PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Receptor noise as a determinant of colour thresholds

M. Vorobyev and D. Osorio

Proc. R. Soc. Lond. B 1998 **265**, doi: 10.1098/rspb.1998.0302, published 7 March 1998

The Royal Society

Receptor noise as a determinant of colour thresholds

Misha Vorobyev[1]* **and D. Osorio**[2]

[1]*Institut für Neurobiologie, Freie Universität Berlin, Königin-Luise-Strasse 28–30, 14195 Berlin, Germany*
[2]*School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK*

Inferences about mechanisms at one particular stage of a visual pathway may be made from psychophysical thresholds only if the noise at the stage in question dominates that in the others. Spectral sensitivities, measured under bright conditions, for di-, tri-, and tetrachromatic eyes from a range of animals can be modelled by assuming that thresholds are set by colour opponency mechanisms whose performance is limited by photoreceptor noise, the achromatic signal being disregarded. Noise in the opponency channels themselves is therefore not statistically independent, and it is not possible to infer anything more about the channels from psychophysical thresholds. As well as giving insight into mechanisms of vision, the model predicts the performance of colour vision in animals where physiological and anatomical data on the eye are available, but there are no direct measurements of perceptual thresholds. The model, therefore, is widely applicable to comparative studies of eye design and visual ecology.

Keywords: colour vision; colour thresholds; spectral sensitivity; receptor noise; colour opponency

1. INTRODUCTION

Perception can be understood as multistage processes, with receptor signals transformed by a sequence of neural mechanisms. In human colour vision the role of receptor mechanisms, described by the Young–Helmholtz theory of trichromacy, has traditionally been contrasted with colour opponency models, which recognize two cardinal axes in perceptual space represented by the yellow–blue and red–green mechanisms, as well as a black–white achromatic axis (Jameson & Hurvich 1955; Wyszecki & Stiles 1982). These theories are not mutually exclusive, but are thought to apply to different stages of the visual pathway. Trichromacy was vindicated by the discovery of three cone types whose spectral sensitivities are predicted by psychophysical methods (figure 1*a*). By comparison, the neural substrate for the psychophysically determined opponency mechanisms is less certain. Primate retinal ganglion cells have colour opponent responses (Lee *et al*. 1989), but their spectral sensitivities do not match those of psychophysical opponent channels (Jameson & Hurvich 1955; Wyszecki & Stiles 1982). Likewise, Webster & Mollon (1991) found that selective adaptation by stimulation along specific axes in colour space causes a loss of sensitivity along the axis of adaptation, which could not be attributed to adaptation of the two independent colour opponency mechanisms. Rather than two opponency channels, Webster & Mollon (1991) infer that there are many.

Here we present evidence that psychophysical thresholds under a fixed adapting stimulus may in fact show nothing about opponency mechanisms. These thresholds are set by noise which arises in receptors and at subsequent neural stages; but where one noise source is dominant, thresholds are set by the mechanism in which it originates. Thus, when thresholds are used to investigate a given mechanism, a key assumption is that noise in this mechanism is dominant. In colour vision, analysis of discrimination thresholds has been based on models which assume performance is limited either by receptor (Helmholtz 1896; Stiles 1946; Trabka 1968), or alternatively by post-receptoral stages (Sperling & Harwerth 1971; Guth *et al*. 1980; Foster & Snelgar 1983; Yeh *et al*. 1993; Sankeralli & Mullen 1996; Cole *et al*. 1993), and only rarely by both (Vos & Walraven 1972).

Predictions based on receptor properties disagree with experimental results (Boynton *et al*. 1964); for example, they do not predict the dips in human threshold spectral sensitivity around 490 nm and 575 nm (Sperling & Harwerth 1971). In contrast, models assuming that colour is coded by opponent chromatic mechanisms and by an achromatic mechanism (Jameson & Hurvich 1955) explain a variety of psychophysical data (Sperling & Harwerth 1971; Guth *et al*. 1980; Yeh *et al*. 1993; Sankeralli & Mullen 1996; Cole *et al*. 1993).

Opponency models have been used to establish receptor inputs to opponent and non-opponent mechanisms for man (Sperling & Harwerth 1971; Sankeralli & Mullen 1996; Cole *et al*. 1993), and for animals (Sperling & Harwerth 1971; Nuboer & Moed 1983; Backhaus 1991). As these models assume that noise in the opponency mechanisms is statistically independent, the probability of detection of a light is given by the probability of its detection by a single post-receptoral mechanism (Sankeralli & Mullen 1996; Cole *et al*. 1993; Wyszecki & Stiles 1982). In the simplest case, the stimulus is assumed to be detected by the most sensitive mechanism, and the threshold spectral sensitivity is given by the 'upper envelope' of the sensitivities of the separate mechanisms (Stiles 1959; Sperling & Harwerth 1971).

*Author for correspondence (vorobyev@zedat.fu-berlin.de).

Received 19 November 1997 *Accepted* 12 December 1997

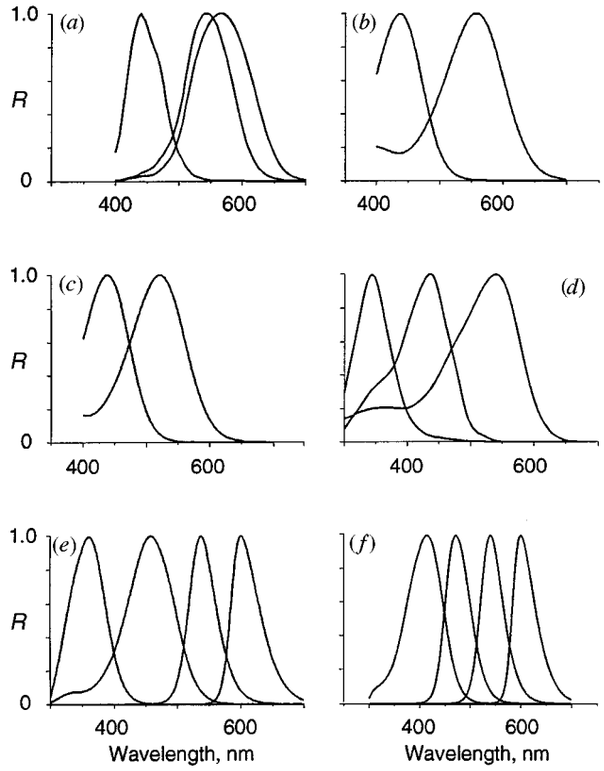

Figure 1. Receptor spectral sensitivities, R, as a function of wavelength, λ, (for details see Appendix 2): (*a*) man (Smith & Pokorny 1972); (*b*) tree shrew (*Tupaia belangeri*; Petry & Harosi 1990); (*c*) ground squirrel (*Spermophilus beecheyi*; Jacobs *et al.* 1985); (*d*) honeybee (*Apis mellifera*; Menzel & Backhaus 1991); (*e*) Pekin robin (*Leiothrix lutea*; Maier & Bowmaker 1993); and (*f*) pigeon (*Columba livia*; Bowmaker *et al.* 1997).

But, as we have observed, if the thresholds are attributable to receptor noise and a single receptor type contributes to more than one opponency mechanism, their noise is generally not independent, and perceptual thresholds cannot characterize post-receptoral mechanisms. We postulate that noise originates in the receptors and that receptor signals are encoded by colour opponency mechanisms, with the achromatic signal being disregarded; beyond this, opponency mechanisms are unspecified. Our model differs from the classical ones (Helmholtz 1896; Stiles 1946; Trabka 1968) because these early receptor noise-limited models were based on the assumption that colour discrimination is mediated by both chromatic and achromatic channels; and the model here is a limiting case of a more general model, accounting for all types of receptor interactions (Brandt & Vorobyev 1997). For natural images, most stimulus power is in the achromatic dimension, so it is perhaps surprising that the achromatic signal is ignored; but in bright illumination for static targets subtending a large visual angle, sensitivity to the achromatic component of colour is indeed low, both for humans (King-Smith & Carden 1976; Thornton & Pugh 1983), and for honeybees (Backhaus 1991; Brandt & Vorobyev 1997; Giurfa *et al.* 1997). The model does not predict thresholds where luminance mechanisms are important, as for small or moving targets, or in dim conditions.

Given the inadequacy of pure receptor models, this receptor noise-limited colour opponent model is the simplest that is physiologically plausible. For an eye with n spectral receptor types, the model requires n parameters, which describe the noise level in n colour channels. Receptor spectral sensitivities can be measured electrophysiologically or modelled from spectrophotometric data, while relative receptor noise levels are estimated from counts of the numbers of spectral receptor types or electrophysiologically. Given these data, the model has no free parameters, and to test it we compare its predictions to psychophysical thresholds from eyes with two, three, or four spectral classes of photoreceptors.

The data modelled are spectral sensitivities for the light adapted eye—that is, the discriminability of minimally saturated colours from a white background. After the pioneering work of Stiles & Crawford (1933), the spectral sensitivity became the most common technique for studying visual thresholds in man and animals. These data are used because they are the most widely available, but provided that the same mechanisms limit discrimination of other spectra, e.g. of the lights reflected from natural objects, the model can predict whether any two spectra are discriminable. This is useful because for many animals there is little or no data on psychophysical thresholds.

2. MODEL

Models which describe sensitivity to small differences by ellipsoids of colour mismatches are useful for predicting contours of equal discriminability in a perceptual space (MacAdam 1942; Poirson & Wandell 1990; Brandt & Vorobyev 1997). Ellipsoid models are valid if the thresholds are small compared to nonlinearities in signal processing, or when discrimination is limited by noise in receptors and in opponency channels. Generally, ellipsoidal contours of equal discriminability are described by 3, 6 or 10 parameters for dichromatic, trichromatic or tetrachromatic vision, respectively (Wyszecki & Stiles 1982), i.e. the number of parameters exceeds the number of receptor types. The values of these parameters depend on noise in receptors, noise added in opponent mechanisms, and on the receptor inputs to opponency mechanisms. The number of parameters can be reduced, if specific assumptions about the colour coding or the factors limiting discriminability are made (Brandt & Vorobyev 1997). The ellipsoid model used to evaluate thresholds here assumes that noise in the n receptor channels sets thresholds, and has just n parameters.

This model is based on three assumptions whose mathematical formulation is given using tensor algebra (Appendix 1).

(1) For a visual system with n receptor channels, colour is coded by $n-1$ unspecified colour opponent mechanisms; the achromatic signal is disregarded.
(2) Colour opponent mechanisms give zero signal for stimuli that differ from the background in intensity only.
(3) Thresholds are set by receptor noise, and not by opponent mechanisms.

These assumptions pose constraints on the conditions where the model may be used: (i) large static stimuli must be presented under bright illumination (conditions which suppress the contribution of an achromatic channel); and (ii) the background must be an achromatic (colour opponent mechanisms give zero signal). Since we do not model chromatic adaptation, we do not describe thresholds for the stimuli presented on chromatic fields, for example, the sensitivity of Stiles's π mechanisms (Stiles 1959). The lack of generality is a consequence of the absence of adjustable parameters.

A colour stimulus is defined by receptor quantum catches:

$$q_i = k_i \int_\lambda R_i(\lambda) I(\lambda) \mathrm{d}\lambda, \tag{1}$$

where $i = 1,2, \ldots n$; q_i is the quantum catch of receptor i; λ is the wavelength; $R_i(\lambda)$ is the spectral sensitivity of receptor i; $I(\lambda)$ is the spectrum of light entering the eye; k_i is an arbitrary scaling factor; and integration is over the visible spectrum. For the sake of simplicity we set k_i so that the quantum catches for the background are equal to unity, giving a receptor contrast space (Cole *et al.* 1993), i.e.

$$k_i = 1 \Big/ \int_\lambda R_i(\lambda) I^{\mathrm{b}}(\lambda) \mathrm{d}\lambda, \tag{2}$$

where $I^{\mathrm{b}}(\lambda)$ is the background spectrum.

Stimuli are indistinguishable if the 'distance' between them in receptor space is less than a 'threshold distance', ΔS^{t}. The value of ΔS^{t} depends on adopted threshold criterion, and often corresponds to 75% correct choices. Let Δq_i be the difference in the quantum catch between the threshold stimuli, and e_i be the standard deviation of the noise in the receptor channel i. Then, for stimuli which are close to the background, the following equations are valid (see derivation in Appendix 1) for dichromatic vision,

$$(\Delta S^{\mathrm{t}})^2 = \frac{(\Delta q_1 - \Delta q_2)^2}{e_1^2 + e_2^2} \tag{3}$$

for trichromatic vision,

$$(\Delta S^{\mathrm{t}})^2 = \frac{e_1^2(\Delta q_3 - \Delta q_2)^2 + e_2^2(\Delta q_3 - \Delta q_1)^2 + e_3^2(\Delta q_1 - q_2)^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2} \tag{4}$$

and for tetrachromatic vision,

$$\begin{aligned}(\Delta S^{\mathrm{t}})^2 = {} & ((e_1 e_2)^2(\Delta q_4 - \Delta q_3)^2 + (e_1 e_3)^2(\Delta q_4 - \Delta q_2)^2 + \\ & (e_1 e_4)^2(\Delta q_3 - \Delta q_2)^2 + (e_2 e_3)^2(\Delta q_4 - \Delta q_1)^2 + \\ & (e_2 e_4)^2(\Delta q_3 - \Delta q_1)^2 + (e_3 e_4)^2(\Delta q_2 - \Delta q_1)^2) / \\ & ((e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2).\end{aligned} \tag{5}$$

The spectral sensitivity is the inverse of threshold intensity, $I^{\mathrm{t}}(\lambda)$, i.e. of the minimum intensity of monochromatic light of wavelength, λ, detectable over an adapting background. The difference in the quantum catch between background and stimulus is given (see equation (1)) by

$$\Delta q_i = k_i R_i(\lambda) I^{\mathrm{t}}(\lambda). \tag{6}$$

Substitution of equation (6) into equations (3)–(5) gives the expressions for threshold spectral sensitivity as a function of wavelength. Since the threshold intensity is defined relative to the background, the shape of the spectral sensitivity curve is dependent upon the background spectrum. For example, low illumination of the background in the UV part of the spectrum gives high sensitivity to UV light. To model spectral sensitivity one needs to know the background spectrum, from which the scaling factors, k_i, are calculated (see equation (2)), the receptor spectral sensitivities, $R_i(\lambda)$, and the standard deviations of the noise in the receptor channels, e_i. While spectral sensitivities are known from electrophysiological and spectrophotometric studies (see figure 1), there are few direct measurements of noise in vertebrate cones.

(a) *Estimation of receptor noise*

To estimate the noise in receptor channels (e_i in equations (3)–(5)), we use the following model. Let ν_i be the standard deviation of the noise in a single receptor cell of type i, and η_i be the number of the cells of type i within the retinal integration area (e.g. a ganglion cell receptive field). Averaging over η_i cells improves the signal to noise ratio as the square root of η_i. Thus the standard deviation of the noise in a receptor mechanism is given by

$$e_i = \nu_i / \sqrt{\eta_i}. \tag{7}$$

Where noise in receptor cells is not known we assume that noise in any single receptor cell is independent of its spectral type, with differences between receptor mechanisms being attributable to differences in their density in the retinal array. Estimates of these densities are obtained from published sources (Appendix 2).

3. RESULTS

Predictions of the model (figures 2–4, solid curves) are compared with threshold spectral sensitivities of six different animals (figures 2–4, symbols). While the model does not have free parameters, and cannot be adjusted, measurements of visual thresholds vary considerably (Wyszecki & Stiles 1982). These variations can be partly attributed to variability of cone densities and of receptor spectral sensitivities *in vivo* (Ruddock 1963), and make it impossible for a unique quantitative model to fit all data. Another source of variability is differences in experimental conditions. For example, goldfish use predominantly chromatic cues on an unilluminated stimulus, but achromatic cues on an illuminated stimulus (Neumeyer *et al.* 1991). Most important, however, are the effects of mean light level, and here we distinguish between bright conditions, which appear to favour colour opponency, from dim conditions which favour non-opponent mechanisms.

To model threshold sensitivities we use equations (3)–(6). The necessary data, namely, the spectrum of the background, receptor spectral sensitivity (figure 1), and receptor noise or relative cone numbers were taken from published sources (Appendix 2).

(a) *Dichromatic vision*

Primates apart, mammals are cone dichromats, as are many colour-deficient humans. A dichromat's spectral sensitivity is given by subtraction of receptor signals (see equation (3)). Consequently, the model predicts that sensitivity approaches zero for a spectral light corresponding to

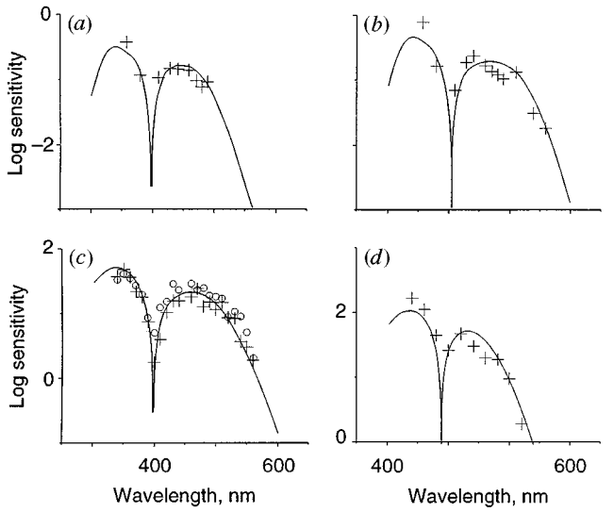

Figure 2. Threshold spectral sensitivity of dichromats as a function of wavelength, λ, (for details see Appendix 2). Sensitivity is expressed in inverse quantum units. Symbols indicate experimental data, the solid line shows the results of the model calculations. Different symbols (crosses or circles) within the same plot indicate different subjects. Curves are shifted on the sensitivity axes to match the experimental data. (*a*) Protanopic human observer (Miyahara *et al*. 1996); (*b*) deuteranopic observer (Miyahara *et al*. 1996); (*c*) tree shrew (*Tupaia belangeri*; Jacobs & Neitz 1986); and (*d*) ground squirrel (*Spermophilus beecheyi*; Jacobs 1990).

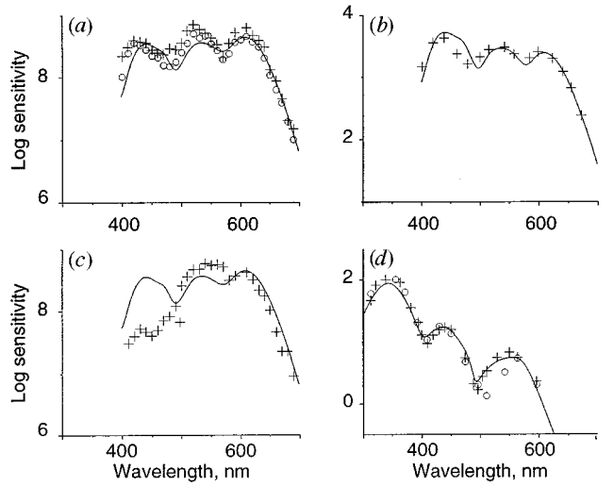

Figure 3. Threshold spectral sensitivity of trichromats (see legend to figure 2). Human observers: (*a*) data of Sperling & Harwerth (1971) for bright illumination; (*b*) data of King-Smith & Carden (1976); (*c*) Sperling & Harwerth's (1971) data for dim illumination. (*d*) Honeybee (*Apis mellifera*; von Helversen 1972).

the dichromatic confusion point, where the ratio of cone excitations equals that of the adapting light. From equation (3) it follows that spectral sensitivity does not depend on the relative noise levels in the two receptor mechanisms.

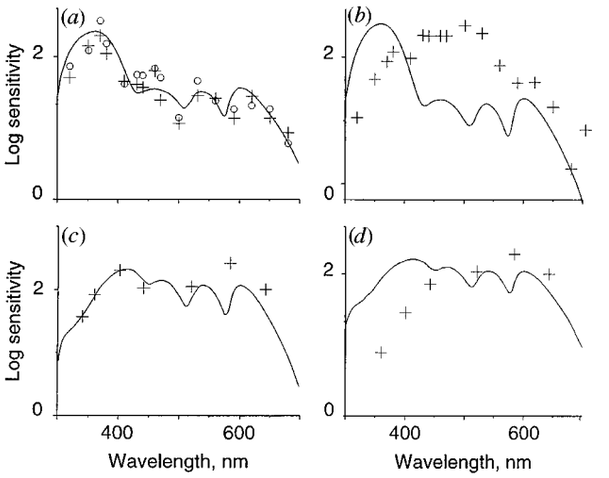

Figure 4. Threshold spectral sensitivities of tetrachromatic birds (see legend to figure 2). Pekin robin (*Leiothrix lutea*; Maier 1992): (*a*) for bright illumination; (*b*) for dim illumination. Pigeon (*Columba livia*; Remy & Emmerton 1989): (*c*) yellow field; (*d*) red field.

Model predictions agree with data for protanopic and deuteranopic humans (figure 2*a*,*b*; Miyahara *et al*. 1996), tree shrews (*Tupaia belangeri*; figure 2*c*; Jacobs & Neitz 1986), and ground squirrels (*Spermophilus beecheyi;* figure 2*d*; Jacobs 1990), in bright illumination. Subtractive combination of receptor signals is known to predict spectral sensitivity of the ground squirrel (Jacobs 1990).

The model does not always explain spectral sensitivities for dichromatic animals. Rabbits' (*Oryctolagus cuniculus*) spectral sensitivity is always non-zero, even in bright illumination (Nuboer & Moed 1983), which is indicative of input from an achromatic channel. Rabbits are crepuscular, and may therefore have a 'mesopic' eye which always uses the achromatic signal.

(b) *Trichromatic vision*

Honeybees, like many primates, are trichromats. Colour vision within these diverse groups is understood in particular detail.

(i) *Man*

Model predictions accord reasonably with measurements made by Sperling & Harwerth (1971), and by King-Smith & Carden (1976) for high intensities (figure 3*a*,*b*). These two studies used different illumination spectra and the model predicts the observed differences in spectral sensitivity. In particular, Sperling & Harwerth's (1971) observers were relatively insensitive to short wavelengths. Although the model predicts the general shape of the curve, the dips in the theoretical curve are shallower than those that actually occur (figure 3*a*), which can be attributed to the noise added at opponency channels. The model does not describe human spectral sensitivities in dim illumination, probably because an achromatic mechanism contributes (figure 3*c*).

(ii) *Honeybee* (Apis mellifera)

Model predictions agree perfectly with the spectral sensitivity of one of the individual bees tested by von

Helversen (1972; figure 3*d*, crosses), while for another the data and model differ slightly (figure 3*d*, circles). Whereas the model does not predict spectral sensitivities of vertebrates, in dim light it works for bees even though they were tested at rather low intensities (von Helversen 1972). It is known that for the task in question—a test of colour memory for large targets—bees do not use the achromatic signal, even in dim light (Backhaus 1991; Brandt & Vorobyev 1997; Giurfa *et al.* 1997; Vorobyev & Brandt 1997).

(c) *Tetrachromatic vision*

Many birds have four types of cone photoreceptor pigment. In single cones these are associated with coloured oil droplets (figure 1*d*,*e*; Bowmaker *et al.* 1997). Birds differ in the peak position of the shortest wavelength pigment; in some, like the Pekin robin, it peaks in the UV (355 nm), while in others, like the pigeon, it peaks in the violet (409 nm) (Bowmaker *et al.* 1997). There is less interspecific variation in the tuning of photopigments in the remaining three cones. Electroretinogram measurements suggest that pigeons have a fifth receptor, peaking in the UV (Hzn *et al.* 1994).

(i) *Pekin robin* (Leiothrix lutea)

Model predictions agree with the spectral sensitivities of two birds tested in bright illumination (Maier 1992) (figure 4*a*). Given the scatter in the behavioural data it is difficult to say if deviations from the model are systematic. One bird was also tested in dim illumination where, as for humans, the model does not work (figure 4*b*).

(ii) *Pigeon* (Columba livia)

In pigeons the relative numbers of the different photoreceptor types varies across the retina. The frontally projecting red field contains predominately red oil droplets, characteristic of single cones containing a 567 nm pigment. The yellow, laterally projecting field, contains a higher number of yellow oil droplets characteristic of cones with a 507 nm pigment (Bowmaker *et al.* 1997). Remy & Emmerton (1989) tested pigeon yellow and red fields separately. Birds were light adapted but tested on a dark field—a condition which makes it difficult to predict adaptation state. A tetrachromatic model predicts mean spectral sensitivity in the yellow field quite well (figure 4*c*), especially at short wavelengths, and there is no evidence for a fifth, UV, receptor (Hzn *et al.* 1994). Deviations from the model predictions in the long wavelength part of the spectrum are consistent with a contribution from the achromatic channel, which probably also accounts for the unimodal sensitivity in the red field (figure 4*d*) where the model fails.

4. DISCUSSION

Given the uncertainty of noise estimates (see Appendix 2), predictions of the model agree well with psychophysical data for diurnal animals in bright illumination. This indicates that photopic detection and discrimination (at least of large static targets) is based on predominantly colour opponent channels, with luminance being disregarded. For the vertebrates, predictions of the model disagree with experimental data for low illumination (figures 3*c*, 4*b*), probably because the achromatic mechanism becomes important.

Where the model predicts experimental data, the implication is that photoreceptor noise limits discrimination, so that threshold sensitivities give no information about the receptor inputs to opponency channels. Models which assume that receptor noise is negligible compared to that in neural mechanisms (Sperling & Harwerth 1971; Guth *et al.* 1980; Backhaus 1991; Yeh *et al.* 1993; Sankeralli & Mullen 1996; Cole *et al.* 1993), also account for psychophysical thresholds. However, the receptor noise-limited model has the virtue of simplicity, making minimal assumptions about post-receptoral processing. Moreover, neural noise-limited models contain free parameters, so that their assumption that receptor noise is negligible cannot be justified simply by the fact that their predictions fit experimental data well. Deviations from the receptor noise model could indicate that noise generated post-receptorally sets thresholds. However, the principal deviations are probably attributable to the intrusion of achromatic mechanisms, and again say nothing about opponency mechanisms.

The conclusion that receptor noise limits the accuracy of colour vision in photopic conditions is consistent with studies which indicate that such noise sets thresholds for other aspects of vision. Examples of receptor noise-limited thresholds reported include the foveal achromatic interval, and threshold colour-naming fluctuations in man (Massof 1977), and also motion coding neurons in insects (de Ruyter *et al.* 1995) and detection of lights by frogs (Aho *et al.* 1993). Finally, the simplicity of the receptor noise-limited colour opponent model and, its ability to predict the threshold spectral sensitivity where receptor spectral tuning and relative numbers are known, mean that we are able to predict colour discrimination in any animal where spectral sensitivities and relative numbers of photoreceptors are known (Osorio & Vorobyev 1996; Vorobyev & Brandt 1997).

We thank Jacky Emmerton for information on conditions in which pigeons were tested, Robert Brandt for discussion and illumination spectra, and Randolf Menzel for support. We also thank the referees for their advice. M.V. was supported by the Deutsche Forschungsgemeinschaft (Me 365/20-1).

APPENDIX 1.

For an eye with n spectral receptor types, colour is considered as a vector in an n-dimensional receptor space, with receptor quantum catches placed along the coordinate axes (see equation (1)). Let X be an arbitrary set of axes in receptor space, which are related to receptor coordinates either by linear or nonlinear transformation. We refer to a vector in these coordinates as $\boldsymbol{x}$, whilst $\boldsymbol{q}$ refers to a vector in receptor contrast coordinates, Q. The ellipsoid of colour mismatches in the coordinate system X is given by a variance–covariance matrix of colour mismatches, $\boldsymbol{R}$, with the elements

$$R_{\alpha\beta} = \langle \delta x_\alpha \delta x_\beta \rangle, \tag{A1}$$

where random variables, δx_α and δx_β, are the mismatches in the direction α and β, respectively; $\langle \ldots \rangle$ denotes the

average (Wyszecki & Stiles 1982). Note that diagonal elements, $R_{\alpha\alpha}$ are equal to dispersions of mismatches. An alternative method of describing the ellipsoid is by a metric tensor in the receptor space, $\boldsymbol{g}$, which is defined as the inverse of $\boldsymbol{R}$, i.e.

$$\boldsymbol{g} = \boldsymbol{R}^{-1}. \tag{A2}$$

The probability of discrimination is defined by the separation of the stimuli relative to the standard deviations of mismatch, and the stimuli are at threshold (i.e. distinguished with a given threshold probability), if the relative separation between them is equal to a 'threshold distance', ΔS^{t}. To understand how thresholds are related to the metric tensor $\boldsymbol{g}$ consider a one-dimensional case. The square of standard deviation (dispersion) of the mismatch in the direction '1' is given by R_{11}, and in the one-dimensional case equation (A2) can be rewritten as $g_{11}=1/R_{11}$. Thus, the stimuli are at threshold if

$$(\Delta x_1)^2/R_{11} = \Delta x_1 g_{11} \Delta x_1 = (\Delta S^{\mathrm{t}})^2. \tag{A3}$$

Generalization of the equation (A3) to n dimensions gives

$$\Delta \boldsymbol{x} \bullet \boldsymbol{g} \Delta \boldsymbol{x} = (\Delta S^{\mathrm{t}})^2. \tag{A4}$$

where $\{\bullet\}$ denotes 'inner product'.

Since a linear approximation is valid when stimuli are similar, a linear transformation, $\boldsymbol{F}$, relates threshold vector coordinates, $\Delta \boldsymbol{x}$, to threshold receptor coordinates, $\Delta \boldsymbol{q}$, by

$$\Delta \boldsymbol{x} = \boldsymbol{F} \Delta \boldsymbol{q}. \tag{A5}$$

Note that if the assumption of local linearity fails, contours of equal discriminability cannot be described by ellipsoids. Let $\boldsymbol{R}^q$ be the covariance matrix of colour mismatches in the receptor contrast coordinates, i.e. the elements of this matrix are given by $\boldsymbol{R}^q_{ik} = \langle \delta q_i \delta q_k \rangle$, then the covariance matrix in coordinates X can be expressed as (see equations (A1) and (A5)):

$$\boldsymbol{R} = \boldsymbol{F} \boldsymbol{R}^q \boldsymbol{F}^T, \tag{A6}$$

where index T denotes the transpose. Equation (A6) is the general form of transformation of tensors with transformation of coordinates. Substitution of equations (A2, A5, A6) into equation (A4) gives an expression for thresholds in the receptor contrast space:

$$(\boldsymbol{F} \Delta \boldsymbol{q}) \bullet ((\boldsymbol{F} \boldsymbol{R}^q \boldsymbol{F}^T)^{-1} \boldsymbol{F} \Delta \boldsymbol{q}) = (\Delta S^{\mathrm{t}})^2. \tag{A7}$$

This equation is equivalent to equation (A4) and is valid for any kind of linear transformation $\boldsymbol{F}$, if $(\boldsymbol{F} \boldsymbol{R}^q \boldsymbol{F}^T)^{-1}$ exists.

Now let X be the set of axes which correspond to neural signals. Our first assumption states that for a visual system with n receptor types, colour is coded by $n-1$ opponent mechanisms. Thus, transformation $\boldsymbol{F}$ is given by a rectangular $(n-1) \times n$ matrix.

Assumption 2 states that background gives zero signal. Since the receptor coordinates are defined so that background corresponds to the unity vector, the components of the tensor $\boldsymbol{F}$ are constrained by

$$\sum_{i=1}^{i=n} F_{\alpha i} = 0, \tag{A8}$$

where index i corresponds to n receptor channels and α to $(n-1)$ opponency mechanisms. If photoreceptor noise limits visual performance (assumption 3), $\boldsymbol{R}^q$ is simply a diagonal matrix, because noise in different receptors is independent. Its non-zero diagonal elements are, by definition, equal to the square of the standard deviation of the noise in the receptor channels, e_i. Thus,

$$R^q_{ik} = e_i^2 \text{ if } i = k; \text{ and } R^q_{ik} = 0 \text{ if } i \neq k. \tag{A9}$$

To obtain the expressions relating thresholds to receptor noise for di-, tri-, and tetrachromatic vision (equations (3),(4),(5)) we rewrite the general expression (equation (A7)), taking into account the constraints on the neural processing (equation (A8)), and on the factors limiting discriminability (equation (A9)). This leads to the expressions which do not contain the components of the tensor $\boldsymbol{F}$. This is consistent with the obvious statement that if discrimination is limited by photoreceptor noise, so discriminability of colours does not depend on how the receptor signals combine in opponent interactions. To illustrate the procedure for evaluation of thresholds (equations (3),(4),(5)) we consider the case of dichromatic vision (Osorio & Vorobyev 1996).

For dichromatic vision $n=2$ and a one colour opponent mechanism is possible: consequently, $\boldsymbol{F}$ has only one row (assumption 1). From equation (A8) it follows that matrix $\boldsymbol{F}$ has components $F_{11} = -F_{12} = F$ (assumption 2). Consequently,

$$\boldsymbol{F} \Delta \boldsymbol{q} = \Delta x = F(\Delta q_1 - \Delta q_2). \tag{A10}$$

From equation (A9) (assumption 3) it follows that

$$(\boldsymbol{F} \boldsymbol{R}^q \boldsymbol{F}^T)^{-1} = 1/(F^2(e_1^2 + e_2^2)). \tag{A11}$$

Substitution of equations (A10) and (A11) into equation (A7) gives the expression for thresholds (equation (3)). Similar, but lengthier calculations give the expressions for trichromatic (equation (4)) and tetrachromatic (equation (5)) vision.

APPENDIX 2. SOURCES OF DATA ON THRESHOLD SPECTRAL SENSITIVITIES

(a) *Man*

Receptor sensitivities (figure 1*a*) are from colour matching data by Smith & Pokorny (1972). The protanope was assumed to have short wavelength (S) and middle wavelength (M) cones; and the deuteranope was assumed to have S and long wavelength (L) cones. Noise in cone channels was calculated from the ratio of the cone numbers (equation (7)), which was assumed to be 1S:16M:32L (Walraven 1974). Receptor quantum catches corresponding to an achromatic background were calculated from the spectra of adapting lights, characterized by their correlated colour temperature. Colour-defective observers were tested at 4600 K (Miyahara *et al.* 1996); threshold spectral sensitivities of the protanope and the deuteranope (figure 2*a*,*b*) correspond to the sensitivities of observers R.R. and M.T. tested with 10° stimuli

(Miyahara *et al.* 1996, fig. 7). Trichromat observers of Sperling & Harwerth (1971) were tested at 5500 K; threshold sensitivities given in figure 3*a* (bright illumination) were obtained at a retinal illuminance of 104 Td (Sperling & Harwerth 1971, fig. 4); data for low illumination (figure 3*c*) correspond to the mean data for a dark adapted subject (Sperling & Harwerth 1971, figure 4, left panel). King-Smith & Carden (1976) used a background with a colour temperature of 3200 K; the sensitivity in figure 3*b* corresponds to a long and large test flash (200 ms, 1°; King-Smith & Carden 1976, figure 4, upper curve).

(b) *Dichromatic mammals: tree shrew* (Tupaia belangeri), *and ground squirrel* (Spermophilus beecheyi)

Receptor sensitivities (figure 1*a*,*b*) were modelled with standard cone pigment curves (Maximov 1988). The tree shrews' pigments peak at 435 nm and 555 nm (Petry & Harosi 1990), the ground squirrels' at 436 nm and 518 nm (Jacobs *et al.* 1985). Threshold data in figure 2*b*,*c* correspond to results obtained with light adapted animals with a background illuminant of 4800 K (Jacobs & Neitz 1986, fig. 3).

(c) *Honeybee* (Apis mellifera)

Receptor sensitivities are from single cell recordings (Menzel & Backhaus 1991). Photoreceptor noise is estimated from electrophysiological data (Peitsch 1992), giving e_i as $e_1 = 0.13$, $e_2 = 0.06$, and $e_3 = 0.12$ (Vorobyev & Brandt 1997), where indexes 1, 2, 3, correspond to receptors peaking at 344 nm, 436 nm and 544 nm, respectively. Receptors were assumed to be adapted to a background with uniform reflectance illuminated by fluorescent lamps (von Helversen 1972). Behavioural sensitivities are for the bees numbered 25 (figure 3*d*, crosses) and 15 (figure 3*d*, circles), of von Helversen's (1972) study.

(d) *Tetrachromatic birds: pigeon* (Columba livia) *and Pekin robin* (Leiothrix lutea)

Receptor spectral sensitivities are approximated by standard cone pigment curves (Maximov 1988), fitted to measured maxima, and combined with the absorption of the ocular media, and of corresponding cone oil droplets (Emmerton *et al.* 1980; Bowmaker *et al.* 1997; Maier & Bowmaker 1993; Maier 1994). We assumed single cones, but not double cones, contributed to discrimination (Maier & Bowmaker 1993). Pekin robin cone pigments peak at 355 nm (UV), 454 nm (S), 499 nm (M) and 568 nm (L), and pigeons' at 409 nm (UV), 453 nm (S), 507 nm (M) and 568 nm (L). In both eyes these are respectively combined with transparent, clear, yellow and red oil droplets (Maier & Bowmaker 1993; Bowmaker *et al.* 1997). Noise in cone channels is given by the ratio of the numbers of cones (equation (7)). We used the following ratios (UV:S:M:L)—Pekin robin, 1:2:2:4 (Maier & Bowmaker 1993), pigeon yellow field, 1:1:1:2 (Bowmaker *et al.* 1997). For Pekin robin the spectrum of an achromatic light was calculated from the spectrum of the halogen light source and the reflectance of the grey plastic (Maier 1992). Pigeons were assumed to be light adapted to daylight lamps (Remy & Emmerton 1989). Threshold data in figure 4*a*,*b* correspond to results obtained with the Pekin robin at 150 lux and at an illumination of less than 1 lux (Maier 1992, figs 5, 6), respectively. Mean threshold data for pigeons (Remy & Emmerton 1989, fig. 3) are shown in figure 4*b*,*c*.

REFERENCES

Aho, A. C., Donner, K. & Reuter, T. 1993 Retinal origins of the temperature effect on absolute visual sensitivity in frogs. *J. Physiol. Lond.* **463**, 501–521.

Backhaus, W. 1991 Color opponent coding in the visual-system of the honeybee. *Vision Res.* **31**, 1381–1397.

Bowmaker, J. K., Heath, L. A., Wilkie, S. E. & Hunt, D. M. 1997 Visual pigments and oil droplets from six classes of photoreceptor in the retina of birds. *Vision Res.* **37**, 2183–2194.

Boynton, R. M., Ikeda, M. & Stiles, W. C. 1964 Interactions among chromatic mechanisms as inferred from positive and negative increment thresholds. *Vision Res.* **4**, 87–90.

Brandt, R. & Vorobyev, M. 1997 Metric analysis of increment threshold spectral sensitivity in the honeybee. *Vision Res.* **37**, 425–439.

Cole, G. R., Hine, T. & McIlhagga, W. 1993 Detection mechanisms in L-cone, M-cone, and S-cone contrast space. *J. Opt. Soc. Am.* A **10**, 38–51.

De Reyuter, R., Steveninck, V. & Bialek, W. 1995 Reliability and statistical efficiency of a blowfly movement-sensitive neuron. *Phil. Trans. R. Soc. Lond.* B **348**, 321–340.

Emmerton, J., Schwemer, J., Muth, J. & Schlecht, P. 1980 Spectral transmission of the ocular media of the pigeon (*Columbia livia*). *Invest. Ophthal. Vis. Sci.* **19**, 1382–1387.

Foster, D. H. & Snelgar, R. S. 1983 Test and field spectral sensitivities of colour mechanisms obtained on small white backgrounds: action of unitary opponent-colour processes? *Vision Res.* **23**, 787–797.

Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. & Menzel, R. 1997 Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *J. Comp. Physiol.* A **180**, 235–243.

Guth, S. M., Massof, R. W. & Benzshawel, T. 1980 Vector model for normal and dichromatic color vision. *J. Opt. Soc. Am.* **70**, 197–212 .

Helmholtz, H. L. F. 1896 *Handbuch der Physiologischen Optik*, 2nd edn. Hamburg:Voss.

Hzn, J. J. V., Coemans, M. A. J. M. & Nuboer, G. F. W. 1994 The photopic sensitivity of the yellow field of the pigeons retina to ultraviolet-light. *Vision Res.* **34**, 1419–1425.

Jacobs, G. H. 1990 Duplicity theory and ground-squirrels—linkages between photoreceptors and visual function. *Vis. Neurosci.* **5**, 311–318.

Jacobs, G. H. & Neitz, J. 1986 Spectral mechanisms and color-vision in the tree shrew (*Tupaia belangeri*). *Vision Res.* **26**, 291–298.

Jacobs, G. H., Neitz, J. & Crognale, M. 1985 Spectral sensitivity of ground squirrel cones measured with ERG flicker photometry. *J. Comp. Physiol.* A **156**, 503–509.

Jameson, D. & Hurvich, L. M. 1955 Some quantitative aspects of an opponent-colors theory. I. Chromatic responses and spectral saturation. *J. Opt. Soc. Am.* **45**, 546–552 .

King-Smith, P. E & Carden, D. 1976 Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration. *J. Opt. Soc. Am.* **66**, 709–717.

Lee, B. B., Martin, P. R. & Valberg, A. 1989 Sensitivity of macaque retinal ganglion-cells to chromatic and luminance flicker. *J. Physiol. Lond.* **414**, 223–243.

MacAdam, L. 1942 Visual sensitivities to color differences in daylight. *J. Opt. Soc. Am.* **32**, 247–274.

Maier, E. J. 1992 Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *J. Comp. Physiol.* A **170**, 709–714.

Maier, E. J. 1994 Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. *Vision Res.* **34**, 1415–1418.

Maier, E. J. & Bowmaker, J. K. 1993 Colour vision in the passeriform bird, *Leiothrix lutea*: correlation of visual pigment absorbance and oil droplet transmission with spectral sensitivity. *J. Comp. Physiol.* A **172**, 295–301.

Massof, R. W. 1977 A quantum fluctuation model for foveal color thresholds. *Vision Res.* **17**, 565–570.

Maximov, V. V. 1988 An approximation of visual absorption spectra. *Sensornye Systemy* **2**, 3–8.

Menzel, R. & Backhaus, W. 1991 Color vision in insects. In *Vision and visual dysfunction. VI. Perception of color* (ed. P. Gouras), pp. 262–293. Houndmills, UK: Macmillan Press.

Miyahara, E., Pokorny, J. & Smith, V. C. 1996 Increment threshold and purity discrimination spectral sensitivities of x-chromosome-linked color-defective observers. *Vision Res.* **36**, 1597–1613.

Neumeyer, C., Wietsma, J. J. & Spekreijse, H. 1991 Separate processing of 'color' and 'brightness' in goldfish. *Vision Res.* **31**, 537–549.

Nuboer, J. F. W. & Moed, P. J. 1983 Increment-threshold spectral sensitivity in the rabbit. *J. Comp. Physiol.* **151**, 353–358.

Osorio, D. & Vorobyev, M. 1996 Color-vision as an adaptation to frugivory in primates. *Proc. R. Soc. Lond.* B **263**, 593–599.

Peitsch, D. 1992 *Contrast responses, signal to noise ratios and spectral sensitivities in photoreceptor cells of hymenopterans.* Ph.D. thesis, F.-U., Berlin.

Petry, H. M. & Harosi, F. I. 1990 Visual pigments of the tree shrew (*Tupaia belangeri*) and greater galago (*Galago crassicaudatus*)—a microspectrophotometric investigation. *Vision Res.* **30**, 839.

Poirson, A. B. & Wandell, B. A. 1990 The ellipsoidal representation of spectral sensitivity. *Vision Res.* **30**, 647–652.

Remy, M. & Emmerton, J. 1989 Behavioral spectral sensitivities of different retinal areas in pigeons. *Behav. Neurosci.* **103**, 170–177.

Ruddock, K. H. 1963 Evidence for macular pigmentation from colour matching data. *Vision Res.* **3**, 417–429.

Sankeralli, M. J. & Mullen, K. T. 1996 Estimation of the L-cone, M-cone, and S-cone weights of the postreceptoral detection mechanisms. *J. Opt. Soc. Am.* A **13**, 906–915.

Smith, V. C. & Pokorny, J. 1972 Spectral sensitivity of color blind observers and the cone photopigments. *Vision Res.* **12**, 2059–2071.

Sperling, H. G. & Harwerth, R. S. 1971 Red–green cone interactions in the increment-threshold spectral sensitivity of primates. *Science* **172**, 180–184.

Stiles, W. S. 1946 A modified Helmholtz line element in brightness–colour space. *Proc. Phys. Soc. Lond.* **58**, 41–51.

Stiles, W. S. 1959 Color vision: the approach through increment threshold sensitivity. *Proc. Natn. Acad. Sci. USA* **45**, 100–114.

Stiles, W. S. & Crawford, B. H. 1933 The liminal brightness increment as a function of wave-length for different conditions of the foveal and parafoveal retina. *Proc. R. Soc. Lond.* B **113**, 496–530.

Thornton, J. E. & Pugh, E. N. 1983 Red–green color opponency at detection threshold. *Science* **219**, 191–193.

Trabka, A. 1968 On Stiles' line element in brightness–color space and the color power of the blue. *Vision Res.* **8**, 113–134.

Von Helversen, O. 1972 Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. *J. Comp. Physiol.* **80**, 439–472.

Vorobyev, M. & Brandt, R. 1997 How do insect pollinators discriminate colours? *Israel J. Plant Sci.* **45**, 103–114.

Vos, J. & Walraven, P. L. 1972 An analytical description of the line element in the zone-fluctuating model of colour vision. I. Basic concepts. *Vision Res.* **12**, 1327–1344.

Walraven, P. L. 1974 A closer look at the tritanopic convergence point. *Vision Res.* **14**, 1339–1343.

Webster, M. A. & Mollon, J. D. 1991 Changes in colour appearance following post-receptoral adaptation. *Nature* **349**, 235–238.

Wyszecki, G. & Stiles, W. S. 1982 *Color science: concepts and methods, quantitative data and formulae*, 2nd edn. New York: Wiley.

Yeh, T., Pokorny, J. & Smith, V. C. 1993 Chromatic discrimination with variation in chromaticity and luminance—data and theory. *Vision Res.* **33**, 1835–1845.