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Tetrachromacy, oil droplets and bird plumage colours

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Abstract There is a growing body of data on avian eyes, including measurements of visual pigment and oil droplet spectral absorption, and of receptor densities and their distributions across the retina. These data are sufficient to predict psychophysical colour discrimination thresholds for light-adapted eyes, and hence provide a basis for relating eye design to visual needs. We examine the advantages of coloured oil droplets, UV vision and tetrachromacy for discriminating a diverse set of avian plumage spectra under natural illumination. Discriminability is enhanced both by tetrachromacy and coloured oil droplets. Oil droplets may also improve colour constancy. Comparison of the performance of a pigeon's eye, where the shortest wavelength receptor peak is at 410 nm, with that of the passerine *Leiothrix*, where the ultraviolet-sensitive peak is at 365 nm, generally shows a small advantage to the latter, but this advantage depends critically on the noise level in the sensitivity mechanism and on the set of spectra being viewed.

Key words Bird · Colour · Vision · UV · Plumage

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Abbreviations *LWS* long-wave sensitive · *MWS* medium-wave-sensitive · *SWS* short-wave-sensitive · *UVS* ultraviolet-sensitive

Introduction

Bird eyes have a number of features which suggest they are well adapted for colour vision. There are four types of cone photopigment with peak sensitivities ranging from 365 nm to 565 nm (Fig. 1), and each cone contains a coloured oil droplet which sharpens spectral tuning (Bowmaker 1980). Given the colourfulness of their plumage to humans, and the evolutionary importance of their visual displays, it is interesting to ask how oil droplets, UV sensitivity and tetrachromacy affect birds' colour vision, and how their perception of plumage coloration might differ from our own (Burkhardt 1989; Bennett et al. 1994).

To provide a framework for understanding the avian view of plumage spectra, we use a model which assumes that photoreceptor noise sets visual thresholds. Performance is predicted most accurately for small differences (i.e. close to threshold). Thus a key notion is that colour is used for precise judgement of object quality; for example, a fruit's ripeness, or health of a potential mate.

Teleost fish evolved four cone opsins (Hisatomi et al. 1994) and most (possibly all) birds have retained them. Spectral sensitivities of cones, and oil droplet absorption spectra, are known for at least 11 species from 8 orders (Fig. 1; Bowmaker et al. 1997; Hart et al. 1998)¹. The four pigments reside in four types of single cone, and

¹In an owl (Strigiformes) *Strix aluco* and a penguin (Sphenisciformes) *Spheniscus humboldti* three types of cone pigment were found, with four in the remaining eight species from the orders: Procellariiformes (*Puffinus puffinus*), Anseriformes (*Anas platyrhynchos*), Psittaciformes (*Melopsittacus undulatus*), Galliformes (*Gallus gallus*, *Coturnix japonica*), Columbiformes (*Columba livia*) and Passeriformes (*Leiothrix lutea*, *Taenopygia guttata*). The starling (*Sturnus vulgaris*), a passerine, also has four cone pigments (Hart et al. 1998).

one also in a double cone. The peaks of the long-wavelength-sensitive (LWS) and medium-wavelength-sensitive (MWS) pigments differ little between species, that of the short-wave-sensitive (SWS) pigment varies over a range of about 25 nm, while the shortest wavelength (UVS) pigment is most variable. In some species (e.g. passerines *Leiothrix lutea* and *Sturnus vulgaris*; and budgerigar *Melopsittacus undulatus*) the UVS peak is at about 365 nm, while in others (e.g. pigeon, *Columba livia*) it is at 410 nm (Bowmaker et al. 1997; Hart et al. 1998). There is evidence from electroretinography of pigeon for a fifth receptor with a peak below 400 nm (Hzn et al. 1994); however this observation is not substantiated by microspectrophotometry or behavioural evidence (see also Vorobyev and Osorio 1998).

Cone inner segments of most classes of vertebrate contain an oil droplet, and these are coloured in lungfish, reptiles and birds (Walls 1942; Robinson 1994). Amongst suggested roles for oil droplets have been: colour vision, prevention of short-wave photodamage and reduction of chromatic aberration (Walls 1942; Bowmaker 1980; Govardovskii 1983; Partridge 1989). In avian single cones, each visual pigment is associated with one type of oil droplet which acts as a cut-off filter, absorbing wavelengths below a critical value, and transmitting longer wavelengths (Maier and Bowmaker 1993; Bowmaker et al. 1997). Oil droplets in the LWS cones and MWS cones, called 'red' and 'yellow', respectively, cut off close to the sensitivity maxima of their photopigments, narrowing spectral tuning and reducing absolute sensitivity by ca. 50% (Fig. 1). By contrast, SWS cone and UVS cone oil droplets, called 'clear' and 'transparent', affect spectral tuning less. Double cones, which contain the LWS opsin, have a droplet of variable colour in their large member (Bowmaker et al. 1997).

The receptor noise model of visual thresholds

To understand performance of the avian eye in discrimination and recognition of plumage colours, we compare eyes modelled on those of the Pekin robin, *Leiothrix lutea* (henceforth called *Leiothrix*) and pigeon (Fig. 1), with modified versions where either one of the receptor types, or the oil droplets are removed. Relating eye design to visual ability is worthwhile only if behaviourally significant discrimination thresholds are set by the eye. Here, performance is predicted using a model of colour coding which attributes thresholds to receptor noise (Osorio and Vorobyev 1996; Brandt and Vorobyev 1997; Vorobyev and Osorio 1998). No assumptions are made about neural mechanisms such as opponency coding, save that the achromatic signal is disregarded. Predictions (Fig. 2) are accurate for *light-adapted* eyes of pigeon (yellow but not red retinal field; Remy and Emmerton 1989) and of *Leiothrix*, as well as for other animals including humans (Vorobyev and Osorio 1998).

A notable prediction of the model is the elevated spectral sensitivity in the near-UV, found in *Leiothrix*

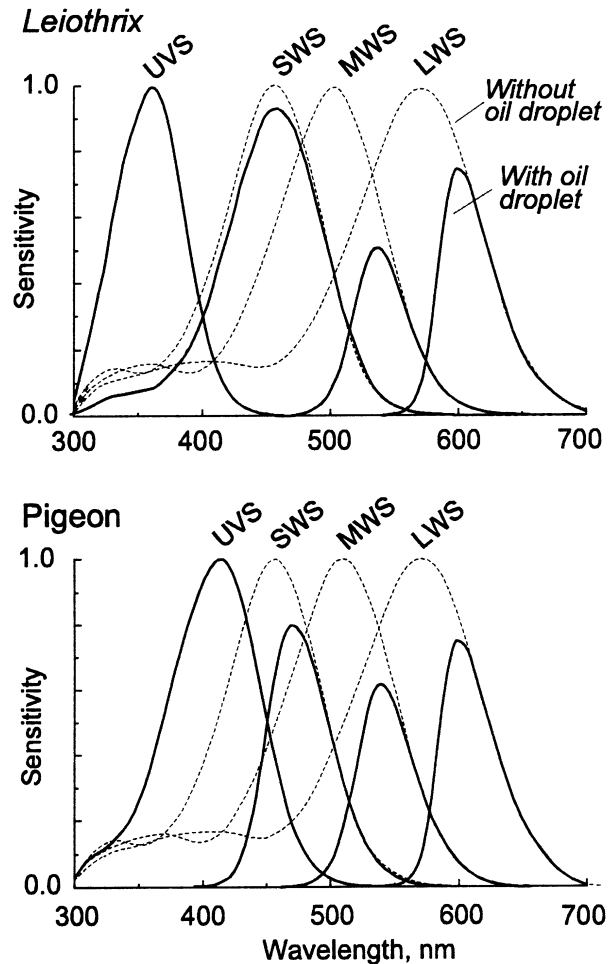


Fig. 1 Spectral sensitivities of single cones in Pekin robin (*Leiothrix lutea*) and pigeon (*Columba livia*) eyes based on optical models derived from microspectrophotometry of the cone photopigments, and of oil droplets. The data are from Bowmaker et al. (1997), and curves fitted to pigment peaks using Maximov's (1988) formula. Optical density of cones at λ_{\max} is assumed to be 0.4. Sensitivity maxima are around 565 nm (long-wavelength-sensitive; LWS), 505 nm (medium-wavelength-sensitive; MWS), 450 nm (short-wavelength-sensitive; SWS), and either around 410 nm (pigeon and chicken) or 365 nm (passerines and budgerigar; violet/UV-sensitive; UVS). 410 nm is close to the 420 nm peak of the human 'blue' cone pigment, but pigeons have greater sensitivity to UV light than humans owing to the high UV transmittance of their ocular media (Emmerton et al. 1980)

and for pigeon (Fig. 2). This is not due to especially high sensitivity of the UV mechanism (which in *Leiothrix* is the noisiest of the four), but rather the combination of UVS–SWS chromatic signals for short-wavelength monochromatic lights, and low adapting intensity in the UV part of the spectrum (c.f. Burkhardt and Maier 1989; Maier 1994). For pigeon the model predicts spectral sensitivity in the short-wave part of the spectrum well, and there is no evidence for a fifth, UV, receptor (c.f. Hzn et al. 1994). Deviations from the predictions, which occur in dim conditions, and in the pigeon red field, are probably attributable to inputs from an achromatic mechanism (Vorobyev and Osorio 1998).