(JND), which is the smallest difference in color or brightness between two stimuli a test animal consistently distinguishes when given a choice. As noted by Olsson et al. (2018) these experiments can obviously only be conducted for a few species across a few comparisons, under a restricted set of viewing conditions, which are affected both by the background and the illuminant. Therefore, models have been developed to generalize the findings. For example, early experiments with birds concerned the ability to distinguish a monochromatic light from background. Ideally, we would like to extrapolate results of such an experiment to other species and to other conditions, such as perception of broad band spectra under varying illuminants and backgrounds. Olsson et al. (2018) review progress in this direction, including summaries of recent behavioral experiments, many of which have been conducted by the authors. In this commentary, we focus on JNDs based on wavelength discrimination ("color") in bright light, i.e. chromatic mechanisms.

In 1998 Vorobyev and Osorio published an elegant model that has subsequently provided the organizational framework for the development of both experiments and predictions in this area. The key to the model is that discrimination in bright conditions is limited mainly by photoreceptor noise (i.e. noise in the cones) and not post-receptoral stages. Given model assumptions, Vorobyev and Osorio (1998) showed that the JND can be predicted from cone catches, and (1) an absolute measure of receptor noise for at least one cone type, (2) the relative number of cones of different types and (3) some way to adjust for background adaptation (usually the so-called von Kries correction, which scales cone catches from the object as a ratio to cone catches from the background). Olsson et al. (2018) note that (1) is hard to measure, but can be derived from experiments, given (2) and (3). Consequently, the model may be thought of as a mathematical transformation that uses the outcome of one behavioral experiment to predict the outcome of another. Olsson et al. (2018) suggest that it works quite well, for example, in predicting JNDs in response to broad band colors.

Nevertheless, progress in this area will require the development of alternative models against which the receptor noise model can be critically assessed, and consequences of relaxing the assumptions evaluated. One assumption of the model is that for n receptors there are $n-1$ independent opponent channels. For example, for a species with three cone types absorbing in the short, medium and long wavelengths respectively, one channel might be written as $[0, 1, -1]$, contrasting medium (M) and long (L) wavelength cone catches, and the other as $[2, -1, -1]$ contrasting short (S) with the sum of medium and long cone catches (Vorobyev and Osorio 1998). In the model, the sum of vector entries must be 0, and the sum of the cross-product of the vectors must be 0 (implying independence); the formulation can accommodate ratios through log transformation. The vectors as we have written them approximate the human opponent channels, but the second channel includes both sums and ratios (a ratio of S cone catch to the sum of the L+M cone catch). We do not know what the opponent channels in birds are, but in turtles, there appear to be many (Rocha et al. 2008), implying both redundancy and a lack of independence. Further, given model assumptions, the actual opponent channels do not matter, which seems unlikely and indeed raises the question of why opponency exists in the retina at all. Another assumption is that differences in noise between photoreceptor classes depends only on their relative abundance. However, in humans, relative abundance and receptive field size vary across the retina (Valberg 2005), and cone morphology also differs (Calkins 2001). Many of these features are likely to apply to other organisms, including birds (Hart 2001; Bloch 2015). As our understanding of behavioral responses

to color improves, the field will also surely benefit from the development of alternative models of color perception, which in turn will guide the development of novel experimental approaches

REFERENCES

Bloch NI. 2015. Evolution of opsin expression in birds driven by sexual selection and habitat. Proc Biol Sci. 282:20142321.

Calkins DJ. 2001. Seeing with S cones. Prog Retin Eye Res. 20:255–287.

Hart NS. 2001. Variations in cone photoreceptor abundance and the visual ecology of birds. J Comp Physiol A. 187:685–697.

Olsson P, Lind O, Kelber A. 2018. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. Behav Ecol. 29:273–282.

Rocha FA, Saito CA, Silveira LC, de Souza JM, Ventura DF. 2008. Twelve chromatically opponent ganglion cell types in turtle retina. Vis Neurosci. 25:307–315.

Valberg A. 2005. Light, vision, color. Chichester, West Sussex: Wiley

Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. Proc Biol Sci. 265:351–358.

Color discrimination is not just limited by photoreceptor noise: a comment on Olsson et al.

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The comprehensive review by Olsson et al. (2018) highlights the versatility and value of Receptor Noise Limited models. Such models are useful in the study of animal vision, because they allow predicting the extent to which biologically salient visual signals and cues are detectable and distinguishable in any species (Clark et al. 2017), based on differences in the number of spectral classes of receptors, their spectral sensitivity functions, and associated noise.

One has to be pragmatic about color spaces for nonhuman animals. Even in humans, where psychophysical data are comparatively easily obtained, it has not been possible to obtain a universal color difference formula that predicts color discrimination in all areas of color space, irrespective of stimulus size, intensity, illumination conditions, etc.—therefore, a rough guidance map is better than no map. Thus, using only (estimated) receptor noise to predict color discrimination is a useful starting point.

However, one must be cautious in assuming that photoreceptor noise is the only factor constraining color discrimination. Noise occurs in all postreceptor neural processes, but various forms of

spatial and temporal integration can counterbalance it. Consider the consequences of spatial summation at the first stage of visual processing. If inputs of multiple receptors are averaged, the signal-to-noise ratio of the receptor channel can be increased at the expense of spatial detail. For example, in honeybees, chromatic contrast sensitivity in behavioral experiments exceeds what we predict from electrophysiological measurements of receptor noise (Dyer et al. 2008); accordingly, the minimal visual angle for color contrast detection (15 degrees) covers 59 ommatidia, equipped with 9 photoreceptors each (Giurfa et al. 1996). It follows that discrepancies between electrophysiological and behavioral estimates of noise from a species (e.g. those reported in Table 1 of Olsson et al. (2018) for rock doves, brown owls, and American kestrels) may actually reflect real differences between the noise of receptors and the noise in more downstream color processing neurons.

The differences in achromatic and chromatic discrimination abilities of any given animal, rightly emphasized by the review, also point to the importance of postreceptor processing. Again, in honeybees, achromatic contrast detection is possible at a visual angle of approximately 5 degrees, employing 7 ommatidia, as opposed to the 15 degrees and 59 ommatidia required for chromatic contrast detection (Giurfa et al. 1996). Thus, both achromatic and chromatic signals are summed up, but to a different extent. As a result, the behaviorally estimated noise of the receptor channel is higher for achromatic than chromatic vision (see Table 1 of Olsson et al. 2018). Interestingly, a similar phenomenon appears in human perceptual studies that indicate a much higher sensitivity to achromatic than chromatic blur (Kingdom et al. 2015). The same distinction does not hold true for bumblebees (Dyer et al. 2008). Such differences originate from species-specific postreceptor processing that should not be ignored when dealing with visual perceptual spaces.

It is also useful to remember that the RNL model was originally introduced for determining color thresholds and not for calculating perceptual differences between easily distinguishable colors. Perceptual differences may or may not scale linearly with differences in opponent receptor responses, and we caution against making such an assumption before this issue has been convincingly settled. In any case, current evidence indicates nonlinearity of visual spaces. For example, a set of behavioral experiments, using several species of bees, showed that the success of discrimination from a gray background scales nonlinearly with color difference (Dyer et al. 2008; Dyer and Neumeyer 2005; Garcia et al. 2017; Spaethe et al. 2014).

Finally, it is important that color vision has many cognitive elements (Skorupski and Chittka 2011). In humans for example, even language constrains color discrimination (Winawer et al. 2007). It is thus impossible to predict receptor noise from behavioral data; instead, noise must be measured with appropriate electrophysiological procedures (e.g. Skorupski and Chittka 2010). Color spaces, including those based on receptor noise, are useful in the same way as a Metro map is: they provide a rough guidance as to what is where, and how far A is from B, but one should be cautious in making overly precise predictions based on them.

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REFERENCES

Clark RC, Santer RD, Brebner JS. 2017. A generalized equation for the calculation of receptor noise limited colour distances in n-chromatic visual systems. R Soc Open Sci. 4:170712.

Dyer AG, Neumeyer C. 2005. Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). J Comp Physiol A. 191:547–557.

Dyer AG, Spaethe J, Prack S. 2008. Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. J Comp Physiol A. 194:617–627.

Garcia JE, Spaethe J, Dyer AG. 2017. The path to colour discrimination is S-shaped: behaviour determines the interpretation of colour models. J Comp Physiol A. doi:10.1007/s00359-017-1208-2.

Giurfa M, Vorobyev M, Kevan P, Menzel R. 1996. Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. J Comp Physiol A. 178:699–709.

Kingdom FA, Bell J, Haddad C, Bartsch A. 2015. Perceptual scales for chromatic and luminance blur in noise textures. J Vis. 15:6.

Olsson P, Lind O, Kelber A. 2018. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. Behav Ecol. 29:273–282.

Skorupski P, Chittka L. 2010. Differences in photoreceptor processing speed for chromatic and achromatic vision in the bumblebee, Bombus terrestris. J Neurosci. 30:3896–3903.

Skorupski P, Chittka L. 2011. Is colour cognitive? Opt Laser Technol. 43:251–260.

Spaethe J, Streinzer M, Eckert J, May S, Dyer AG. 2014. Behavioural evidence of colour vision in free flying stingless bees. J Comp Physiol A. 200:485–496.

Winawer J, Witthoft N, Frank MC, Wu L, Wade AR, Boroditsky L. 2007. Russian blues reveal effects of language on color discrimination. Proc Natl Acad Sci USA. 104:7780–7785.

Do not be distracted by pretty colors: a comment on Olsson et al.

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The review by Olsson and colleagues on chromatic and achromatic models is a very useful read for the many behavioral ecologists and neuroethologists confused on how to do this, for those that may want to improve what they are already doing and for those at the point of deciding whether or not to do it. That said, it is not a guide on how to do it, but more, as the title states, a guide on pitfalls and the "limitations" of the currently favored model, the Vorbyev/Osorio receptor noise limited model (V/O RNL) (Vorobyev and Osorio 1998). Perhaps most importantly, Olsson et al. (2018) repeatedly note that some sort of behavioral calibration or verification is, if not essential, at least very desirable.

This paper is by no means an easy read and will certainly be of most use to those who have already had a go at using the V/O RNL model. I personally hope it will be very useful to those who have had a go and reached the wrong conclusion because there are many out there that have and have nonetheless got the results published. One of the caveats, in fact not mentioned until the end of the review, is that this model is not suited for examining large just noticeable differences (jnds) but operates best around threshold jnd of 1–3 for example. This, along with other considerations also covered in the review, is often ignored and it has become difficult to decide where the right conclusion for the wrong reason or just the wrong conclusion has been drawn. This cautionary missive will help and should probably be read alongside existing papers under the microscope. It will also be of great benefit to editors and reviewers.