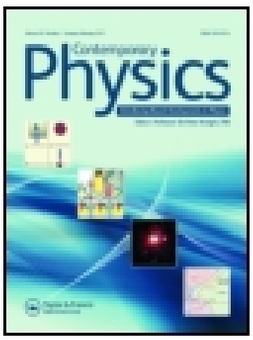

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Colour Vision

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ABSTRACT. This article reviews research into human colour vision, most information about which has been derived by psychophysical methods. Thus, the sensitivity of the eye to light of different wavelengths over the spectrum has been accurately estimated for the initial photoreceptor stage which converts light incident on the retina into neural signals. Spectral sensitivities have also been obtained, in part at least, for the subsequent post-receptoral neural pathways that apparently recode colour information into separate signals specifying luminance and chromaticity. These and other findings on receptoral and post-receptoral spectral sensitivities are considered in relation to techniques for functionally isolating colour-processing pathways in the human visual system. Also discussed briefly are models of colour vision, the relationship between form perception and colour vision, and inherited and acquired colour-vision deficiencies.

1. Introduction

Research into human colour vision has been strongly influenced by the theoretical approach and experimental methods of *psychophysics*, this being the study of the quantitative relationship between the physical characteristics of sensory stimuli and the corresponding sensory experience reported by an observer. In the archetypal experiment, stimulus variables are adjusted to achieve a constant observer response, which might correspond either to a threshold condition or to the indistinguishability of the response from a response to some reference or control stimulus. This technique has proved remarkably successful in revealing the functional properties and organization of the human visual system, from the peripheral levels involving the absorption of radiant flux by the light-sensitive visual pigments of the retinal end-organs, the *photoreceptors*, to the more central pathways and structures which subserve visual perception.

The basic notion that human colour vision is associated with three independent retinal mechanisms with different sensitivities to light of different wavelengths over the visible spectrum was clearly expressed over one-hundred and eighty years ago by Thomas Young (1802 a, pp. 20–21) in his Bakerian Lecture: 'Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colours red, yellow, and blue... and that each of the particles is capable of being put into motion less or more forcibly, by undulations differing less or more from a perfect unison'. Subsequently, Young (1802 b, p. 395) modified these three principal colours to red, green, and violet. Much research in human colour vision has since been directed towards determining the variation in sensitivities of these retinal mechanisms to light of different wavelengths, their *spectral sensitivities*. Two main psychophysical techniques have been used: in the one, following A. König (König and Dieterici 1886, König 1903), measurements were made by normal observers and observers with defective colour vision of the *colour-matching* characteristics of the eye, the latter notably investigated and systematicized by W. D. Wright (1934, 1946, 1952); in the other, determinations were made of the *detection thresholds* of various combinations of spectral stimuli in an important paradigm introduced and developed by W. S. Stiles (1939, 1953, 1959).

These and related techniques provided fundamental information concerning, not necessarily uniquely, the characteristics of the receptoral or receptor-determined level of human colour vision. In the last decade, there has been increasing interest in the processing of colour information at *post-receptoral* levels. This article reviews some of the recent advances that have occurred in the understanding of human colour vision, and, in particular, post-receptoral colour processing. The emphasis is on the psychophysics of colour vision rather than on the anatomy and physiology of the underlying pathways. A review introducing the physiology of colour vision has been given by K. H. Ruddock (1971) in a previous article in this journal.

The present article is organized as follows. First, a brief summary is given of the elementary structure and function of the visual system. Separate sections then deal in turn with: cone mechanisms and their spectral sensitivities, post-receptoral colour processes, models of colour vision and colour appearance, colour vision and form perception, and, finally, inherited and acquired colour-vision deficiencies. In addition to the specific references cited in this article, background material on general vision, including colour vision, can be obtained from books by Davson (1980), Brindley (1970), and Graham (1965); for colour vision in particular there is an introductory book by Boynton (1979), and a conference proceedings edited by Mollon and Sharpe (1983).

2. Elementary structure and function of the visual system

Figure 1 (a) shows a horizontal section of the eye. Light incident on the eye enters the *cornea*, traverses the optic media, and finally penetrates the retina at the back of the eye where it is absorbed by the retinal photoreceptors. The *visual axis* of the eye, the line joining the point on which the eye is fixated to the object nodal point of the eye, does not coincide with the *optic axis*, the axis of approximate symmetry of the refracting surfaces. The *visual angle* that the optic axis makes with the visual axis is about 5 degrees. The non-coincidence of the two axes is probably an evolutionary consequence

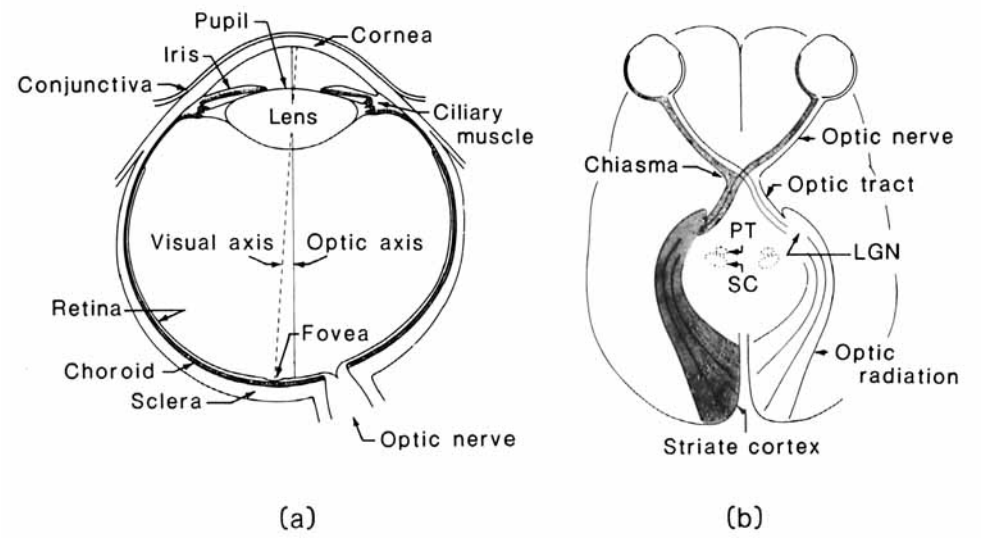

Figure 1. (a) Horizontal section of the left human eye. (b) The central visual pathways (LGN: lateral geniculate nucleus; PT: pretectal region; SC: superior colliculus).

of the development of the frontal position of the eyes from their earlier lateral position. The total refractive power of the eye is about 60 dioptres (reciprocal of the focal length in metres). Most of this power is associated with the anterior surface of the cornea, which accounts for about 48 dioptres; in addition to its relaxed power, the *lens* acts to provide power to accommodate objects placed at a finite distance from the eye. The *pupil* allows some control of the total light reaching the retina, but its dynamic range, 1 to about 16, is very small in relation to the range of light levels, 1 to about 10^{10}, over which the eye can operate. This large dynamic range results mainly from neural activity within the retina itself. The image formed by the optical system of the eye suffers from aberrations and diffraction effects. Under light-adapted conditions, where pupil diameter may be as small as 2 mm, diffraction effects dominate. The eye also suffers from chromatic aberration. The magnitude of the effect, equivalent to almost 3 dioptres over the full spectrum (Palmer and Sivak 1981), is not perceived under normal conditions of viewing.

The retina is a multilayered structure. Electrical signals from the two types of retinal receptors, the *rods* and *cones*, undergo transmission and coding in the retina by *bipolar* and *ganglion* cells, with lateral interactions arising in *horizontal* and *amacrine* cells, before leaving the eye along the *optic nerve*, which comprises approximately one million nerve fibres, the *axons* of the retinal ganglion cells. There is a partial cross-over or *decussation* of these nerve fibres at the *optic chiasma* (figure 1 b). About 70 per cent of these fibres then pass to intermediate bodies, the *lateral geniculate nuclei* (LGN), and then on to the *striate cortex* (figure 1 b). The residual 30 per cent of fibres of the optic tract run mainly to other parts of the brain, the *superior colliculus* (SC) and the *pretectal region* (PT) (figure 1 b). The striate cortex is associated mainly with detailed vision, particularly in the centre of the field of view, whereas the superior colliculus seems to be involved in visual function over the whole visual field, including detection of movement and change. The pretectum is associated with pupiliary control.

2.1. *Photoreceptors*

There are about 120 million rod receptors and about 7 million cone receptors, and their distributions vary over the retina. Cones are most densely packed at the *fovea* (figure 1 a), a region of about 5 degrees visual angle centred about the visual axis where vision is most acute. The density of cones declines with increasing visual angle. Rods are absent over approximately 1 degree of the central fovea, and their density reaches a maximum at about 20 degrees and then falls again in the periphery. Although rods and cones derived their names from their shapes, inside the central fovea cones are more rod-like in shape, and their diameters here and those of rods are about the same, of the order of 1 μ. Cone sensitivity varies with the angle of inclination of incoming light. The angle of incidence depends on the point of entry of light on the pupil, and the variation in sensitivity is known as the *Stiles–Crawford effect*. Rods exhibit little such variation.

The rod system operates in low light levels, and is associated with low acuity, achromatic vision; the cone system operates in medium-to-high light levels, and is associated with high acuity, colour vision. The absolute sensitivity of rods is greater than that of cones, and rods can respond to the absorption of single photons. There is considerably more neural pooling of signals from rods both over area and over time (*spatial integration* and *temporal integration*) than there is for cones. The maximum frequency of a flashing light that can be detected as flashing by the rod system is about 16 Hz whereas by the cone system it is about 60 Hz, though even higher values have been reported under special conditions of stimulation (Brindley 1970).

2.2. *Spectral sensitivity and wavelength discrimination*

The sensitivities of the rod and cone systems over the visible spectrum are shown in figure 2 (a). The curves are normalized to have maximum values of unity. Rod-mediated sensitivity, the *scotopic* spectral luminous efficiency function, denoted by V_λ', peaks at about 507 nm; cone-mediated sensitivity, the *photopic* spectral luminous efficiency function, denoted by V_λ, peaks at about 555 nm. This dependence of sensitivity on wavelength does not determine the characteristic feature of colour vision, namely, the capacity to discriminate light stimuli of different spectral compositions *independent* of their total radiant energies. Figure 2 (b) shows for the normal eye the smallest detectable difference $\Delta\lambda$ in wavelength of two monochromatic lights of wavelengths λ and $\lambda+\Delta\lambda$ (or $\lambda-\Delta\lambda$) as a function of λ under small-field conditions. Wavelength discrimination is poor at both ends of the spectrum and is best at approximately 440, 490, and 590 nm, where values of the discrimination step $\Delta\lambda$ are of order of a few nm. With larger fields, discrimination improves further and, for some observers, $\Delta\lambda$ approaches the difference in wavelength of the sodium D-lines. The total number of visually discriminable colours, spectral and non-spectral, has been estimated as 7–10 million.

2.3. *Trivariance*

Individual cones (and rods) are colour-blind. A photon may be absorbed by only one receptor at a time, and once this has occurred, all information about its wavelength or frequency (which determines its probability of absorption) is lost. This property is sometimes called the *principle of univariance*. The capacity to discriminate stimuli of different spectral compositions is achieved in the human visual system by a system of three classes of cone with different spectral sensitivities. This three-channel property is known generally as *trichromacy* or *trivariance*. An involvement by rods in colour vision is only revealed under special conditions of retinal stimulation, and no particular colour sensation results from this involvement.

Evidence for trivariance comes primarily from colour-matching experiments. Under normal conditions, a stimulus of any spectral composition may be matched to (i.e. rendered indistinguishable in colour from) an appropriate mixture of not more

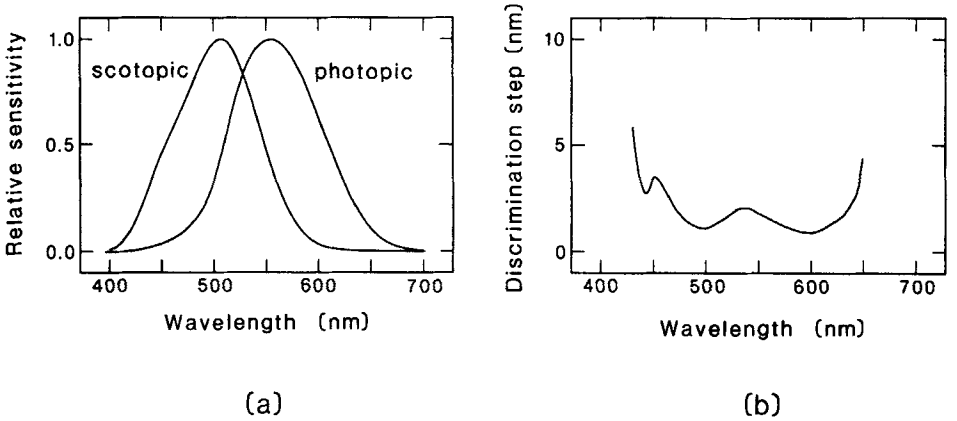

Figure 2. (a) Standard spectral luminous efficiency functions of the eye under scotopic (rod-mediated) and photopic (cone-mediated) conditions. (Curves plotted from abridged CIE data listed in Wyszecki and Stiles, 1982, Table 1 (4.3.2).) (b) Wavelength discrimination function for the normal eye. (Curves replotted from data given in Wright and Pitt, 1934.)

than three stimuli, sometimes known as *primary colour stimuli,* which may be monochromatic, and typically red, green, and blue. The amount of one of the stimuli in these additive mixtures may sometimes be negative, equivalent to adding the stimulus from the mixture to the stimulus being matched. This is called *desaturation.* Under some conditions, and for some observers, fewer than three primary colour stimuli are sufficient for colour matching. Such observers are referred to as *colour defective.* Complete *colour blindness* is very rare (see below).

Evidence for trivariance also comes from application of the *two-colour threshold method* to the investigation of spectral sensitivities of colour mechanisms (see below), from measurements *in vitro* of the absorbance spectra of individual cones of the human retina (see below), and indirectly from single-cell micro-electrode recordings in animals.

3. Cone mechanisms and their spectral sensitivities

As already noted, the trivariance of colour vision is determined initially by the existence of three classes of cone receptor, with different spectral sensitivities. These different kinds of cone or, more generally, cone mechanism are sometimes referred to as red-, green-, and blue-sensitive, although a better nomenclature is long-, medium-, and short-wavelength-sensitive, for the wavelengths of the peak sensitivities of cone mechanisms do not correspond well to these nominal colours. Cone-mechanism spectral sensitivities are broad-band and there is considerable overlap of the spectral sensitivities of the long- and medium-wavelength-sensitive mechanisms. In so far as spectral sensitivity functions determined psychophysically involve the manipulation of stimuli to produce a constant perceptual effect, for example a threshold response, they are sometimes referred to as *action spectra.*

3.1. *Spectral sensitivities*

Determination of the spectral sensitivities of cone mechanisms has been approached by a variety of techniques.

3.1.1. *Colour matching*: From colour-matching experiments (section 2.3.), it is possible to derive a set of three theoretical spectral sensitivities which define at each wavelength the amounts of the three matching colour stimuli required to match a monochromatic stimulus of an equal-radiance spectrum. These *colour-matching functions* embody the colour-matching properties of the observer's eye in the particular system of matching stimuli used in the experiment. Standardized colour-matching functions for fields subtending 2 degrees visual angle were specified by the Commission Internationale de l'Eclairage (CIE) in 1931 based on data by Wright (1928–29) and Guild (1931), and on earlier work on the spectral sensitivity function V_λ (section 2.2.). These colour-matching functions were extended by the CIE in 1964 to include data by Stiles and Burch (1959) for fields of 10 degrees visual angle.

Colour-matching functions are not unique and may be linearly transformed into any one of an infinite number of equivalent sets of colour-matching functions (see for example Wright 1946, Wyszecki and Stiles 1982). It may be assumed, however, that one particular set of colour-matching functions is correct in the sense that it corresponds to the actual spectral sensitivities of the three distinct response mechanisms of the normal eye. It may be further assumed that in observers with *dichromatic* vision, a defect in which just two rather than three primaries suffice for colour-matching, the remaining two response mechanisms are the same as in the normal observer. Under these assumptions (König and Dieterici 1886, König 1903), colour-matching data derived

from these colour-defective observers allow a unique set of colour-matching functions to be obtained, the *König fundamentals*. A less restrictive alternative to König's theory assumes that the response mechanisms in dichromats consist of two independent linear combinations of the response mechanisms in the normal observer. The functions are called the *Fick fundamentals*. These and other derivations of König fundamentals have been reviewed by Wyszecki and Stiles (1982).

3.1.2. *Spectral compensation*: Given rough estimates for the spectral sensitivities of two of the three classes of cone mechanism, it is possible to arrange the spectral composition of stimuli, usually gratings with time-varying modulation, to appear substantially uniform to those two classes of cone mechanism. Provided this condition is maintained, any visible changes in the stimuli must be detected by the third class of cone mechanism, which property may be used to investigate the spectral sensitivity of the third class of cone mechanism (Cavonius and Estévez 1975). The technique, also known as *silent substitution* or the *exchange threshold* method, may be used iteratively to provide accurate estimates of all three cone-mechanism spectral sensitivities.

3.1.3. *Two-colour threshold method*: This sophisticated technique was developed by Stiles (1939, 1946, 1949, 1953, 1959), collected papers in Stiles (1978), and, because of its importance in colour vision, an account of its essentials is given here. In the experimental situation, the eye is fully adapted to a large, spatially uniform, monochromatic *conditioning* field, of wavelength μ, and on this conditioning field a monochromatic *test* stimulus, typically 1 degree angular subtense, duration 200 ms, and wavelength λ, is presented (figure 3, inset). The smallest detectable radiant intensity N_λ of the test stimulus is evaluated at a number of different conditioning-field radiant

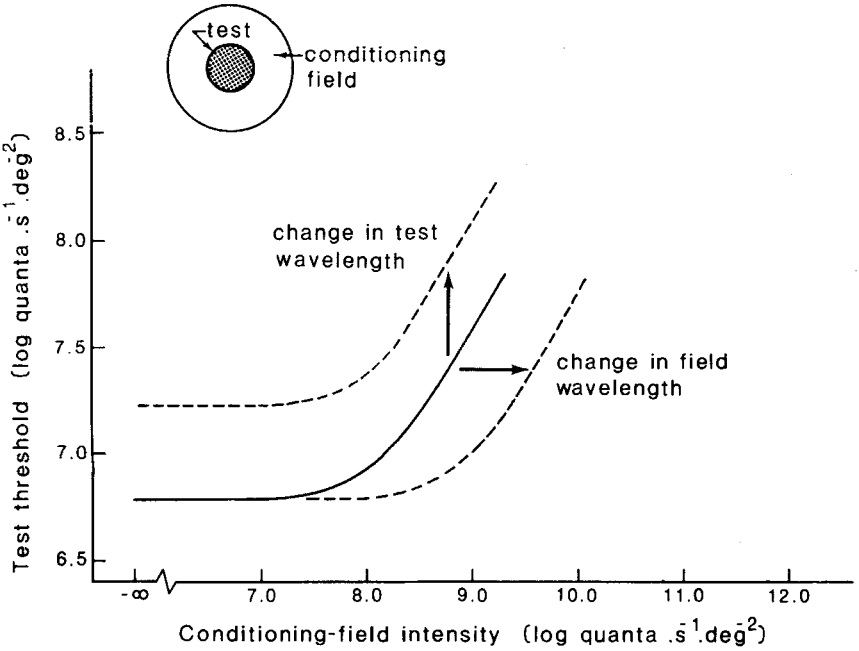

Figure 3. Threshold-*versus*-intensity (tvi) curves for a colour mechanism. The inset shows the spatial arrangement of the stimuli.

intensities M_μ. These *threshold* settings may be determined by a number of techniques, but results do not depend critically on the particular method chosen. The continuous curve in figure 3 shows typical results for the variation of N_λ with M_μ. Note that radiant intensities, usually expressed in quantum units, have been transformed to a $\log_{10}$ scale. This is conventional, and has a number of advantages including stabilizing the variance associated with each experimental measurement at each conditioning-field intensity. For clarity, a radiant intensity of 10^N quanta.s^{-1}.deg^{-2} is written as N log quanta.s^{-1}.deg^{-2}. (Since threshold and sensitivity are inversely proportional, a threshold with that value would correspond to a sensitivity of $-N$ log quanta.sec^{-1}.deg^{-2}.)

The form of the dependence of test threshold on conditioning-field intensity was explained by Stiles in the following way. Stimuli were assumed to detected by an association of cones (or rods), called generically π *mechanisms*, that could be considered to act as independent units. The observed threshold was assumed to depend only on the threshold of the most sensitive π mechanism under the conditions of the particular experiment. The value N_λ of that threshold was further assumed to depend on the conditioning-field intensity M_μ only in so far as the particular π mechanism was excited by the conditioning field: excitation of other π mechanisms by the conditioning field was considered, to a first approximation, to be negligible. Thus, in figure 3, as the conditioning-field intensity is progressively increased from zero, threshold for the test flash first remains the same as its value on zero background, and then increases as the sensitivity of say the i^{th} π mechanism π_i detecting the test flash is reduced by the conditioning field. The shape of the resulting *threshold-versus-intensity* or tvi curve depends on the particular conditions of the experiment.

If the wavelength λ of the test flash is altered, the resulting tvi curve should be displaced vertically, parallel to the axis of test intensity, according to the sensitivity of the i^{th} π mechanism to variations in test-flash wavelength (the displacement property being dependent on the use of a logarithmic scale). At any fixed conditioning-field wavelength μ and intensity M_μ, the latter typically zero, the dependence of the reciprocal of N_λ upon λ defines the *test spectral sensitivity*, denoted by $\pi_{i\lambda}$, of the i^{th} π mechanism. Conversely, if the wavelength μ of the conditioning field is altered, the resulting tvi curve should be displaced horizontally, parallel to the axis of conditioning-field intensity, according to the sensitivity of the i^{th} π mechanism to variations in conditioning-field wavelength. At any fixed test wavelength λ and intensity N_λ, defined conventionally as 1 log unit above threshold on zero field (*absolute* threshold), the dependence of the reciprocal of M_μ on μ defines the *field spectral sensitivity*, denoted by $\Pi_{i\mu}$, of the i^{th} π mechanism.

Under the assumptions of independence of π mechanisms outlined earlier, these two spectral sensitivities $\pi_{i\lambda}$ and $\Pi_{i\mu}$ should have the same shape, over those parts of the spectrum where both can be measured. Stiles (1946, 1949, 1953) found this to be so, providing that the excursions along the ordinate and abscissa caused by variations in λ and μ were not too great. Eventually, however, the dependence illustrated by the continuous tvi curve in figure 3 fails, and threshold was then assumed to be determined by a different π mechanism with a different tvi curve.

Using this technique, Stiles derived three main classes of π mechanism, the principal members of which had peak sensitivities at 440 nm (π_3), 540 nm (π_4), and 575 nm (π_5) (Stiles 1959). Field spectral sensitivities (which can be determined over more of the spectrum than test spectral sensitivities) are shown in figure 4, for (a) Π_3, (b) Π_4, and (c) Π_5. As has been conventional, a wavenumber rather than wavelength scale is used.

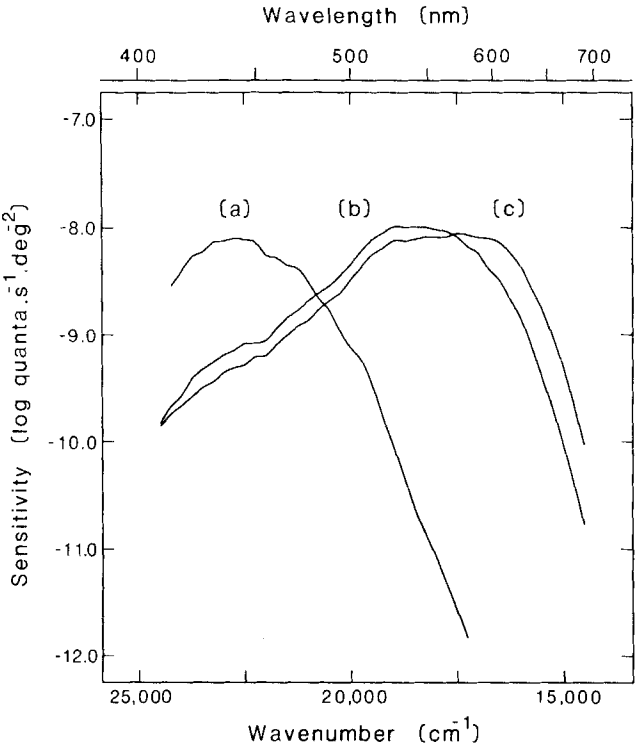

Figure 4. Field spectral sensitivities of Stiles's colour mechanisms (a) π_3, (b) π_4, and (c) π_5. (Curves plotted from average data listed in Wyszecki and Stiles, 1982, Table 2(7.4.3). The curve for π_3 in the figure has been raised by 1 log cycle.)

Stiles found it necessary to postulate additional π mechanisms to account for the various breakdowns in tvi dependence obtained under some adaptational conditions, and so not all π-mechanism spectral sensitivities could represent cone spectral sensitivities.

Detailed examinations of the field sensitivities of the mechanisms π_3, π_4, and π_5 have indicated that although π_5 and apparently π_3 are each adaptationally sensitive to signals from only one class of cone (Sigel and Pugh 1980, Pugh and Mollon 1979), this is not true for π_4, for changes in the shape of the π_4 tvi curve have been shown to occur with long-wavelength conditioning fields (Sigel and Brousseau 1982). Despite these technical difficulties, it has been possible to demonstrate a broad qualitative agreement between the spectral sensitivities of π_3, π_4, and π_5 and the fundamental spectral sensitivities of small-field colour matching (Estévez and Cavonius 1977, Pugh and Sigel 1978, Wyszecki and Stiles 1980).

3.1.4. *Microspectrophotometry*: It is possible to measure the absorbance of individual photoreceptors using the techniques of microspectrophotometry (MSP). Marks *et al.* (1964) and Brown and Wald (1964) made axial recordings from human cones in whole mounts of the retina. These measurements were of *difference* spectra, that is, the difference in optical density before and after bleaching the photopigment, thus avoiding artifacts due to the optically stable constituents of the retina. Because of the difficulty of

the technique and the small number of cones examined, the spectra obtained were of limited accuracy. J. K. Bowmaker and his colleagues subsequently made measurements of *transverse* absorbance of a large number of cones excised from the retinae of seven human eyes (Bowmaker and Dartnall 1980, Dartnall *et al.* 1983). Figure 5 shows their results for (a) short-wavelength-sensitive cones, (b) medium-wavelength-sensitive cones, and (c) long-wavelength-sensitive cones. Wavelengths for peak absorbance were at approximately 419, 531, and 558 nm. These values cannot be compared directly with the previously described psychophysical estimates because the latter are modified by absorption in the ocular media, particularly in the lens of the eye and in an inert yellow retinal pigment, the *macula lutea*, which extends beyond the fovea. It is, however, possible to estimate these prereceptoral losses. This was done by Bowmaker *et al.* (1980) and Bowmaker and Dartnall (1980), and the authors obtained a generally satisfactory agreement between the spectral sensitivities of π mechanisms and those obtained by MSP.

3.2. *Receptor photopigments*

The photopigment in rods is *rhodopsin*, and its absorption spectrum matches well the spectral sensitivity of the dark-adapted eye (figure 2 a). It has not, however, been possible to isolate *in vitro* the photopigments in cones, despite the considerable body of empirical data relating to their absorption characteristics *in vivo*. The continuing failure to extract cone photopigments has led to other explanations of the differing spectral sensitivities of human cones, including the possibility of waveguide modes of action (the dimensions of cones being compatible with such effects), and the possibility of coloured filters in front of receptors (as occur in the form of oil droplets in the eyes of some birds). Both explanations have been highly controversial (see Ruddock 1971).

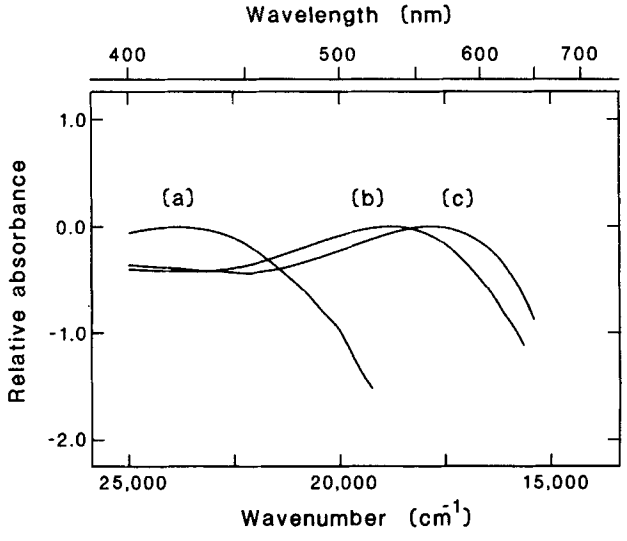

Figure 5. Absorbance spectra obtained by microspectrophotometry for (a) short-wavelength-sensitive cones, (b) medium-wavelength-sensitive cones, and (c) long-wavelength -sensitive cones of the human eye. (Curves plotted from average proportional absorbance data listed in Dartnall *et al.*, 1983, Table 2.)

3.3. *Retinal distributions of different classes of cone*

The populations and distributions over the retina of the long-, medium-, and short-wavelength-sensitive cones are not the same. Estimates may be made by both psychophysical and histochemical techniques. From the latter, it has been suggested that at the central fovea of the primate retina there are probably about twice as many medium-wavelength-sensitive cones as long-wavelength-sensitive cones; in more parafoveal regions, respective proportions of long-, medium-, and short-wavelength-sensitive cones are approximately 33, 55, and 12 per cent (Marc and Sperling 1977). Short-wavelength-sensitive cones are almost certainly absent from the central 20 min arc of the fovea and reach their greatest density, albeit still low, at 1–1·5 degrees eccentricity (Marc and Sperling 1977, de Monasterio *et al.* 1981).

4. Post-receptoral colour processes

There is considerable evidence from psychophysics, some already touched upon, and from perceptual psychology and electrophysiology, that the initial encoding of colour in terms of the activities of three classes of cone is not preserved throughout the visual system. At post-receptoral levels, cone signals are combined in different ways so that they represent quantities related to stimulus luminance and chrominance or chromaticity (colourfulness). A broad class of theories that deal with this kind of post-receptoral encoding are called *opponent-process* theories (Hurvich and Jameson 1957, Jameson 1972). Two parallel systems are usually assumed: a *non-opponent* system, which transmits cone signals combined with the same sign, and which typically signals luminance; and an *opponent-colour* system, which transmits cone signals combined with different signs, and which typically signals hue. The two systems are sometimes referred to as *achromatic* and *chromatic* systems, respectively.

The description of all post-receptoral processing in terms of opponent-process theory is clearly an oversimplification, but the functional division of processing into receptoral and post-receptoral levels has proved useful. The detailed characteristics of opponent-colour processes, particularly their sensitivity to spatial organization of the retinal image and the form of their spectral sensitivities, may vary from level to level in the visual pathway (Gouras 1972, de Monasterio and Gouras 1975, de Monasterio 1978, Marrocco 1976, Dow 1974, Zeki 1977), although one analysis (de Monasterio and Schein 1982) of electrophysiological data has suggested that there may be substantial constancy in the bandwidths of colour-opponent cells from retina to cortex.

4.1. *Characteristics of chromatic and achromatic systems*

Critical experimental properties of the chromatic, opponent-colour system and the achromatic, non-opponent system have been postulated as follows. Supporting evidence has been cited in Foster and Snelgar (1983 a).

(*a*) Relative to the non-opponent system, the opponent-colour system has poor high-spatial-frequency response (greater spatial integration).

(*b*) Relative to the non-opponent system, the opponent-colour system has poor response to temporal transients (greater temporal integration).

(*c*) The sensitivity of the non-opponent system is preferentially depressed by white conditioning fields of moderate-to-high intensity.

(*d*) Unlike signals from long- and medium-wavelength-sensitive cones, signals from short-wavelength-sensitive cones have access only to the opponent-colour system.

It should be noted that these proposed characteristics, particularly (*a*) and (*b*), relate to a general, psychophysically defined, opponent-colour system. Such a system may reflect the activity of an ensemble of retinal colour-opponent cells that individually have spatial characteristics different from colour-opponent cells in some areas of cortex (Gouras 1968, 1972, Dow and Gouras 1973, de Monasterio and Gouras 1975, Zeki 1977, 1980, de Monasterio 1978).

4.2. *Isolation of chromatic pathways*

If stimuli are constituted in accord with the above properties, it is possible to stimulate preferentially or selectively the opponent-colour or non-opponent systems. Experimentally, selective stimulation of the non-opponent system is not difficult to achieve. The following techniques have been used to allow selective stimulation of the opponent-colour system.

4.2.1. *Detection determined by short-wavelength-sensitive cones*: When a short-wavelength test flash, typically 420 nm, is presented on a large, concentric, medium-to-long-wavelength, steady conditioning field, in the manner of Stiles described in section 3.1.3., detection is determined by short-wavelength-sensitive cones. Under the assumption that short-wavelength-sensitive cones have access only to opponent-colour pathways, it may be expected that the properties of the latter may determine some of the characteristics of test-flash detection. Unfortunately, it may not always be possible to distinguish receptoral and post-receptoral contributions to observed performance. Thus spatial acuity determined by the short-wavelength-sensitive mechanism is low (Brindley 1954), consistent with the proposed properties of opponent-colour pathways, but the retinal distribution of short-wavelength-sensitive cones is also much sparser than the distribution of medium- and long-wavelength-sensitive cones. Likewise, temporal frequency response determined by the short-wavelength-sensitive mechanism is low, so that the maximum frequency of a flashing light that can be detected as flashing by the short-wavelength-sensitive mechanism is about 18 Hz, compared with more than 50 Hz for the medium- and long-wavelength-sensitive mechanisms, in one particular set of conditions (Brindley *et al.* 1966); this poor temporal resolution by the short-wavelength-sensitive mechanism is, however, a probable consequence of both receptoral and post-receptoral factors. One phenomenon involving the short-wavelength pathways that almost certainly does reflect opponent-colour processing was reported by Stiles (1949) and subsequently investigated by Mollon and Polden (1977). If the eye is adapted to a medium- or long-wavelength conditioning field and the field is suddenly removed, the threshold of the short-wavelength-sensitive mechanism is raised rather than lowered. Recovery may take seconds (see Mollon and Polden 1977).

Despite its experimental simplicity, there are inherent limitations attached to the use of the short-wavelength-sensitive mechanism for the investigation of opponent-colour pathways, not least of which is the spectral restriction on test stimuli.

4.2.2. *Introduction of a large white conditioning field*: According to the proposed properties (section 4.1.) of the opponent-colour system, the use of a relatively large (e.g. 1 degree) and relatively long (e.g. 200 ms) test flash on a large white (*auxiliary*) conditioning field should facilitate detection by the opponent-colour system. This hypothesis has been confirmed experimentally. Test spectral sensitivity obtained by an observer using a simple detection criterion has been shown (King-Smith and Carden 1976) to correspond, over most of the spectrum, to the spectral sensitivity obtained with the use of a *colour*-detection criterion, the latter presumably dependent on the spectral sensitivity of the opponent-colour system. The upper broken line (a) in figure 6 shows test spectral sensitivity, for simple detection, obtained with a large white auxiliary conditioning field. The isolation of the opponent-colour system in this kind of measurement can be improved further, as follows.

4.2.3. *Introduction of a white conditioning field spatially coincident with the test field*: The technique for deriving the field spectral sensitivity of a colour mechanism was outlined in section 3.1.3. The procedure was to determine, at a number of different wavelengths, the reciprocal intensity M_μ of a large, monochromatic conditioning field that raised the threshold intensity N_λ of a small superimposed test flash, of fixed wavelength λ, by a constant multiple of its value on zero field. The resulting sensitivity function reflects an *adaptational* sensitivity of the mechanism. When, however, field spectral sensitivities of the medium- and long-wavelength-sensitive mechanisms, corresponding normally to Stiles's mechanisms π_4 and π_5 (figures 4 b and 4 c) are obtained with a long-duration test flash presented on a white auxiliary conditioning field, *spatially coincident* with the test field, the resulting curves may appear narrowed or sharpened with their peaks shifted away from each other along the wavelength scale. Results are illustrated in the lower half of figure 6. The field spectral sensitivity of the long-wavelength-sensitive mechanism π_5, normally rather flat-topped, with maximum sensitivity at about 575 nm (figure 4 c) becomes attenuated on the short-wavelength side and acquires a relatively sharp peak at 615–625 nm (figure 6 e). The field spectral sensitivity of the medium-wavelength-sensitive mechanism π_4, also fairly flat-topped with maximum sensitivity at about 540 nm (figure 4 b), becomes attenuated on the long-wavelength side and peaks a little more sharply close to 530 nm (figure 6 d). The field spectral sensitivity of the short-wavelength-sensitive mechanism π_3 (figure 4 a) shows no sharpening over the range 400–500 nm (figure 6 c) here with a coincident white auxiliary conditioning field or with a monochromatic auxiliary field of moderate-to-high intensity (Foster 1981). (It should be noted that the data shown in figures 4 and 6 are averages over different groups of observers. Detailed comparisons for the same observers have been given in Foster 1981).

These results, like those for test spectral sensitivity obtained on large white conditioning fields, have been interpreted (Foster 1981) within the framework of an opponent-process theory of colour vision. The basic hypothesis is that in the region of the boundary of the small auxiliary conditioning field there is a selective loss (by processes such as spatial adaptation, see section 6) of high-spatial-frequency sensitivity. The response to the spatial transient associated with the boundary of the test field, normally mediated by the high acuity, non-opponent system, is suppressed.

It seems possible that the sharpened field spectral sensitivities of the long- and medium-wavelength-sensitive mechanisms may represent, in part at least, the field spectral sensitivities of opponent-colour processes defining a 'red–green' channel. The

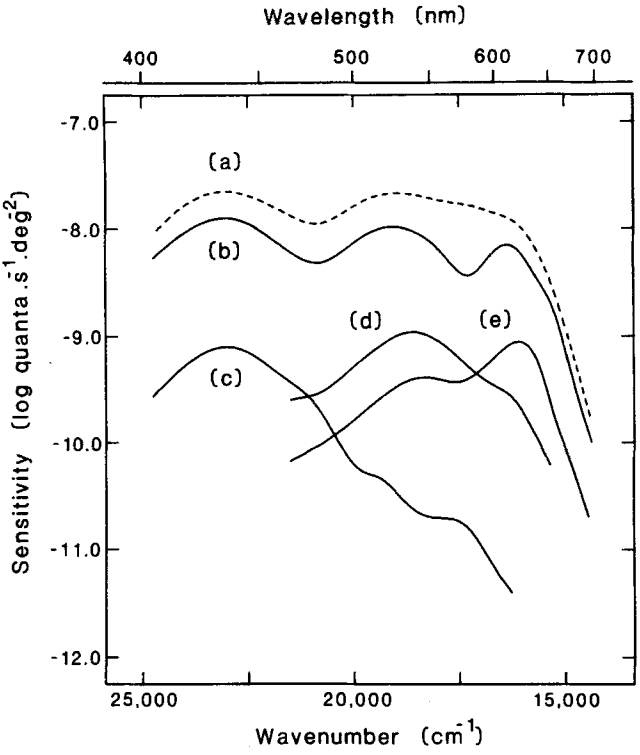

Figure 6. Spectral sensitivities of colour mechanisms obtained on a white auxiliary conditioning field (retinal illumination level 1000 td). Test spectral sensitivities are shown (a) for the auxiliary field larger than the test field, and (b) for the auxiliary field spatially coincident with the test field. Field spectral sensitivities are shown (c) for the short-wavelength-sensitive mechanism, (d) for the medium-wavelength-sensitive mechanism, and (e) for the long-wavelength-sensitive mechanism, each obtained with the auxiliary field spatially coincident with the test field. (Curves averaged from data given in Foster and Snelgar, 1983 a, Fig. 1. The field spectral sensitivity of the short-wavelength-sensitive mechanism (c) in the figure has been displaced downwards by 1 log cycle.)

sharpened field spectral sensitivity of the long-wavelength-sensitive mechanism (figure 6 e) would involve signals from medium-wavelength-sensitive cones inhibiting signals from long-wavelength-sensitive cones; and conversely the sharpened field spectral sensitivity of the medium-wavelength-sensitive mechanism (figure 6 d) would involve signals from long-wavelength-sensitive cones inhibiting signals from medium-wavelength-sensitive cones. These inhibitory interactions are apparently asymmetric (compare (d) and (e) in figure 6), and have been revealed in other visual phenomena (Stromeyer *et al.* 1978). At present, the contributions of post-receptoral adaptation and pure receptoral adaptation to the field spectral sensitivities (c), (d), and (e) of figure 6 have not been distinguished (Foster 1981, Foster and Snelgar 1983 a, 1983 b).

The continuous curve (b) in the upper half of figure 6 shows test spectral sensitivity determined on a white auxiliary conditioning field spatially coincident with the test field. The peaks in test spectral sensitivity at medium and long wavelengths are more clearly demarcated than with the non-coincident large white auxiliary conditioning field (figure 6 a) and presumably result from the increased isolation of the opponent-colour system achieved by the combined effects of achromatic and spatial adaptation of

the non-opponent system. The positions of these peaks, at approximately 440, 520–530, and 605–615 nm, are characteristic of opponent-colour processes revealed in *hue-cancellation* experiments (Hurvich and Jameson 1957) in which subjects made judgements about the 'redness' or 'greenness' of stimuli. The close fit of the full test spectral sensitivity curve (figure 6 b) and the upper envelope of the field spectral sensitivities (figures 6 c, 6 d, 6 e), all obtained on the coincident auxiliary conditioning field, suggests the involvement of common opponent-colour processes.

4.2.4. *Isoluminant stimulation*: A different approach to the isolation of chromatic pathways entails the use of chromatic stimuli that appear spatially and temporally constant to the luminance system. A typical arrangement comprises two monochromatic square-wave gratings, the one of long wavelength, the other of medium wavelength, superimposed in antiphase. If the two gratings have precisely the same luminance, then in principle the combined stimulus should appear uniform to the luminance system. The response of the opponent-colour system may then be explored as the spatial period, time course, or other attributes of the stimulus are varied. The technique is analogous to the spectral-compensation method (section 3.1.2.) used for isolating cone mechanisms.

There are a number of technical difficulties associated with the use of this method, including the introduction of ocular chromatic differences of magnification of the retinal image and equalization of luminances at different spatial frequencies. Work by K. T. Mullen has, however, circumvented many of these problems (e.g. Mullen 1982). Results on spatial and temporal frequency response characteristics obtained by this method are consistent with the properties (a) and (b) listed in section 4.1.

5. Models of colour vision and colour appearance

Most models of colour vision based on opponent-process theory have involved the introduction of some inhibitory interaction between signals from long- and medium-wavelength-sensitive cones. Models have differed, however, in how the inhibitory interaction is computed and how the resulting signals are combined with signals resulting from non-inhibitory interactions to determine overall visual performance.

Following E. Hering (1874), D. Jameson and L. M. Hurvich developed a quantitative opponent-process theory (e.g. Hurvich and Jameson 1957). They specified (Jameson 1972) three kinds of response: an achromatic response V_1 that consisted of a linear combination of cone-mechanism responses with positive coefficients only; and two chromatic responses V_2 and V_3 that consisted of linear combinations of cone-mechanism responses with both positive and negative coefficients.

Subsequent models of receptoral and post-receptoral encoding by S. L. Guth and by C. R. Ingling and their co-workers have been characterized as *vector* models. In one such model (Ingling and Tsou 1977), the response to an arbitrary stimulus may be represented as a point in Euclidean 3-space, the normalized co-ordinates (x_1, x_2, x_3) of which are defined typically as a sum and two differences thus:

$$x_1 = a_{12}\beta + a_{13}\gamma$$

$$x_2 = a_{21}\alpha - a_{22}\beta + a_{23}\gamma$$

$$x_3 = -a_{31}\alpha + a_{32}\beta + a_{33}\gamma$$

where α, β, and γ are responses determined by the fundamental spectral sensitivity functions, equivalent to the spectral sensitivities of the short-, medium-, and long-wavelength-sensitive cone mechanisms, and the coefficients a_{ij}, all positive at suprathreshold levels, depend on the precise conditions of adaptation. The coordinate x_1 corresponds to the luminance response, and x_2 and x_3 to chromaticity responses in two separate chromaticity channels, the one 'red-green', the other 'yellow-blue'. Note that there is no input by the short-wavelength-sensitive mechanism to the luminance response x_1, and that in this model there is an input, although it is normally small, from the short-wavelength-sensitive mechanism to the 'red-green' response x_2. The size S of the total response is given by the Euclidean metric:

$$S^2 = Q^2(x_1^2 + x_2^2 + x_3^2)$$

where Q is a scaling factor determined by light intensity. By these means, spectral sensitivities, hue discrimination, apparent hue of monochromatic stimuli, and other kinds of visual performance were all well predicted (Ingling and Tsou 1977, Guth *et al.* 1980).

Other opponent-process models have introduced nonlinear transformations of cone-mechanism responses (see for example King-Smith and Kranda 1981, who improved on a linear model by Sperling and Harwerth 1971, of test spectral sensitivities on white backgrounds; see also Foster and Snelgar 1983 b). One model designed specifically for predicting colour appearance was proposed by R. W. G. Hunt (1982, 1983). It was assumed that signals from cones were subjected to a nonlinear compression by a power function with exponent 0·5. An achromatic signal was obtained as a linear combination with positive coefficients of compressed signals from long- and medium-wavelength-sensitive cone mechanisms; three chromatic signals were obtained as linear combinations with positive and negative coefficients of compressed signals from all three possible pairings of the three mechanisms (Hunt 1983). The model gave good predictions for loci of constant hue plotted in colour-matching space (*chromaticity diagram*) and good approximations to standard descriptions of surface colours, and to data on the appearance of spectral colours.

Less commonly, models of colour vision have included dynamical aspects of opponent-colour and non-opponent performance. Some which have dealt with temporal function have been proposed by Koenderink *et al.* (1972), and Pugh and Mollon (1979).

6. Colour vision and form perception

There are a wide range of visual phenomena involving both colour vision and pattern or form perception. Some involve the selective habituation or adaptation of the underlying sensory processes.

6.1. *Spatial adaptation*

The visual system has the capacity to adapt selectively to the spatial structure of stimuli. Typically, prolonged viewing of a grating while constantly moving the gaze will reduce sensitivity to a subsequently presented test grating that is close in spatial frequency to the original grating, whereas sensitivity to a test grating that is very different in spatial frequency, for example beyond one octave of the adaptation frequency, will not be affected (Gilinsky 1968, Pantle and Sekuler 1968, Blakemore and Campbell 1969). When the test and adaptation gratings were presented to the same eye, it was found that

the adaptation effect was spectrally selective; for example, threshold for a long-wavelength grating was raised by adaptation to a long-wavelength grating, but not to a medium-to-short-wavelength grating (May 1972, Maudarbocus and Ruddock 1974). When the experiment was performed *dichoptically*, with the adaptation grating presented to one eye and the test grating to the other, this spectral selectivity was lost (Maudarbocus and Ruddock 1973). But, when the dichoptic paradigm was modified so that the test eye was adapted to a grating and the other eye to a matrix of circular spots, the detection of the test grating was found to be dependent on the wavelength of the adapting matrix (Hendricks *et al.* 1982). The authors obtained spectral sensitivity functions of an opponent-colour type: extrema in interactions occurred at about 600, 520, and 450 nm (see section 4.2.3.). The medium- and long-wavelength-sensitive functions were interpreted (Hendricks *et al.* 1982) in terms of subtractive interactions between signals from medium- and long-wavelength-sensitive cones, probably within the 'red-green' opponent-colour channel (see section 5).

6.2. *Form-contingent colour after-effects*

There are a number of related phenomena in which coloured after-images, produced classically by adapting the eye to a uniform coloured field and then inspecting a uniform neutral test field, are made contingent upon the spatial structure of the adaptation and test fields. The best known of these form-contingent colour after-effects is the *McCollough effect*. The eye is adapted, for example, to alternately presented gratings: the one composed of vertical red and black bars, and the other of horizontal green and black bars. After this adaptation period, a neutral vertical test grating appears pale greenish, and a neutral horizontal test grating appears pinkish. The effect is long-lasting and may extend over days. It is not merely contingent upon orientation; it may also be made to depend on spatial frequency and motion. The effect has been attributed variously to the selective adaptation of populations of neurones affected jointly by colour and spatial structure, and to the associative habituation or modification of neural connections. Stromeyer (1978) has given a survey of form-contingent colour after-effects.

Form-contingent colour after-effects are sometimes cause for a mildly disturbing concomitant of prolonged viewing of text on VDU screens with the currently common, green P31 phosphor. Neutral patterned fields, for example white printed type on a dark background, can at the appropriate viewing distance subsequently appear pinkish in the localized region of gaze.

6.3. *Colour and form coding*

Information about the precise form of a visual stimulus is carried by the luminance system; information about the spatial variation of its colour is given less precision. As R. L. Gregory (1977) has pointed out, it is surprising, given the separate character of the two systems, that 'misregistration' of the perceptual images does not occur, particularly at the boundaries. The interesting notion has been proposed by Gregory that the luminance system provides a master spatial signal to which there is slave locking of chromatic signals. Under some conditions, for example, motion of a blue-and-white target on a bright yellow background, a perceptual misregistration does occur, but this is a consequence of the slowness of the chromatic system relative to the luminance system. Form information carried by the chromatic system, although coarse, is sufficient for most of the classical geometrical distortion illusions to be maintained or only slightly impaired under isoluminant conditions, where stimuli are

defined by their chromatic variation, luminance remaining substantially uniform over the field. Some illusions that depend on complex spatial structure, however, are destroyed under isoluminant conditions (Gregory 1977).

Separate processing of some spatial information by chromatic and luminance systems has been reported in a correlate of the spatial adaptation phenomenon described in section 6.1. Prolonged viewing of a grating pattern gives rise to a shift in the perceived spatial frequency of a subsequently presented test grating (Blakemore and Sutton 1969). In the induction of these effects, the luminance and chromaticity systems appear to operate independently of each other (Favreau and Cavanagh 1981).

6.4. *Central visual processes*

Experimental data from anatomy and physiology have suggested separate areas in the visual cortex and *prestriate* visual cortex that are specific for form, colour, motion, and depth (Zeki 1978; see also reviews by Van Essen and Maunsell 1983, Mishkin *et al.* 1983). In one area, known as V4, the majority of cells have been found to be colour-coded with large receptive fields, responding to the same stimulus over a large region of the retina (Zeki 1977, 1980; compare Schein *et al.* 1982). Moreover, the cells in this region have no discernible *retinotopic* organization, such as that found elsewhere in the visual cortex, so that recordings by microelectrode along oblique penetrations in the cortex showed little relation to the geometry of the visual field (Zeki 1980). Some colour-coded cells in V4 have been found (Zeki 1980, 1983) to respond to *apparent* colour. Thus, the spectral composition of the light within the nominal receptive field of the cell was not sufficient to determine its response: regions surrounding the field also influenced its activity. These responses have been related (Zeki 1980, 1983) to the perceptual phenomenon of *colour constancy*, where the appearance of colours remains the same independent of changes in illuminant.

7. Colour-vision deficiencies

It has been traditional to divide deficiencies in human colour vision into those which are inherited and those which are acquired. Congenital disorders of the long- and medium-wavelength-sensitive cone mechanisms result from sex-linked inheritance, whereas those of the short-wavelength-sensitive mechanism result from autosomal inheritance. Because some nominally acquired deficiencies, due for example to disease, may have a genetic component, the division of deficiencies into inherited and acquired is essentially conventional.

7.1. *Inherited colour-vision deficiencies*

Classification of the inherited deficiencies has derived from colour-matching experiments. Thus, as already noted, some observers do not need three independent primaries to make a colour match. For about 2–3 per cent of males and less than 0·05 per cent of females, two primaries are sufficient. These observers are called *dichromats*. For an even smaller proportion of the population, about 0·005 per cent, one primary is sufficient for colour matching. For such *monochromats*, all matches are brightness matches. There is, in addition, a class of observers, about 5·5 per cent of males and about 0·4 per cent of females, that, like normal observers, require three primaries for colour matching, but use abnormal combinations of those primaries. These observers are known as *anomalous trichromats* and they usually have impairment in other aspects of colour function (see Wyszecki and Stiles 1982, Pokorny *et al.* 1979).

Dichromacy, investigated most notably by Pitt (1935) and Wright (1952), has three possible forms called *protanopia*, *deuteranopia*, and *tritanopia*, which may be viewed as reductions of normal trichromacy caused by the loss of function of respectively the long-, medium-, or short-wavelength-sensitive cones. Monochromacy may manifest itself as either cone monochromacy, which is very rare, or rod monochromacy. In the former there is at least one functional cone photopigment; in the latter only rods function. Anomalous trichromacy results from modification of the spectral sensitivities of one or more cone types. (For further discussion of inherited and acquired deficiencies in colour vision, see Pokorny *et al.* 1979, and Verriest 1980.).

7.2. *Acquired colour-vision deficiencies*

Deficiencies of colour vision may be acquired as a result of disease, toxic agents, physical injury, or the normal processes of ageing. Curiously, the short-wavelength-sensitive mechanism, only rarely involved in inherited colour-vision deficiency, is far more likely to be affected in disease. Because of the differences in causation and in sites of action, acquired colour-vision deficiences cannot be classified satisfactorily using the system devised for inherited colour-vision deficiencies.

Disease processes affecting the blood or blood vessels may modify colour vision (see reviews in Pokorny *et al.* 1979). For example, in diabetes mellitus, with inadequately maintained insulin activity, there is a deficiency in retinal circulation that leads to deterioration in colour discrimination either generally or specifically in the short-to-medium-wavelength end of the spectrum accompanied by losses in function of the short-wavelength-sensitive mechanism (Birch *et al.* 1980). Impairment in discrimination and losses of function of the short-wavelength-sensitive mechanism may also occur in glaucoma, in which there is an intra-ocular elevation in pressure and damage to the eye, in turn leading to nerve fibre bundle damage. In multiple sclerosis, a disease that causes lesions in the optic nerve and tract (and elsewhere in the central nervous system), there is often general impairment in visual function, including the apparent desaturation of coloured stimuli, reduction in colour discrimination, and reduction in chromatic sensitivity (Perkin and Rose 1979, Pokorny *et al.* 1979). The characteristics and sometimes unilateral nature of acquired colour-vision deficiencies are often of diagnostic use for the clinician.

Drugs sometimes have side-effects on vision, and deficiencies in colour vision, manifested as losses in colour discrimination or as changes in colour perception, often arise as one of the first clinical symptoms of the effects of toxic agents. Drugs that may cause such side-effects include tobacco (leading to tobacco amblyopia), some antibiotics, some oral contraceptives, and some chemotherapeutics (Pokorny *et al.* 1979). For example, the drug ethambutol, used as a tuberculostaticum, appears mainly to affect the function of the opponent-colour system involving post-receptoral inhibitory interactions between signals from long- and medium-wavelength-sensitive cones (Zrenner and Krüger 1981). The three-peaked test spectral sensitivity curve of the form illustrated in the upper half of figure 6 has been found to be modified: the notch at about 580 nm, characteristic of 'red-green' opponent-colour interaction, was absent in patients (Zrenner and Krüger 1981).

Colour-vision abnormalities secondary to damage of the cortex have occasionally been reported. In one case (Young *et al.* 1980), a patient with previously normal colour vision exhibited losses in colour discrimination and of function of the short-wavelength-sensitive mechanism following a blow to the back of the head. This pattern of colour impairment was tentatively attributed to a loss of function of (central)

chromatic processes. An unusual central deficit in colour vision has also been reported (Hendricks *et al.* 1981) in which an observer experienced a spreading loss in vision associated with long-wavelength stimuli. The effect could be sufficiently strong to obliterate perception of a large area of the field containing the long-wavelength light. The likely site for the deficit was thought to be the area V4 referred to in section 6.4.

Although a number of novel aids for impaired colour vision have been proposed, there is no cure for inherited colour-vision deficiency; any recovery of colour vision in acquired colour-vision deficiency depends on the course of the disease or injury.

8. Conclusion

As this article has indicated, substantial progress has been made in the understanding of receptoral and post-receptoral colour-vision function. At present, the outstanding problems in colour vision appear to divide naturally into three main types: the problem of the detailed functional organization of post-receptoral chromatic and achromatic systems; the problem of the reconciliation of the presently simple description of colour processing offered by psychophysics with the complex body of data derived from single-cell microelectrode recordings; and, most central of all, the problem of the visual combination of information concerning object colour and object form to produce a unitary perceptual experience. For the first problem, the introduction of new psychophysical techniques for the isolation of chromatic pathways offers the possibility of elucidating further the organization of the opponent-colour system. The second problem should be amenable to combined techniques involving behavioural, electrophysiological, and anatomical work on animals. As for the third problem, new techniques from psychophysics, perceptual psychology and mathematics have provided information about the spatial encoding processes used by the visual system in form perception and pattern recognition (see Foster 1984, for review); a great deal more work will have to be done, however, on the processes encoding form and colour before substantial progress is made on the fundamental question of their perceptual synthesis.

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