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Special Issue: Unasked Questions

Understanding how neural responses contribute to the diversity of avian colour vision

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The past 20 years have seen a surge of interest in how animals perceive colour, setting the stage for a much more detailed examination of how colour perception differs among species, how a species' colour perception relates to its environment and how it all fits into the framework of animal communication. We need to address two major questions: first, how do general mechanisms of signal processing work within whole clades of animals, and second, how do these mechanisms modulate differences among related species within clades? The receptor noise-limited (RNL) model (Vorobyev & Osorio, 1998) has made a critical advance in the field. Relevant parameters of the model, including screening pigments in the eye, visual pigments and relative numbers of the different receptor cells, can be measured to predict how species detect objects in their environment, based on wavelength. Details of the opponent channels, however, which compare the outputs of the retinal receptors and can determine the signals sent to the brain, are unknown for most species and are not required by the model. Here, we unpack the RNL model, focusing on experiments in humans and birds, and explore the impact of including specific opponent channels in the model. Incorporating opponent channels into the RNL model could help us better understand the selective forces and coevolutionary processes that shape the visual system and determine visual adaptations. Present evidence shows that the RNL model works as a good first approximation and points to critical parameters we need to measure, such as noise in receptor cells.

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How an animal perceives colour depends on the properties of its visual system. Differences in the light environment, habitat and behaviour of different species could lead to very different colour vision systems. Despite this, species in large clades are thought to share quite similar perceptual systems (Cronin, Johnsen, Marshall, & Warrant, 2014; Land & Nilsson, 2012). Such a similarity is often considered to apply across birds, in which species most notably differ in the extent of their ultraviolet (UV) sensitivity (Bitton, Janisse, & Doucet, 2017; Hart & Hunt, 2007; Lind, Mitkus, Olsson, & Kelber, 2013a, 2013b). However, many possible differences in the visual system remain to be evaluated and may result in even close relatives differing in how they perceive the world. We know that many features of the processing of light in the eye and brain may affect perception, but we have only a rudimentary understanding of how these features differ among species and how they affect colour perception. Investigating any differences in visual systems across species will also contribute to understanding the diversity of colour in nature, and ultimately how signallers coevolve with receivers (Price, 2017).

A basic principle of colour processing is that outputs from different receptor cells are contrasted in the retina, a process termed opponency. This is by far best understood in humans and related primates. We are trichromats, with three types of retinal receptors mediating colour vision: the short wavelength (S, peak absorption at a wavelength of 420 nm), medium wavelength (M, 530 nm) and long wavelength (L, 560 nm) cone cells (summarized in Valberg, 2005; see Fig. 1, left). Processing involves comparing photon catches from the different cone (receptor) cells across a small area of the retina, termed the receptive field. The catch of photons by a given receptor class depends on both the spectrum of light impacting the receptor and the receptor's absorption

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spectrum. Subsequently, the catch may be transformed in various ways in the receptor itself and in the retina, to generate neural signals that are transmitted to the brain. These signals are the opponent channels. Humans process two opponent channels, written as $S-(M+L)$, which is a comparison of S cone output to summed M and L cone outputs (Shevell & Martin, 2017) and $L-M$ (a comparison of L to M). Here italicized letters are used to indicate the signals from each receptor summed across the receptive field. For example, a long-wavelength stimulus excites the L cones more than the M and S cones. This is translated in the retina into a low $S-(M+L)$, as well as high $L-M$ signal, and it is these two signals that the brain processes, leading to our perception of red.

In dichromats, which include most mammals apart from some primates, only a single opponent channel is possible, contrasting outputs from the two different receptor cell types. Beyond dichromats, a basic challenge in colour vision for the majority of species with more than two receptor types, including all bird species, is that we do not know how receptor signals are combined into opponent channels. We do, however, have some evidence from the turtle, *Trachemys scripta,* which has a very similar visual system to that of most birds (tetrachromats with four classes of receptor cells). In this species it appears opponency works in a very different way than it does in primates, with many possible channels each contrasting outputs from all receptor classes (Rocha, Saito, Silveira, De Souza, & Ventura, 2008). To circumvent the uncertainty about the specifics of the opponent channels, Vorobyev and Osorio (1998) developed an elegant and innovative model, now termed the receptor noise-limited (RNL) model. The model is regularly used to ask how readily a signal can be detected against the background, or how well two signals can be discriminated from each other, for a particular species. The strength of the RNL model is that it is rooted in the concept of opponency, even if the actual opponent mechanisms are unknown. The model, along with technological advances facilitating measurement of parameters important to the model, has led to a surge of interest in colour perception in nature (Olsson, Lind, Kelber, & Simmons, 2018). It has been used as the basis for asking how detection and discrimination vary as a species encounters different environments, where signals appear against a variety of background colours. It has also been used to ask how different species should differ in detection and discrimination abilities, as various parameters in the model are varied (Bitton et al., 2017; Lind, Henze, Kelber, & Osorio, 2017; Lind & Kelber, 2009).

In this paper, we assume that the opponency mechanism, while not known, is the same across all species of birds. We ask if our knowledge of that mechanism might change our inferences about discrimination and detection when compared to the standard RNL model, in which the opponent channels are unspecified. In other words, we ask if the details of the opponent channels change predictions about how colour perception could vary across species. To do this, we have three specific goals, as follows.

(1) To develop and explain the model from first principles, highlighting how it can be used for both detection and discrimination problems. We describe the assumptions of the model that make it robust to the actual opponent channels present, and how outputs from different channels are combined.

(2) To ask if experiments in humans, in which colour vision is relatively well understood, are consistent with the standard RNL model.

(3) To review some experiments in birds, in order to ask how explicit knowledge of opponent channels might alter our understanding of bird colour vision.

OPPONENCY AND THE RECEPTOR NOISE-LIMITED MODEL

The RNL model is not a model of colour vision, but of sensitivity to differences between an object and background (detection) and between two objects (discrimination), based on wavelength. This is an important consideration. Notably, wavelength differences may be placed into different categories by different species even if these species have similar thresholds (Caves, Green, Zipple, Peters, Johnsen, Nowicki, 2018), an issue we do not consider further in this paper. Furthermore, the RNL model is concerned primarily with detection and discrimination at threshold (the 'just noticeable difference'). How differences beyond threshold should be modelled remains a contentious issue (Kemp, Herberstein, Fleishman, Endler, Bennett, Dyer, 2015).

The RNL model assumes that all error associated with signal processing is confined to the receptor cells, before the opponent signals are computed, and that there are exactly $n-1$ opponent channels, where n is the number of different receptor types. Given several additional assumptions, which we

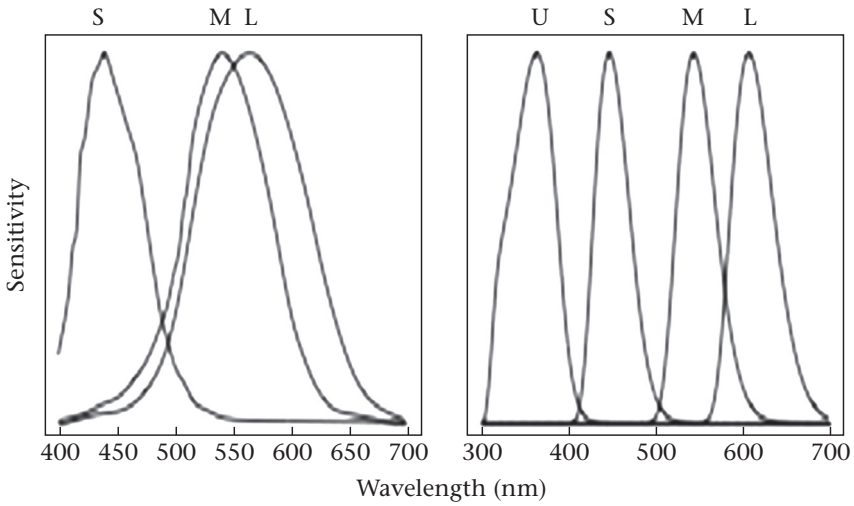

Figure 1. Estimated absorbance spectra for humans (from Stockman, Sharpe, Merbs, & Nathans, 2000) and zebra finches, *Taeniopygia guttata* (from Lind, 2016). Letters above peaks refer to the ultraviolet (U), short (S), medium (M) and long (L) wavelength-sensitive cones.

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describe below, Vorobyev and Osorio (1998) then showed that the specific channels used are not critical. Vorobyev and Osorio (1998) used their results to summarize the ability of an observer to discriminate an object, based on empirically measurable parameters, including the receptor absorption curves and the relative densities of the different kinds of receptors. Here, we restrict ourselves to observations in ample illumination (photopic vision). To develop the model from first principles, we consider three separate sections that respectively cover dichromats, trichromats and tetrachromats. In the first section we introduce the simplest detection system, where there are only two classes of receptor cells (dichromats). Next, we extend this to discrimination tasks. Then we consider trichromats and some salient results from humans. Finally, we turn to experiments on birds, which are tetrachromats. In the discussion, we consider the extent to which assumptions of the model are violated when we consider the specific opponent mechanisms, and how considering the actual bird opponent channels in the model might lead to us re-evaluating the consequences of changes in other parameters currently believed not to impact colour discrimination (Lind et al., 2017).

DICHROMATS

The simplest application of the model involves a single opponent mechanism comparing outputs from two cone receptor classes. For example, most mammals are dichromats with long-wavelength (L) and short-wavelength (S) cones. In a dichromat, only one possible opponent channel exists, which compares the output from the two receptor classes. The first step in the RNL model is to write this opponent channel as a vector, **F**, of coefficients: $\mathbf{F} = [1, -1]$. The coefficients in the vector **F** are additive and sum to 0. Hence, the vector **F** summarizes a contrast between the L receptors and the S receptors. We can write the outputs (that is, the strength of the neural signal) from the L and S cones as a vector $\mathbf{C} = [L_1, S_1]$, where the subscript 1 refers to the object being viewed and italics are used to indicate outputs summed across the receptive field. The opponent signal contrasts the output from the L and S cones, which is given by the vector product $\mathbf{F} \times \mathbf{C}^{\mathrm{T}} = L_1 - S_1$ (where $\mathbf{C}^{\mathrm{T}}$ is the transpose of the vector **C**).

Chromatic Adaptation

Output from the receptor cells depends on the light arriving at the receptor cell and its absorption spectrum, but an additional factor needs to be incorporated. The receptors themselves modulate output, depending on the spectrum of the background. The process is termed adaptation to the background (chromatic adaptation). For example, in the presence of a great deal of short-wavelength light in the background, output from the S cones is downregulated, altering the difference between L and S outputs. This would improve detection of an object reflecting long wavelengths, which appears red. Assessment of the background spectrum appears to result from eye movements over the scene, but also includes post-receptoral communication between cells (Vanleeuwen, Joselevitch, Fahrenfort, & Kamermans, 2007). Chromatic adaptation is often approximated by dividing the photon catch from the signal by the photon catch from the background, separately for each receptor class. The transformation is referred to as the von Kries correction. However, in humans, the von Kries correction does not fully capture colour adaptation. Post-receptoral cross talk between different cone cell classes, as well as higher-order mechanisms (e.g. in the brain itself), are also involved in this process (reviewed by Vanleeuwen et al., 2007). It is not known how well the von Kries correction models chromatic adaptation in birds.

Detection

In the case of dichromats, the opponent channel signal from the object after a von Kries transformation becomes

$$L_1/L_{\mathrm{b}} - S_1/S_{\mathrm{b}} \tag{1}$$

where L_1 is the photon catch of L cones from the object and L_{b} is the photon catch of L cones from the background, and similarly for the S cones. Now consider one part of the retina receiving input from the background and the other input from the object in the foreground. The difference in photon catches between receptors responding to the background and to the object is $\Delta L = L_1 - L_{\mathrm{b}}$ and $\Delta S = S_1 - S_{\mathrm{b}}$, hence $L_1 = L_{\mathrm{b}} + \Delta L$ and $S_1 = S_{\mathrm{b}} + \Delta S$. Substituting these expressions into equation (1), the difference in opponent channel signal output from the object and the background is

$$\Delta L/L_{\mathrm{b}} \; - \; \Delta S/S_{\mathrm{b}}. \tag{2}$$

Hence, the von Kries correction is consistent with Weber's law (Brainard, 1996), which states that the magnitude of the difference needed to detect an object becomes larger as intensity in the background increases (i.e. $\Delta L/L_{\mathrm{b}} =$ constant, a principle true also for other senses such as sound). When the first and second terms are equal, no discrimination based on wavelength is possible. Mammals use input from the L cones to detect objects based on intensity, so if $\Delta L/L_{\mathrm{b}}$ is large, the object may still be detected because it is darker or lighter than background.

The squared version of equation (1), $(L_1/L_{\mathrm{b}} - S_1/S_{\mathrm{b}})^2$ is the variance in the catches of the two receptor classes, and it is useful to write it in this way because it can be scaled by error variance. Vorobyev and Osorio (1998) started with equation (1) and set up a model in which the major cause of error lies in the receptors themselves, before the opponent signals are computed. There are many possible sources of error at the receptor level. The number of photons captured varies (termed photon shot noise), receptors spontaneously fire in the absence of stimulation (termed dark noise), and error is expected during transduction and early synaptic processes. Large variation in output obscures any average difference in the receptor signal comparisons, resulting in a failure to detect the object consistently. One possible mechanism to reduce error is to average output across all cells in a receptive field. Assuming errors from each cone cell are independent, the error variance is proportional to $\frac{1}{n}$, where n is the number of cells in a receptor channel (the variance of a mean is $1/n$, where n is the number of observations). The final equation is written as the square root of the ratio of variance in output to variance in error:

$$\Delta O = \sqrt{\frac{(L-S)^2}{K \times \left(\frac{1}{n_{\mathrm{L}}} + \frac{1}{n_{\mathrm{S}}}\right)}}. \tag{3}$$

ΔO is the signal in the opponent channel and measures sensitivity to the object. A large value implies high sensitivity, hence consistent detection, and is achieved when either variance in output (numerator, as in equation (2)) is large, or error variance (denominator) is small. Vorobyev and Osorio (1998) symbolized sensitivity as ΔS but here we use ΔO throughout to avoid confusion with S cone output. L and S are used as shorthand for von Kries-adjusted receptor outputs, n_{L} and n_{S} are the number of long- and short-wavelength receptors in the receptive field, and K is a constant. One feature of this equation is that for a given number of cells present in the field, sensitivity is maximized when $n_{\mathrm{L}} = n_{\mathrm{S}}$, i.e. each

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receptor class consists of the same number of cones in the receptive field. For example, if $n_L = n_S = 4$, the denominator in equation (3) is = 0.5, whereas if $n_L = 2$ and $n_S = 6$, the term in parentheses becomes = 0.66. Hence in this model, if detection is a primary selective force driving receptor cell numbers, we predict that all species should evolve to have an equal number of cones in each receptor class. This comes with the proviso that individual cells in each receptor class come with similar errors of output, which appears unlikely (see Discussion).

A second feature of equations (1–3) is that total light intensity does not alter detection, because it results in an increase in both background and signal, which cancel out assuming a linear system. This is consistent with the data. For example, between perception thresholds, if the intensity of light illuminating a scene increases, the object does not generally become easier to detect. It should be possible to directly estimate receptor cell error from neurophysiological experiments, but this has yet to be done. Instead, parameterization of the model has been based on behavioural experiments (Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). First, one sets a criterion for sensitivity to object and background in trials (e.g. the difference required for the correct choice to be made 75% of the time). Second, one computes von Kries-corrected cone catches (the numerator in equation (3)) based on optical properties of the eye. Third, one computes the denominator in equation (3) from these measurements. Once this is done, sensitivity to different tasks can be predicted from knowledge of light spectra, and sensitivities of a different species can be predicted from knowledge of receptor cell distributions in that species, assuming noise at the level of the receptor is the same across species.

Discrimination

Vorobyev et al. (1998) placed the RNL model in the context of discrimination of two objects, both of which are scaled by background, rather than detection of object against background. Again, the data indicate receptor outputs should be compared as a ratio because objects do not become easier to discriminate as they both become brighter. To accomplish this, while at the same time retaining an additive contrast in the vector **F**, Vorobyev et al. (1998) log-transformed the cone outputs. By transforming in this way, difference in outputs from the opponent channels can now be written as in equations (1) and (3):

$$\Delta O = \sqrt{\frac{(\Delta L - \Delta S)^2}{K \times \left(\frac{1}{n_L} + \frac{1}{n_S}\right)}}, \qquad (4)$$

where ΔL and ΔS refer to the difference in log-transformed photon catches from the two objects. The von Kries correction may be applied, but it is now irrelevant because receptors receiving input from one object are affected in exactly the same way by the transformation as those receiving input from the other object and therefore cancel out.

DETECTION AND DISCRIMINATION IN TRICHROMATS

The principles outlined above for dichromats also apply to trichromatic species. However, with three receptor classes we have many possible opponent channels. For example, in humans the comparisons could potentially be $L - S$ and $M - S$, rather than, or as well as, $(L + M) - S$ and $L - M$. Only three pieces of information are available from the cone outputs of a given receptive field, that is *L, M, S*; hence, two contrasts capture all the available information on differences in wavelength. Vorobyev et al. (1998) assumed that exactly $n - 1$ opponent channels are present, where n is the number of receptor classes. They then showed that the specific opponent channels are irrelevant, provided they are not linearly dependent (i.e. they capture all the wavelength information between them). In the trichromatic case, **F** is a matrix with two rows (representing the number of opponent channels), and three columns, representing the coefficients for each receptor class. Therefore, for humans we might write **F** as:

$$\mathbf{F} = \begin{vmatrix} +2 & -1 & -1 \\ 0 & +1 & -1 \end{vmatrix}$$

The top row in this matrix contrasts *S* cones with the $L + M$ cones (i.e. $S - (L + M)$), and the second row is a contrast of *M* to *L* cones ($M - L$). As in the dichromat case, the rows of the matrix compare outputs additively, and they sum to 0. Also, as in the dichromatic case, the opponent signals are obtained by multiplying each row of the matrix by a vector whose three entries summarize output from each receptor cell. The result is a second vector with two entries, quantifying the signals from each of the opponent channels when viewing an object. The difference between the vectors summarizing the signal coming from the object and the background, or from the object and another object, then need to be combined into a single measure that translates how easily these can be detected and/or discriminated. Importantly, Vorobyev and Osorio (1998) assumed the two differences were combined simply, as the square root of the sums of squares (that is, the distance from the origin of the point in two-dimensional space). Given these assumptions, Vorobyev and Osorio (1998) showed that the sensitivity of a trichromat is:

$$\Delta O = \sqrt{\frac{\frac{1}{n_S}(\Delta L - \Delta M)^2 + \frac{1}{n_M}(\Delta L - \Delta S)^2 + \frac{1}{n_L}(\Delta M - \Delta S)^2}{K \times \left(\frac{1}{n_L} \times \frac{1}{n_M} + \frac{1}{n_L} \times \frac{1}{n_S} + \frac{1}{n_M} \times \frac{1}{n_S}\right)}} \qquad (5)$$

The elegance of the RNL model is that both the signal in the numerator and error in the denominator are transformed in the same way by the **F** matrix and cancel out, making the actual opponent channels employed irrelevant. If the relative number of cone cells is the same (i.e. all are 33%), then the formula reduces to a straightforward measure of the standard deviation in differences in photon catch by the cones, ΔL, ΔM, ΔS. The equation applies equally to detection and discrimination, with present approaches applying von Kries transformation to detection cases, and log transformation to discrimination cases.

Detection

We focus on empirical studies of detection in humans, as any deviations in predictions from the RNL model should apply equally to detection and discrimination tasks. Detection is more easily studied, because discrimination depends in poorly understood ways on the background (Stockman & Brainard, 2010). Consider detection of a monochromatic light against a background: assume this light excites the L and M cones but excitation of the S cones is negligible, that is, its wavelength is above about 550 nm (Fig. 1). In this case, equation (5) reduces, given $S_1 = 0$, to:

$$\Delta O = \sqrt{\frac{\frac{1}{n_S}(L - M)^2 + \frac{1}{n_M}L^2 + \frac{1}{n_L}M^2}{K \times \left(\frac{1}{n_L} \times \frac{1}{n_M} + \frac{1}{n_L} \times \frac{1}{n_S} + \frac{1}{n_M} \times \frac{1}{n_S}\right)}} \qquad (6)$$

Here, because we are dealing with a detection problem, the cone outputs are not log-transformed but are scaled by background (see equation (3)). The first term represents the $L - M$ channel. The second two terms emerge from $S - (L + M)$ comparisons. In this

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case, S catches come only from the background. After von Kries transformation, the signal from background to the M cone (second term in the numerator) or to the L cone (third term) is the same as signal to the S cone and cancels, which is why no S entry appears in the equation.

From equation (6), two peaks in sensitivity should correspond to maxima in the positive and negative $L - M$ differences, derived from the first term in the numerator. One can see from the left graph in Fig. 1 that these may be at about 525 nm and 625 nm: at 525 nm, the $M - L$ catch may be approximately maximized, and at 625 nm, the $L - M$ catch may be approximately maximized. However, in the RNL model, additional contributions to detection come from the second two terms, which compare the L to S outputs and M to S (again, where S from the object is 0 but S from the background is positive). The two terms are L^2 and M^2 and their sum will be maximized at intermediate values (~560 nm, Fig. 1, left). Hence including S cone contributions can obliterate the valley in the detection landscape. In fact, human data indicate two peaks that do roughly correspond to the first term alone (e.g. Fig. 2c), suggesting that the influence from the S channel is small.

Given this finding, the question then becomes how to down-weight the background contributions from the S cones in the model (second and third terms in equation (6)) to match the data. Vorobyev and Osorio (1998) assumed the S cones to be about 2% of the cell population. This gives large error associated with the second and third terms, and high weighting to the first term ($1/n_S = 50$), i.e. the $L - M$ channel. Vorobyev and Osorio (1998) were thereby able to replicate the two-peak pattern in the region where the monochromatic light does not stimulate the S cones (Fig. 2a, grey line). However, the S cone population is now known to comprise about 7% of the total cones (Schmidt, Touch, Neitz, & Neitz, 2016), and in this case, under the RNL model mechanism, the two-peak pattern becomes obscured, and the match with the data weakens (Fig. 2a, black line). One plausible explanation for the mismatch of data with predictions from the RNL model based on cell numbers alone is that individually the S cones have noisier output (see Discussion).

In the human literature, signal outputs are combined in a different way from the RNL model (Stockman & Brainard, 2010). In this case, if output from either one or the other channel, rather than the combination, exceeds a certain value, the object is detected. Empirically, in humans, detection as a function of channel inputs often follows an elliptical shape (Fig. 3). In the human literature, the explanation is that detection requires crossing a threshold in either of the two channels. At the arrowed position in Fig. 3, signals from $L - M$ or $S - (M + L)$ channel are large, and by chance either one could cross the threshold required for detection. On the other hand, if one looks along the X axis, only the $L - M$ channel is stimulated, and hence a larger signal is required because it is the only one that can cross threshold. Although we have not seen this discussed anywhere, the explanation for the elliptical shape in the RNL model would be that because both channels are stimulated to some extent and because outputs are combined together, less signal in each is required than when only one channel is stimulated. Results from additional studies on humans seem to offer more support to the model in the human literature (termed 'probability summation'), because the threshold often appears as a rectangle with rounded corners rather than an ellipse (summarized by Stockman & Brainard, 2010, 2015). Theoretically as well, this model fits with a general principle of neural nets, that a large signal from a few neurons is a more efficient means of transmitting signals than smaller signals across many (e.g. Renoult, Bovet, & Raymond, 2016).

An additional feature of the empirical results from human research is that the intensity of monochromatic light needed to cross threshold is not always symmetrical around the X or Y axes, especially in the S cone direction, implying that the $S - (M + L)$ signal differs from $(M + L) - S$; this is not allowed in the RNL model, which always assumes symmetry. The data on humans are generally fitted by assuming that a threshold mechanism in each channel is associated with a probability of crossing the threshold, and taking signs of the difference into account. That requires a five-parameter model, making the fit unsurprising (Stockman & Brainard, 2010). In summary, the crossing of a threshold by a single opponent channel appears likely to contribute to detection/discrimination in humans, but a role for summed contributions from both, as in the RNL model, remains difficult to rule out.

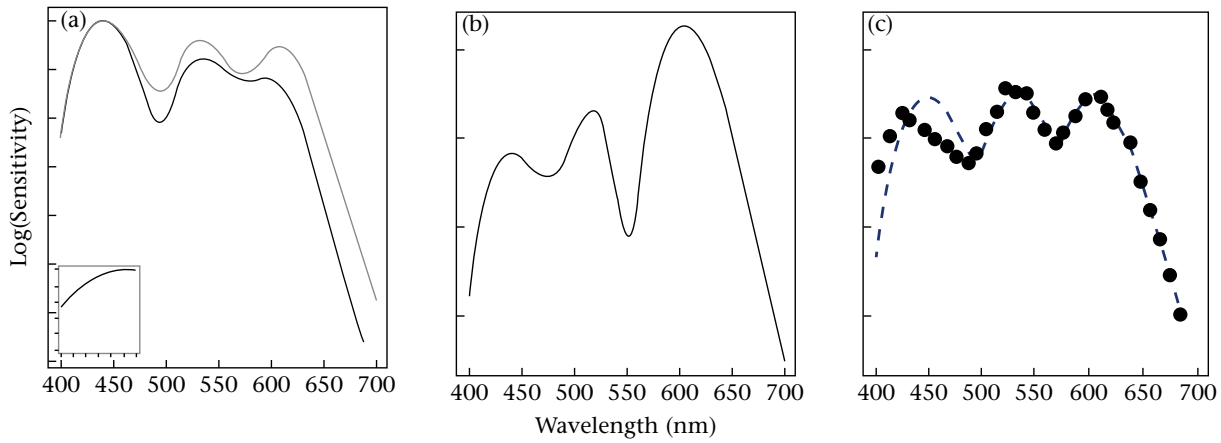

Figure 2. (a) Modelled human sensitivity for the receptor noise model to monochromatic light viewed against a background with spectrum matching a 5500 K black body radiator, following Vorobyev and Osorio (1998); inset is the assumed background, quantal catch against wavelength. Grey line: cone ratios 2:33:65 (Short:Medium:Long), as assumed by Vorobyev and Osorio (1998). Black line: cone ratios 7:46.5:46.5, computed using the R package Pavo (Maia, Eliason, Bitton, & Doucet, 2013). (b) A simple model where output from the opponent channel with the highest sensitivity is assumed to determine threshold. The two channels were modelled as $S - (L + M)$ and $L - M$ (not log-transformed), with the sensitivity (Weber fraction) of $S - (M + L)$ channel set 9× lower than the $L - M$ channel, in accord with experimental data (see Fig. 3). (c) Experimental data (points; from Figure 17 in Stockman & Brainard, 2010) and a complex five-parameter model fit (a, b, c, d, e) assumed to more closely match mechanisms in humans, in which the sign of the opponent signal matters: $b\ |aL - M| + c\ |M - aL| + d\ |S - e(L + 0.5M)|$.

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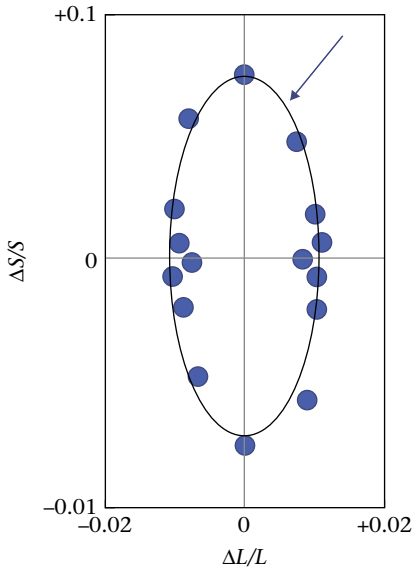

Figure 3. Detection thresholds in humans, based on an experiment with a single individual. Luminance, which in humans is given by the summed output of the long and medium cells ($L + M$), is held constant. The axes are the increment in photon catch by the cones over baseline, and the ellipse demarcates the point at which the observer could reliably distinguish 200 ms flashes against background. Note the different X and Y scales. The point of the arrow highlights that the shape is not a rectangle. In the receptor noise model, an ellipse may be expected because the signal is modelled as the square root of the squared outputs from the two opponent channels. In models from the human literature, rounded corners on a rectangle result because when both channels are close to threshold, the chances of at least one crossing threshold is increased. Redrawn from Figure 1 in Eskew, Newton, and Giulianini (2001).

DETECTION AND DISCRIMINATION IN TETRACHROMATS

We now turn to consider bird perception. Most bird species are likely tetrachromats and rely on four types of retinal receptors to mediate colour vision: the ultraviolet (U, peak sensitivity varies between 370 nm and 425 nm among species studied so far), short wavelength (S, 450–475 nm), medium wavelength (M, 535–545 nm) and long wavelength (L, 601–612 nm) cone cells (Hart & Hunt, 2007; see Fig. 1 for an example). The RNL model for a tetrachromat introduces no new principles over a trichromat, and the general equation for sensitivity is a more complicated version of equation (5). It has been reproduced many times since it was introduced by Vorobyev and Osorio (1998), e.g. see Endler and Mielke (2005) and Lind et al. (2017).

Evaluations of the appropriateness of the RNL model in animals have most often been based on experiments that studied the detection of narrow band stimuli (near monochromatic) lights against background (Goldsmith & Butler, 2003; Maier, 1992; Olsson, Lind, & Kelber, 2018). Because the pattern of sensitivity as a function of the wavelength of the light follows model predictions, the RNL model is regularly quoted as adequately representing perceptual systems (Endler & Mielke, 2005). However, care is needed with this inference because many other models may be consistent with these data. For birds, the spectra of the four colour cone types overlap little (Fig. 1), so sensitivity to a monochromatic light closely matches the receptor absorption spectra themselves. Hence, radically different models that do not consider opponency at all fit the data equally well (e.g. see the supplement in Lind, Chavez, & Kelber, 2014).

A few studies have evaluated responses to broader band light. Some have achieved this by using mixtures of monochromatic lights (Goldsmith & Butler, 2005), while others have examined discrimination of reflected light from coloured disks (Caves et al., 2018; Lind & Kelber, 2009; Osorio, Vorobyev, & Jones, 1999). We have no information on the opponent channels in birds with which to compare against the RNL. Because opponent channels in birds are not known, we consider two possibilities. First, in the turtle, Rocha et al. (2008) used electrophysiology to find evidence for three common channels, plus three others rarely observed (i.e. just once or twice in their experiments). The commonly observed channels were $L - (U + S + M)$, $U - (S + M + L)$ and $(U + S) - (M + L)$ and the less commonly observed ones were $(U + M) - (S + L)$, $(U + L) - (S + M)$, $(U + M + L) - S$. The title to their paper indicates a possible total of 12 channels because positive and negative differences were evaluated separately. In all channels, output from all receptor classes are contrasted. Here, we consider just the three common classes. In the experiments we illustrate in Fig. 4, stimulation of the U channel was either specifically eliminated through the use of monochromatic light (Goldsmith & Butler, 2005) or thought to make a negligible contribution (Caves et al., 2018). Hence, only two of the three common turtle channels are relevant, and without U cone stimulation they become: $L - (S + M)$ and $S - (M + L)$. We also consider the possibility of an $L - M$ channel.

Goldsmith and Butler (2005) used a mixture of monochromatic lights in the red–green region, so only the L and M cones should be excited (they also conducted experiments elsewhere in the spectrum, but here we review these data alone). In this case, the $L - (S + M)$ channel is the only one operating, with the signal being $L - M$. Here, the predictions of the receptor noise model are essentially identical to a model of $L - M$ opponency, with the exception that $L - M$ might differ from $M - L$ in opponent models. The data are largely consistent with the predictions from the RNL model, but it does appear possible that the sign matters (Fig. 4a). Caves et al. (2018) studied broadband light reflected from coloured disks, where both the channels $L - (S + M)$ and $S - (M + L)$ should be operating. In Fig. 4b we show predictions from these two channels, plus $L - M$. We also show predictions from the RNL model, and from a model in which disk brightness matters. The absolute height of each of these five lines is not relevant, or known, because it depends on how signals are weighted (i.e. their Weber fraction; in humans the $L - M$ channel is much more sensitive than the $S - (L + M)$ channel; Fig. 3). Therefore, we can only compare across tasks within each line. The two comparisons that were well discriminated are 4 versus 6 and 5 versus 7 (Fig. 4b; Caves et al., 2018). For 5 versus 7, the luminance difference is large, making it difficult to exclude this as the driver of strong discrimination, rather than any effect of colour. For 4 versus 6, the RNL model is at a maximum, and luminance differences are moderate; together these effects may also lead to strong discrimination. One opponent channel alone ($S - (M + L)$) gives a very similar pattern to the RNL model, but the other opponent channels predict discrimination poorly. Hence, at present, these data are consistent with both the RNL model and one in which a single opponent channel is driving the threshold.

DISCUSSION

The extent to which perception of colour varies across related animal species is a crucial question that we feel deserves careful attention. This will require both an improved understanding of the basic mechanics of colour vision and how anatomical and physiological differences affect perception. As we gain knowledge about the visual system of animals, particularly birds, the RNL model continues to be a widely used and valuable predictor for colour detection and discrimination in these clades. Here we have

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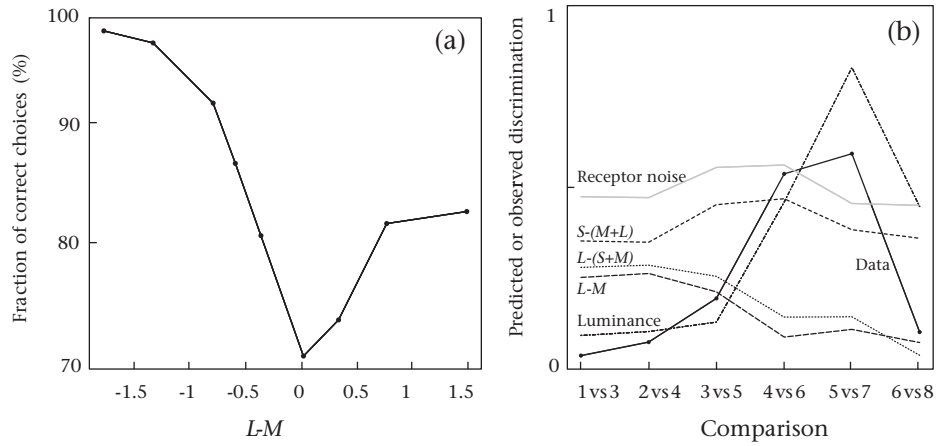

Figure 4. Discrimination thresholds in birds (solid lines with points). (a) In the budgerigar, *Melopsittacus undulates*, percentage correct in a discrimination task is plotted as a function of the difference in photon catch by long (L) and medium (M) wavelength-sensitive cones ($\log(L_1/L_2) - \log(M_1/M_2)$, based on Figure 8 in Goldsmith and Butler (2005), with catches computed from the absorbance spectra in Lind et al. (2013a, 2013b). The use of monochromatic light implies the ultraviolet (U) and short (S) wavelength-sensitive cones were not involved. (b) Thresholds and differences in cone catches from a series of choice tests in zebra finches along the orange to red part of the spectrum. The solid black line with black circles represents the proportion of passes in discrimination tests performed by Caves et al. (2018) (from Figure 3 of their paper); that is, discriminability of different coloured disks. On the *X* axis, numbers refer to the particular coloured disks being compared. Dotted lines consider predictions from three possible opponent channels ($S - (M + L)$, $L - (S + M)$ and $L - M$) and luminance contrast based on photon catch by the double cones (not considered elsewhere in this paper). All are calculated as the absolute differences in log-transformed cone catches, with predicted cone catches taken from Caves et al. (2018). Finally, the solid grey line corresponds to the choice test's discrimination thresholds calculated using the receptor noise model, assuming an S:M:L ratio of 1.5:2:3 (Lind, 2016) and a Weber fraction of 0.1. Thresholds were divided by 5 to match the same scale as the rest of the graph.

unpacked the model to explain its 'backbone' and asked how variation in the critical parameters of the RNL model and the inclusion of specific knowledge of the opponent channels might affect its predictions on colour discrimination. One of the great values of the RNL model lies in its power to highlight directions for future research. Some come from obvious gaps in our knowledge and others from experimentally demonstrated deviations from the assumptions of the RNL model.

Assumptions

In humans we know that many assumptions of the RNL model are not perfectly met. Earlier sections considered some implicitly or explicitly, and we summarize them here: (1) for discrimination problems, one opponent channel in humans ($S - (M + L)$) (and all inferred for turtles) cannot be written in terms of additive contributions even on a log scale (that is, the channel output should be written as $\log(S) - \log(M + L)$, which cannot be not achieved by log transforming *S*, *M* and *L* separately); (2) noise is known to affect transmission beyond the receptors (Stockman & Brainard, 2010); (3) chromatic adaptation is not simply achieved by the von Kries transformation even for detection problems (Vanleeuwen et al., 2007; Worthey & Brill, 1986); (4) additional S cone inputs to the L or M cones are likely in some receptive fields (Schmidt et al., 2016). The tetrachromatic turtle may also employ more than the three channels required to capture all wavelength information (Rocha et al., 2008); (5) the L:M cone ratio varies across individuals in humans (from about 1:1 (M:L) to 1:4, Schmidt et al., 2016) and the ratio and number of cone types forming the receptive field varies across the retina and across individuals (there are no S cones at all in the central fovea); (6) detection ellipses sometimes follow those in Fig. 3, but in other experiments they appear closer to a rectangle with rounded corners, suggesting that thresholds are indeed set by responses in a single channel (Stockman & Brainard, 2010); (7) detection thresholds may not be symmetrical around the axes, suggesting that the sign of the signal in the opponent channel makes a difference (e.g. $S - (L + M)$ appears to give a different threshold than $(L + M) - S$; Stockman & Brainard, 2010). All these details could make a difference for perception – and cause deviations from the predictions of the RNL model – but we are unsure to what extent. We consider these issues in more detail, first with respect to noise, and then with respect to signal.

Noise in the RNL Model

Given the assumption that all noise is at the level of the receptors, the RNL model depends critically on knowledge of what that noise is. At present, estimates of noise – at least in birds – come from behavioural experiments (Vorobyev et al., 1998). This has the advantage that detection and discrimination are being measured in units relevant to ecology and behaviour. The RNL model is generalized from these experiments to other situations and species (Price & Fialko, 2018) by assuming that noise *per* receptor cell is the same across receptor classes and species, so the only contribution to differences in noise comes from cone numbers, which are measurable. While absolute noise from a cone could in principle be measured electrophysiologically, that has not been done. If it becomes known, it could be incorporated along with cone numbers to make a more refined model of receptor noise. At present, however, cone ratios are the critical feature of the RNL model that affect our estimates of noise across species. Therefore, we review explanations for why the number of cone cells in the different receptor classes are not equal, which runs counter to the to the expectation (supported by the model) that equal cone densities should be optimal for reducing receptor noise in detection and discrimination problems (equation 1).

If the properties of the U, S, M and L cones are selected to optimize sensitivity to colour across the entire spectrum and each has the same noise per cell, the RNL model predicts them to be in equal abundance. This often seems to be approximately the case (Hart, 2001a). For example, in the most thorough study to date, American goldfinch, *Spinus tristis*, cone ratios approximate 1:2:2:2 (U:S:M:L, Baumhardt, Moore, Doppler, & Fernández-Juricic, 2014). Across birds, relatively small deviations from this ratio are

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common, but U cones are always the rarest and L cones generally the commonest (Hart, 2001b; Hart, Partridge, Cuthill, & Bennett, 2000). One possible reason for the differences is that they compensate for noise in each channel, because dark noise is highest in the L cones (associated with lower energy, longer-wavelength photons) and lowest in the S cones. Supporting this, cone size is correlated with cone number and the diameter of the U cones is one-third that of the L cones in some species (Hart et al., 2000). Together these considerations suggest that noise in all receptor classes could be quite similar, even as the ratios differ. However, if receptor noise is indeed the same in each channel, it can be simply ignored (e.g. see equation (5), where setting all cone classes equal results in the numerator and denominator terms cancelling out). In consequence, the receptor noise model reduces to Euclidean distance on a standard colour space (Stoddard & Prum, 2008).

Despite predictions of the presence of similar cone numbers, in some bird species, ratios differ greatly from unity. For example, Hart (2001b) found a species of kingfisher where the L cones were about twice the abundance of all the other cones combined, for which no explanation has been forthcoming (Hart, 2001a). One explanation for deviations such as these is that certain regions of the spectrum require better discrimination than others because of the tasks set for that species. However, Lind et al. (2017) modelled a variety of discrimination tasks for both birds and butterflies using the RNL model. They found that a decrease in the relative abundance of the M cells always increased discrimination, suggesting that factors other than noise reduction should affect cone cell numbers. In summary, we suggest that the receptor noise model may be an adequate measure of avian perception given current knowledge. It is less clear, however, that cone ratios are valid indicators of noise, and setting noise equal across receptors may be equally justified, in which case the model reduces to other distance measures in colour spaces (Kemp et al., 2015; Renoult, Kelber, & Schaefer, 2017; Stoddard & Prum, 2008).

Signal

Beyond noise, signals in the opponent channel depend on the photon catches of the receptor classes. The best studied causes of variation in photon catch across species lie in the absorption spectra of the cones. Bird species vary considerably in the tuning of the ultraviolet visual pigment (Hart & Hunt, 2007), which should affect discrimination and detection in the very shortest wavelengths (Bitton et al., 2017; Lind et al., 2013a; 2013b), but tuning of the other visual pigments does not vary much (Hart & Hunt, 2007; Lind et al., 2017). Other features also vary across species. For example, the S, M and L cones are associated with a pigmented oil droplet that screens out the lower wavelengths. The concentration and absorbance spectra of these droplets vary across species (Hart & Vorobyev, 2005; Toomey et al., 2016). Ocular media transmittance also differs among bird species (Lind et al., 2013a; 2013b). Lind et al. (2017) used the RNL model to consider effects of transmission properties of the ocular media and oil droplets. They found that, individually, these features made a small difference, but noted the possibility that different features could act synergistically, in which case perception may be more strongly affected. This is a crucial point as it is in line with the possibility that including opponent channels in our current models of colour perception could reveal more variability across birds than currently appreciated. Still other features affecting the signal remain to be modelled. The concentration of the visual pigments themselves is likely to differ between species, because Bloch (2015) found large differences in opsin gene expression across a clade of birds. An effect of increased densities of the opsin pigments within cones is to increase the width of the absorption spectrum, and hence the overlap between spectra of different receptor classes (Thomas, Formankiewicz, & Mollon, 2011). Because of the presence of oil droplet pigments that shield out short wavelengths, a broadening of the absorption spectrum can also lead to a shift in the absorbance peak (N. I. Bloch & K. Norden, personal observations). Absorbance spectra of receptors have been shown to vary among individuals within populations (Ronald, Ensminger, Shawkey, Lucas, & Fernández-Juricic, 2017), between subspecies (Knott, Berg, Ribot, Endler, & Bennett, 2017), and among species (Hart & Hunt, 2007), all of which suggest that perception varies among species in meaningful ways.

We argue here that opponent channels are worth considering. In the absence of data for avian opponent channels, one could consider the three common channels detected in turtles (Rocha et al., 2008). Ultimately, we will need to know what the opponent channels are and filling this significant gap in our knowledge is long overdue. Electrophysiological techniques can be used to do this, whereby neural signals are measured in response to light stimulants (Rocha et al., 2008; Shevell & Martin, 2017). In humans, opponent channels have been supported by behavioural experiments (e.g. adding light that alone appears green to a light that appears red can result in a colour that has no hint of either redness or greenness; Hurvich and Jameson, 1957). Behavioural tests are a challenge in other animals, but results from neural studies may make it possible to substantially narrow the range of appropriate experiments.

Conclusions

We believe the RNL model remains the best model of detection and discrimination in animals based on wavelength differences, as it is currently understood. Despite many deviations from the assumptions of the model identified in human studies, limited empirical evidence suggests that predictions from the RNL model are likely to approximately match those based on explicit consideration of the opponent channels. Indeed, we suggest that the RNL model might be profitably applied to studies in humans, where it has been neglected. Ultimately, refined understanding of perception in other animals is going to come from further extensive neural studies (e.g. measurement of noise in the receptors themselves and identification of the opponent channels) and behavioural experiments (e.g. uncovering the effects of background on discrimination: Lind, 2016; translating discrimination into categorization: Caves et al., 2018). Much of this work will be guided by the RNL model, which clearly lays out the assumptions, and by consideration of explicit opponent channels.

In nature, many factors affect detection and discrimination beyond those considered in the models and in the laboratory, including motivation, experience, habituation and background (Renoult et al., 2017). For example, males choose only a specific subset of environments in which to display, which are those that generally increase their conspicuousness to females (Endler & Théry, 1996; Ligon et al., 2018). We believe that studies on colour perception are about to grow rapidly, and as we gain increased understanding, this will lead to many insights into how animals communicate. Our ultimate goal – to understand the diversity of colour perception and colour in nature – will be achieved by integrating neural and anatomical studies with behaviour and by validating these ideas in a variety of natural settings.

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proving that when the rows of **F** sum to zero, the receptor noise model is general, and that when the cone cell numbers are equal, sensitivity is proportional to the standard deviation of the differences in cone outputs. This work was partly funded by Marie Sklodowska-Curie Fellowship 654699 and National Science Foundation Postdoctoral Fellowship in Biology 1523669 to N.I.B.

Supplementary data

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