

A. G. Dyer

Broad spectral sensitivities in the honeybee's photoreceptors limit colour constancy

Accepted: 14 August 1999

Abstract Colour constancy allows for visual systems to be view stimuli independent of changes in spectral illumination. Chromatic adaptation is likely to be an important mechanism in colour constancy and can be explained by use of the von Kries coefficient law. Chromatic adaptation is compared for the honeybee and three hypothetical visual systems. It is shown that the spectral breadth and asymmetry of photoreceptors in the honeybee may limit colour constancy. In particular, it is demonstrated that the absorption of short-wavelength radiation by the *cis*-band of chromophore is responsible for a poorer correction for bee colours rich in ultraviolet reflectance. The results are discussed in relation to theoretical considerations of von Kries colour constancy and the physiology of eye design in some other species for which colour constancy has been demonstrated.

Key words Bees · Colour constancy · Photoreceptors · Spectrally variable illumination · Flower colour

Abbreviations *UV* ultraviolet · *CCT* correlated colour temperature · *HVS* hypothetical visual system · *SWS* short-wavelength-sensitive · *MWS* medium-wavelength-sensitive · *LWS* long-wavelength-sensitive

Introduction

Spectrally variable illumination is a problem for colour visual systems because the spectral reflectance of an object is determined both by its spectral absorption characteristics and the spectral composition of the radiation source. Sunlight is the primary illumination for most diurnal animals and is highly variable in spectral

content due to many modifiers including wavelength-specific scattering and filtering in the atmosphere (Konradtsev 1969), filtering by forest canopies (Endler 1993), and selective absorption of radiation in water (Lythgoe 1979). The ability to respond accurately to colours in spite of changes in spectral illumination is termed colour constancy (Hurvich 1981; MacAdam 1985) and has been demonstrated in primates, birds, fishes, cats, amphibia and insects (see Neumeyer 1998 for review). One model of colour constancy is von Kries chromatic adaptation where the spectral sensitivity of each photoreceptor does not change, but the scalar coefficients of the photoreceptors vary to achieve constancy (von Kries 1902 in MacAdam 1970; Hurvich 1981; MacAdam 1985). Worthey and Brill (1986) produced a theoretical analysis which showed that the correction offered by von Kries adaptation is limited by both an increase in the breadth of photoreceptor spectral sensitivity functions, and an increase in the overlap between photoreceptors. They show that the von Kries coefficient law would achieve only approximate colour constancy when considering broad overlapping photoreceptors.

The honeybee (*Apis mellifera*) has trichromatic colour vision with photoreceptors maximally sensitive at about 350 nm, 440 nm and 540 nm (Autrum and Zwehl 1964; Menzel and Blakers 1976; Menzel et al. 1986). Each of the bee's three photoreceptors also has a second common absorption peak at about 340 nm due to absorption of radiation by the *cis*-band of the chromophore (Stavenga et al. 1993). The main absorption peak is termed the α -band and the secondary absorption peak the β -band. Figure 1A shows the spectral sensitivity of the honeybee's three photoreceptors plotted with a vitamin A₁ photopigment spectral absorption template described by Stavenga et al. (1993). The β -band has little effect on the relative spectral sensitivity of the short-wavelength-sensitive (SWS) photoreceptor, but becomes distinctly noticeable for the medium-wavelength-sensitive (MWS) and long-wavelength-sensitive (LWS) receptors. The β -band results in the MWS and LWS

A.G. Dyer
Faculty of Science, Monash University,
Clayton, Victoria 3168, Australia
e-mail: adrian.dyer@sci.monash.edu.au
Fax: +61-3-9905-3637

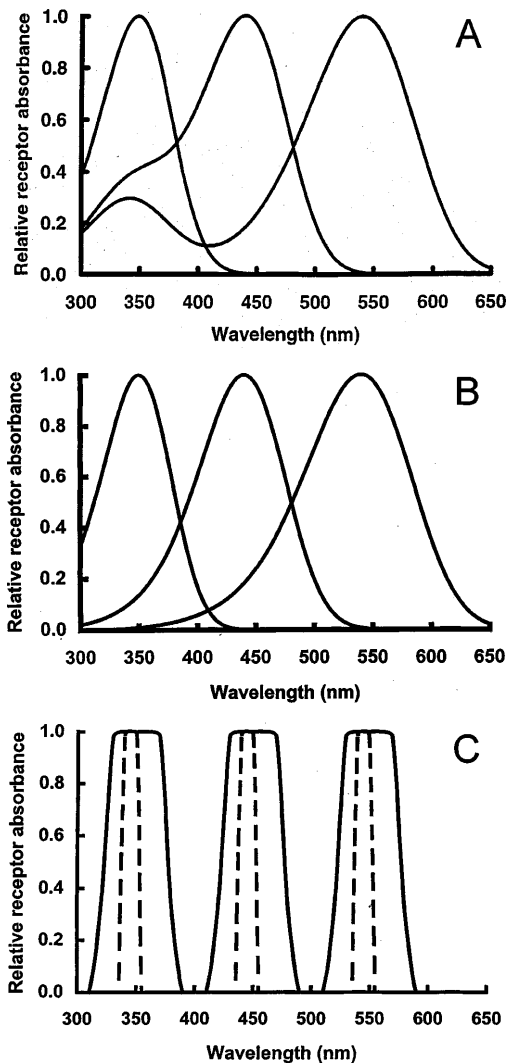


Fig. 1A–C Spectral sensitivity of various visual systems with the height of the photoreceptors arbitrarily adjusted to a maximum of 1.0. **A** The honeybee (*Apis mellifera*) plotted using a vitamin A₁ template described by Stavenga et al. (1993) and considering the α -band photoreceptor peaks to be maximally sensitive at 350 nm, 440 nm and 540 nm, and the β -band peaks to be maximally sensitive at 340 nm. **B** A hypothetical vision system (HVS1) based only on the α -band photoreceptor peaks described above for the honeybee. **C** A broad non-overlapping set of photoreceptors (HVS2, *unbroken line*) and a narrow non-overlapping set of photoreceptors (HVS3, *dashed line*). The breadth of these photoreceptors approximately matches that of the hypothetical retinas described by Worthey and Brill (1986)

photoreceptors being spectrally broad and having considerable overlap with the SWS photoreceptor.

Behavioural experiments have shown that bees can discriminate colours as food signals (von Frisch 1914a, b; Daumer 1956, 1958; Helversen 1972), and colour is an important cue for insects orientating to flowers (Daumer 1958; Chittka et al. 1997). It is important then for insects to be able to detect flower stimuli relatively independent of changes in spectral illumination, and behavioural studies have demonstrated colour constancy in bees (Mazokhin-Porshnjakov 1966; Neumeyer 1981; Werner et al. 1988). Neumeyer (1981) showed that bees have

colour constancy by training single freely flying bees to land on one of nine sequentially coloured test fields that were presented on a grey background. The illumination source was then changed with coloured filters to see if a bee could still correctly choose the training field. The field was preferred under nearly all the new illumination sources, but the frequency of correct choices fell the more the new source colour varied from the training source, showing that bees have approximate colour constancy. In similar behavioural experiments bees demonstrate simultaneous colour contrast (Neumeyer 1980) and successive colour contrast (Neumeyer 1981). The results suggest that chromatic adaptation could be an important mechanism in colour constancy and Neumeyer (1981, 1998) suggests that physiological mechanisms underlying chromatic adaptation may include neuronal interactions between photoreceptor channels, variations in the equilibrium of visual pigment concentrations due to relatively slow mechanisms of receptor adaptation, and central retuning processes that adjust a neutral point of colour perception.

It has been observed that insect pollinators sometimes restrict their visits to one flower type even when other rewarding flowers are available (Bennett 1884; Christy 1884; Heinrich 1976; Chittka et al. 1997). This temporary loyalty to one species is termed flower constancy (see Waser 1986 for review) and increases the fitness of angiosperms by enabling the effective and efficient transfer of genetic material between plants of the same species (Waser 1983a, b, 1986; Barth 1985; Proctor et al. 1996). Flower constancy may benefit insects because of improved foraging efficiency once a flower's characteristics have been learnt (Darwin 1876; Waser 1983a, b, 1986; Chittka and Thomson 1997; Chittka et al. 1997). Flower colour is an important determinant in flower constancy (Waser 1983a, b; Chittka and Menzel 1992; Chittka et al. 1997) and the reproductive success of some plants may depend on the ability of insects to correctly choose flower colours in spectrally variable illumination. Dyer (1998) showed that a model of honeybee vision based on the von Kries coefficient law leads to a correction to spectrally variable illumination that depends on the position of a colour in bee colour space. Reflectance curves that have colour loci in the centre right-hand side of colour space are well corrected for, but the correction is relatively poorer for bee colours on the left-hand side of colour space (Fig. 3B). This region represents colours that are relatively rich in ultraviolet (UV) reflectance, and Chittka et al. (1994) reports that UV-coloured flowers are rare in nature and comprise only about 1.6% of a worldwide sample of flowers. It was thus suggested by Dyer (1998) that the relatively poorer solution of chromatic adaptation for UV-coloured flowers is a possible or part explanation for the rarity of these flowers in nature, because they are harder for insects to identify (and hence visit constantly) in spectrally variable illumination. Other possible reasons for the rarity of certain flower colours in nature may include phylogenetic or biochemical constraints (Menzel and Shmida 1993; Chittka 1997),

although it is likely that most plant families have the potential to generate a wide variety of flower colours (Menzel and Shmida 1993).

In this study it is hypothesised that: (1) the absorption of short-wavelength radiation by the *cis*-band of chromophore is responsible for the asymmetry of chromatic adaptation reported in Dyer (1998), and (2) the breadth of spectral-sensitivity curves limits the accuracy of colour constancy for all colours in colour space. To test these hypotheses, a series of 99 computer-generated reflectance curves that provide a good coverage of a Maxwell colour triangle (Dyer 1998) are plotted considering spectrally variable illumination and three hypothetical visual systems (HVS): HVS1, three photoreceptors based only on the α -band sensitivities of vitamin A₁; HVS2, three non-overlapping broad photoreceptors; and HVS3, three non-overlapping narrow photoreceptors. Each of the visual systems is evaluated both without any mechanism for colour constancy, and with a model of von Kries colour constancy. The results are compared with the model of honeybee vision in spectrally variable illumination (Dyer 1998).

Materials and methods

The methods used to model chromatic adaptation for the three HVSs are those used previously for honeybee colour vision (Dyer 1998). The only parameters varied are the spectral sensitivities of the HVS (Fig. 1B, C), and the resulting von Kries scalar coefficients (Table 1). The four visual systems evaluated were determined as follows.

The honeybee visual system

The results are taken directly from Dyer (1998). The spectral sensitivity of the photoreceptors was modelled using a photopigment

Table 1 The colour of radiation sources and the weighting (W) of short-, medium- and long-wavelength-sensitive photoreceptors to plot a stimulus reflecting radiation equally in the centre of a Maxwell colour triangle according to the von Kries coefficient law

Radiation source colour in terms of correlated colour temperature (K)	Short (W)	Medium (W)	Long (W)
The honeybee (from Dyer 1998)			
10 000	1.94	1.01	1.00
6500	3.54	1.32	1.00
4800	7.10	1.80	1.00
Hypothetical visual system (HVS) 1			
10 000	2.22	1.01	1.00
6500	4.31	1.35	1.00
4800	8.98	1.85	1.00
HVS2			
10 000	1.57	1.00	1.44
6500	2.50	1.00	1.06
4800	5.43	1.32	1.00
HVS3			
10 000	1.60	1.00	1.46
6500	2.61	1.00	1.07
4800	5.73	1.32	1.00

spectral absorption template (Stavenga et al. 1993) and assuming the α -bands absorb radiation maximally at 350 nm, 440 nm and 540 nm, and the β -bands all absorb radiation maximally at 340 nm (Fig. 1A).

HVS1

A template of photopigment spectral absorption described by Stavenga et al. (1993) was used to determine the α -band spectral absorbance of vitamin A₁. The absorption peaks for the three HVS1 photoreceptors were taken to be 350 nm, 440 nm and 540 nm to match the α -band absorption peaks of the honeybee. This produces a hypothetical visual system with three well spaced and approximately symmetric photoreceptors (Fig. 1B). The HVS1 photoreceptors are essentially honeybee photoreceptors without the radiation absorption by the *cis*-band of the chromophore. A comparison of HVS1 and bee visual systems allows an evaluation of the effect of the β -band absorption peaks on von Kries colour constancy. The theoretical considerations of von Kries colour constancy demonstrated by Worthey and Brill (1986) suggest that the narrower HVS1 photoreceptors should provide improved colour constancy. Since the photoreceptors for HVS1 are well spaced and approximately symmetric, it is also expected that the von Kries coefficient law should produce a symmetric solution of colour constancy in colour space.

HVS2 and HVS3

To model the theory that non-overlapping, and narrower photoreceptors should improve von Kries colour constancy (Worthey and Brill 1986), a set of three broad non-overlapping photoreceptors (HVS2), and a set of three narrow non-overlapping receptors (HVS3) were used. The breadth of the HVS2 and HVS3 photoreceptors approximately matches that of the hypothetical retinas (HR3 and HR1, respectively) described by Worthey and Brill (1986). The photoreceptors were chosen to be sensitive in the UV, blue (400–500 nm) and green (500–600 nm) regions of the spectrum (Fig. 1C) to allow the changes in spectral illumination to match those modelled for the honeybee.

Illumination sources

The illumination sources used for the modelling were equivalent to a correlated colour temperature (CCT) of 4800 K, 6500 K, and 10 000 K (Fig. 2), based on the data of Judd et al. (1964). A CCT of between 4800 K and 6500 K approximates direct sunlight, and a CCT of 10 000 K approximates diffuse skylight (examples in Dyer

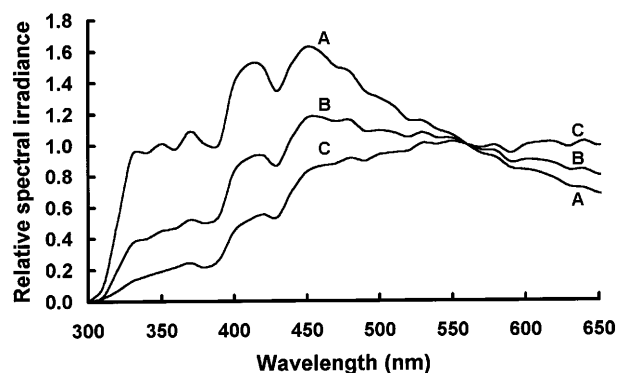


Fig. 2 Spectral distribution of typical daylight with the relative quantity of radiation normalised to 1.0 at 560 nm. Curves are based on the data of Judd et al. (1964) and represent correlated colour temperatures of A 10 000 K, B 6500 K and C 4800 K

1998). Varying the spectral quality of illumination from 4800 K to 10 000 K simulates a problem that foraging insects would encounter when visiting flowers in both direct sunlight and shade.

Computer-generated reflectance curves

The most frequently occurring flower colours do not cover the whole of bee colour space (Menzel and Shmida 1993; Chittka et al.

colour distance (Backhaus and Menzel 1987) but are used to evaluate relative colour shift in different areas of colour space. Possible errors from mapping reflectance curves onto a two-dimensional colour space (Backhaus 1991, 1992; Chittka 1992) were minimised by using broad-band reflection spectra and limiting theoretical variations in illumination to natural daylight conditions (see Dyer 1998 for discussion).

The distance between colour loci of a reflectance curve in spectrally variable illumination is given by:

$$cs = 100 \times \sqrt{\left[\left(\frac{1 - s_{ws1}}{\cos 30^\circ} - m_{ws1} \times \tan 30^\circ \right) - \left(\frac{1 - s_{ws2}}{\cos 30^\circ} - m_{ws2} \times \tan 30^\circ \right) \right]^2 + [m_{ws1} - m_{ws2}]^2}, \quad (4)$$

1994). To examine the effect of spectrally variable illumination on a broad range of colours theoretically visible to the honeybee a series of 99 computer-generated reflection curves has previously been used (Dyer 1998). The reflectance curves were derived from the many flower colours that have a steep gradient at about 375 nm and 500 nm (Chittka and Menzel 1992). The generated reflectance curves were tested for the three HVSs and found to also give a good coverage of their respective colour spaces.

where s_{ws1} , s_{ws2} and m_{ws1} , m_{ws2} are the chromaticity coordinates of $I(\lambda)$ under two spectrally different illumination sources.

Colour triangle contour plots of reflectance curves in spectrally variable illumination

For each of the visual systems, the amount of radiation absorbed by the photoreceptors P (SWS, MWS, LWS) was calculated by numerically integrating the product of photoreceptor absorption $S(\lambda)$, relative spectral illumination $D(\lambda)$, and spectral reflectance $I(\lambda)$ at 10-nm steps from 310 nm to 670 nm (Eq. 1). The variable W was used to weight each of the three photoreceptors:

$$P = W \cdot \int_{310}^{670} S(\lambda)I(\lambda)D(\lambda)d\lambda. \quad (1)$$

The values of P (SWS), P (MWS) and P (LWS) were then used to calculate chromaticity coordinates (Eq. 2) (Wyszecki and Stiles 1967). Chromaticity coordinates (s_{ws} , m_{ws} , l_{ws}) are given by:

$$\begin{aligned} s_{ws}/P(\text{SWS}) &= m_{ws}/P(\text{MWS}) = l_{ws}/P(\text{LWS}) \\ &= 1/(P(\text{SWS}) + P(\text{MWS}) + P(\text{LWS})), \\ &\text{and } s_{ws} + m_{ws} + l_{ws} = 1 \end{aligned} \quad (2)$$

Maxwell colour triangles are conventionally used to plot chromaticity coordinates for trichromatic visual systems (Rushton 1972; Goldsmith 1990) and the values were plotted in separate equilateral triangles to represent the colour spaces of the honeybee, HVS1, HVS2, and HVS3 (see below).

For each visual system, the three photoreceptors P (SWS, MWS and LWS) were weighted by the variable W to simulate chromatic adaptation to the various illumination sources (4800 K, 6500 K and 10 000 K, see Fig. 2). The value of W (Table 1) was determined by the ratio of the three photoreceptors required to plot a stimulus reflecting radiation equally (equal white) in the centre of a colour triangle for a given illumination source (Eq. 3). This simulates colour constancy based on the von Kries coefficient law.

For chromatic adaptation to equal white reflecting an illumination source, the ratio of the values of W were varied such that:

$$s_{ws} = m_{ws} = l_{ws} = 1/3. \quad (3)$$

The relative colour shift (cs) of a reflectance curve $I(\lambda)$ in two spectrally different illumination sources was quantified by converting chromaticity coordinates to Cartesian coordinates and applying Pythagoras' theorem (Eq. 4, derivation given in Dyer 1998). The resulting unit of measure is relative to the height of a colour triangle (100 units), and represents the change in the position of a reflectance curve in colour space for a given change in the spectral quality of illumination. The values cannot be treated as perceptual

Results

The visual systems with no colour constancy

The effect of spectrally variable illumination for each of the visual systems without colour constancy was determined by maintaining a set value of W for a CCT of 6500 K (Table 1), and varying the value of $D(\lambda)$ such that CCT = 4800, 6500 and 10 000 K. The colour shift of the 99 reflectance curves as illumination varied from 4800 K to 10 000 K was calculated for each visual system (Eq. 4). These numeric values were plotted onto separate colour triangles, representing each of the visual systems, at the coordinates where the 99 reflectance curves would lie for a CCT of 6500 K. The numeric values were then converted into contour lines of constant colour shift. The distribution of some plant colours that are very common in nature (Dyer 1998) were plotted onto the triangles considering a CCT of 6500 K to evaluate the correlation between plant colour loci and contour shape.

The results for HVS3 with no colour constancy were very similar to HVS2 and are not separately shown. Without any mechanism for colour constancy, spectrally variable illumination produces a large colour shift for all of the visual systems with values ranging from 8 units to 40 units (Fig. 3A, C, E). Each of the 99 reflectance curves are able occupy a large number of positions in colour space, and without colour constancy colour recognition in spectrally variable illumination would be impossible for any of the visual systems. The shape of the contours is symmetric in the colour spaces, with a similar degree of colour shift on either side of the triangle. There is no correlation between contour shape and the colour loci of common plant colours (Fig. 3A, C, E).

Chromatic adaptation based on the von Kries coefficient law

Chromatic adaptation for the various hypothetical vision systems was simulated by using a specific value of

W for each photoreceptor depending upon the illumination source used (Table 1). The colour shift of the 99 reflectance curves as illumination varied from 4800 K to 10 000 K was calculated (Eq. 4), and these numeric values were plotted onto separate colour triangles at the coordinates where each of the 99 curves would lie for a CCT of 6500 K. The numeric values were then converted to contour lines of constant colour shift, and the distribution of plant reflectance curves that are common in nature (Dyer 1998) were plotted onto the colour spaces (Fig. 3B, D, F). The results for HVS3 are not shown since the calculated values were extremely small.

Chromatic adaptation for the honeybee visual system (results from Dyer 1998)

Compared with the system of no colour constancy (Fig. 3A), chromatic adaptation for honeybee shows a reduced colour shift with values ranging from 0 to 11.0 units (Fig. 3B). The chromatic adaptation model predicts an asymmetric correction that is best in the centre right-hand side of bee colour space, and this is the region where the loci of many common plant colours lie.

Chromatic adaptation for HVS1

Chromatic adaptation for HVS1 shows a large reduction in the degree of colour shift for all reflectance curves, with the best correction in the centre of colour space (Fig. 3D). The relative colour shift values range from 0 to 6.0 units, and provide a better overall correction than chromatic adaptation for the bee where values range from 0 to 11.0 units (Fig. 3B). Contours of colour shift for HVS1 are symmetric in colour space, offering a correction that is similar on either side of the triangle. There is no correlation between contour shape and plots of common plant reflectance curves, and the contours are different in shape from chromatic adaptation for the bee (Fig. 3B).

Chromatic adaptation for HVS2

The correction to spectrally variable illumination resulting from chromatic adaptation for HVS2 (Fig. 3F) shows a large improvement over the correction for HVS1 (Fig. 3D). The colour shift values range from 0 to 2.0 units. The contours are approximately symmetrically orientated in colour space with a high level of correction in the centre of the triangle. There is also a high level of correction shown on the bottom left-hand side of the triangle because these reflectance curves only stimulate the SWS photoreceptor, guaranteeing colour constancy.

Chromatic adaptation for HVS3

Chromatic adaptation to spectrally variable illumination for HVS3 provides for almost perfect colour constancy

for all theoretically visible colours. A small colour shift was calculated for some reflectance curves resulting in a mean colour shift of 0.03 units ($SD = 0.03$). As colour constancy is nearly perfect, there are no contours of colour shift to plot. The results for the hypothetical visual systems are in agreement with the theoretical considerations proposed by Worthey and Brill (1986), that non-overlapping and narrower photoreceptors improve von Kries colour constancy.

Discussion

The contour plots of colour shift for HVS1 show that for approximately symmetric and evenly spaced photoreceptors the von Kries coefficient law produces a symmetric solution in colour space (Fig. 3D). The correction is incomplete, however, showing that chromatic adaptation for HVS1 achieves only approximate colour constancy. A comparison of chromatic adaptation for HVS1 (Fig. 3D) and for the honeybee (Fig. 3B) shows that absorption of UV radiation by the *cis*-band of the chromophore is responsible for the asymmetric solution of chromatic adaptation reported previously for the honeybee. Dyer (1998) suggests that the poorer solution of bee chromatic adaptation for colours that are relatively rich in UV reflectance is a possible or part explanation for the rarity of UV-coloured flowers in nature, because these flowers might be harder for bees to constantly find using colour as a cue. If this is the case, then the absorption of UV radiation by the *cis*-band of the chromophore may have played an important role in natural selection not favouring some flower colours. However, behavioural studies that demonstrate different levels of colour constancy for different bee colours would be required to substantiate this hypothesis.

Electrophysiological measurements of photoreceptor spectral sensitivities (e.g. Peitsch et al. 1992) show that for some insects that the sensitivities may vary from Stavenga et al. (1993) photopigment template predictions, probably because of spectral filtering by screening pigments, waveguide effects and/or self-screening in the photoreceptors (Stavenga et al. 1993; Gribakin et al. 1995). Peitsch et al. (1992) recorded that in some hymenopteran species that the spectral sensitivities of the MWS and LWS receptors had considerable overlap with the SWS receptor, whilst in other species the overlap was small. In a study of white-eyed insect mutants Gribakin et al. (1996) showed that spectral sensitivities of visual pigments may also vary from the predictions made by the template, and that the effect of the β -band on receptor sensitivities in some insects may be smaller than template predictions. A comparison of Figs. 3B and 3D shows that as there is a change in the effect of the β -band on the absorption of radiation by the MWS and LWS receptors, there should be a relative change in the performance of von Kries chromatic adaptation.

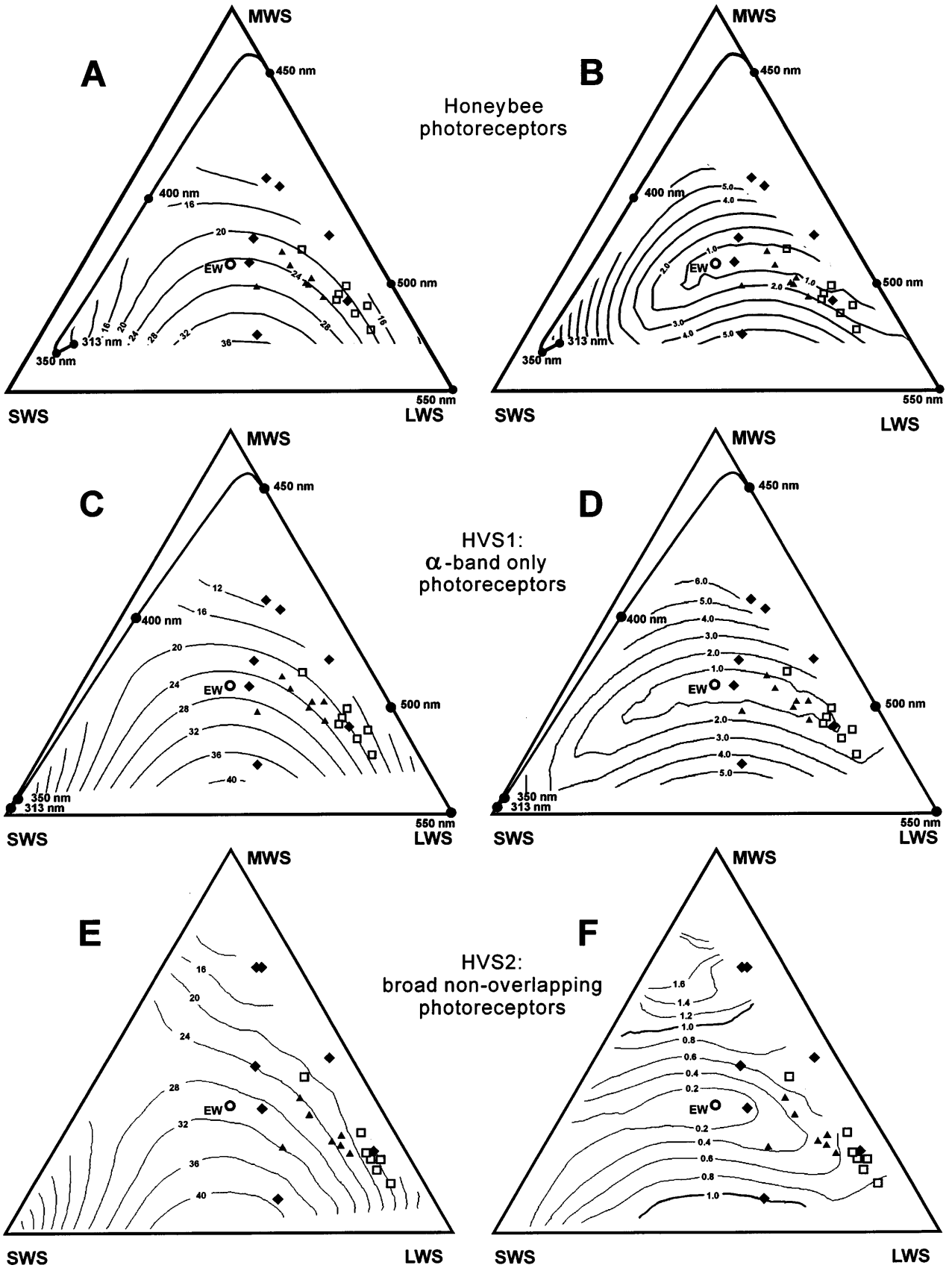




Fig. 3A–F Interpolated contour plots of colour shift in a Maxwell colour triangle for spectral illumination varying from a correlated colour temperature (CCT) of 4800 K to 10 000 K. The contours represent colour shift for 99 computer-generated reflectance curves whose loci provide a good coverage of the Maxwell triangle. The colour shift distance is relative to the height of the triangle (100 units). *Numbers on the contours* represent the distance a colour in that region of colour space would shift under the spectral illumination change. *Triangles on the left-hand side* of the figure (**A, C, E**) show plots made with the weighting of photoreceptors kept constant for a CCT of 6500 K to simulate no colour constancy. *Triangles on the right-hand side* of the figure (**B, D, F**) show plots made with the weighting of receptors varied based on the von Kries coefficient law (see text). Note that the colour shift values are much lower for triangles on the right-hand side, and the contour intervals are different. **A, B** Predicted colour shift for honeybee photoreceptors. **C, D** Predicted colour shift for a hypothetical visual system (HVS1) which is based only on the α -band spectral sensitivities of vitamin A₁. **E, F** Predicted colour shift for a hypothetical visual system (HVS2) based on three broad non-overlapping photoreceptors. The centre of the triangle represents a stimulus that reflects radiation equally at all wavelengths (*EW*). The corners of the triangles represent short-, medium- and long-wavelength-sensitive photoreceptors (*SWS*, *MWS* and *LWS*), respectively. The distribution of common plant colours is shown on all colour triangles: petals (◆); flower centres (□); and foliage (▲). The spectral locus is a plot of pure spectral radiation, but is not shown for the non-overlapping photoreceptors as the locus would be incomplete

A comparison of Figs. 3B, 3D and 3F shows that chromatic adaptation to spectrally variable illumination is improved by narrowing photoreceptor spectral sensitivity breadth. Improved colour constancy has been suggested as a possible function of oil droplets in pigeons and Pekin robins (Vorobyev et al. 1998). The spectral sensitivity of the birds' four photoreceptors is narrowed by the coloured oil droplets present in the eye, and modelling shows that this reduces the expected colour shift of natural colours in avian tetrachromatic space when considering von Kries colour constancy. They also show that spectral tuning by oil droplets may improve the discrimination of some coloured objects, but the benefits of narrower receptors may be traded off against increased receptor noise and poorer discrimination of monochromatic lights.

The spacing, number and spectral breadth of photoreceptors in visual systems is likely to be influenced by many different needs and constraints including colour constancy, colour discrimination, receptor noise, visual acuity (e.g. Barlow 1982; Goldsmith 1990) and chemistry of the visual pigments (e.g. Goldsmith 1990; Britt et al. 1993). For narrow non-overlapping photoreceptors (HVS3), nearly perfect colour constancy is achieved for a broad range of theoretically visible colours. In nature, however, visual systems based on non-overlapping photoreceptors would be poor at discriminating the broad range of reflectance curves available as information to animals. For example, in the honeybee it has been shown that the regions of the spectrum where colour discrimination is highest is where there is overlap between two photoreceptors of different spectral sensitivity (Helfersen 1972; Chittka and Menzel 1992; Peitsch et al. 1992), because small differences in the wavelength

of reflected radiation cause a large difference in the excitation of the two photoreceptors, and thus maximise signal divergence for the bee's colour opponent system (Chittka and Menzel 1992).

For a vision system based on the three HVS3 photoreceptors there would be a number of different reflectance curves that would produce identical stimulation of the receptors, and it would be poorly suited to foraging amongst natural colours. To achieve good colour discrimination a natural vision system may thus have limitations on the correction to spectrally variable illumination available through chromatic adaptation. A solution to this constraint may be evident in stomatopod crustaceans, which have ten or more classes of spectrally narrow photoreceptors (Cronin and Marshall 1989; Osorio et al. 1997). Modelling shows that stomatopods' narrow but overlapping photoreceptors would provide improved von Kries colour constancy compared to spectrally broader receptors, and would still allow for good colour discrimination (Osorio and Vorobyev 1997; Osorio et al. 1997).

In human vision the photosensitive pigments are based on vitamin A₁ (see Stavenga et al. 1993) and absorb radiation maximally at about 420 nm, 534 nm and 564 nm (Bowmaker and Dartnall 1980). The photoreceptors also have the potential to absorb UV radiation because of the *cis*-band of the chromophore (Stavenga et al. 1993), and this produces spectrally broad photoreceptors. The retina is not exposed to UV radiation, however, due to the strong absorption of radiation below 400 nm by pigmentation in the lens (Wald 1952). Pigmented lenses that absorb short-wavelength radiation are common in fishes, primates and sciurid mammals, and are present in some other mammals, amphibia, and reptiles (see Muntz 1972; Douglas and Marshall 1999 for reviews). Several reasons have been suggested for the function of the pigmentation in the optics of some animals, including limiting chromatic aberration, protection of the retina from damaging UV radiation, reduction of haze and glare (Muntz 1972; Douglas and Marshall 1999). It is also possible that pigmentation in the optics of the eye improves colour constancy by narrowing spectral-sensitivity curves (although colour vision and colour constancy is yet to be demonstrated in many animals possessing pigmented lenses). In particular, filtering out UV radiation before it is absorbed by the *cis*-band of the chromophore may prevent the asymmetric type solution of chromatic adaptation shown for the honeybee (Fig. 3B).

Colour constancy is important if animals are to make robust judgements about reflectance spectra in variable illumination conditions. Colour constancy has apparently evolved independently in primates, birds, fishes, amphibia and insects (Neumeyer 1998), which is strong evidence that it has importance in the survival or reproductive success of many species. Theoretical considerations of von Kries colour constancy (Worthey and Brill 1986), and the models presented here, show that only approximate colour constancy would be achieved

for animals with broad overlapping photoreceptors. The inability of colour constancy to fully correct for changes in illumination may place selective pressure on some species. For example, Endler and Thery (1996) report that birds displaying in forests compete for patches of specific illumination, which might be to maximise the communication of colour signals in the absence of perfect colour constancy, and the relatively poorer solution of chromatic adaptation for honeybees may place selective pressure on plants with UV-coloured flowers (Dyer 1998). The results presented here support the hypotheses that the absorption of short-wavelength radiation by the *cis*-band of the chromophore is responsible for the asymmetric results of chromatic adaptation for the honeybee, and that the breadth of spectral-sensitivity curves limits the accuracy of colour constancy for all colours in colour space.

Acknowledgements I wish to thank Professor W.R.A. Muntz, Dr Bill Jagger, Dr Lalina Muir and two unknown referees for their valuable comments on the manuscript. I also thank Mr Richard Crompton for his assistance with one of the figures. I am grateful for resources provided by Monash University and RMIT University.

References

- Autrum H, Zwehl V von (1964) Spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. *Z Vergl Physiol* 48: 357–384
- Backhaus W (1991) Color opponent coding in the visual system of the honeybee. *Vision Res* 31: 1381–1397
- Backhaus W (1992) The Bezold-Brücke effect in the color vision system of the honeybee. *Vision Res* 32: 1425–1431
- Backhaus W, Menzel R (1987) Color distance derived from a receptor model of color vision in the honey bee. *Biol Cybern* 55: 321–331
- Barlow HB (1982) What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Res* 22: 635–643
- Barth FG (1985) *Insects and flowers – the biology of a partnership*. Princeton University Press, Princeton, New Jersey
- Bennett AW (1884) On the constancy of insects in their visits to flowers. *Zool J Linn Soc* 17: 175–185
- Bowmaker JK, Dartnall HJA (1980) Visual pigments of rods and cones in a human retina. *J Physiol (Lond)* 298: 501–511
- Britt SG, Feiler R, Kirschfeld K, Zuker CS (1993) Spectral tuning of rhodopsin and metarhodopsin in vivo. *Neuron* 11: 29–39
- Chittka L (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J Comp Physiol A* 170: 533–543
- Chittka L (1997) Bee color vision is optimal for coding flower color, but flower colors are not optimal for being coded – why? *Isr J Plant Sci* 45: 115–127
- Chittka L, Menzel R (1992) The evolutionary adaptation of flower colours and the insect pollinators' colour vision. *J Comp Physiol A* 171: 171–181
- Chittka L, Thomson JD (1997) Sensory motor learning and its relevance for task specialisation in bumble bees. *Behav Ecol Sociobiol* 41: 385–398
- Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Res* 34: 1489–1508
- Chittka L, Gumbert A, Kunze J (1997) Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behav Ecol* 8: 239–249
- Christy RM (1884) On the methodic habits of insects when visiting flowers. *Zool J Linn Soc* 17: 186–194
- Cronin TW, Marshall NJ (1989) Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. *J Comp Physiol A* 166: 261–275
- Darwin C (1876) *On the effects of cross and self fertilisation in the vegetable kingdom*. John Murray, London
- Daumer K (1956) Reizmetrische Untersuchung des Farbensehens der Bienen. *Z Vergl Physiol* 38: 413–478
- Daumer K (1958) Blumenfarben, wie sie die Bienen sehen. *Z Vergl Physiol* 41: 49–110
- Douglas RH, Marshall NJ (1999) A review of vertebrate and invertebrate ocular filters. In: Archer SN, Djamgoz MBA, Loew ER, Partridge JC, Vallerga S (eds) *Adaptive Mechanisms in the Ecology of Vision*. Kluwer, Dordrecht, The Netherlands, pp 95–162
- Dyer AG (1998) The colour of flowers in spectrally variable illumination and insect pollinator vision. *J Comp Physiol A* 183: 203–212
- Endler JA (1993) The color of light in forests and its implications. *Ecol Monogr* 63: 1–27
- Endler JA, Thery M (1996) Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest dwelling birds. *Am Nat* 148: 421–452
- Frisch K von (1914a) Demonstration von Versuchen zum Nachweis des Farbensinnes bei angeblich total farbenblinden Tieren. *Verh Dtsch Zool Ges Freiburg* 24: 50–58
- Frisch K von (1914b) Der Farbensinn und Formensinn der Biene. *Zool J Physiol* 37: 1–238
- Goldsmith TH (1990) Optimization, constraint, and history in the evolution of eyes. *Q Rev Biol* 65: 281–322
- Gribakin F, Alekseyev E, Shukolyukov S, Gogala M (1995) Unconventional ultraviolet sensitivity spectra of *Ascalaphus* (Insecta, Neuroptera). *J Comp Physiol A* 177: 201–206
- Gribakin FG, Alekseyev YeN, Ukhonov KYu (1996) Spectral sensitivity of white-eyed insect mutants in the UV, blue and green. *Photochem Photobiol B* 35: 13–18
- Heinrich B (1976) The foraging specializations of individual bumblebees. *Ecol Monogr* 46: 105–128
- Helversen O von (1972) Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. *J Comp Physiol* 80: 439–472
- Hurvich LM (1981) *Color Vision*. Sinauer, Sunderland, Mass., USA
- Judd DB, MacAdam DL, Wyszecki G (1964) Spectral distribution of typical daylight as a function of correlated color temperature. *J Opt Soc Am* 34: 1031–1040
- Kondratyev KYA (1969) *Radiation in the atmosphere*. Academic Press, New York
- Lythgoe JN (1979). *The ecology of vision*. Clarendon Press, Oxford
- MacAdam DL (1970) *Sources of color science*. MIT Press, Cambridge, Mass., USA
- MacAdam DL (1985) *Color measurement: theme and variations*. Springer, Berlin Heidelberg New York
- Mazokhin-Porshnjakov GA (1966) Recognition of coloured objects by insects. In: Bernhard CG (ed) *The functional organization of the compound eye*. Pergamon Press, Oxford, pp 163–170
- Menzel R, Blakers M (1976) Colour receptors in the bee eye-morphology and spectral sensitivity. *J Comp Physiol A* 108: 11–33
- Menzel R, Shmida A (1993) The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case. *Biol Rev* 68: 81–120
- Menzel R, Ventura DF, Hertel H, de Souza JM, Greggers U (1986) Spectral sensitivity of photoreceptors in insect compound eyes: comparison of species and methods. *J Comp Physiol A* 158: 165–177
- Muntz WRA (1972) Inert absorbing and reflecting pigments. In: Dartnall H (ed) *Handbook of sensory physiology*, vol. 7. Springer, Berlin Heidelberg New York, pp 529–565
- Neumeyer C (1980) Simultaneous color contrast in the honeybee. *J Comp Physiol A* 139: 165–176
- Neumeyer C (1981) Chromatic adaptation in the honey bee: successive color contrast and color constancy. *J Comp Physiol A* 144: 543–553

- Neumeyer C (1998) Comparative aspects of color constancy. In: Walsh V, Kulikowski J (eds) *Perceptual constancies*. Cambridge University Press, Cambridge, pp 323–351
- Osorio D, Vorobyev M (1997) *Sepia* tones, stomatopod signals and the uses of colour. *Trends Ecol Evol* 12: 167–168
- Osorio D, Marshall NJ, Cronin TW (1997) Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vision Res* 37: 3299–3309
- Peitsch D, Fietz A, Hertel H, Souza J de, Ventura DF, Menzel R (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J Comp Physiol A* 170: 23–40
- Proctor M, Yeo P, Lack A (1996) *The natural history of pollination*. Timber Press, Portland, Oregon
- Rushton WAH (1972) Pigments and signals in colour vision. *J Physiol (Lond)* 220: 1–31
- Stavenga DG, Smits RP, Hoenders BJ (1993) Simple exponential functions describing the absorbance bands of visual pigment spectra. *Vision Res* 33: 1011–1017
- Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC (1998) Tetrachromacy, oil droplets and bird plumage colours. *J Comp Physiol A* 183: 621–633
- Wald G (1952) Alleged effects of the near ultraviolet on human vision. *J Opt Soc Am* 42: 171–173
- Waser NM (1983a) Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In: Jones CE, Little RJ (eds) *Handbook of experimental pollination biology*. Scientific and Academic Editions, New York, pp 277–293
- Waser NM (1983b) The adaptive nature of floral traits: ideas and evidence. In: Real LA (ed) *Pollination biology*. Academic Press, New York, pp 241–285
- Waser NM (1986) Flower constancy: definition, cause, and measurement. *Am Nat* 127: 593–603
- Werner A, Menzel R, Wehrhahn C (1988) Color constancy in the honeybee. *J Neurosci* 8: 156–159
- Worthey JA, Brill MH (1986) Heuristic analysis of von Kries color constancy. *J Opt Soc Am A* 3: 1708–1712
- Wyszecki G, Stiles WS (1967) *Colour science: concepts and methods, qualitative data and formulas*. John Wiley, New York