

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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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 Vorobyev/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.

As a good review should, this work contains a wealth of secondary references in this area and a very valuable table of chromatic and achromatic thresholds. A couple of recent publications missing are the recent special edition of *Philosophical Transactions of the Royal Society B* (Caro et al. 2017) that these authors also contribute to, and a thorough discussion by Price (2017).

Based on this collective knowledge, as Olsson et al. point out, anyone can have a go at these models, even if there is missing data. Some sensible estimates can be made and as long as the results are treated as guidelines and ideas only. Go for it! The danger comes when one desired result from modeling is fed into a secondary conclusion without sufficient caution and attention to the caveats mentioned in this review. Perhaps the most important point in this respect is not to get distracted by pretty colors alone but include luminance contrast using a best estimate of the photoreceptors responsible for this. Also, do not expect to know exactly how luminance information interacts with color (or indeed polarization), this is a complex area needing more neurophysiology and behavioral dissection than most want to enter into.

To hopefully paraphrase this valuable work in a paragraph. Do your best to measure or find the parameters needed, estimate sensibly where necessary, don't become too wedded or proud of your results and try and both back up and also feed numbers into your modeling with some behavioral observation. All of us could do with a good dose of Konrad Lorenzian perspective. Go look at your animal in the real world, not a deconstruction of it on a little screen. Recognize that what it is telling you is defined by how you are observing it, stimulus size, context, illumination level, etc, not what it is actually capable of throughout life.

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Models for a colorful reality?: a response to comments on Olsson et al.

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In her commentary to our review (Olsson et al. 2018), Stuart-Fox (2018) asks “What do animals see” and continues that we cannot imagine, but attempt to model it. Price and Fialko (2018)

begin their commentary saying: “Behavioral experiments are crucial to understanding animal vision.” We agree and add: if behavioral experiments are carefully designed, these can answer even complex questions about the visual world of animals. However, behavioral experiments even on a small number of specimens can take weeks or months, and thus can only be performed on a limited number of species, asking a limited range of questions. Tests are also performed in laboratory settings and thus not under the most ecologically realistic conditions. Finally, tests often separate single sensory modalities, even submodalities, testing either spatial resolution, color discrimination, or the sensitivity of an animal for achromatic contrasts. All of this is necessary to keep the test simple and thus allow for unambiguous conclusions.

Even in carefully controlled experiments, results vary between individuals, with behavioral context, motivation and yet other factors. Thus, behavioral tests are painstaking and time-consuming and cannot answer all questions that we would like to pose. Here, well-informed models can help. It is the beauty of the receptor noise limited (RNL) model of color discrimination that is discussed in the review and commentaries, that it can predict absolute discrimination thresholds using a very limited number of parameters based on receptor physiology. As Osorio and Vorobyev (2018), who conceived this ingenious model 20 years ago, point out in their commentary, this model “provides an excellent basis for comparative and evolutionary studies.” The model can be used to better understand behavioral results and to make predictions that can be tested in further behavioral experiments. If behavioral tests indeed measure absolute discrimination thresholds, we would argue, contrary to Vasas et al. (2018), that model calculations do allow the estimation of the underlying receptor noise (Olsson et al. 2015, 2018). Yet, we fully agree with Vasas et al. 2018 in that electrophysiological measurements are crucial.

Therefore, unfortunately, in times when the number of papers and citations are used to measure the quality of science, it is tempting to replace experiments with model calculations, instead of combining behavioral tests, physiology and models. Sadly, as Marshall (2018) points out, this can very easily lead to wrong conclusions, many of which have been published, which does not bring the field forward. Instead of developing alternative models, as suggested in the commentary by Price and Fialko (2018), we suggest a generally careful use of any model, and more efforts invested in behavioral and physiological experiments.

Interestingly, all 5 commentaries mostly discuss the original, chromatic version of the RNL model. Our review, however, was initially inspired by our observation that the more recent adaptation of the RNL model for achromatic discrimination thresholds is often used without parameter validation. The table of physiologically or behaviorally determined real thresholds (Olsson et al. 2018) can be used to directly predict achromatic discrimination by animals. Our main point is to explain is how they can be used to inform the RNL model. And the commentary by Vasas et al (2018) nicely points out the important point that noise levels differ between chromatic and achromatic channels, in some species, but not others.

We hope that the review and commentaries contribute to a more cautious use of model predictions in general, and inspire more researchers to perform controlled behavioral or electrophysiological experiments on their animals!

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