Avian colour vision: Effects of variation in receptor sensitivity and noise data on model predictions as compared to behavioural results

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ABSTRACT

Colour vision models require measurement of receptor noise and the absorbance of visual pigments, oil droplets, and ocular media. We have studied how variation in these parameters influences colour matching, spectral sensitivity, and colour discrimination predictions in four bird species. While colour match predictions are sensitive to variation in visual pigment and oil droplet absorbance data, discrimination predictions are mostly sensitive to variation in receptor noise. Ocular media transmittance influences only modelled spectral sensitivities at short wavelengths. A comparison between predicted and measured spectral sensitivities in domestic fowl and duck revealed large discrepancies, likely because of influences from achromatic mechanisms.

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1. Introduction

Birds use colours in various tasks such as foraging and mate choice (see e.g. Bennett & Cuthill, 1993; Cuthill, Bennett, Partridge, & Maier, 1999; and references therein). To understand bird behaviour it is therefore important to gain knowledge about avian visual processing, the link between the spectral composition of stimuli and the perception of colours.

There may be many stages of signal processing between the response of the photoreceptors and the behavioural outcome. Still, the most commonly used models suggest that certain behavioural responses can be predicted from the calculations of colour representation at the photoreceptor and early post-receptor (colour opponency) level (as reviewed in Kelber, Vorobyev, & Osorio, 2003).

Diurnal birds, with few exceptions, sample visual information by a retinal array consisting of four types of single cones, one type of double cone, and one type of rod (Hart, 2001b). However, it is generally assumed that only single cones are involved in colour vision (Maier & Bowmaker, 1993; reviewed in Martin & Osorio, 2008). The visual pigments of the single cones are grouped into four classes designated SWS1, SWS2, RH2, and M/LWS (Ebrey & Koutalos, 2001; Yokoyama, 2000). These are found in the ultraviolet or violet-sensitive (UVS/VS), the short-wavelength-sensitive (SWS), medium-wavelength-sensitive (MWS), and the long-wavelength-sensitive (LWS) cone, respectively (Hart, 2001b).

The spectral sensitivities of bird cones also depend on pigmented oil droplets in the cone inner segments by which incident light is filtered. The oil droplets act as long-pass cut-off filters that narrow the spectral sensitivity of the photoreceptors and shift their spectral position of peak absorbance towards longer wavelengths (Goldsmith, Collins, & Licht, 1984; Hart & Vorobyev, 2005; Partridge, 1989). This is true for all oil droplets but those of the UVS/VS cones that absorb insignificant amounts of light from 300 to 800 nm. Even before reaching the cones, light is filtered through the ocular media that absorb light of short wavelengths (e.g. Hart, 2004; Hart, Partridge, Bennett, & Cuthill, 2000; Hart, Partridge, Cuthill, & Bennett, 2000; Jane & Bowmaker, 1988; Wright & Bowmaker, 2001). The spectral sensitivity of a cone is thus a function of the ocular transmittance together with the absorbance of the cone's oil droplet and visual pigment.

The absorbance of the visual pigments and the oil droplets are commonly described by models of which the most frequently used are those suggested by Govardovskii, Fyhrquist, Reuter, Kuzmin, and Donner (2000; for the visual pigments), and by Hart and Vorobyev (2005; for the oil droplets). These models are convenient since they can be used to reconstruct the sensitivity of a cone from only a few known parameters; the spectral position of the visual pigment's peak absorbance (λ_{max}) and the oil droplet's cut-off wavelength (λ_{cut}). The cut-off wavelength is the shortest wavelength at which there still is a significant transmittance of light (Hart & Vorobyev, 2005; Lipetz, 1984). In addition to this, also the wavelength of 50% transmittance (λ_{mid}) of the oil droplet is

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needed for the model calculations. However, there is a correlation between λ_{cut} and λ_{mid} that makes it possible to approximate λ_{mid} when only λ_{cut} is known (Hart & Vorobyev, 2005).

The parameters (λ_{max}, λ_{cut}, λ_{mid}) required in the models are estimated by microspectrophotometry (MSP; Hart, 2001b; Liebman, 1972). Due to the small dimensions of the oil droplets and the photoreceptors, MSP measurements are noisy (Bowmaker, Heath, Wilkie, & Hunt, 1997; Hart & Vorobyev, 2005; Lipetz, 1984; MacNichol, 1986), which leads to a considerably amount of variation in the parametric values. Hence, there is a certain level of uncertainty in the model predictions.

Cone spectral sensitivities can also be explored in colour matching experiments. These tests are based on the theory that any spectral stimulus coded by n receptors can be matched by a specific mixture of n other spectral stimuli (Goldsmith & Butler, 2005; Kelber et al., 2003). When a match is established, the single stimulus and the mixture excite the receptor array equally and are thus inseparable. Colour matching results are thus directly related to the absorbance properties of the cones. This allows for a direct comparison between receptor responses that are measured through the behavioural experiments and those that are estimated through model predictions based on MSP measurements (Goldsmith & Butler, 2005).

A colour matching test provides information on the number of active, colour coding receptor types and their spectral sensitivities. Another behavioural experiment, the spectral sensitivity threshold test can also be used to explore these properties and this test might also serve to reveal mechanisms in colour vision such as the post-receptor processing of receptor outputs (Kelber et al., 2003).

The spectral sensitivity experiment tests a subject for its performance in distinguishing large chromatic stimuli presented on an adapting background (Goldsmith & Butler, 2003; Kelber et al., 2003; Maier, 1992). In 1998, Vorobyev and Osorio proposed a model in which they assumed that spectral sensitivity thresholds are set by receptor noise as it is propagated into higher-order neural mechanisms. The model is most carefully tested for honeybees (Vorobyev, Brandt, Peitsch, Laughlin, & Menzel, 2001) but has also been used for several other di-, tri-, and tetrachromats (Vorobyev & Osorio, 1998). The receptor noise-limited model allows for an estimation of discrimination thresholds. It is today widely used in various studies to answer the questions whether, and how well, birds (or other animals) can detect and discriminate objects such as fruit, other birds, or other stimuli (e.g. Håstad, Victorsson, & Ödeen, 2005; Herrera et al., 2008; Schaefer, Schaefer, & Vorobyev, 2007; Vorobyev, Osorio, Bennet, Marshall, & Cuthill, 1998; Vorobyev, 2003).

Considering the frequent use of colour vision models it is of importance to determine how sensitive they are to parametric variation. With such information it is possible to appreciate how precise the model predictions are and to what extent it is possible to rely on model predictions instead of performing time-consuming behavioural tests on a large number of species.

In this study we examine how sensitive the models describing colour matching, spectral sensitivity, and wavelength discrimination thresholds are to variation in receptor noise, visual pigment absorbance, oil droplet absorbance, and ocular media absorbance. This is done by comparing model predictions to behavioural data describing the same properties. Four species of bird are included in the study; the budgerigar (*Melopsittacus undulatus*), the pigeon (*Columba livia*), the domestic chicken (*Gallus gallus*), and the domestic duck (*Anas platyrhynchos*). For this purpose, we also measured the ocular media transmittance in the budgerigar, the pigeon, and the chicken, for which data are either missing (budgerigar) or ambiguous (chicken and pigeon; Emmerton, Schwemer, Muth, & Schlecht, 1980; Govardovskii & Zueva, 1977).

2. Methods and theory

2.1. Experimental data

Experimental data from earlier studies presented in graphic form were digitized using WinDig 2.5 (Lovy, 1996) and Plot Digitizer 2.4.1 (Huwaldt, 2005). The stimuli spectral distributions used in the budgerigar colour matches were provided by the authors directly (Goldsmith, personal communication). The monochromatic stimuli used in the colour matches of the pigeon were assumed to be Gaussian functions with full bandwidths at half maximum as specified in the articles (Palacios, Martinoya, Bloch, & Varela, 1990; Palacios & Varela, 1992).

2.2. Measurements of pre-retinal tissue transmittance

Three budgerigars were anaesthetized with carbon dioxide and decapitated. The eyes were excised and a small portion (approximately 3×3 mm) of the sclera and retina at the posterior pole of the eye was removed. The eye was placed with the pupil facing downwards in a plastic container (12 mm path length), through which a 4 mm hole had been drilled in the bottom and covered by a fused silica window (UQG optics). Metallic ring inserts were used to stabilize the position of the eye. Eyes were bathed and measured in 340 mosmol kg^{-1} PBS. Reference scans were made with the same container including the inserts and PBS. The light source was a xenon lamp (Cermax Xenon Fiberoptic Light Source, ILC Technologies). The transmittance of the ocular media of each eye was measured with five repeats at 1 nm steps from 220 to 1050 nm with a spectroradiometer (International light, RPS 900-R) attached to a 3 mm hole in the top cover of the container. One eye was damaged by the preparations and data from this eye were therefore excluded from further analysis.

The data from each eye were smoothed with an 11-step running average to reduce noise. The transmittance was normalized to the value at 700 nm, where we assume that only insignificant amounts of light are absorbed by the ocular media. As a final step the mean transmittance of the 25 measurements of all five eyes was calculated. The experiments were approved and followed the ethical guidelines of the Swedish board of agriculture (M206-07).

This procedure was repeated for the domestic fowl and the pigeon with few modifications. The excised portions of the sclera at the posterior pole of the eye were approximately 4×4 mm and the eyes were placed in a plastic container similar to that used in the budgerigar measurements but larger (26 mm path length). Four eyes from two domestic fowls and seven eyes from four pigeons (one pigeon eye was damaged and could not be used) were measured and each eye was sampled three times.

2.3. Colour match model

A colour match is established when an array of n photoreceptors is stimulated equally by a single spectral stimulus and the mixture of n other stimuli (Kelber et al., 2003). For the budgerigar and the pigeon we can limit the number of photoreceptors to $n = 2$ because these species have cones with narrow spectral sensitivities so that their eyes are functionally dichromatic in each spectral region for which colour match tests have been performed. The double cones are assumed to transfer achromatic information only and are ignored in this study.

For a dichromatic colour match two photoreceptors, P_s and P_l, respond to a single stimulus, S_0, and the mixture of two stimuli, $S_s + S_l$ (the subscripts refer to the relative wavelength position of peak absorbance or quantum flux, s = shorter, l = longer). The expected ratio, r, of the stimuli intensities, I, in the mixture at match is then related to the quantum catches of the photoreceptors, q, through,