

Coloured oil droplets enhance colour discrimination

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The eyes of most diurnal reptiles and birds contain coloured retinal filters—oil droplets. Although these filters are widespread, their adaptive advantage remains uncertain. To understand why coloured oil droplets appeared and were retained during evolution, I consider both the benefits and the costs of light filtering in the retina. Oil droplets decrease cone quantum catch and reduce the overlap in sensitivity between spectrally adjacent cones. The reduction of spectral overlap increases the volume occupied by object colours in a cone space, whereas the decrease in quantum catch increases noise, and thus reduces the discriminability of similar colours. The trade-off between these two effects determines the total benefit of oil droplets. Calculations show that coloured oil droplets increase the number of object colours that can be discriminated, and thus are beneficial for colour vision.

Keywords: colour vision; oil droplets; evolution; birds; reptiles

1. INTRODUCTION

Different animals have different eyes, and this variability in eye design may reflect the adaptation of animals to their specific habits and habitats (Lythgoe 1979). However, some features of eye design are shared by many animals, and it is interesting to ask what selective advantage such features provide. Most vertebrates have several types of cone photoreceptor cell whose sensitivities are tuned to different parts of the spectrum. Comparison of signals from these photoreceptors makes it possible to perceive colours. Cone sensitivities are mainly determined by their visual pigments. However, many animals have evolved devices that modify photoreceptor sensitivity by selective filtering of light (Douglas & Marshall 1999). Such filters—coloured oil droplets—are responsible for the strikingly colourful appearance of the retinae of many diurnal reptiles and birds (Walls 1942). Oil droplets, located in the cone inner segments, selectively absorb light before it reaches the visual pigment housed in the cone outer segments. This changes the spectral sensitivities of cones and thus modifies colour vision (Bowmaker 1980; Govardovskii 1983; Partridge 1989; Goldsmith 1991). Coloured retinal filters probably appeared early in the evolution of terrestrial vertebrates—a lungfish, the closest living relative of the first terrestrial vertebrates, has coloured oil droplets (Robinson 1994). Coloured oil droplets were retained in diurnal lizards, turtles and birds (Walls 1942). However, they were lost in amphibians, snakes, crocodiles and mammals, presumably when ancestors of these animals lived in dim light conditions (Walls 1942). Because coloured oil droplets occur in animals with substantially different lifestyles, it is probable that they are generally useful regardless of specific visual tasks.

Early workers attributed a variety of functions to oil droplets (Walls 1942), most notably that they were a means by which animals, assumed to have only a single visual pigment, could produce a system for colour vision (Walls 1942; King-Smith 1969). However, animals with coloured oil droplets turned out to have multiple visual pigments (Govardovskii & Zueva 1977; Bowmaker &

Knowles 1977). Moreover, recent spectral measurements of both oil droplets and visual pigments in the same cone clearly show that in birds oil droplets are not used to increase the number of spectral types of single cones (Bowmaker *et al.* 1997; Hart 2001).

Coloured oil droplets act as cut-off filters, absorbing wavelengths below a critical value. Thus, they narrow the spectral sensitivity functions of cones and simultaneously reduce the overall quantum catch (figure 1). Consequently, where receptor noise depends on the number of absorbed quanta, any benefits from oil droplets are traded against increased noise. Narrowing spectral sensitivity leads to a reduction in spectral overlap. Because monochromatic lights are discriminated best where receptor spectral sensitivities overlap, coloured oil droplets impair wavelength discrimination ($\Delta\lambda/\lambda$ function) (Arnold & Neumeyer 1987). Hence, it has been suggested that the selective advantage of oil droplets lies in spatial rather than colour vision (Arnold & Neumeyer 1987).

However, the discrimination of monochromatic lights is an unusual visual task—in natural conditions, animals have to discriminate broad-band lights reflected from objects. Reduction of spectral overlap may improve the discriminability of such spectra, and thus coloured oil droplets may enhance colour vision in these more natural conditions (Barlow 1982; Govardovskii 1983). Direct computations have shown that changes in receptor spectral sensitivity caused by oil droplets should improve discrimination of plumage colours (Vorobyev *et al.* 1998). Plumage colours are important components of bird sexual displays, but whether oil droplets also improve the discriminability of other biologically significant colours remains uncertain. Moreover, we do not know which colours it is important for diverse groups of birds and reptiles to discriminate.

To evaluate the benefits or costs of filtering by oil droplets I consider the task of discriminating *all* possible surface colours. This method is based on the analysis of the spread of mathematically realizable reflectance spectra in a colour space. Such spectra correspond to all possible object colours, and these colours occupy only a limited

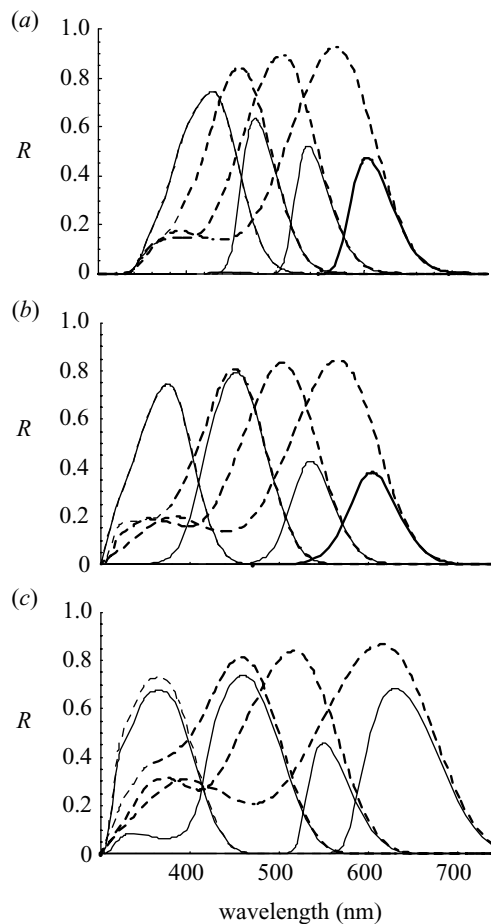


Figure 1. Receptor spectral sensitivities (R) of four cone types in (a) the peacock, *Pavo cristatus* (Hart 2002); (b) the blue tit, *Parus caeruleus* (Hart *et al.* 2000); and (c) the freshwater turtle, *Pseudemys scripta elegans* (Loew & Govardovskii 2001) (solid lines). Dashed lines show the hypothetical sensitivities of cones not equipped with oil droplets. Sensitivities are given in inverse quantum units. The cone pigment curves are scaled to one at their maxima. Sensitivities of cones not equipped with oil droplets do not reach one, because the ocular media absorb light. Absorption by oil droplets additionally decreases the sensitivity. Note that oil droplets decrease the overlap between the sensitivity curves.

part of the colour space, an object-colour solid (Luther 1927; Nyberg 1928; MacAdam 1935). The concept of the object-colour solid has been applied to animal vision by Maximov (1984) and later was used to study the role of oil droplets in colour vision (Govardovskii & Vorobyev 1989). I present a quantitative estimate of both the benefits and the drawbacks of coloured oil droplets, based on accurate new spectral measurements of visual pigments and oil droplets (Hart *et al.* 2000; Loew & Govardovskii 2001; Hart 2002).

2. THEORY

(a) *Receptor-based colour space and the object-colour solid*

For a colour vision system with n spectral receptor types, colour can be represented as a point in n -dimensional colour space, where the receptor quantum catches are placed along the coordinate axes. For an eye viewing

the surface of an object, the quantum catch of the receptor i , Q_i , is given by the following expression:

$$Q_i = \int_{\lambda_{\min}}^{\lambda_{\max}} R_i(\lambda) S(\lambda) I(\lambda) d\lambda, \quad (2.1)$$

where λ denotes wavelength, λ_{\min} and λ_{\max} denote the lower and upper limits of the visible spectrum, respectively, $R_i(\lambda)$ is the spectral sensitivity of receptor i , $S(\lambda)$ is the reflectance spectrum and $I(\lambda)$ is the illumination spectrum.

Mathematically realizable reflectance spectra are positive functions that do not exceed one, i.e. $0 < S(\lambda) < 1$. The points corresponding to such functions occupy an object-colour solid (figure 2). A method for constructing the object-colour solid is given in Appendix A. The boundaries of the colour solid are formed by optimal colour stimuli (Luther 1927; Nyberg 1928; MacAdam 1935). These optimal colour stimuli correspond to reflectance functions that are limited to values of either zero or one, and for a visual system with n types of receptors the transitions may occur $n - 1$ times (figure 3). Optimal colour stimuli are imaginary stimuli, in the sense that no real reflectance spectrum has sharp transitions of this kind. The object-colour solid is a centrally symmetric shell-shaped body, with one apex at the origin, which corresponds to an ideal black surface ($S(\lambda) \equiv 0$), and the other at the corner corresponding to an ideally white reflector ($S(\lambda) \equiv 1$). If receptor sensitivities do not overlap, the object-colour solid fills the entire cubic volume between these apexes. For overlapping receptor sensitivities, the object-colour solid fills only a limited part of the cubic volume (figure 2; Govardovskii & Vorobyev 1989).

(b) *The number of discriminable colours*

A point in colour space is surrounded by a small elementary volume of the colours indistinguishable from that point. The number of object colours that the visual system is able to discriminate is equal to the number of these elementary volumes needed to fill the object-colour solid. Let V be the volume of the object-colour solid and u be the volume of indistinguishable colours. If u were constant then the ratio, V/u , would give the number of discriminable colours. In reality, u depends on the position of the point in the colour space, which means that the number of discriminable colours is given by an integral of $1/u$ over the volume of the solid, i.e. the number of discriminable colours, N , is given by:

$$N = \int_V \frac{1}{u} \prod_{i=1}^{i=n} dQ_i. \quad (2.2)$$

Thus, the larger the volume of the object-colour solid compared with the volume of indistinguishable colours, the higher is the number of discriminable colours.

Colours are discriminated if the distance between them in colour space exceeds a certain threshold distance. This distance, in turn, depends on noise, which originates in the receptors and at subsequent stages of the neural processing of receptor signals. The assumption that the threshold distance is determined by receptor noise leads to predictions that agree nicely with behavioural colour thresholds in a variety of animals, including humans and birds (Vorobyev & Osorio 1998; Vorobyev *et al.* 2001).

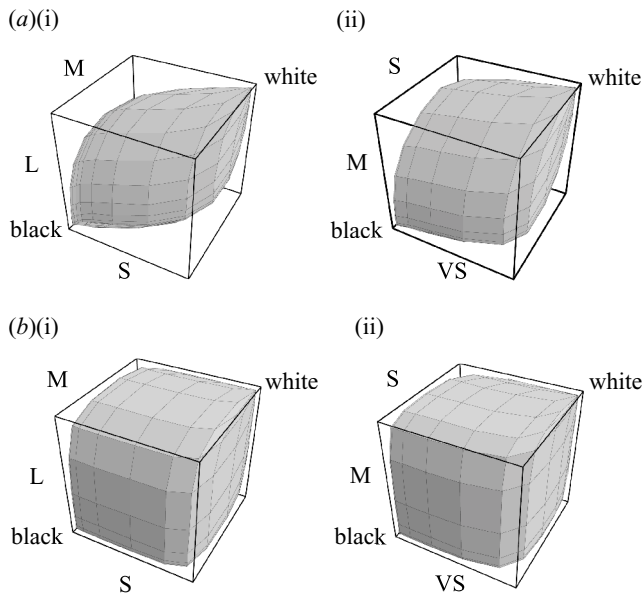


Figure 2. Object-colour solids of the blue tit. Calculations are for eyes (a(i,ii)) without and (b(i,ii)) with oil droplets. A tetrachromatic colour space is shown by projecting it onto the spaces defined by quantum catches of (a(i),b(i)) S, M and L cones and (a(ii),b(ii)) VS, S and M cones.

This indicates that receptor noise plays an important role in setting thresholds. However, the contribution of additional post-receptor noise cannot be ruled out (Vorobyev *et al.* 2001). To estimate the volume of indistinguishable colours, I assume that colour thresholds are determined by receptor noise alone. Because receptor noise sets the upper limit for colour discrimination, the calculations presented here give the upper boundary of the number of discriminable colours. I also assume that chromatic and achromatic (brightness) aspects of colour are equally important for colour discrimination.

In conditions of relatively dim light, receptor noise is determined by the fluctuations of absorbed quanta (quantum noise). Then, noise is proportional to the square root of receptor quantum catch (Rose-de Vries law) (Rose 1948). As the intensity of the illumination increases, the noise is better described by direct proportionality dependence on quantum catch or the Weber law (Wysszecki & Stiles 1982). The Weber law implies that the contrast threshold (or the signal-to-noise ratio) remains constant when the signal varies. Mathematical formulations of these two laws and the corresponding dependence of the volume of indistinguishable colours (u) on the receptor quantum catches are given in Appendix B. The formulae given in Appendix B also predict the dependence of the number of discriminable colours on the intensity of the ambient illumination.

3. RESULTS

The number of discriminable colours is given by the volume of the object-colour solid relative to the volume of indistinguishable colours (equation (2.2)). Oil droplets change the shape of the object-colour solid (figure 2) and decrease the receptor sensitivity (figure 1), and the goal of this study is to understand whether these changes are

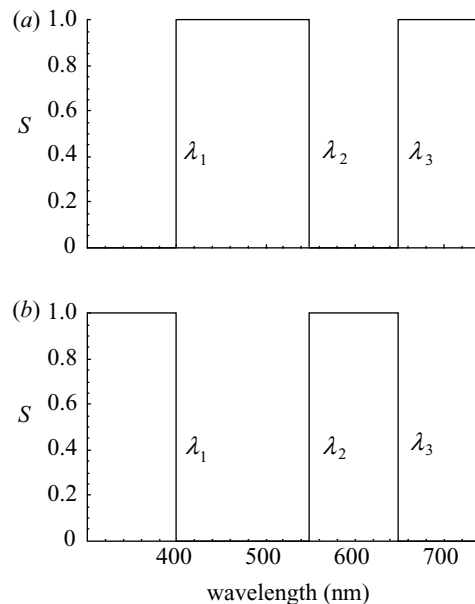


Figure 3. Reflectance spectra (S) of optimal colour stimuli for tetrachromatic vision. Such stimuli have three sharp transitions from zero to one at wavelengths λ_1 , λ_2 and λ_3 and may belong to one of two types: (a) reflectance is equal to 0 for $\lambda < \lambda_1$, or (b) reflectance is equal to 1 for $\lambda < \lambda_1$ (see Appendix A).

beneficial or not. To construct the object-colour solid, one needs first to model the receptor spectral sensitivities.

Typically, diurnal birds and reptiles have four cone visual pigments, which are housed in single and double cones. Analysis of behavioural spectral sensitivity indicates that double cones are not used for colour vision (Maier & Bowmaker 1993; Vorobyev & Osorio 1998), and therefore I consider colour spaces corresponding to single cones only. The four single cone types are termed L for the long-, M for the middle-, S for the short- and VS for the very short-wavelength (UV or violet) parts of the spectrum. The oil droplets are named according to their appearance as 'red', 'yellow', 'clear' and 'transparent'; 'clear' oil droplets absorb UV light, while the 'transparent' ones transmit it. In single cones, the visual pigments are usually combined with a single type of oil droplet (Hart 2001). L, M, S and VS pigments are combined with 'red', 'yellow', 'clear' and 'transparent' oil droplets, respectively. The spectra of oil droplets may vary, but the main differences between species result from the tuning of visual pigments. In birds, visual pigments are based on vitamin A1, and in some reptiles they are based on vitamin A2 (Provencio *et al.* 1992; Loew & Govardovskii 2001). While the peak positions of the S, M and L visual pigments in birds are relatively stable, the position of the VS pigment peak is quite variable and may be close to either 370 nm (UV) or 415 nm (violet) (Hart 2001).

To cover variability in eye design, I considered the visual systems of the peacock, *Pavo cristatus* (A1 visual pigments, violet receptor) (Hart 2002), the blue tit, *Parus caeruleus* (A1 visual pigments, UV receptor) (Hart *et al.* 2000) and the freshwater turtle, *Pseudemys scripta elegans* (A2 visual pigments, UV receptor) (Loew & Govardovskii 2001) (figure 1). Receptor spectral sensitivities are modelled using the standard curves of visual pigment optical

Table 1. The drawback, d , of oil droplets to tetrachromatic colour vision resulting from the reduction in cone quantum catches.

(k_i and k_i^0 denote quantum efficiencies of cone mechanisms with and without oil droplets, respectively; $d = \prod_{i=1}^4 \sqrt{k_i^0/k_i}$ (equation (B 14)). Calculations are performed with equation (B 6) using the spectral sensitivities shown in figure 1 and standard daylight (D65) (Wyszecki & Stiles 1982) scaled to one at its maximum.)

	peacock	blue tit	turtle
k_{VS}^0/k_{VS}	1	1	1.1
k_S^0/k_S	2.1	1.1	1.3
k_M^0/k_M	3.6	3.4	4.2
k_L^0/k_L	4.3	4.2	2.4
d	5.7	4.0	3.7

density (absorbance) (Govardovskii *et al.* 2000) fitted to measured maxima and combined with the transmittances of the ocular media and oil droplets (Hart *et al.* 2000; Loew & Govardovskii 2001; Hart 2002) (Appendix C, equation (C 1)). Because ‘red’ and ‘yellow’ oil droplets are strongly absorbing, the spectral sensitivities of L and M cones are significantly changed by filtering; ‘clear’ oil droplets change the quantum catch of the S cones less, and ‘transparent’ ones barely alter the spectral sensitivity of the VS cones. For any given reflectance spectrum the quantum catch is determined by receptor spectral sensitivity and the illumination spectrum (equation (2.1)). Here, calculations are for standard daylight illumination D65 (Wyszecki & Stiles 1982).

Since for diurnal birds and reptiles colour is defined by the signals of four types of cone, their colour spaces are four-dimensional. To visualize four-dimensional colour spaces, I used projections onto three-dimensional subspaces defined by S–M–L and VS–S–M cone axes (figure 2). Oil droplets reduce the overlap of the receptor sensitivities. Hence, the object-colour solids occupy a greater part of the available colour space. However, the reduction in the quantum catch caused by the oil droplets increases receptor noise. The trade-off between these two effects determines the benefit of oil droplets.

A quantitative measure of the benefit of oil droplets is given by the ratio, r , of the number of discriminable colours for the eye with oil droplets to that without oil droplets (see Appendix B, equation (B 11)). The benefit so defined is equal to the ratio b/d (equation (B 12)), where the numerator b describes the benefit resulting from the change of the shape of the object-colour solid (equation (B 13)), and the denominator d describes the drawback resulting from the reduction of the quantum catch (equation (B 14)). I assume that the volume of indistinguishable colours is determined by receptor noise and consider two cases: (i) receptor noise is determined by the fluctuations in the number of absorbed quanta (relatively low illumination level); and (ii) both quantum fluctuations and receptor noise obeying the Weber law (constant signal-to-noise ratio) affect colour discrimination (moderate and bright illumination). Formulae are given in Appendix B, and the results of the calculations are summarized in tables 1 and 2.

(a) Quantum noise

In this case the benefit does not depend on the light intensity (see Appendix B). Reductions of quantum catches decrease the number of discriminable colours by factors of 5.7, 4.0 or 3.7 (table 1), while the benefit resulting from the change of the shape of the object-colour solid is equal to 8.9, 4.2 or 4.2 for the peacock, blue tit and turtle, respectively (table 2). Hence, oil droplets slightly increase the number of discriminable colours.

(b) Weber noise

In this case, the benefit increases with increasing light for any values of Weber fractions (Appendix B). The benefit for bright light always exceeds that for the quantum noise limited scenario, and calculations show that in daylight ($T > 500$; see Appendix C) oil droplets markedly increase the number of discriminable colours (table 2). Exact values of the benefit depend on the Weber fractions of cone mechanisms (equation (B 9)). The Weber fractions can be estimated from cone densities, and the validity of the estimates can be verified by comparing behavioural thresholds with modelled ones (Vorobyev & Osorio 1998). I use here the Weber fractions of a passerine bird, *Leiothrix lutea* ($\omega_L = 0.05$, $\omega_M = 0.07$, $\omega_S = 0.07$, $\omega_{VS} = 0.1$); it is the only non-mammalian vertebrate whose Weber fractions have been accurately estimated (Maier & Bowmaker 1993; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). The Weber fractions for other diurnal birds and reptiles may differ from this estimate, but they are likely to be of the same order of magnitude.

4. DISCUSSION

The results of the calculations show that coloured oil droplets are beneficial for colour discrimination and that the benefit increases with increasing light (table 2). This benefit is the result of the reduction of overlap between receptor spectral sensitivities, which leads to an increase in the volume of the object-colour solid (figures 1 and 2). Absorption by oil droplets decreases the quantum catch, reducing this benefit, especially in conditions of dim light. However, coloured oil droplets are still beneficial even when colour discrimination is limited by fluctuations in the number of absorbed quanta.

I considered colours corresponding to all possible object spectra, rather than colours of real objects. The latter do not occupy the whole volume of the object-colour solid, because the colours at the boundaries are formed by step functions, i.e. by unnatural spectra. Nevertheless, oil droplets increase the discriminability of many reflectance spectra including those of objects that are important for birds, for example those of plumage (Vorobyev *et al.* 1998).

While coloured oil droplets modify colour vision, their value may also lie in spatial vision. Because coloured oil droplets absorb in the short-wavelength part of the spectrum, they are likely to reduce chromatic aberration and glare in much the same way as do the yellow filters used in photography (Walls 1942; Douglas & Marshall 1999). Coloured oil droplets may also protect delicate cone outer segments from the damage caused by ultraviolet light (Douglas & Marshall 1999). However, the results presented here favour the hypothesis that coloured oil

Table 2. The benefit of oil droplets, r , increases with increasing ambient illuminant intensity.

(The illuminant intensity, T , is given as the number of quanta per receptive field and summation time that would be effectively absorbed by L receptors lacking oil droplets. During the day T may vary from *ca.* 5×10^2 to 5×10^5 (Appendix C). The 'shape factors' G^0 and G correspond, respectively, to eyes lacking and having oil droplets; $b = G/G^0$ describes the benefit resulting from the change of the shape of the object-colour solid. The total benefit of oil droplets, r , is equal to b/d , where d denotes the drawback resulting from decreased quantum catch (table 1). The shape factors are calculated using equation (B 10) for the quantum noise limited scenario, and using equation (B 9) where both quantum noise and Weber noise play a role.)

	peacock				blue tit				turtle			
	G^0	G	b	r	G^0	G	b	r	G^0	G	b	r
quantum noise	0.90	8.0	8.9	1.5	2.1	8.9	4.2	1.05	2.3	9.7	4.2	1.14
$T = 500$	0.22	2.3	10	1.8	0.67	3.0	4.5	1.1	0.79	3.6	4.6	1.2
$T = 1000$	0.16	2.1	13	2.3	0.47	2.6	5.4	1.4	0.59	3.2	5.4	1.5
$T = 10\,000$	0.014	0.44	32	5.6	0.05	0.54	11	2.7	0.067	0.64	9.5	2.6

droplets are an adaptation that improves the colour vision of diurnal animals (Barlow 1982; Govardovskii 1983; Goldsmith 1991). Coloured oil droplets could have evolved to enhance discrimination of objects that were important for the extinct ancestors of terrestrial vertebrates, and they were retained (or evolved independently) in lungfishes, diurnal reptiles and birds (Walls 1942; Robinson 1994) because they enhance the discrimination of almost any object spectra.

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APPENDIX A: A METHOD OF CONSTRUCTING AN OBJECT-COLOUR SOLID

The reflectance spectra of 'optimal' colour stimuli for a tetrachromatic visual system have three sharp transitions at wavelengths $\lambda_1 < \lambda_2 < \lambda_3$ (figure 3). Such stimuli may have values of either 0 or 1. Thus, any set of three numbers, $\lambda_1, \lambda_2, \lambda_3$, define two types of stimuli, which add up to one for all λ (figure 3). Boundaries of a four-dimensional object-colour solid are three-dimensional surfaces, which can be defined as functions of λ_1, λ_2 and λ_3 . The coordinates of those boundaries can be obtained by substitution of the reflectance shown in figure 3 into equation (2.1), which gives

$$Q_i = \int_{\lambda_1}^{\lambda_2} R_i(\lambda)I(\lambda)d\lambda + \int_{\lambda_3}^{\lambda_{\max}} R_i(\lambda)I(\lambda)d\lambda$$

or

$$Q_i = \int_{\lambda_{\min}}^{\lambda_1} R_i(\lambda)I(\lambda)d\lambda + \int_{\lambda_2}^{\lambda_3} R_i(\lambda)I(\lambda)d\lambda, \quad (\text{A } 1)$$

where i denotes one of the four receptor types (VS, S, M, L). The object-colour solid has two-dimensional edges at $\lambda_1 = \lambda_2$ and $\lambda_2 = \lambda_3$ (two sharp transitions) and a one-dimensional edge at $\lambda_1 = \lambda_2 = \lambda_3$ (one sharp transition).

APPENDIX B: RECEPTOR NOISE, THE VOLUME OF INDISTINGUISHABLE COLOURS AND THE DEPENDENCE OF THE NUMBER OF DISCRIMINABLE COLOURS ON ILLUMINANT INTENSITY

Let Q_i be the number of effectively absorbed quanta in receptor mechanism i per receptive field and summation time, and δQ_i be the standard deviation of the noise in this mechanism. If the fluctuations in the number of absorbed quanta determine the receptor noise then

$$\delta Q_i = \sqrt{Q_i}. \quad (\text{B } 1)$$

If quantum catch is high, equation (B 1) is no longer valid, and the Weber law better describes the noise:

$$\delta Q_i = \omega_i Q_i, \quad (\text{B } 2)$$

where ω_i is the Weber fraction. For intermediate values of quantum catch, the dispersion of the noise is given by the sum of the dispersions of the noises obeying the Weber law and that originating from quantum fluctuations. Then,

$$\delta Q_i = \sqrt{Q_i + \omega_i^2 Q_i^2}. \quad (\text{B } 3)$$

This equation is equivalent to equation (B 1) when quantum catch is low, and to equation (B 2) when quantum catch is high.

Consider an elementary volume with sides equal to the noise level (standard deviation) in each receptor channel, δQ_i . The volume of indistinguishable colours, u , differs from this elementary volume (it is, generally, ellipsoidal), but its value is proportional to the elementary volume, i.e.

$$u = C \prod_{i=1}^{i=n} \delta Q_i, \quad (\text{B } 4)$$

where n is the number of receptor types, and C is the proportionality factor. The constant C depends on the definition of the threshold. Because C does not depend on the presence or absence of oil droplets, its value is not important here. Substitution of equation (B 3) into equation (B 4) gives an expression relating the volume of indistinguishable colours to the receptor quantum catches, i.e. to the position in the colour space.

The dependence of the number of discriminable colours on the intensity of the ambient illumination is implied by the direct proportionality dependence of the quantum catch on illuminant intensity. Let $j(\lambda)$ be the illumination spectrum scaled to one at its maximum; then the illumination spectrum $I(\lambda)$ is related to the intensity of the ambient illuminant, T , by

$$I(\lambda) = Tj(\lambda). \tag{B 5}$$

For the sake of convenience we use scaled receptor sensitivities, $r_i(\lambda)$, which are related to the original ones by $R_i(\lambda) = k_i r_i(\lambda)$, where

$$k_i = \int_{\lambda_{\min}}^{\lambda_{\max}} R_i(\lambda)j(\lambda)d\lambda. \tag{B 6}$$

The scaling factors, k_i , so defined, denote the quantum efficiency of receptor mechanism i for a given shape of illumination spectrum, $j(\lambda)$. Then expression (2.1) for the quantum catch can be rewritten as

$$Q_i = Tk_i x_i, \tag{B 7}$$

where $x_i = \int_{\lambda_{\min}}^{\lambda_{\max}} r_i(\lambda)S(\lambda)j(\lambda)d\lambda$ (see equation (2.1)).

Note that x_i is equal to one for an eye viewing an ideally reflecting white surface ($S(\lambda) \equiv 1$). Absolute values of the quantum efficiencies depend on the units of the illuminant intensity, T (note that $R_i(\lambda)$ is measured in units reciprocal to those of T). To define the units of T , we set the ‘efficiency’ of an L cone devoid of coloured droplet, k_L^0 , to one. Then the illuminant, T , is measured in photons absorbed per receptive field and integration time; T is equal to the number of photons that would be absorbed by an L cone devoid of coloured droplet viewing an ideally white surface.

Substitution of the expression for the volume of indistinguishable colours (equation (B 4)) into the expression for the number of discriminable colours (equation (2.2)) and subsequent use of the relation of the noise to the quantum catch (equation (B 3)) with quantum catch expressed as in equation (B 7) gives

$$N = \frac{1}{C} T^{n/2} G \prod_{i=1}^{i=n} \sqrt{k_i}. \tag{B 8}$$

The ‘shape factor’, G , depends on the shape of the object-colour solid and is given by

$$G = \int_V \frac{1}{\prod_{i=1}^{i=n} \sqrt{x_i + \omega_i^2 T k_i x_i^2}} \prod_{i=1}^{i=n} dx_i, \tag{B 9}$$

where integration is performed over the volume of the object-colour solid with the point ‘white’ scaled to one. In the case of the quantum noise limited scenario, G does not depend on illuminant intensity, T :

$$G = \int_V \frac{1}{\prod_{i=1}^{i=n} \sqrt{x_i}} \prod_{i=1}^{i=n} dx_i. \tag{B 10}$$

Consequently, in the quantum noise limited scenario the number of discriminable colours is proportional to $T^{n/2}$.

Let N and N^0 be the numbers of discriminable colours

for eyes with and without coloured oil droplets, respectively. Then, the benefit resulting from oil droplets can be expressed as

$$r = N/N^0. \tag{B 11}$$

Substitution of equation (B 8) into equation (B 11) gives

$$r = b/d, \tag{B 12}$$

where

$$b = G/G^0 \tag{B 13}$$

and

$$d = \prod_{i=1}^{i=n} \sqrt{\frac{k_i^0}{k_i}}, \tag{B 14}$$

where the index 0 corresponds to the eye without coloured oil droplets. The numerator b describes the benefit resulting from the change of the shape of the object-colour solid, while the denominator d describes the drawback resulting from the reduction in the quantum catch. To understand how the benefit depends on the light intensity, T , consider equation (B 9). The shape factor, G , decreases with increasing T , and the higher the quantum efficiencies, k_i , the faster the decline of G . Because oil droplets decrease quantum efficiencies, the benefit increases with increasing T , for any values of Weber fractions, ω_i . Note that in the case of quantum noise limited scenario the benefit is independent of light intensity (see equation (B 10)).

APPENDIX C: ABSOLUTE SENSITIVITY OF CONE MECHANISMS AND RELATION OF CONE QUANTUM CATCH TO THE INTENSITY OF DAYLIGHT

The light intensity, T , is measured in photons absorbed per receptive field and integration time (see Appendix B). To convert T into conventional units, we need to estimate the absolute spectral sensitivity of cones, $R_i(\lambda)$. Simple geometric considerations (Land 1981) led to the following formula:

$$R_i(\lambda) = \nu\tau(\pi/4)^2 \Delta\rho^2 D^2 O(\lambda)A_i(\lambda) [1 - \exp(-\mu_i(\lambda) l)], \tag{C 1}$$

where $O(\lambda)$ and $A_i(\lambda)$ are transmittances of the ocular media and an oil droplet of type i , respectively, $\mu_i(\lambda)$ is the optical density of the visual pigment of type i , l is the length of the outer segment, ν is the number of cones per receptive field, τ is the summation time, $\Delta\rho$ is the acceptance angle of a cone and D is the pupil diameter. In the case of the short outer segments of diurnal birds $R_i(\lambda) \sim O(\lambda)A_i(\lambda)\mu_i(\lambda)$. The parameters determining the absolute sensitivity of cones vary among species, but estimates can be made using the data available in the literature. At its maximum the optical density of cones, μ_{\max} , is $0.015 \mu\text{m}^{-1}$ (Bowmaker & Knowles 1977), the length of the outer segments of single cones in birds, l , is $16 \mu\text{m}$ (Hart 2001), pupil diameter, D , is 2 mm and integration time, τ , is 14 ms (flicker fusion frequency of 70 Hz ; Jarvis *et al.* 2002); acceptance angle can be estimated as $\Delta\rho = df/f$, where the diameter of the receptor, d , is $3.8 \mu\text{m}$ (Hart 2002) and the distance to the nodal point, f , is 5 mm

(Martin 1986), hence $\Delta\rho = 7.6 \times 10^{-4}$ rad (0.044°). Assuming $A_i(\lambda) = 1$, $O(\lambda) = 1$ and $\nu = 1$, we estimate from equation (C 1) the peak sensitivity: $R_{\max} = 4.3 \times 10^{-15}$ m² sr s. On a bright sunny day the irradiance at 560 nm is 174 $\mu\text{W cm}^{-2} \text{nm}^{-1}$ (Dixon 1978); in quantum units this value corresponds to a radiance of 7.8×10^{17} photons m⁻² sr⁻¹ s⁻¹ nm⁻¹. Using equation (2.1) I calculate the quantum catch of an L cone without an oil droplet viewing an ideal white surface. By definition, T is equal to this value (see Appendix B). On a bright sunny day (D65 illumination) T calculated for the eye of a peacock (figure 1) is equal to 4.5×10^5 photons (variations in the sensitivity of the L cone affect T only slightly). Illumination during twilight can be decreased by three orders of magnitude (Dusenbery 1992). Thus, during the day T may vary from approximately 5×10^5 to 5×10^2 .

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