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Section 1

Visual pigments, cone oil droplets, ocular media and predicted spectral sensitivity in the domestic turkey (*Meleagris gallopavo*)

N.S. Hart [a,b,*], J.C. Partridge [a], I.C. Cuthill [a]

[a] *School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*
[b] *Vision, Touch and Hearing Research Centre, University of Queensland, Brisbane, Queensland 4072, Australia*

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Abstract

A microspectrophotometric survey conducted on the retinal photoreceptors of the domestic turkey (*Meleagris gallopavo*) revealed the presence of five different types of vitamin A_1-based visual pigment (rhodopsin) in seven different types of photoreceptor. A single class of rod contained a medium wavelength-sensitive visual pigment (wavelength of maximum absorbance, λ_{max}, 504 nm). Four different types of single cone contained visual pigment maximally sensitive to wavelengths in either the long (LWS, λ_{max} 564 nm), medium (MWS, λ_{max} 505 nm), short (SWS, λ_{max} 460 nm) or violet (VS, λ_{max} 420 nm) spectral ranges. The LWS, MWS and SWS single cones contained pigmented oil droplets with cut-off wavelengths (λ_{cut}) at 514, 490 and 437 nm, respectively. The VS single cone contained a transparent oil droplet which displayed no significant absorbance above 330 nm. A single class of double cone was also identified, both the principal and accessory members of which contained the LWS cone visual pigment. The principal member contained an oil droplet with a λ_{cut} at 436 nm. No oil droplet was observed in the accessory member. The use of a glycerol-based cell mountant, which reduced wavelength dependent measurement artefacts in the microspectrophotometric measurements, is described. Predictions of cone effective spectral sensitivity, incorporating measurements of the spectral transmission of the ocular media, suggest that turkeys have considerable sensitivity to wavelengths in the ultraviolet-A (UV-A, 315–400 nm) spectral range. This has implications for both the visual ecology of wild birds and the welfare of intensively farmed individuals.

Keywords: Microspectrophotometry; Visual pigment; Oil droplet; Turkey; Ocular media

1. Introduction

Neognathus bird species have among the most complex retinae of any vertebrate (Meyer, 1977). In addition to a single class of medium wavelength-sensitive rod, the retinae of most diurnal birds studied to date contain a single class of long wavelength-sensitive double cone, and four classes of single cone with maximum sensitivities to different regions of the spectrum (Bowmaker, Heath, Wilkie & Hunt, 1997; Hart, Partridge & Cuthill, 1998). Each cone class contains a particular type of oil droplet. Oil droplets are highly refractile spherical organelles located in the photoreceptor between the visual pigment and the incident light. Most contain carotenoid pigments (Wald & Zussman, 1937; Goldsmith, Collins & Licht, 1984), which alter the spectral transmission characteristics of the oil droplets, and are generally considered to act as long-pass cut-off filters (Liebman & Granda, 1975; Bowmaker, 1977; Partridge, 1989). Consequently, the effective spectral sensitivity of a cone photoreceptor is determined by both the spectral transmission of the oil droplet (and that of other pre-retinal filters, particularly the lens and cornea) and the spectral absorptance of the visual pigment (Baylor & Hodgkin, 1973; Neumeyer & Jäger, 1985; Kawamuro, Irie & Nakamura, 1997).

The ability of birds to detect wavelengths in the ultraviolet-A (UV-A, 315–400 nm) spectral range was first demonstrated in hummingbirds (*Colibri serriros-tris*) (Huth & Burkhardt, 1972) and pigeons (*Columba livia*) (Wright, 1972). Avian retinae contain a cone visual pigment maximally sensitive to wavelengths be-

* Corresponding author. Tel.: +61-7-33654484; fax: +61-7-3365-4522.
E-mail address: n.hart@vthrc.uq.edu.au (N.S. Hart)

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tween 403 and 426 nm, as in the duck *Anas platyrhynchos* (Jane & Bowmaker, 1988), pigeon (Bowmaker et al., 1997), chicken *Gallus gallus* (Fager & Fager, 1981; Yoshizawa & Fukada, 1993; Bowmaker et al., 1997), penguin *Spheniscus humboldtii* (Bowmaker & Martin, 1985) and Japanese quail *Coturnix coturnix japonica* (Bowmaker, Kovach, Whitmore & Loew, 1993), or between about 355 and 380 nm, as in the Pekin robin *Leothrix lutea* (Maier & Bowmaker, 1993), zebra finch *Taeniopygia guttata*, budgerigar *Melopsittacus undula-*

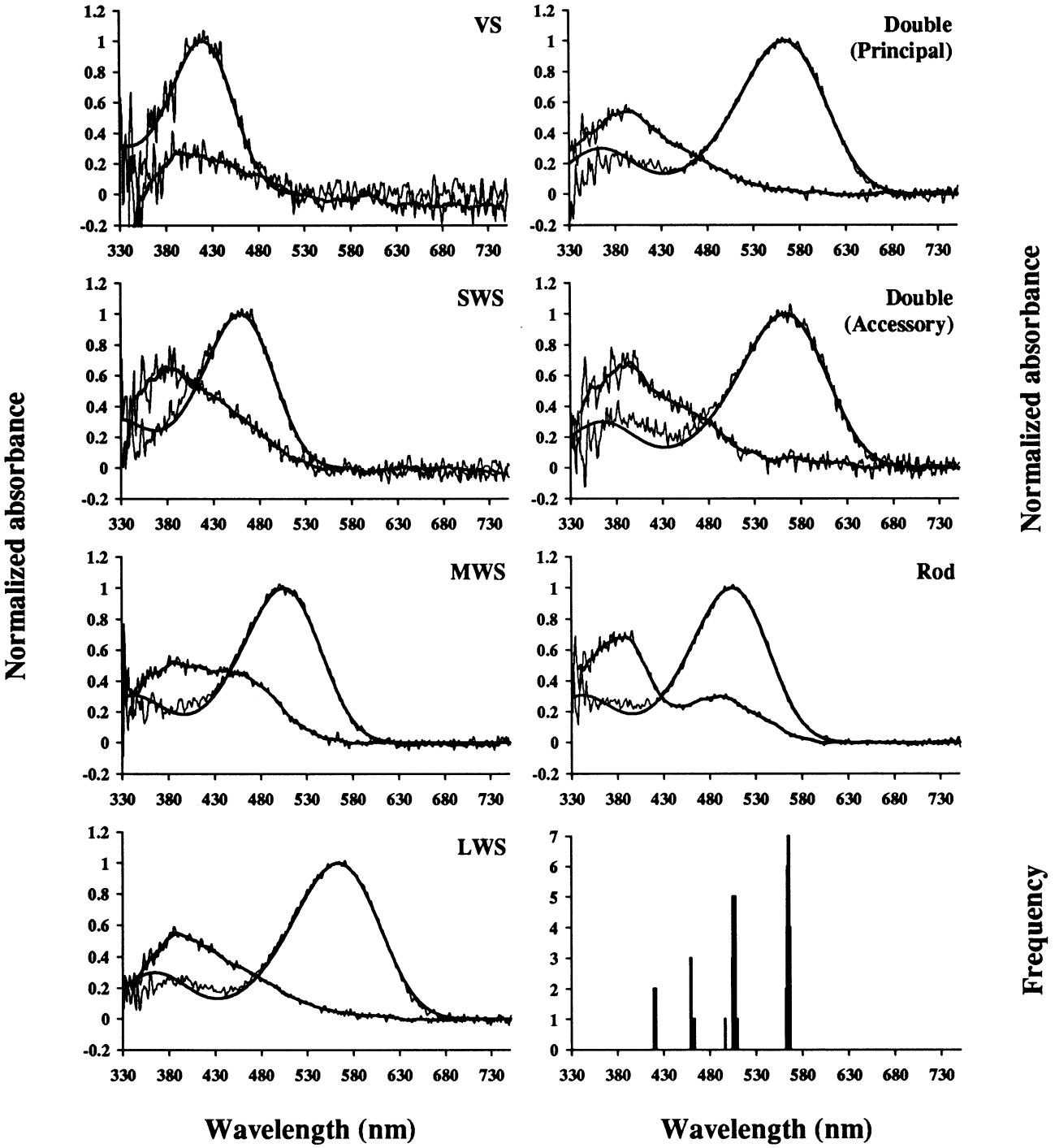

Fig. 1. Normalized mean absorbance spectra of visual pigments in the rod, double and single cones from *Meleagris gallopavo* measured whilst mounted in a solution of phosphate buffered saline containing 75% glycerol (GPBS). Mean pre-bleach spectra (upper traces) are shown with superimposed best-fitted visual pigment templates (solid lines) and mean post-bleach spectra (lower traces) with their running averages (solid lines). The histogram shows the wavelengths of maximum absorbance (λ_{max}) obtained for the analysis of the visual pigments of single and double cone photoreceptors. VS, violet-sensitive; SWS, short wavelength-sensitive; MWS, medium wavelength-sensitive; LWS, long wavelength-sensitive single cones.

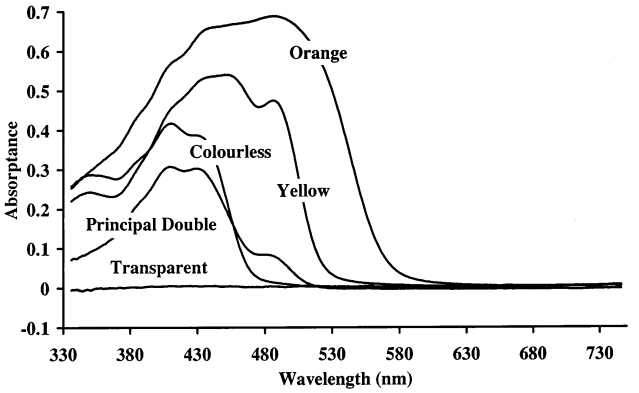

Fig. 2. Mean absorptance spectra of oil droplets in the cone photoreceptors of the turkey. Each line represents an 11-point running average passed through the averaged absorptance spectra data. No oil droplet was observed in the accessory member of the double cone. Rods do not contain an oil droplet.

tus (Bowmaker et al., 1997) and starling *Sturnus vulgaris* (Hart et al., 1998).

The UV-A waveband is an essential component of the visual ecology of many birds. Conspecific signals in Pekin robins (Maier, 1993), zebra finches (Bennett, Cuthill, Partridge & Maier, 1996; Hunt, Cuthill, Swaddle & Bennett, 1997), starlings (Bennett, Cuthill, Partridge & Lunau, 1997), bluethroats *Luscinia svecica svecica* (Andersson & Amundsen, 1997) and blue tits *Parus caeruleus* (Hunt, Bennett, Cuthill & Griffiths, 1998) are affected if the UV component of plumage coloration is removed. The role of UV in prey detection predicted by Burkhardt (1982) and has been demonstrated in hummingbirds *Archilochus alexandri*, *Lampornis clemenciae*, and *Eugenes fulgens* (Goldsmith, 1980), kestrels *Falco tinnunculus* (Viitala, Korpimaki, Palokangas & Koivula, 1995) and blue tits (Church, Bennett, Cuthill & Partridge, 1998). In this communication, we provide physiological evidence that a widely

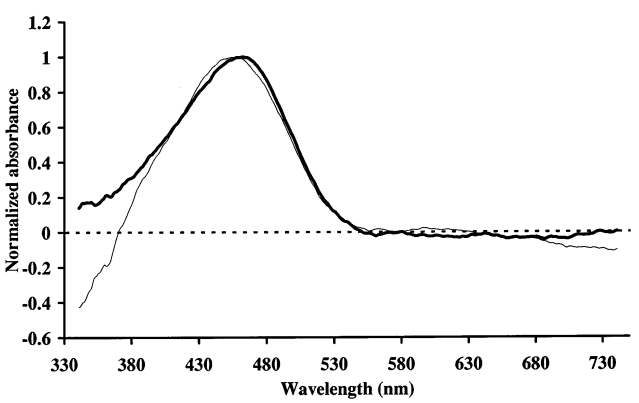

Fig. 3. Normalized mean prebleach absorbance spectra of the SWS cone outer segment mounted in 5% dextran in phosphate buffered saline (DPBS, thin line), or in 75% glycerol in phosphate buffered saline (GPBS, bold line). Each line is a 21-point unweighted running average applied to the raw data.

farmed commercial species of poultry, the domestic turkey (*Meleagris gallopavo*), which is known to display preferences for both the chromatic composition (Smith, McDaniel, Skotko & Owen, 1989) and intensity (Sherwin, 1998) of some ambient irradiance regimes, also has the potential for vision in the UV-A spectral range.

In addition, we describe the use of an alternative cell mountant (a solution of phosphate buffered saline containing 75% glycerol) developed to reduce measuring artefacts due to refractive index discontinuities in MSP preparations. Outer segments typically have a high refractive index (RI, 1.39 cones, 1.41 rods, Sidman, 1957) relative to the surrounding medium and take on a granular appearance as they deteriorate following enucleation (Levine & MacNichol, 1985). These properties are likely to cause Rayleigh and Mie scattering, both of which are wavelength-dependent and increase at short wavelengths (Born & Wolf, 1970). Scattering of light by outer segments may increase the apparent short wavelength absorbance in MSP measurements of visual pigments and shift the apparent λ_{max} to shorter wavelengths (Levine & MacNichol, 1985). However, scattering or refraction might also change the apparent absorbance by focusing the MSP measuring beam onto the photomultiplier tube (PMT) differently between sample and baseline scans, or by changing the path of the transmitted light through the collecting objective optics, which may differ in their absorption of short wavelengths. In the worst cases, this can produce an apparent negative absorption when the signal from the PMT is higher for the sample than the baseline. Because scattering is greater at short wavelengths, this artefact is most apparent in MSP measurements below 400 nm where the signal to noise ratio is often low due to the paucity of short wavelength photons from many MSP light sources. Scattering occurs when light undergoes a change in phase at the interface between media of different refractive index. MSP preparations are usually mounted in saline with additional high molecular weight dextran to reduce cellular movement (Mollon, Bowmaker & Jacobs 1984; Hart et al., 1998). The RI of this mountant is relatively low (RI 10% 242 00 RMM dextran in PBS approximately 1.34). Using glycerol as a mountant (RI 75% glycerol in PBS approximately 1.43) reduces the difference in RI between the outer segment and the surrounding medium, and in this paper we demonstrate its advantages in microspectrophotometry of small photoreceptors.

2. Materials and methods

2.1. Microspectrophotometry

Measurements were made of the absorbance spectra of retinal photoreceptors from 5 and 24 week old male

Table 1
Wavelengths of maximum sensitivity (λ_{max}) for the visual pigments found in the retinal photoreceptors of the domestic turkey *Meleagris gallopavo* measured in different mountants[a]

	VS	SWS	MWS	LWS	Principal double	Accessory double	Rod
Photoreceptors mounted in phosphate buffered saline containing 5% dextran (DPBS)							
λ_{max} of mean prebleach spectrum	417.9 ± 1.9	457.6 ± 1.5	504.3 ± 0.7	563.4 ± 2.9	564.2 ± 1.0	–	503.5 ± 0.5
Mean λ_{max} of prebleach spectra	417.8 ± 2.4	456.7 ± 2.3	504.6 ± 3.4	563.1 ± 0.4	563.8 ± 2.6	–	503.5 ± 1.3
No. of cells	2	4	9	3	9	0	6
Photoreceptors mounted in phosphate buffered saline containing 75% glycerol (GPBS)							
λ_{max} of mean prebleach spectrum	419.7 ± 1.96	459.3 ± 1.4	505.4 ± 0.9	563.4 ± 1.0	563.8 ± 1.3	563.4 ± 2.6	504.2 ± 0.7
Mean λ_{max} of prebleach spectra	419.6 ± 1.3	459.9 ± 1.9	505.2 ± 3.6	563.6 ± 1.3	564.1 ± 1.2	563.9 ± 1.1	504.2 ± 0.5
No. of cells	4	5	10	10	8	5	6

[a] Values are ± 1 S.D. Standard deviations for the λ_{max} value of each mean visual pigment absorbance spectrum refer to the variance in λ_{max} estimates obtained from data points on the long wavelength limb of the mean absorbance spectrum using the polynomial of Partridge and DeGrip (1991), as described in Section 2. Standard deviations for the mean λ_{max} values represent the observed variance of individual records used to create the mean spectra. The effect of mountant type on λ_{max} was non-significant ($P = 0.128$; see Section 3). VS, violet-sensitive; SWS short wavelength-sensitive; MWS, medium wavelength-sensitive; LWS, long wavelength-sensitive single cones.

domestic turkeys (strain BUT8). Subjects were held in darkness for several hours prior to sacrifice by approved humane methods. Preparation of retinal tissue for analysis using a microspectrophotometer (MSP) was as described previously (Hart et al., 1998). Photoreceptors were mounted either in a 75% glycerol solution (BDH) or a 5% dextran solution (Sigma 242 000 RMM), here referred to as GPBS and DPBS, respectively, both of which were diluted with phosphate buffered saline (PBS; Dulbecco A tabletised PBS made to a concentration of 340 mOsm kg^{-1}, Oxoid Ltd, Basingstoke, UK) and adjusted to pH 7.3 using 1 M NaOH. Separate retinal preparations were made for the measurement of oil droplet absorption spectra and these samples were mounted in pure glycerol. Although glycerol has been used without apparent detriment to the measurement of oil droplet absorption spectra by MSP (e.g. Partridge, 1989; Hart et al., 1998), the use of GPBS for outer segment preparations has several potential problems. Firstly, glycerol, even when diluted with saline, has a very high osmolality (75% glycerol $> 8.33 \times 10^3$ mOsm kg^{-1}). However, it appears that the osmotic shock occurs so quickly as to avoid damage by swelling and bursting of cells, presumably because the glycerol rapidly infiltrates the outer segment. Secondly, glycerol does not act as a buffer, but dilution with PBS maintains a suitable pH in the mountant for the duration of MSP recordings, albeit with low buffering capability. Thirdly, GPBS contains a lower concentration of chloride ions (41 mM) than isosmotic DPBS (162 mM). Chloride depletion causes hypsochromatic shifts in the λ_{max} of the LWS cone visual pigment (iodopsin) in extracts from chicken retinae (Knowles, 1976; Shichida, Kato, Sasayama, Fukada & Yoshizawa, 1990). At the chloride ion concentration of GPBS, however, less than 2% of the total iodopsin in a digitonin extract would be chloride depleted (Shichida et al., 1990). GPBS solution does, however, have the advantage of absorbing less light, particularly of short wavelengths, than DPBS, and is sufficiently viscous to prevent significant cell movement. The MSP used is a computer-controlled, single beam, wavelength-scanning design, the construction and operation of which is described in detail elsewhere (Hart et al., 1998).

2.2. Analysis of visual pigment absorbance spectra

MSP baseline and sample scans, made from tissue-free and cellular samples, respectively, were converted

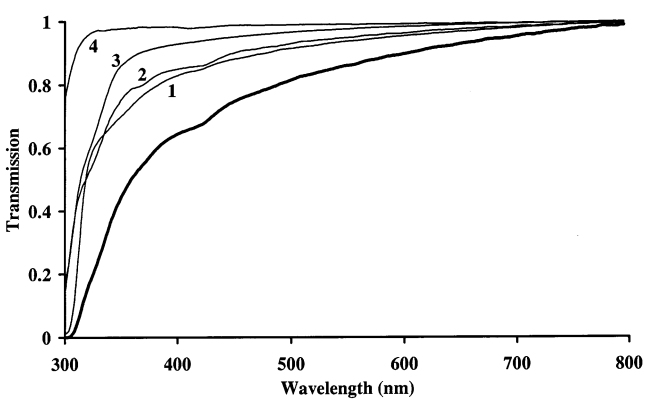

Fig. 4. Calculated transmission spectra, on the optic axis of the eye, of the ocular media of *Meleagris gallopavo*. Thin lines: (1) lens; (2) cornea; (3) aqueous humour; and (4) vitreous humour. Thick line, combined ocular media. The wavelength of 0.5 transmission of the combined ocular media was 358 nm. Each line represents an 11-point unweighted running average applied to the raw data.

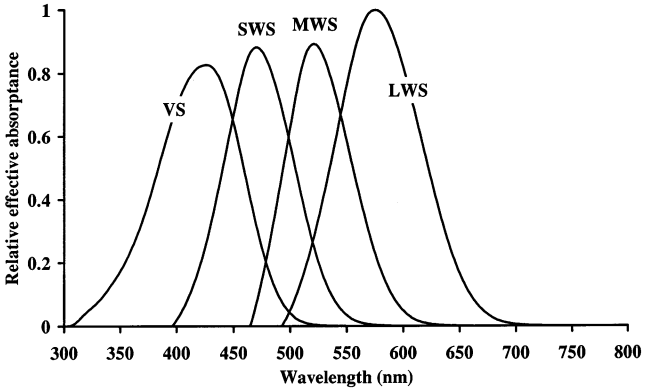

Fig. 5. Calculated spectral sensitivities of the four single cone types in the domestic turkey, expressed as effective absorptance relative to the LWS single cone. The wavelengths of peak sensitivity for the VS (violet-sensitive); SWS (short wavelength-sensitive); MWS (medium wavelength-sensitive) and LWS (long wavelength-sensitive) cones are 426, 470, 521 and 575 nm, respectively.

into absorbance values at 1 nm intervals. Absorbance was measured at each odd wavelength on the downward long wavelength to short wavelength spectral pass and at each interleaved even wavelength on the upward short wavelength to long wavelength spectral pass. The upward and downward scans were averaged by fitting a weighted (delta function) three point running average to the data. Specifically, the two absorbance values on either side of a datum were averaged and this mean averaged with the datum.

The data were analysed as described previously (Hart et al., 1998), and the wavelength of maximum absorbance (λ_{max}) was determined using the polynomial derived by Partridge and DeGrip (1991). Specifically, each point on the long wavelength limb of the absorbance spectrum with an absorbance between 80 and 20% of the normalized maximum was used to estimate the λ_{max}, the average of all these estimates being taken as the best estimate of the λ_{max} of the visual pigment (Partridge & DeGrip, 1991). For display, the λ_{max}/λ transformed rhodopsin template of Stavenga, Smits and Hoenders (1993) was used, but with the β-peak of the absorbance spectrum shifted linearly with respect to the α-peak as suggested by Palacios, Goldsmith and Bernard (1996), and utilising the relative extinction coefficients of the α- and β-peaks proposed by Stavenga et al. (1993).

Visual pigment absorbance spectra were subjected to an acceptance procedure, the justification of which has been explained by Levine and MacNichol (1985). Scans were accepted for averaging if: (i) the template spectrum fell within the peak-to-peak noise of the data between 80% normalized maximum absorbance on the short wavelength limb and 20% normalized maximum absorbance on the long wavelength limb; (ii) the absorbance spectra were flat for at least 100 nm beyond the wavelength at which the long wavelength limb first falls to an absorbance of zero; (iii) were confirmed as photolabile by bleaching; and (iv) were free from obvious distortions at wavelengths longer than the λ_{max} (Levine & MacNichol, 1985).

2.3. Analysis of oil droplet absorptance spectra

Because of their small size, spherical shape, high refractive index and high carotenoid concentration (Goldsmith et al., 1984), light leakage around oil droplets during MSP measurement is considerable. Consequently, recorded absorptance spectra tend to be limited to a maximum absorptance of approximately 0.9, and display a flat-topped cut-off character (Liebman & Granda, 1975). Oil droplets are described by their cut-off wavelength (λ_{cut}), which is the wavelength of the intercept at the value of maximum measured absorptance by the line tangent to the oil droplet absorptance curve at half maximum measured absorptance (Lipetz, 1984).

2.4. Spectrophotometry of pre-retinal tissue and ocular humours

Absorbance measurements of the cornea, aqueous humour, lens and vitreous humour were made over the range 200–800 nm using a Shimadzu UV2101 PC UV-VIS scanning spectrophotometer fitted with a Shimadzu ISR-260 integrating sphere assembly to reduce the effects of light scattering by the tissue samples. The cornea was excised from the sclera and measured whilst sandwiched between two stainless steel mesh inserts inside a standard (10 mm pathlength) quartz cuvette. The lens was dissected away from the anterior segment of the eye and measured using an aluminium insert, designed to fit inside a standard cuvette, in which a 6.0 mm hole (the same diameter as the lens) had been drilled to coincide with the measuring beam of the spectrophotometer, and in which the lens could be positioned in its normal orientation to the incident light. Vitreous humour was removed from the vitreal body and measured in a similar fashion, but using an insert with a 4.5 mm hole. The vitreous, which is a highly viscous gel, was trimmed in the insert to give a pathlength of exactly 10 mm. For measurement, the cornea, lens and vitreous humour were bathed in 340 mOsm kg^{-1} PBS, which was also placed in the identical inserts and cuvettes in the reference channel of the spectrophotometer. Aqueous humour was removed from the anterior chamber, using a hypodermic syringe, and measured in a 200 μl, 1 cm pathlength quartz cuvette relative to distilled water. The absorbance measurements of both the aqueous and vitreous humour were scaled arithmetically to correspond to in vivo ocular pathlengths. These were determined from scaled

photographs of a hemisected frozen eye, taken from the same individual used for the spectrophotometric measurements of the pre-retinal media and sectioned using a cryostat.

3. Results

3.1. Photoreceptors

The turkey retinae contained five types of rhodopsin (vitamin A_1-based) visual pigments (Fig. 1) and five types of oil droplet (Fig. 2) in seven different types of photoreceptor. A single class of rod contained a medium wavelength-sensitive visual pigment with a mean wavelength of maximum sensitivity (λ_{max}) at 504.2 nm (standard deviation of the mean of λ_{max} measurements ± 0.5 nm, $N = 6$ cells). Rods do not contain oil droplets. Cone photoreceptors containing an orange oil droplet (mean λ_{cut} 514.2 ± 9.2 nm, $N = 26$) were associated with a long wavelength-sensitive (LWS) visual pigment (mean λ_{max} 563.6 ± 1.3 nm, $N = 10$). Cones containing a yellow oil droplet (mean λ_{cut} 490.1 ± 2.9 nm, $N = 36$) were associated with a medium wave-sensitive (MWS) visual pigment (mean λ_{max} 505.2 ± 3.6 nm, $N = 10$). Cones containing a 'colourless' oil droplet (mean λ_{cut} 437.4 ± 2.5 nm, $N = 10$) were associated with a short wavelength-sensitive (SWS) visual pigment (mean λ_{max} 459.9 ± 1.9 nm, $N = 5$). Cones containing a truly transparent oil droplet, with no detectable absorbance between 330 and 750 nm, were associated with a violet-sensitive (VS) visual pigment (mean λ_{max} 419.6 ± 1.3 nm, $N = 4$). Both members of the double cone pair contained the LWS visual pigment, but an oil droplet was only detected in the principal member (mean λ_{cut} 436.4 ± 3.9 nm, $N = 12$).

The effect of using a 75% glycerol in PBS solution (GPBS) instead of a 5% dextran in PBS solution (DPBS), to reduce the difference in refractive index (RI) between the outer segment and the surrounding medium, is evident in Fig. 3 (Table 1). The apparent negative absorption by the visual pigment (thin line in Fig. 3) at short wavelengths is due to wavelength-dependent scattering and/or refraction of the measuring beam by the outer segment when mounted in a suspension medium of relatively low RI. A high concentration of glycerol in the suspension medium increases its RI and reduces this effect (thick line in Fig. 3). Mounting cells in the GPBS solution did not affect the λ_{max} of visual pigments measured in this study. A two-way analysis of variance (ANOVA, MiniTab 10.51, Minitab, Inc.) was performed on the rank-transformed (Seamen, Walls, Wise & Jaeger, 1994) λ_{max} values obtained for each of the photoreceptor types measured using the two mountants (except the accessory member of the double cone, which was not measured in retinae mounted in DPBS), and the effect of mountant was found to be non-significant ($F_{1, 69} = 2.37$; $P = 0.128$). The benefit of using GPBS will be more obvious in the determination of λ_{max} values for visual pigments with maximum sensitivity in the UV-A spectral range. A drop in apparent absorbance below 380 nm is still evident in some of the scans displayed in Fig. 1. This may be attributable to light scatter within the outer segment and due to differences in RI between the cytoplasm and lipid membranes.

3.2. Ocular media

The spectral transmission of the combined ocular media of the domestic turkey is shown in Fig. 4, as are the spectral transmissions of the individual components (cornea, aqueous humour, lens and vitreous humour). Each line represents an 11-point unweighted running average fitted to the raw data to smooth random noise. The pathlength for light travelling along the optic axis of a juvenile turkey eye was calculated as follows. The cornea and lens were measured entire so no further correction of measured pathlength was required. The in vivo pathlengths of the aqueous and vitreous humours were determined from a photograph of a frozen, hemisected eye from the same individual, sectioned along the optic axis, and were 2.7 and 10.4 mm respectively. Measured absorbance spectra (pathlength 10.0 mm) for these two ocular media were scaled appropriately, summed with the absorbance data for the cornea and lens, and the combined absorbance converted to transmission for display. The wavelength of 0.5 transmission of the combined ocular media was 358 nm.

3.3. Calculated effective spectral sensitivities

Spectral sensitivities of the four types of single cone, expressed as effective absorptance relative to the LWS single cone, are displayed in Fig. 5 and were calculated as follows. The visual pigment absorbance spectrum template of Stavenga et al. (1993) was used in preference to data obtained by microspectrophotometry to remove noise from the calculations and eliminate measurement artefacts. The effective absorbance was then calculated for an outer segment with a pathlength of 10 μm and a specific absorbance of 0.015 μm^{-1}. The effective absorbance of the outer segment was then converted into absorptance and multiplied with the transmissions of its respective oil droplet and the combined ocular media at each wavelength. The effective spectral sensitivity of the VS cone suggests that the domestic turkey will have considerable sensitivity to wavelengths between 300 and 400 nm.

4. Discussion

The use of a glycerol-based mountant significantly reduced the effects of wavelength-dependent light scattering and/or refraction by photoreceptor outer segments. Because there was no significant shift in visual pigment λ_{max} associated with the incorporation of high concentrations of glycerol into the suspension medium, it is advised for single-cell MSP.

The number and type of photoreceptor cells present in the turkey retina and the spectral location of their visual pigment λ_{max} values are consistent with the other galliform species investigated so far (Japanese quail and chicken; Govardovskii & Zeuva, 1977; Bowmaker et al., 1993, 1997). Our data also support the findings of Crescitelli, Wilson and Lilyblade (1964) who, by spectrophotometry of retinal extracts, identified the LWS cone visual pigment and the medium wavelength-sensitive rod pigment of the broad-breasted bronze turkey (λ_{max} 562 and 504 nm, respectively).

In many species it is possible to measure either a formed oil droplet or to detect the presence of carotenoid-like absorbing substances in the inner segments of the accessory member of the double cone pair (Bowmaker et al., 1997; Hart et al., 1998). No such oil droplet or absorbance was observed in the turkey. This may be a consequence of the apparent carotenoid deficiency observed in all types of pigmented cone oil droplet, evident by comparison of the oil droplet absorption spectra of this study with those obtained in a previous microspectrophotometric investigation on the American bronze turkey (Strother, 1963). Strother identified red, orange, green and yellow oil droplets which absorbed more short wavelengths than the corresponding droplets measured in this study. The carotenoid pigments responsible for oil droplet coloration (astaxanthin, lutein, zeaxanthin, galloxanthin and ε-carotene) must be obtained from dietary sources (Davies, 1985). The reduction in oil droplet pigmentation in the domestic turkeys examined here is presumably either a result of selective breeding for domestication, the light environment in which they were raised, or carotenoid deficiency in commercially available feed.

Plumage feathers are at least one aspect of the domestic turkey's environment that may contain visual information in the UV-A region of the spectrum (unpublished observations). However, lamps of the type normally used in poultry housing, either fluorescent or incandescent, emit little UV radiation and as such many objects may appear unnatural to the turkeys. If, as the predictions of cone effective spectral sensitivity suggest, domestic turkeys are sensitive to wavelengths in the UV-A spectral range, the provision of supplementary UV to levels found in their natural environment may improve the welfare of intensively farmed birds, for example by redirecting aberrant visually-mediated behaviours generated as a result of an unnatural light environment (Sherwin, personal communication), in addition to any non-visually mediated benefits (Lewis & Morris, 1998).

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