

OCULAR FILTERING OF ULTRAVIOLET RADIATION AND THE SPECTRAL SPACING OF PHOTORECEPTORS BENEFIT VON KRIES COLOUR CONSTANCY

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Summary

Ocular filters in the eyes of many vertebrates, including humans, absorb wavelengths shorter than approximately 400 nm. These filters prevent the β -band of a visual pigment from being exposed to ultraviolet radiation, essentially narrowing the spectral sensitivity of the different photoreceptor classes. A comparison of different hypothetical visual systems is used to show that von Kries colour constancy is improved by ocular filtration of ultraviolet radiation, whilst there is no reduction in

colour discrimination. Furthermore, it is shown that the asymmetric spectral spacing of different photoreceptor classes present in the human visual system may benefit colour constancy. The results are interpreted in relation to predictions of von Kries colour constancy for a standard human observer.

Key words: colour vision, colour space, illumination, Old-World primate.

Introduction

The eyes of many vertebrates contain ocular filters that absorb ultraviolet radiation (300–400 nm) (Fig. 1). For example, in primates protein pigmentation in the lens of the eye prevents radiations with wavelengths shorter than approximately 400 nm from reaching the retina (Zigman et al., 1976). The possible function of this type of optical filtering has previously been explained as improving optical performance through reduced chromatic aberration, haze and glare, or to prevent damaging ultraviolet radiation from reaching the retina (for reviews see Muntz, 1972; Douglas and Marshall, 1999).

Human colour vision is based on three classes of photoreceptor with spectral absorbance maxima at approximately 420, 534 and 564 nm (Bowmaker and Dartnall, 1980). These receptor peaks can be taken as reasonably representative of the asymmetrically spaced receptors in many Old-World primates (Bowmaker, 1991). Each class of photoreceptor also has the potential to absorb ultraviolet radiation as a result of the *cis*-band of the chromophore, which produces a common secondary absorbance peak at approximately 340 nm (Stavenga et al., 1993). The primary receptor peak is termed the α -band and the secondary peak the β -band. Interestingly, the perception of ultraviolet radiation by humans has been directly observed in aphakic patients who have had their lenses surgically removed (Wald, 1945; Davenport and Foley, 1979).

Illumination quality for most diurnal animals is highly variable because of continuously changing atmospheric conditions (Lythgoe, 1979), and the ability of a visual system to correctly identify a coloured stimulus in spectrally variable

illumination is termed colour constancy (Hurvich, 1981; MacAdam, 1985; Kaiser and Boynton, 1996). Colour constancy is usually considered to be complete only if the colour of a stimulus is identical in spectrally different illumination sources, and an incomplete correction is described as approximate colour constancy. It is known that in many circumstances colour constancy is imperfect in humans (Hurvich, 1981; MacAdam, 1985; Kaiser and Boynton, 1996). Chromatic adaptation is likely to be an important mechanism of colour constancy and can be explained by the von Kries coefficient law (von Kries, 1902 in MacAdam, 1970; Hurvich, 1981; MacAdam, 1985; Kaiser and Boynton, 1996). von Kries colour constancy assumes that the relative spectral sensitivity of different photoreceptor classes does not change, but that the relative sensitivity of photoreceptors vary to achieve constancy.

Theoretical analyses show that von Kries colour constancy is limited both by an increase in the spectral breadth and an overlap of different photoreceptor classes (Worthey and Brill, 1986; Dyer, 1999; Kevan et al., 2001), and recent studies have suggested that one purpose of ocular filters may be to improve von Kries colour constancy (Vorobyev et al., 1998; Dyer, 1999). For example, Vorobyev et al. (Vorobyev et al., 1998) modelled the tetrachromatic colour visual systems of two birds, the pigeons and the Pekin robins, and showed that coloured oil droplets above the bird's cones would narrow the spectral sensitivities of the photoreceptors and improve von Kries colour constancy. Dyer (Dyer, 1999) modelled the trichromatic colour vision of the honeybee (*Apis mellifera*), which has photoreceptor peaks at approximately 350, 440 and 540 nm

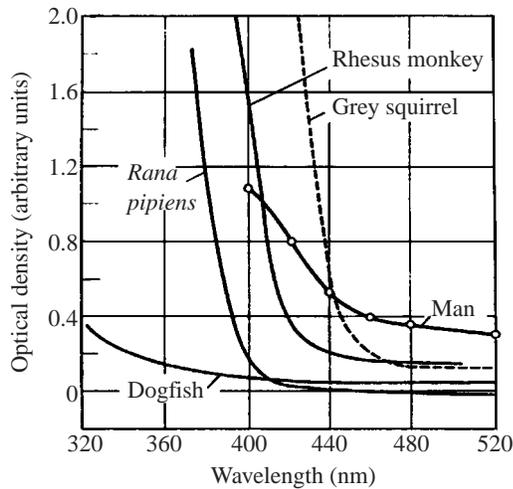


Fig. 1. The spectral absorbance of ocular filters in the eyes of various vertebrates. (Redrafted from Muntz, 1972, with the permission of Springer-Verlag and W. R. A. Muntz.)

(Peitsch et al., 1992), and showed that increases in the spectral breadth of the photoreceptors caused by the β -band peaks limit von Kries colour constancy. It was therefore suggested that screening pigments in the eyes of some insects (e.g. Peitsch et al., 1992) may serve to reduce the influence of the β -band peak. For animals with visual systems that do not have an α -band photoreceptor absorbing in the ultraviolet and do not need to have optics that transmit these wavelengths, it may thus be beneficial for colour constancy to have ocular filters that absorb ultraviolet radiation before it reaches the retina.

An intriguing question in the evolution of trichromatic colour visual systems for Old-World primates and humans is that the three receptor classes are asymmetrically spaced (Mollon, 1989; Goldsmith, 1990). In humans, the short-wavelength-sensitive (SWS) and long-wavelength-sensitive (LWS) cones absorb radiation maximally at approximately 420 nm and 564 nm, respectively, so the medium-wavelength-sensitive (MWS) cones would need to be maximally sensitive at approximately 492 nm for the three receptor classes to be evenly spaced, assuming the same region of the spectrum is to be sampled. Theoretical analyses of colour visual systems suggest that symmetrically spaced receptors across the spectrum should be optimal for the discrimination of differently coloured stimuli (Barlow, 1982; Vorobyev and Menzel, 1999). Several authors have suggested that the asymmetric trichromatic visual systems in Old-World primates may be an adaptation that is well suited to detecting yellow- and orange-coloured fruits from green foliage (Mollon, 1989; Regan et al., 1998; Sumner and Mollon, 2000), and Barlow (Barlow, 1982) demonstrated that the small spectral separation of the MWS and LWS cones may benefit spatial resolution in human vision. Another possible explanation for asymmetric receptor spacing lies in the genetic evolution of human trichromatic vision: the MWS receptor may lie at approximately 534 nm because of how far and how fast the spectral position of this receptor is able to evolve from

the long-wavelength subfamily of pigments in mammals (Goldsmith, 1990). However, the green opsin genes of rabbits (*Oryctolagus cuniculus*) and rats (*Rattus norvegicus*) have been sequenced (Radlwimmer and Yokoyama, 1998), and an absorbance maximum at about 509 nm was demonstrated. Sun et al. (Sun et al., 1997) sequenced the mouse green cone, which has a maximum absorbance of radiation at approximately 508 nm, and suggested that there are genetic tuning mechanisms that could allow the long-wavelength subfamily of pigments in mammals to have absorption maxima at wavelengths as short as 487 nm. Studies of the evolution of visual pigments indicate that genetic tuning may occur over relatively short periods; for example, divergent fish species possess photoreceptors that appear to have adapted to their present photopic environment over the last 20000 years (Bridges and Yoshikami, 1970; Bridges, 1974). This suggests that the asymmetric spacing of receptors in Old-World primates may be an adaptation to their visual environment, rather than a result of genetic invariability. Osorio (Osorio, 1997) suggested an alternative possibility for the asymmetric spectral spacing of receptors by demonstrating that a reduction in the spectral separation of the MWS and LWS receptors benefits von Kries colour constancy for coloured fruits. This idea, together with the optimised ability to detect stimuli against a mature leaf background (Sumner and Mollon, 2000), provides an interesting and plausible explanation for the curious spectral spacing of photoreceptors in Old-World primates.

In the present study, hypothetical visual systems (HVSs) are used to approach two questions about colour vision. (i) Are ocular filters that absorb ultraviolet radiation likely to benefit colour constancy? (ii) Is the asymmetric spectral spacing of photoreceptor classes in Old-World primates and humans likely to benefit colour constancy? The efficiency of von Kries colour constancy is also determined for a standard human observer to allow a calculation of perceptual colour difference in spectrally variable illumination (MacAdam, 1985).

Materials and methods

Measuring the reflectance spectra of stimuli

The reflectance spectra of 24 differently coloured stimuli (Table 1) were measured using a Varian DMS100 spectrophotometer fitted with a diffuse reflectance attachment. The spectral range examined included 300–700 nm, to allow an analysis of how a visual system including the β -band peak might view the stimuli. The spectrophotometer was calibrated against a Varian pressed polytetrafluoroethylene powder standard. The 24 stimuli include 12 man-made and 12 naturally occurring samples, and represent a range of colours for normal human vision. These included fruit items, coloured card (Optix Australia), white paper (Reflex Australia), coloured fabric material and a piece of sawn mountain ash wood (all purchased from local stores). In addition, leaf and bark samples were collected from the gardens at Monash University. To measure the reflectance spectra of the fruit, leaf and bark samples, a cut

Table 1. Stimuli and the number of just-noticeable differences considering a change in the spectral quality of illumination from a correlated colour temperature of 6500 K to 10000 K and von Kries colour constancy

Stimulus and observed colour	Number of just-noticeable differences
1. Green card	1
2. Yellow lemon	5
3. Yellow banana	4
4. Green apple	4
5. Green banana	4
6. Green <i>Eucalyptus</i> sp. leaf	1
7. Green <i>Hibbertia</i> sp. leaf	1
8. Green cloth	2
9. Orange card	3
10. Orange orange	5
11. Pink cloth	2
12. Red pepper	4
13. Red cloth	3
14. Brown wood	3
15. Brown dry <i>Eucalyptus</i> sp. leaf	3
16. Red apple	3
17. Yellow card	3
18. White paper	0
19. Yellow cloth	5
20. Cream cloth	1
21. Purple card	3
22. Light blue card	2
23. Brown tree bark	2
24. Blue cloth	9

The just-noticeable differences are calculated for a CIE 1931 standard observer using MacAdam's ellipses to estimate perceptual colour distance (MacAdam, 1985).

3 cm×2 cm section was used. Measurements were made immediately, and no visible discolouration of the fruit occurred in this time (Fig. 2).

Illumination sources

From the data of Judd et al. (Judd et al., 1964) two radiation sources were used to represent spectrally different distributions of daylight. These included direct daylight (a mixture of direct sunlight and diffuse skylight) with a correlated colour temperature (CCT)=6500 K, and shade (diffuse skylight only) with a CCT=10000 K (Fig. 3). The two radiation sources represent the problem for the animal of identifying objects illuminated alternatively by sunlight and shade, as finding food might be in a natural foraging environment (Dyer, 1998).

CIE 1931 standard observer

To model von Kries colour constancy for normal human colour vision the $\bar{x}(\lambda)$ (red), $\bar{y}(\lambda)$ (green) and $\bar{z}(\lambda)$ (blue) colour-matching functions for a standard observer as specified by the Commission Internationale de l'Eclairage (CIE) 1931 (see Wyszecki and Stiles, 1967 for details) were used. These

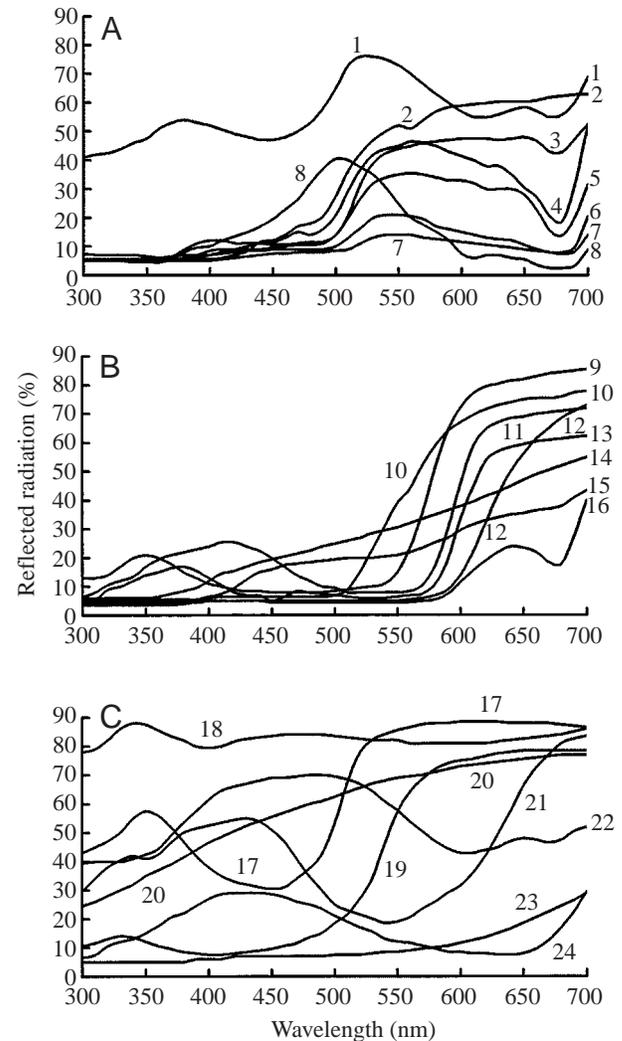


Fig. 2. Reflectance spectra of the 24 stimuli (numbered 1–24) described in Table 1. Division of the stimuli into A, B and C is purely to aid the reading of the reflectance curves.

colour-matching functions are an internationally agreed standard for quantitatively specifying colour for an average or typical human observer (Wyszecki and Stiles, 1967; MacAdam, 1985). To estimate the efficiency of von Kries colour constancy for a CIE 1931 standard observer it is possible to use MacAdam's ellipses (MacAdam, 1942; MacAdam, 1985) to calculate a just-noticeable distance in colour space. MacAdam's ellipses are an experimentally determined set of ellipses for different regions of CIE 1931 colour space that allow the calculation of a perceivable difference in stimuli colour for a CIE 1931 standard observer (Wyszecki and Stiles, 1967; MacAdam, 1985).

For a given stimulus $I(\lambda)$ viewed under an illumination $D(\lambda)$, the tristimulus values (X , Y and Z) are given by.

$$T_i = K \int_{400}^{700} \bar{t}_i(\lambda) I(\lambda) D(\lambda) d\lambda, \quad (1)$$

for $i=1-3$, where λ is wavelength, $\bar{t}_1(\lambda)=\bar{x}(\lambda)$, $\bar{t}_2(\lambda)=\bar{y}(\lambda)$ and $\bar{t}_3(\lambda)=\bar{z}(\lambda)$,

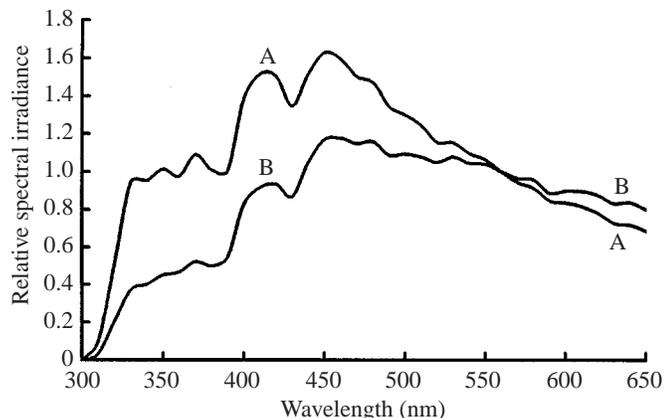


Fig. 3. Spectral distribution of typical daylight with the relative quantity of radiation normalised to 1.0 at 560 nm. Curves are based on the data of Judd et al. (Judd et al., 1964) and represent correlated colour temperatures of (A) 10 000 K and (B) 6500 K.

respectively, and $T_i=X, Y$ and Z , respectively. The variable K is the von Kries coefficient (see equation 2), and the visual system is assumed to be adapted to a stimulus reflecting radiation equally at all wavelengths. As the goal of the calculation is to determine the colour shift of a given stimulus in spectrally different illumination, the absolute brightness of the stimulus is considered to remain constant and the only change is to the relative spectral signal. As colour matching data does not exist for ultraviolet wavelengths (since we do not normally see these wavelengths), the integration was calculated over the range 400–700 nm.

$$K = 1 / \int_{400}^{700} \bar{t}_i(\lambda) D(\lambda) d\lambda, \quad (2)$$

for $i=1-3$.

Chromaticity coordinates (x, y, z) are computed from the tristimulus values $(X, Y$ and $Z)$ (equation 3). The value of z is defined since $z=1-(x+y)$ (Wyszecki and Stiles, 1967):

$$x/X = y/Y = z/Z = 1/(X + Y + Z). \quad (3)$$

The chromaticity coordinates were plotted in CIE 1931 colour space (see Fig. 4) and constant metric coefficients for MacAdam’s ellipses were used to calculate the perceptible change in the colour of a stimulus $I(\lambda)$ considering spectrally variable illumination and von Kries colour constancy (Wyszecki and Stiles, 1967; MacAdam, 1985). Using equation 4, a calculated distance of 2.0 units is equivalent to one just-noticeable distance, or the smallest perceivable colour step for a standard observer (Wyszecki and Stiles, 1967; MacAdam, 1985), and Table 1 shows the predicted colour shift in just-noticeable distances. The choice of one just-noticeable distance as a criterion to designate approximate colour constancy (i.e. the perceived colour of a stimulus is not exactly the same) is probably very strict. Colour constancy in the biological sense is concerned with correctly identifying a stimulus by its reflectance properties independently of illumination colour (i.e. how similar is stimulus colour when illumination colour changes), whilst the formulation

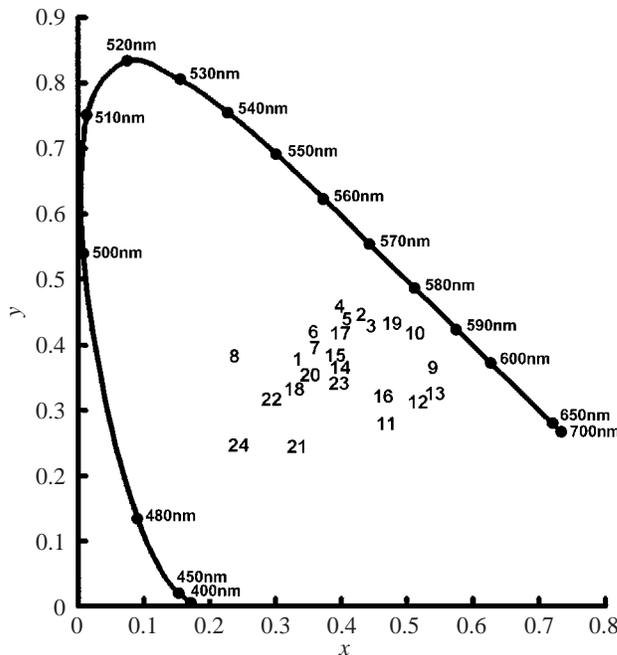


Fig. 4. Plots of 24 coloured stimuli (numbered as in Table 1) in CIE 1931 colour space. The chromaticity coordinates (x, y) of the stimuli are plotted considering an illumination of correlated colour temperature=6500 K, and the spectral locus is a plot of pure spectral radiation.

for MacAdam’s ellipses are based on the perception of small colour differences (i.e. can two stimuli be perceived as different). However, it is useful to have a benchmark to quantify the change in the appearance of a stimulus in spectrally variable illumination, and colour difference Δc is more tangible than colour similarity:

$$\Delta c = \sqrt{[g_{11}(\Delta x)^2 + 2g_{12}(\Delta x)(\Delta y) + g_{22}(\Delta y)^2]}, \quad (4)$$

where Δx and Δy are the differences in the coordinates of the stimulus in colour space for spectrally different illumination conditions (assuming von Kries colour constancy). The constant metric coefficients g_{11}, g_{12} and g_{22} are based on MacAdam’s ellipses and are given elsewhere (Wyszecki and Stiles, 1967; MacAdam, 1985).

Hypothetical visual systems

Three HVSs were used in the study to allow a comparative evaluation of how visual systems with different features might perform in spectrally variable illumination. The relative spectral sensitivity of different photoreceptor classes for each HVS were calculated using the vitamin A₁ template (Stavenga et al., 1993). The region of the spectrum considered for these visual systems included 300–700 nm.

HVSI

For HVS1, the SWS, MWS and LWS receptor peaks were taken to be 420, 534 and 564 nm, respectively, on the basis of data for cones in human colour vision (Bowmaker and Dartnall, 1980). These receptor peaks are very similar to those reported

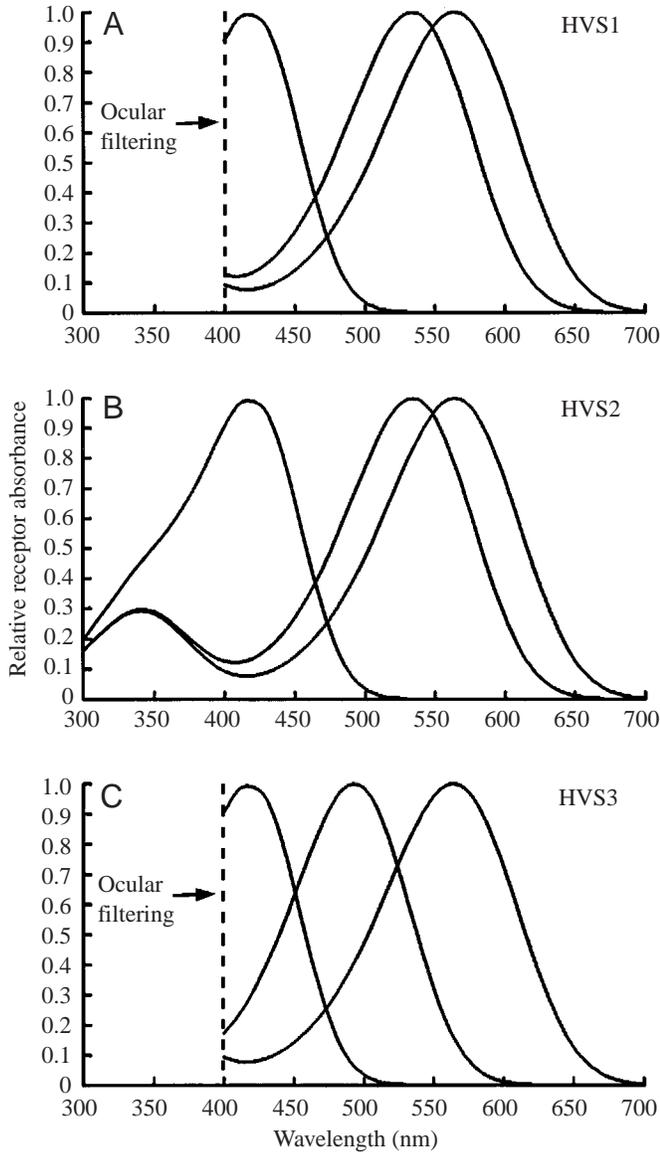


Fig. 5. Spectral sensitivity of various hypothetical visual systems (HVSs) plotted using a vitamin A₁ template described by Stavenga et al. (Stavenga et al., 1993) with the height of the photoreceptors adjusted to a maximum of 1.0. (A) HVS1 is based on human photoreceptor peaks at 420, 534 and 564 nm (Bowmaker and Dartnall, 1980) and assumes that all radiations shorter than 400 nm are absorbed by ocular filters. (B) HVS2 is based on the same photoreceptor peaks as HVS1, but assumes no ocular filtration and that ultraviolet radiations are absorbed by common β -band peaks maximally sensitive at 340 nm. (C) HVS3 is based on three symmetrically spaced photoreceptors maximally sensitive at 420, 492 and 564 nm and assumes that all radiations shorter than 400 nm are absorbed by ocular filters.

in a number of different Old-World primate species (Bowmaker, 1991). Radiation with a wavelength shorter than 400 nm was assumed to be totally absorbed by ocular filters (Fig. 5A). This HVS approximately represents human colour vision.

HVS2

The HVS2 α -band receptor peaks are identical to HVS1;

however, it is assumed that there is no filtration of radiation by ocular filters, and ultraviolet radiation is absorbed by a common β -band peak maximally sensitive at 340 nm (Stavenga et al., 1993) (Fig. 5B). There is some evidence that the spectral position of the β -band peak may vary with the spectral position of the α -band receptor (Palacios et al., 1998); however, an invariable position is used here to simplify the model and because of the paucity of other data. Minor shifts of the β -band peak towards longer wavelengths should not greatly change the spectral breadth and overlap of the three receptor classes, nor the overall predictions of the model.

HVS3

For HVS3, the SWS and LWS receptors are identical to HVS1, but the MWS receptor is assumed to absorb radiation maximally at 492 nm. All radiation at wavelengths shorter than 400 nm is assumed to be absorbed by ocular filters. This visual system represents approximately symmetrically spaced receptors without a β -band peak (Fig. 5C). The placement of the MWS receptor at 492 nm seems plausible because of the findings (Sun et al., 1997) suggesting that mammals may have the genetic tuning mechanisms to have 'green' cone pigments with absorption maxima as short as 487 nm.

Colour distance for HVS

For the three HVSs the amount of radiation absorbed by each receptor P (SWS, MWS and LWS) was calculated using equations 5 and 6. Chromaticity coordinates (s_{ws} , m_{ws} and l_{ws}) were calculated using equation 7, and these were subsequently plotted onto Cartesian coordinates to represent colour space for each HVS (see Fig. 6A–C). A Euclidean colour distance was calculated using Pythagoras' theorem (equation 8) (Wyszecki and Stiles, 1967).

For a given stimulus $I(\lambda)$ viewed under an illumination $D(\lambda)$ by receptor type $S(\lambda)$, the relative amount of radiation absorbed by each receptor is given by:

$$P(\text{SWS, MWS, LWS}) = K \int_{300}^{700} S(\lambda)I(\lambda)D(\lambda)d\lambda, \quad (5)$$

where the von Kries coefficient (K) is given by:

$$K(\text{SWS, MWS, LWS}) = 1 / \int_{300}^{700} S(\lambda)D(\lambda)d\lambda. \quad (6)$$

Chromaticity coordinates were calculated as described by Wyszecki and Stiles (Wyszecki and Stiles, 1967).

$$\begin{aligned} s_{ws}/P(\text{SWS}) &= m_{ws}/P(\text{MWS}) = \\ l_{ws}/P(\text{LWS}) &= 1/[P(\text{SWS}) + P(\text{MWS}) + P(\text{LWS})]. \end{aligned} \quad (7)$$

The relative colour shift of a stimulus considering spectrally variable illumination is given by:

$$\text{Relative colour shift} = \sqrt{[(\Delta l_{ws})^2 + (\Delta m_{ws})^2]}, \quad (8)$$

where Δl_{ws} and Δm_{ws} are the differences in the coordinates of

the stimulus in colour space for different illumination conditions (assuming von Kries colour constancy).

To determine the relative performance of von Kries colour constancy for HVS2 (visual system with no ocular filtering) compared with HVS1 (visual system with ocular filtering), the percentage difference in relative colour shift was calculated. An increase in colour shift (e.g. colour shift for HVS2 is greater than colour shift for HVS1) is represented by a positive number, and a decrease in predicted colour shift is represented by a negative number. This method was repeated for each of the 24 stimuli individually, and the data are presented as a percentage increase (or decrease) in colour shift (Fig. 7). This procedure was also repeated for each of the 24 stimuli to compare HVS3 (symmetrically spaced photoreceptors) with HVS1 (asymmetrically spaced photoreceptors), and again the data are presented as a percentage increase (or decrease) in colour shift (Fig. 7).

Relative colour discrimination of the stimuli for HVS

To evaluate the relative ability of the three HVSs to discriminate the 24 stimuli in Table 1, the standard deviation of the distribution of the loci in each of the respective colour spaces (Fig. 6) was calculated. This was done by calculating the mean of the 24 *lws* and the 24 *mws* chromaticity coordinates (i.e. the centre of gravity of the 24 stimuli in colour space), and the mean distance (standard deviation) of loci from this point in colour space. A larger standard deviation represents a larger spread of loci and indicates a relatively better ability to discriminate between stimuli.

Results

The reflectance spectra of the 24 stimuli are shown in Fig. 2. For clarity of display, the curves are presented in

separate graphs (Fig. 2A–C), but no special significance applies to these divisions. All the naturally occurring samples (fruit, leaves, bark) reflect less than 10% ultraviolet radiation.

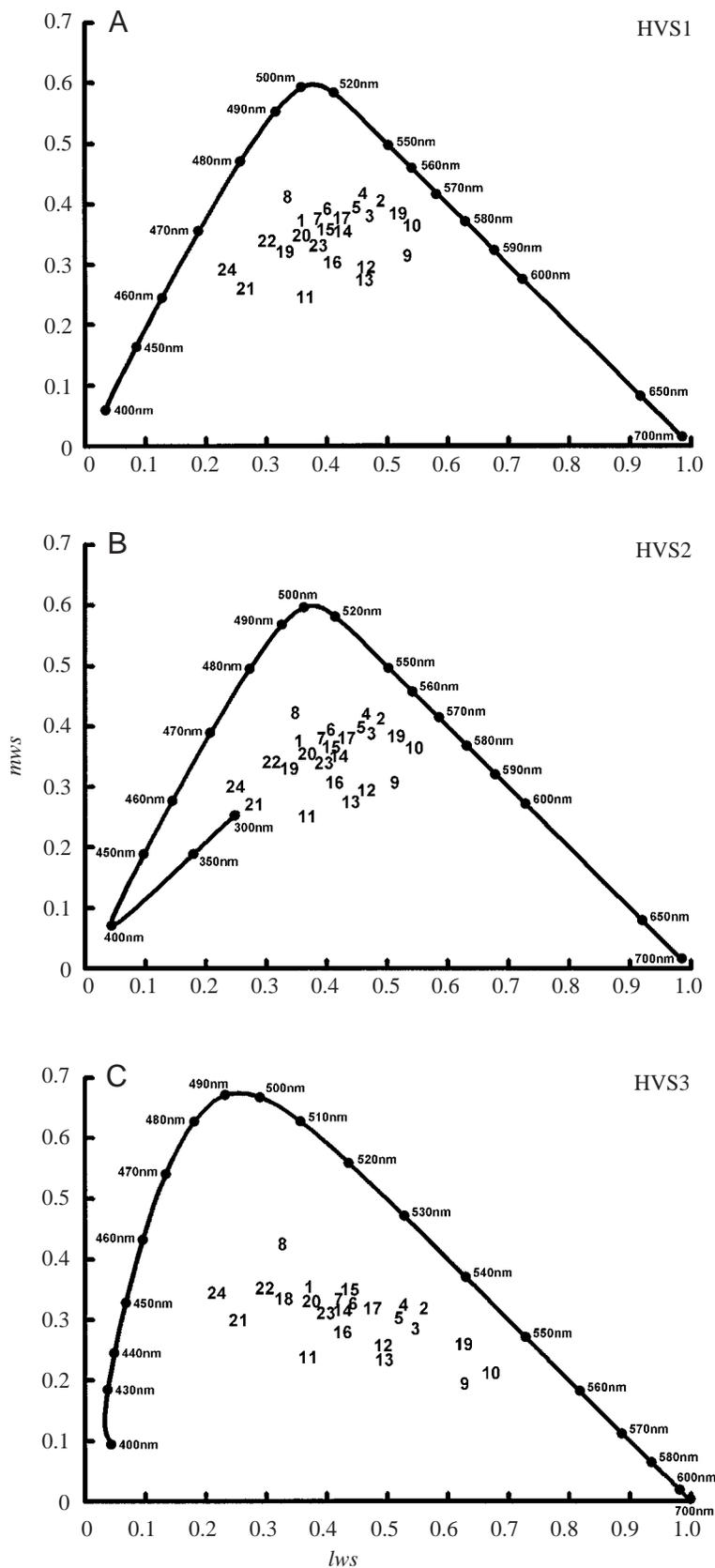
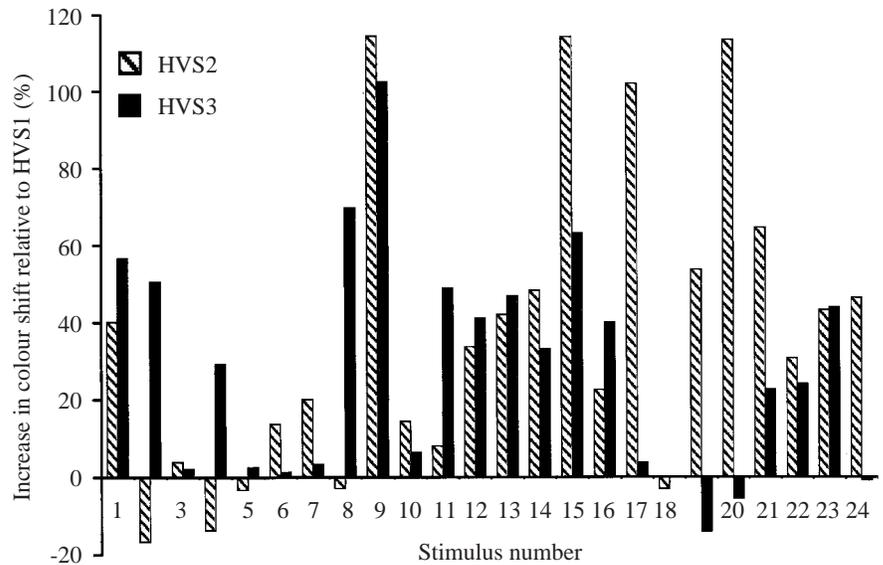


Fig. 6. Plots of 24 coloured stimuli (numbered as in Table 1) onto Cartesian coordinates to represent the colour space of various hypothetical visual systems (HVSs) considering an illumination of correlated colour temperature=6500 K. Chromaticity coordinates (*lws*, *mws*) are the normalised stimulations of the long-wavelength-sensitive and medium-wavelength-sensitive photoreceptors. (A) Colour space for HVS1, which is a visual system based on human colour receptor peaks (420, 534 and 564 nm; Bowmaker and Dartnall, 1980) and ocular filters absorbing radiations shorter than 400 nm. (B) Colour space for HVS2, which is a visual system based on human colour receptor peaks and no ocular filters. Ultraviolet radiation is assumed to be absorbed by secondary β -band peaks that are maximally sensitive to 340 nm radiation. (C) Colour space for HVS3, which is a visual system based on symmetrically spaced photoreceptors maximally sensitive at 420, 492 and 564 nm and assumes that all radiations shorter than 400 nm are absorbed by ocular filters (see Fig. 5). The spectral locus is a plot of pure spectral radiation.

Fig. 7. The relative performance of two hypothetical visual systems (HVS2 and HVS3) compared with HVS1 for a variety of differently coloured stimuli (numbered 1–24; see Table 1) when considering spectrally variable illumination and von Kries colour constancy. The change in illumination colour is from a correlated colour temperature of 6500 K to 10000 K. A positive number indicates a relative increase in the predicted colour shift of a stimulus in colour space (poorer performance), and a negative number indicates a reduced colour shift (better performance). For example, an increase of 100% means the predicted colour shift is twice the magnitude of that calculated for HVS1. If the performance is identical to that of HVS1, then the relative increase is zero. HVS1 is based on three receptors with maximum absorption of radiation at 420, 534 and 564 nm, plotted with a vitamin A₁ template (Stavenga et al., 1993) and assuming all radiations shorter than 400 nm are absorbed by ocular filters. HVS2 has the same main receptor peaks as HVS1, but does not have ocular filters that prevent the β -band absorbing short-wavelength radiations. HVS3 is based on symmetrically spaced receptors with maximum absorption of radiation at 420, 492 and 564 nm and has ocular filters absorbing radiations shorter than 400 nm (see Fig. 5).



The results for leaf foliage are consistent with larger studies of foliage reflectance spectra (Chittka et al., 1994). Since fruits and foliage have a similar ultraviolet reflectance, it may be of little value for a visual system trying to discriminate these stimuli to evaluate this region of the spectrum. However, many of the man-made stimuli reflect significant proportions of ultraviolet radiation (Fig. 2).

Fig. 4 shows the distribution of the 24 stimuli in colour space for a CCT=6500 K and the colour matching functions of a CIE 1931 standard observer. The perceptual change in colour of these stimuli, considering spectrally variable illumination and von Kries colour constancy, are given in Table 1. For 23 of the 24 stimuli only, approximate colour constancy is achieved by chromatic adaptation as the predicted colour distance exceeds the threshold for one just-noticeable distance. This result is consistent with other findings that von Kries-type colour constancy achieves approximate colour constancy for normal human vision (MacAdam, 1985). It should be noted that the values of just-noticeable differences for a CIE standard observer cannot be directly compared with relative colour shift values for the HVSs. The calculations of just-noticeable differences are based on data from colour-matching experiments with CIE 1931 specified standard human viewers (MacAdam, 1985), whilst the calculation of relative colour shift is simply the Euclidean distance for a HVS that does not actually exist in nature. The just noticeable differences are used here to demonstrate that von Kries colour constancy is not complete (except in one case) for a standard human viewer. The purpose of the colour-shift values is that they allow a comparison of performance for HVSs that natural selection has not favoured.

To evaluate how an increase in the spectral breadth of the photoreceptors due to the inclusion of the β -band might affect von Kries colour constancy, it is possible to compare the

relative performance of HVS2 with that of HVS1. The calculated values do not represent perceptual colour distance, but the relative performance indicates which visual system is better able to correct for spectrally variable illumination. Fig. 7 shows that for most of the 24 stimuli, there is predicted to be a larger colour shift for HVS2, and for a few of the stimuli (e.g. 9, 15 and 20) the predicted colour shift is over twice as large as for HVS1. A comparison of the mean colour distances of all 24 stimuli for HVS1 and HVS2 suggests that HVS1 is approximately 33% better at correcting for spectrally variable illumination. Since von Kries colour constancy is predicted to be approximate for a CIE 1931 standard observer, a decrease in the ability to identify coloured stimuli in spectrally variable illumination is likely to reduce the effectiveness of colour vision. It appears, therefore, that ocular filters that prevent ultraviolet radiation reaching the β -band improve the effectiveness of colour constancy, which agrees with the theoretical considerations suggested by Worthey and Brill (Worthey and Brill, 1986). However, it is interesting to note that the relative performance of colour constancy for five of the stimuli is predicted to be slightly better for HVS2 (Fig. 7). The explanation for this may be that, for some long-wavelength-rich stimuli that also weakly reflect ultraviolet radiation, the degree of adaptation for a visual system with β -peaks is enhanced compared with that of a visual system without β -peaks. This appears to be because whilst a weak ultraviolet reflectance has little influence on the overall colour signal of a stimulus, the state of adaptation of the receptors is benefited by the input of the β -band. Similar anomalies of chromatic adaptation are discussed elsewhere (Jameson and Hurvich, 1989).

The performance of HVS3 compared to HVS1 shows that, for most of the 24 stimuli, von Kries colour constancy is predicted to be better for the asymmetrically spaced

photoreceptors (Fig. 7). A comparison of the mean colour distances of all 24 stimuli for HVS3 and HVS1 suggests that HVS1 is approximately 34% better at correcting for spectrally variable illumination. Using a different method from that of Osorio (Osorio, 1997), these results support his findings that the asymmetric spacings of colour receptor peaks present in Old-World primates improve von Kries colour constancy (compared with a symmetrically spaced visual system). Again, because colour constancy is predicted to be approximate for most stimuli considering a CIE 1931 standard observer (Table 1), it is hypothesised that a decrease in the performance of colour constancy could reduce the reliability of colour vision. Vorobyev and Menzel (Vorobyev and Menzel, 1999) show that symmetrically spaced receptors should maximise the discriminability of different stimuli. The standard deviations of the distribution of 24 stimuli in separate colour spaces for HVS1, HVS2 and HVS3 were 0.092, 0.089 and 0.128 units, respectively. A larger standard deviation represents a larger mean distance between all of the stimuli and, hence, relatively better discriminability. For HVS1 and HVS2, discriminability is predicted to be similar, although the calculated value is slightly lower for HVS2 as a result of the desaturation of the receptor signals by the β -bands. The discrimination of stimuli by HVS3 is predicted to be better than that of HVS1. However, greater discriminability may result in a more difficult problem to solve in spectrally variable illumination and, hence, the possibility of poorer colour constancy.

Discussion

Without any mechanism of colour constancy, reliable colour vision in spectrally variable illumination would be impossible. This is because, without colour constancy, a stimulus can occupy a very large number of positions in colour space (Dyer, 1998). When a visual system is able to partially correct for changes in illumination colour then colour constancy is described as approximate. The value of approximate colour constancy (i.e. the colour of a given stimulus does not appear identical in different illumination conditions) may be of great value to animals. For example, if the perceived colour of a stimulus changes under different illumination conditions, but to such a small extent that it can still be reliably identified from alternative stimuli, then approximate colour constancy is sufficient to meet the demands on that visual system.

Colour constancy, or approximate colour constancy, is likely to be achieved in the visual systems of animals through a variety of mechanisms. There is evidence that the problem of identifying stimuli by their reflectance properties in spectrally variable illumination may be partially solved at both the receptor and neural levels of visual processing. Zeki (Zeki, 1983) demonstrated that the V4 region of the cerebral cortex in monkeys appears to be important for constant colour recognition. However, colour constancy has also been demonstrated in goldfish (*Carassius auratus*) (Ingle, 1985; Dörr and Neumeyer, 1996; Dörr and Neumeyer, 2000), and these animals have virtually no cerebral cortex (Hubel, 1995).

Evidence of chromatic adaptation contributing to colour constancy in humans has been demonstrated by Uchikawa et al. (Uchikawa et al., 1989). The predictions of von Kries colour constancy for a CIE 1931 standard observer suggest that approximate colour constancy is possible through chromatic adaptation (Table 1), with the implication that any reduction in the performance of constancy could affect reliable colour vision. The comparative results for the three HVSs suggest that two features present in the visual systems of Old-World primates aid von Kries colour constancy (Fig. 7). These include a narrowing of receptor spectral sensitivities by ocular filters that prevent ultraviolet radiation reaching the retina (compare Fig. 5A,B), and an asymmetric spacing of the spectral sensitivities of the photoreceptor classes (compare Fig. 5A,C). The finding that asymmetric receptor spacing is predicted to improve colour constancy agrees with the results of Osorio (Osorio, 1997). However, Sumner and Mollon (2000) have recently demonstrated that the spectral positions of the MWS and LWS receptors in Old-World primates appears to be ideally suited to detecting stimuli presented against a mature leaf background, and improved colour constancy due to asymmetric receptor spacing may be a fringe benefit of other demands on the visual system.

Goldsmith (Goldsmith, 1990) suggests that, whilst the nervous systems of different animals may manipulate the signals received at the photoreceptor level of the visual process, the spectral breadth and λ_{\max} position of the photoreceptors will influence the character of a visual system. Spectrally broad photoreceptors may reduce the effectiveness of von Kries colour constancy because for a given receptor class there can be different visual stimuli that can produce the same receptor stimulation (brightness metamerism), which can reduce independent adaptation or lightness constancy (Worthey and Brill, 1986). Overlapping photoreceptors reduce the effectiveness of colour constancy because changes in illumination magnitude at a given wavelength can affect multiple receptor classes, preventing independent lightness constancy (Worthey and Brill, 1986). For photoreceptors with increased spectral overlap, there is also increased spectral breadth, and this may partially (or substantially) limit colour constancy in visual systems (Dyer, 1999). In the case of trichromatic visual systems with broad overlapping photoreceptors, approximate colour constancy may be a result of compromise with other constraints on the visual system. For example, if a visual system is to sample a given section of the electromagnetic spectrum, say from 400 nm to 700 nm, then the use of spectrally narrower receptors may require an increase in the number of receptor classes in order to retain sufficient overlap to ensure good colour discrimination. A reduction in the spectral breadth of photoreceptors can also adversely affect both colour discrimination and receptor signal-to-noise ratio (Osorio et al., 1997; Vorobyev et al., 1998). Improved colour constancy has been suggested as one possible explanation for the large number of ten or more classes of spectrally narrow photoreceptors in stomatopod crustaceans (Osorio and Vorobyev, 1997; Osorio et al., 1997). In these animals the

necessity for accurate colour constancy may be highly critical in situations where reliable identification is necessary to avoid potentially fatal conflicts with other members of the species (Osorio et al., 1997). However, an increase in the number of receptor classes is likely to result in additional neural processing complexity. Hence, for many animals it may be sufficient to have visual systems with fewer colour receptors, and to tune receptor breadth in order to achieve the best possible approximate colour constancy. As the β -peaks of visual pigments are unlikely to significantly benefit an animal's discrimination of coloured stimuli, the use of ocular filters to absorb ultraviolet radiation and, hence, narrow receptor breadth appears to be a realistic method of improving colour constancy at little cost to the visual system.

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References

- Barlow, H. B.** (1982). What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Res.* **22**, 635–643.
- Bowmaker, J. K.** (1991). Visual pigments and colour vision in primates. In *From Pigments to Perception* (ed. A. Valberg and B. B. Lee), pp. 1–9. New York: Plenum Press.
- Bowmaker, J. K. and Dartnall, H. J. A.** (1980). Visual pigments of rods and cones in a human retina. *J. Physiol. Lond.* **298**, 501–511.
- Bridges, C. D. B.** (1974). Evolution of visual pigments. *Exp. Eye Res.* **18**, 323–332.
- Bridges, C. D. B. and Yoshikami, S.** (1970). Distribution and evolution of visual pigments in salmonid fishes. *Vision Res.* **10**, 609–626.
- Chittka, L., Shmida, A., Troje, N. and Menzel, R.** (1994). Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Res.* **34**, 1489–1508.
- Davenport, D. and Foley, J. M.** (1979). Fringe benefits of cataract surgery. *Science* **204**, 454–457.
- Dörr, S. and Neumeyer, C.** (1996). The goldfish – a colour-constant animal. *Perception* **25**, 243–250.
- Dörr, S. and Neumeyer, C.** (2000). Color constancy in goldfish: the limits. *J. Comp. Physiol. A* **186**, 885–896.
- Douglas, R. H. and Marshall, N. J.** (1999). A review of vertebrate and invertebrate ocular filters. In *Adaptive Mechanisms in the Ecology of Vision* (ed. S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge and S. Vallerger), pp. 95–162. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Dyer, A. G.** (1998). The colour of flowers in spectrally variable illumination and insect pollinator vision. *J. Comp. Physiol. A* **183**, 203–212.
- Dyer, A. G.** (1999). Broad spectral sensitivities in the honeybee's photoreceptors limit colour constancy. *J. Comp. Physiol. A* **185**, 445–453.
- Goldsmith, T. H.** (1990). Optimization, constraint, and history in the evolution of eyes. *Quart. Rev. Biol.* **65**, 281–322.
- Hubel, D. H.** (1995). *Eye, Brain, and Vision*. New York: Scientific American Library.
- Hurvich, L. M.** (1981). *Color Vision*. Sunderland, MA, USA: Sinauer Associates Inc.
- Ingle, D.** (1985). The goldfish as a retinex animal. *Science* **227**, 651–654.
- Jameson, D. and Hurvich, L. M.** (1989). Essay concerning color constancy. *Annu. Rev. Psychol.* **40**, 1–22.
- Judd, D. B., MacAdam, D. L. and Wyszecki, G.** (1964). Spectral distribution of typical daylight as a function of correlated color temperature. *J. Opt. Soc. Am.* **34**, 1031–1040.
- Kaiser, P. K. and Boynton R. M.** (1996). *Human Color Vision*. Washington DC: Optical Society of America.
- Kevan, P. G., Chittka, L. and Dyer, A. G.** (2001). Limits to the salience of ultraviolet: lessons from colour vision in bees and birds. *J. Exp. Biol.* **204**, 2571–2580.
- Lythgoe, J. N.** (1979). *The Ecology of Vision*. Oxford: Clarendon Press.
- MacAdam, D. L.** (1942). Visual sensitivities to colour differences of daylight. *J. Opt. Soc. Am.* **32**, 247–274.
- MacAdam, D. L.** (1970). *Sources of Color Science*. Cambridge, MA, USA: MIT Press.
- MacAdam, D. L.** (1985). *Color Measurement. Theme and Variations*. Berlin: Springer-Verlag.
- Mollon, J. D.** (1989). 'Tho she kneel'd in that Place where they grew...'. *J. Exp. Biol.* **146**, 21–38.
- Muntz, W. R. A.** (1972). Inert absorbing and reflecting pigments. In *Handbook of Sensory Physiology*, vol. 7 (ed. H. Dartnall), pp. 529–565. Berlin: Springer-Verlag.
- Osorio, D.** (1997). A functional view of cone pigments and colour vision. In *John Dalton's Colour Vision Legacy* (ed. C. M. Dickinson, I. J. Murray and D. Carden), pp. 483–489. London: Taylor and Francis.
- Osorio, D., Marshall, N. J. and Cronin, T. W.** (1997). Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vision Res.* **37**, 3299–3309.
- Osorio, D. and Vorobyev, M.** (1997). *Sepia* tones, stomatopod signals and the uses of colour. *Trends Ecol. Evol.* **12**, 167–168.
- Palacios, A. G., Srivastava, R. and Goldsmith, T. H.** (1998). Spectral and polarization sensitivity of photocurrents of amphibian rods in the visible and ultraviolet. *Vis. Neurosci.* **15**, 319–331.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F. and Menzel, R.** (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* **170**, 23–40.
- Radlwimmer, F. B. and Yokoyama, S.** (1998). Genetic analyses of the green visual pigments of rabbit (*Oryctolagus cuniculus*) and rat (*Rattus norvegicus*). *Gene* **218**, 103–109.
- Regan, B. C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P. and Mollon, J. D.** (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Res.* **38**, 3321–3327.
- Stavenga, D. G., Smits, R. P. and Hoenders, B. J.** (1993). Simple exponential functions describing the absorbance bands of visual pigment spectra. *Vision Res.* **33**, 1011–1017.
- Sumner, P. and Mollon, J. D.** (2000). Catarrhine photopigments are optimized for detecting targets against a foliage background. *J. Exp. Biol.* **203**, 1963–1986.
- Sun, H., Macke, J. P. and Nathans, J.** (1997). Mechanisms of spectral tuning in the mouse green cone pigment. *Proc. Natl. Acad. Sci. USA* **94**, 8860–8865.
- Uchikawa, K., Uchikawa, H. and Boynton, R. M.** (1989). Partial color constancy of isolated surface colors examined by color-naming method. *Perception* **18**, 83–91.
- Vorobyev, M. and Menzel, R.** (1999). Flower advertisement for insects: bees, a case study. In *Adaptive Mechanism in the Ecology of Vision* (ed. S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge and S. Vallerger), pp. 537–553. Dordrecht: Kluwer Academic Publishers.
- Vorobyev, M., Osorio, D., Bennett, A. T. D., Marshall, N. J. and Cuthill I. C.** (1998). Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* **183**, 621–633.
- Wald, G.** (1945). Human vision and the spectrum. *Science* **101**, 653–658.
- Worthey, J. A. and Brill, M. H.** (1986). Heuristic analysis of von Kries color constancy. *J. Opt. Soc. Am. A* **3**, 1708–1712.
- Wyszecki, G. and Stiles, W. S.** (1967). *Color Science: Concepts and Methods, Qualitative Data and Formulas*. New York: Wiley.
- Zeki, S.** (1983). Colour coding in the cerebral cortex: the responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition. *Neuroscience* **9**, 767–781.
- Zigman, S., Groff, J. and Griess, G.** (1976). Light extinction and protein in lens. *Exp. Eye Res.* **23**, 555–567.