromatic aberrations of the lens in focusing the visual image on the fixation point. The same argument will apply to understand the proximity of peaks of the 'red' and 'green' mechanisms. Barlow (1982) suggests that the proximity

of the 'red' and 'green' mechanisms may also be constrained by spatial considerations of the visual system.

Another issue stems from the nonlinear nature of the cone phototransducers. We simulated the effects of changes in the relative sensitivity of the three classes of photoreceptor using a von Kries coefficient scheme through the matrix K (§4). Because of the overlapping sensitivities of the three phototransducers, the elements of the K matrix are related to one another through the stimulus. An auxiliary model of the phototransduction process that captures this relation is necessary to achieve a realistic simulation of the adaptive state.

A current limitation of the analysis is that little is known about the distribution of typical colour signals, an issue already discussed by Stiles *et al.* (1977). This issue is much broader than mere determination of the useful frequency limits of colour signals (see §5) as it also impacts on a preferred optimal shape for the colour mechanisms. In §5 it was shown that a trichromatic system can provide an adequate representation of colour spectra band-limited by $0.005 \text{ cycles nm}^{-1}$. Optimally, for signal representation purposes, the colour mechanisms would be flat low pass filters with a cut-off frequency of 0.005 cycles ; this, obviously, is not the case (Barlow 1982, figure 5). Because of this, energy outside the established band-limit appears in a system capable of adequately representing only signal energies within the band-limit. This may produce distortions in the colour signal representation similar to aliasing and aperture-effect distortions in communication systems (Oppenheim & Schaffer 1975). So, either an ideal filter is not realizable as a cone pigment, or typical colour spectra are suitably band-limited such that ideal filters are not required. Resolution of this issue requires detailed knowledge of the distribution of typical colour stimuli.

Other theoretical issues stem from the relation of the present model to psychophysics. Having developed a model of the optimal manner in which to convey colour information to higher neural centres, we have only provided a bound on colour signal processing by the visual system. Detection and estimation of colour signal attributes are limited by the amount of information placed in the channel (as a function of time and space) and distortions produced by the channel noise. Auxiliary models are needed to understand how the information in the various channels is used to determine or discriminate colour attributes. For example, the combination of chromatic and achromatic channels for the detection of coloured flashes may be different from those for hue naming, brightness discrimination, detection threshold, etc. More psychophysical and physiological evidence encompassing the significant signal parameters may be needed to provide useful answers.

7. CONCLUSIONS

(i) Opponent type processing in the visual system can be deduced as the next logical step after the initial three cone mechanisms. The basic hypothesis is optimizing efficiency of colour signal transmission in the visual system. Opponent type processing fulfills the optimality requirements.

(ii) Chromatic adaptation and its effect on the colour channels in the visual system can be shown, under the basic hypothesis, to be a dynamic adjustment that

corrects the response of the colour channels such that efficient colour information transmission is achieved.

(iii) The issue of the number of spectrally different colour mechanisms in the retina is discussed in terms of colour signal variability. It is argued that the number of significant degrees of freedom of typical colour spectra is three. The requirement for three degrees of freedom is satisfied by the trichromacy of the visual system and is matched by the low pass filtering properties of the cone photopigments (Barlow 1982).

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