Vision in the peafowl (Aves: Pavo cristatus)

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Summary

The visual sense of the Indian blue-shouldered peafowl Pavo cristatus was investigated with respect to the spectral absorption characteristics of the retinal photoreceptors, the spectral transmittance of the ocular media and the topographic distribution of cells in the retinal ganglion cell layer. Microspectrophotometry revealed a single class of rod, four spectrally distinct types of single cone and a single class of double cone. In the case of the single cone types, which contained visual pigments with wavelengths of maximum absorbance ($\lambda_{\text{max}}$) at 424, 458, 505 and 567 nm, spectral filtering by the ocular media and the different cone oil droplets with which each visual pigment is associated gives predicted peak spectral sensitivities of 432, 477, 537 and 605 nm, respectively. Topographic analysis of retinal ganglion cell distribution revealed a large central area of increased cell density (at peak, 35,609 cells mm$^{-2}$) with a poorly defined visual streak extending nasally. The peafowl has a calculated maximum spatial resolution (visual acuity) in the lateral visual field of 20.6 cycles degrees$^{-1}$. These properties of the peafowl eye are discussed with respect to its visual ecology and are compared with those of other closely related species.

Key words: microspectrophotometry, colour vision, avian retina, visual pigment, cone oil droplet, photoreceptor, visual ecology, ganglion cell topography, ocular media, peafowl, Pavo cristatus.

Introduction

The peafowl Pavo cristatus is a lekking species and males (peacocks) do not provide resources for offspring. It is essential, therefore, for a female (peahen) to reliably assess the genetic ‘fitness’ of a given peacock prior to mating, so that she may adjust her reproductive investment proportionately. The elaborate train of the peacock represents at least one important indicator of male quality that is used by peahens in their assessment; peacocks with more elaborate trains have increased mating success (Petrie and Halliday, 1994), their offspring show improved growth and survival (Petrie, 1994) and peahens lay more eggs for peacocks with larger trains (Petrie and Williams, 1993).

Vision is the primary sense for most birds and, in addition to predator and prey detection, vision is obviously extremely important for intraspecific communication among peafowl, particularly in the assessment of male quality. However, almost nothing is known about their visual capabilities. This paper reports microspectrophotometric measurements of the spectral absorption characteristics of the visual pigments and oil droplets found in their retinal photoreceptors. These data are combined with measurements of the spectral transmittance of the ocular media to predict photoreceptor spectral sensitivities. Data on the topographic organization of the retinal ganglion cell layer are also presented.

Materials and methods

Adult (1 year old) Indian blue-shouldered peacocks Pavo cristatus L. obtained from commercial breeders were euthanased by approved humane methods (overdose of barbiturate anaesthetic). Birds for microspectrophotometric analysis were held in darkness for at least 1 h prior to sacrifice.

Microspectrophotometry

Following enucleation, retinal tissue was prepared for analysis using a microspectrophotometer (MSP) as described elsewhere (Hart et al., 1998, 1999, 2000a,c). Photoreceptors were mounted in a solution of 340 mosmol kg$^{-1}$ phosphate-buffered saline (PBS; Oxoid, UK) diluted 1:3 with glycerol (BDH) and adjusted to pH 7.3 with 1 mol l$^{-1}$ NaOH. Separate retinal preparations were made for the measurement of oil droplet absorbance spectra and these samples were mounted in pure glycerol.

Absorbance spectra (330–750 nm) of individual photoreceptor outer segments and oil droplets were measured using a computer-controlled, wavelength-scanning, single beam MSP (Hart et al., 1998). Sample and baseline scans were made from cellular and tissue-free regions of the preparation, respectively. The dimensions of the measuring beam were adjusted according to the size of the outer segment being measured, and varied from approximately 1 $\mu$m x 1 $\mu$m for oil droplets and small cones to 2 $\mu$m x 10 $\mu$m for rods. Rod outer
segments were fairly robust, measuring approximately 15 μm long and 3–3.5 μm in diameter. Cone outer segments, on the other hand, were usually folded over, or otherwise distorted, so it was difficult to estimate transverse pathlength or outer segment length. For this reason, specific absorbance per mm of cone outer segment was not calculated and the absorbance at the \( \lambda_{\text{max}} \) of the mean difference spectrum was given instead (Table 1).

Data were recorded at each odd wavelength on the ‘downward’ long- to short-wavelength spectral pass and at each interleaved even wavelength on the ‘upward’ short- to long-wavelength spectral pass. Each scan (either sample or baseline) consisted of two downward and two upward spectral passes in alternate succession; spectral passes of the same direction were averaged together. To reduce the effects of in-scan bleaching, only one sample scan was made of each outer segment, but this was combined with two separate baseline scans. Averaging the two absorbance spectra obtained in this way improved the signal-to-noise ratio of the spectra used to determine the wavelengths of maximum absorbance (\( \lambda_{\text{max}} \)) of the visual pigments (Bowmaker et al., 1997). Following the ‘pre-bleach’ scans, outer segments were bleached with full spectrum ‘white’ light from the monochromator for 5 min and an identical number of sample and baseline scans made subsequently. The ‘post-bleach’ average spectrum thus created was deducted from the pre-bleach average to produce a bleaching difference spectrum for each outer segment.

To establish visual pigment-oil droplet pairings, the spectral absorptance of the oil droplet associated with the outer segment (if present) was also measured. A single sample scan was made of each droplet and combined with a single baseline scan. Each scan consisted of only one downward and one upward spectral pass, which were not averaged together. Higher quality oil droplet spectra, showing less evidence of by-passing light (Lipetz, 1984), were obtained from the retinal preparations mounted in pure glycerol, which reduces wavelength-dependent scattering of the MSP measuring beam (Hart et al., 1999).

### Analysis of visual pigment absorbance spectra

Baseline and sample data were converted to absorbance values at 1 nm intervals. Upward and downward scans were averaged together by fitting a weighted (delta function) three-point running average (Hart et al., 2000c). Pre- and postbleach absorbance spectra were then normalized to the peak and long-wavelength offset absorbances determined by fitting a variable-point unweighted running average to the data. Following the method of MacNichol (1986), a regression line was fitted to the normalized absorbance data between 30% and 70% of the normalized maximum absorbance. The regression equation was used to predict the wavelength of maximum absorbance.

### Table 1. Characteristics of rod and cone photoreceptors in the retina of the peafowl (Pavo cristatus) measured using microspectrophotometry

<table>
<thead>
<tr>
<th>Visual pigments</th>
<th>Single cones</th>
<th>Double cones</th>
<th>Rods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>VS</td>
<td>SWS</td>
<td>MWS</td>
</tr>
<tr>
<td>( \lambda_{\text{max}} ) of pre-bleach absorbance spectra (nm)</td>
<td>423.7±2.3</td>
<td>458.0±2.0</td>
<td>504.6±1.9</td>
</tr>
<tr>
<td>( \lambda_{\text{max}} ) of mean pre-bleach absorbance spectrum (nm)</td>
<td>423.3</td>
<td>457.6</td>
<td>504.5</td>
</tr>
<tr>
<td>Mean ( \lambda_{\text{max}} ) of difference spectra (nm)</td>
<td>420.6±4.8</td>
<td>464.6±2.8</td>
<td>510.1±2.2</td>
</tr>
<tr>
<td>( \lambda_{\text{max}} ) of mean difference spectrum (nm)</td>
<td>421.6</td>
<td>463.9</td>
<td>509.7</td>
</tr>
<tr>
<td>Absorbance at ( \lambda_{\text{max}} ) of mean difference spectrum</td>
<td>0.004</td>
<td>0.013</td>
<td>0.017</td>
</tr>
<tr>
<td>Number of cells used in analysis</td>
<td>4</td>
<td>10</td>
<td>5</td>
</tr>
</tbody>
</table>

**Oil droplets**

<table>
<thead>
<tr>
<th>T-type</th>
<th>C-type</th>
<th>Y-type</th>
<th>R-type</th>
<th>P-type (dorsal)</th>
<th>P-type (ventral)</th>
<th>A-type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean ( \lambda_{\text{cut}} ) of absorptance spectra (nm)</td>
<td>(&lt;330)</td>
<td>448.5±3.8</td>
<td>511.3±1.9</td>
<td>569.4±3.9</td>
<td>479.1±9.0</td>
<td>499.6±1.4</td>
</tr>
<tr>
<td>( \lambda_{\text{cut}} ) of mean absorptance spectrum (nm)</td>
<td>(&lt;330)</td>
<td>449.5</td>
<td>511.4</td>
<td>569.6</td>
<td>482.5</td>
<td>499.6</td>
</tr>
<tr>
<td>Mean ( \lambda_{\text{mid}} ) of absorptance spectra (nm)</td>
<td>(&lt;330)</td>
<td>462.1±3.3</td>
<td>525.4±2.3</td>
<td>591.9±4.3</td>
<td>498.8±5.0</td>
<td>513.6±1.4</td>
</tr>
<tr>
<td>( \lambda_{\text{mid}} ) of mean absorptance spectrum (nm)</td>
<td>(&lt;330)</td>
<td>462.7</td>
<td>525.6</td>
<td>592.4</td>
<td>500.4</td>
<td>513.6</td>
</tr>
<tr>
<td>Mean diameter (μm)</td>
<td>3.2±0.8</td>
<td>3.6±0.2</td>
<td>3.6±0.3</td>
<td>3.8±0.3</td>
<td>3.8±0.4</td>
<td>4.0±0.3</td>
</tr>
<tr>
<td>Mean maximum transverse absorptance</td>
<td>(&lt;0.01)</td>
<td>0.88±0.02</td>
<td>0.90±0.02</td>
<td>0.92±0.02</td>
<td>0.48±0.11</td>
<td>0.90±0.03</td>
</tr>
<tr>
<td>Number of oil droplets used in analysis</td>
<td>8</td>
<td>9</td>
<td>28</td>
<td>29</td>
<td>9</td>
<td>22</td>
</tr>
</tbody>
</table>

Values are means ± 1 S.D.

\( \lambda_{\text{max}} \), wavelength of maximum absorbance; \( \lambda_{\text{cut}} \), 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 absorbance; \( \lambda_{\text{mid}} \), wavelength of half maximum measured absorbance (Lipetz, 1984).

Avian rods do not contain oil droplets. T-, C-, Y-, R-, P- and A-type oil droplets are located in the VS, SWS, MWS and LWS single cones and the principal and accessory members of the double cone pair, respectively. Spectra of P-type oil droplets vary considerably between the dorsal and ventral retina.

See list of abbreviations and text for more details.
absorbance ($\lambda_{\text{max}}$) following the methods of Govardovskii et al. (2000). Scans from each photoreceptor type that satisfied established selection criteria (Hart et al., 1999; Levine and MacNichol, 1985) were averaged and reanalysed. Criteria were relaxed for SWS single cones (see Abbreviations), as it was impossible to obtain spectra that did not show at least some distortion of the short wavelength limb.

**Analysis of oil droplet absorptance spectra**

Sample and baseline data were converted into absorptance and normalized to the maximum and long-wavelength offset absorbances obtained by fitting an unweighted 13-point running average to the data (Hart et al., 1998). Oil droplet absorptance spectra are described by their $\lambda_{\text{cut}}$, which is the wavelength of the intercept at the value of maximum measured absorbance by the line tangent to the oil droplet absorptance curve at half maximum measured absorbance (Lipetz, 1984). For comparison with other studies (e.g. Partridge, 1989), the wavelength corresponding to half maximum measured absorbance ($\lambda_{\text{mid}}$) is also given (Lipetz, 1984).

**Spectrophotometry of ocular media**

Absorbance measurements of the cornea, aqueous humour, lens and vitreous humour from one bird 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. Because the eyes were too big to measure in their entirety, the ocular media were measured separately (Hart et al., 1999), and pathlengths were determined from measurements of a radially sectioned frozen eye (see below).

The lens was dissected away from the anterior segment of the eye and placed in a rectangular aluminium insert, designed to fit inside a standard (10 mm pathlength) quartz cuvette, in which a 7.3 mm diameter 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 relative to the incident light. Thin plastic rings were lodged inside the insert hole in front of and behind the lens to prevent movement. The cornea was excised from the sclera and measured whilst sandwiched between two stainless steel mesh inserts inside a standard cuvette. Both cornea and lens were bathed in 340 mosmol kg$^{-1}$ PBS, which was also placed in the identical inserts and cuvettes as reference samples.

Vitreous humour was removed from the vitreal body and placed in the hole (4.5 mm diameter) of an aluminium cuvette insert identical to that used to measure lenticular absorbance. The vitreous, which is a highly viscous gel, was trimmed in the insert to give a pathlength of exactly 10 mm. Aqueous humour was removed from the anterior chamber, using a hypodermic syringe, and measured in a 200µl, 10 mm pathlength quartz cuvette. Both humours were measured relative to distilled water.

The spectrophotometer performed a single spectral pass from 800 nm to 200 nm, recording absorbance at 1 nm intervals. The spectral full width at half maximum bandwidth of the monochromator used by the spectrophotometer was set at 5 nm to maximise light transmission and signal-to-noise ratio, which are otherwise low when using an integrating sphere.

**Determination of optical pathlengths in the peafowl eye**

Pathlengths of the aqueous and vitreous humours along the optic axis were estimated from scaled photographs of a frozen eye, hemisected sagittally using a cryostat. Eyes were frozen at $-20^\circ$C and attached to the chuck of a motor driven microtome using OCT embedding compound (BDH). The eye was orientated such that sections made by the cryostat were parallel to the optic axis, and 10 µm sections were made at $-20^\circ$C until the edge of the lens was visible. Photographs of the eye, and a scale ruler positioned adjacent to the cut face of the eyeball, were then taken after every 10 sections, approximately 0.1 mm intervals. The negatives obtained were projected with a magnification of approximately $\times 13$ using a photographic enlarger and the pathlengths of the aqueous and vitreous calculated according to the scale ruler.

Expansion of the eye upon freezing has a negligible effect on the calculated pathlengths. If the eye is modeled as a sphere 21 mm in diameter (mean of axial and equatorial diameters), and it is assumed that the thermal expansivity of the aqueous and vitreous humours is similar to that of water, the total pathlength along the optic axis of the frozen eye would only be approximately 35 µm longer than at body temperature. This increase in pathlength due to freezing (approximately 0.2%) was less than the likely error in estimating the pathlength by measuring an enlarged photograph (±1.4–5.3%).

**Retinal whole-mount preparation and analysis**

The retina and vitreous of one eye was removed intact by dissection in 340 mosmol kg$^{-1}$ PBS and the pigment epithelium adhering to the photoreceptor layer removed gently with a fine paintbrush. The free-floating retina was fixed for 30 min in 4% paraformaldehyde in 0.1 mol kg$^{-1}$ phosphate buffer (pH7.2) and then washed in PBS. The retina was cleared of vitreous and floated onto a gelatinised slide (Fol’s mounting medium; Stone, 1981) with the ganglion cell layer uppermost. Relieving cuts were made at the periphery to enable the retina to lie flat, and the preparation flooded with fresh Fol’s medium. The retina was covered with Whatman #50 filter paper soaked in 16% paraformaldehyde in 0.1 mol$^{-1}$ phosphate buffer (pH7.2) and then washed in PBS. A large coverslip was placed on top of the filter paper and a small weight (85 g) applied to the coverslip to ensure that the retina flattened onto the slide (modified from Moroney and Pettigrew, 1987). The preparation was stored in a moist chamber for 24 h, after which the weight was removed and the slide washed in distilled water. The retina was then allowed to dry on the slide slowly in a moist chamber over several days to avoid cracking.

The retina was defatted in xylene (two changes, each 30 min), rehydrated through a descending alcohol series (100%, 95%, 70%, 50% ethanol and then distilled water for 10 min each) and stained for Nissl substance in an aqueous solution of 0.05% Cresyl Violet titrated to pH4.3 with glacial acetic acid for 25 min. After rinsing in distilled water, the stained retina was passed through 70% and 95% ethanol (30 s
Estimating visual resolution

Peak cell density data from counts of the whole-mounted retina were used to estimate the theoretical resolution limits for the peafowl eye. The posterior nodal distance (PND) of the eye was estimated by multiplying its axial length (measured from an enlarged scaled photograph) by 0.60. This ratio is identical to that measured empirically for the chicken (Schaeffel and Howland, 1988), starling Turdus vulgaris (Martin, 1986) and blackbird Turdus merula (Donner, 1951), and similar to the mean for diurnal eyes (0.67) from a variety of vertebrate species calculated by Pettigrew et al. (1988).

The distance $d$ subtended by one degree on the retina was determined from the calculated PND and the formula:

$$d = (2 \text{mPND})/360. \quad (1)$$

Assuming that ganglion cells are the limiting factor for spatial resolution and that they are packed in a hexagonal array, the mean cell-to-cell spacing $S$ was calculated using the formula:

$$S^2 = 2/(D \sqrt{3}), \quad (2)$$

where $D$ is the density of ganglion cells per mm$^2$. The maximum spatial (Nyquist) frequency $v$ of a sinusoidal grating resolvable by this array was then defined (Snyder and Miller, 1977) as:

$$v = 1/(S \sqrt{3}). \quad (3)$$

This value was multiplied by $d$ to give spatial resolution in cycles per degree.

Results

Microspectrophotometry

Microspectrophotometric data for visual pigments (Figs 2, 3, 4, 5).
Vision in the peafowl

3) and oil droplets (Fig. 4) are summarized in Table 1. The peafowl retina contains five different types of vitamin A₁-based visual pigment (on the basis of their similarity to rhodopsin, rather than porphyropsin, visual pigment templates) in seven different types of photoreceptor cell. Rods contained a medium wavelength (‘green’) sensitive (MWS) visual pigment with a \( \lambda_{\text{max}} \) at 504 nm. There were four spectrally distinct types of single cone. Firstly, a violet sensitive (VS)
type with a visual pigment $\lambda_{\text{max}}$ at 424 nm and a transparent T-type oil droplet that showed no detectable absorptance between 330 and 750 nm. Secondly, a short wavelength ('blue') sensitive (SWS) type with a 458 nm $\lambda_{\text{max}}$ visual pigment and a colourless/pale green C-type oil droplet with a $\lambda_{\text{cut}}$ at 449 nm. Thirdly, a MWS type with a 505 nm $\lambda_{\text{max}}$ visual pigment and a golden yellow Y-type oil droplet with a $\lambda_{\text{cut}}$ at 511 nm. Finally, the fourth type of single cone was maximally sensitive to long ('red') wavelengths (LWS) and contained a 567 nm $\lambda_{\text{max}}$ visual pigment and a red R-type oil droplet with a $\lambda_{\text{cut}}$ at 596 nm.

Good quality absorbance spectra were obtained for almost
Note that P-type oil droplets measured in the ventral retina have a C-, Y-, R- and P-type oil droplets used to create the mean spectra. Consequently, bleaching, similar to those that can be seen in the post-bleach photoproducts in the outer segment as a result of in-scan bleaching, similar to those that can be seen in the post-bleach photoproducts in the outer segment. The wavelength of 0.5 transmittance \( \lambda_{T,0.5} \) was 365 nm.

**Spectrophotometry of ocular media and calculated pathlengths**

Calculated pathlengths of the aqueous and vitreous humours along the optic axis of the peafowl eye were 3.2 mm and 10.6 mm, respectively, for an eye measuring 19.8 mm in axial length. The wavelength of 0.5 transmittance \( \lambda_{T,0.5} \) was 365 nm and the ocular media ceased to transmit light below approximately 330 nm.

**Retinal ganglion cell distribution**

The isodensity contour maps of both total cell counts (Fig. 6A) and presumptive ganglion cells only (Fig. 6B) are similar and reveal a prominent area centralis in the central
The density of presumptive ganglion cells (Fig. 6B) in the ganglion cell layer decreased concentrically from a peak of approximately 35,609 cells mm$^{-2}$ in the area centralis to a minimum of 816 cells mm$^{-2}$ at the dorsal periphery. Closer examination reveals a poorly defined horizontal visual streak of high cell density extending nasally from the area centralis.

**Resolution limit**

The unfixed eye from which the counted retina was taken had a measured axial length of 19.4 mm and an estimated PND of 11.6 mm (see Materials and methods). Thus, one degree of visual angle subtended 0.20 mm on the retina. The Nyquist frequencies calculated from the highest cell density counts for all cells in the ganglion cell layer (37,649 cells mm$^{-2}$) and presumptive ganglion cells only (35,609 cell mm$^{-2}$) were 21.2 cycles degrees$^{-1}$ and 20.6 cycles degrees$^{-1}$, respectively (not corrected for retinal shrinkage).

**Discussion**

**Microspectrophotometric data**

The spectral characteristics of the visual pigments and oil droplets in the retinal photoreceptors of the Indian blue-shouldered peafowl *Pavo cristatus* are very similar to those described in the other galliform species studied to date: the domestic chicken *Gallus gallus* (Bowmaker et al., 1997), domestic turkey *Meleagris gallopavo* (Hart et al., 1999) and Japanese quail *Coturnix coturnix japonica* (Bowmaker et al., 1993) (for a review, see Hart, 2001b). They also resemble those measured in the mallard duck *Anas platyrhynchos* (Jane and Bowmaker, 1988), which belongs to the order Anseriformes that is thought to be closely related phylogenetically to the Galliformes (Sibley and Monroe, 1990). Galliform and anseriform photoreceptors are characterised by a VS ($\lambda_{\text{max}}$ 415–426 nm) rather than UVS ($\lambda_{\text{max}}$ 362–373 nm) visual pigment in the single cone containing a transparent T-type oil droplet. The possession of a VS visual pigment is correlated with a shift in SWS visual pigment $\lambda_{\text{max}}$ to longer wavelengths relative to SWS visual pigments found in birds with UVS visual pigments (Hart et al., 2000a) and increased spectral filtering (higher transverse absorptance and $\lambda_{\text{cut}}$ at longer wavelengths) in the C-type oil droplet with which the SWS visual pigment is associated (Bowmaker et al., 1997). Both of these factors will serve to reduce the overlap between the spectral sensitivities of the VS and SWS cone classes (Fig. 7), potentially improving colour discrimination and colour constancy under a variety of illumination conditions (Barlow, 1982; Govardovskii, 1983; Vorobyev et al., 2001, 1998).

As well as reducing the overlap between adjacent spectral classes, spectral filtering by the oil droplets in the SWS, MWS and LWS single cones shifts the peak sensitivity of each cone to a longer wavelength than the $\lambda_{\text{max}}$ of the visual pigment it contains; in the case of the peafowl, to 477, 537 and 605 nm, respectively (Figs 7, 8). The peak sensitivity of the VS cone is shifted to about 432 nm because of increasing absorption at short wavelengths by the ocular media. Excluding double cones, the potentially tetrachromatic colour vision system of the peafowl has, therefore, three spectral loci of maximal wavelength discrimination, where the cone spectral sensitivities overlap (Delius and Emmerton, 1979; Jacobs, 1981), at approximately 462, 517 and 576 nm (Figs 7 and 8).

The visual systems of birds have presumably evolved primarily for finding food and avoiding enemies (Lythgoe,
of all single cones were assumed to be 16 μm long (as for the chicken, Morris and Shorey, 1967) and contain a visual pigment with an end-on specific absorbance of 0.015 μm⁻¹ (Bowmaker, 1977). The calculated spectral absorbance of each visual pigment was multiplied by the spectral transmittance of the combined ocular media (Eye in Fig. 4), the spectral transmittance (1-absorptance), and cross-sectional area (diameters from Table 1) of the relevant oil droplet, and normalized to the SWS cone.

Microspectrophotometric data, together with estimates of the relative abundance of the different cone types in the retina, can be used to predict the relative threshold spectral sensitivity of a visual system (Vorobyev and Osorio, 1998). Such estimates have been shown to match behaviourally measured threshold spectral sensitivities well for di-, tri- and tetrachromatic colour vision systems operating under photopic light levels. The model of Vorobyev and Osorio (1998) assumes that photoreceptor noise limits discrimination and that noise in a given receptor colour channel is proportional to the reciprocal of the square root of the relative proportion of that cone type in the retina, and that the level of noise in a cone is independent of spectral sensitivity. VS, SWS, MWS and LWS single cones were assumed to be present in the ratio 1:1.9:2.2:2.1, respectively (Hart, 2001a). Spectral sensitivities for the different cone types were those presented in Fig. 7.

Spectrophotometry of ocular media

As with other species that possess a VS visual pigment (wavelength of 0.5 transmittance, λT0.5, 358–380 nm), the ocular media of the peafowl (λT0.5=365 nm; Fig. 4) transmit fewer short wavelengths than species with UVS visual pigments (λT0.5=316–343 nm; for a review, see Hart, 2001b). Consequently, while the VS visual pigment confers considerable sensitivity to near ultraviolet wavelengths (at least in the mallard duck; Parrish et al., 1981), it is clear that the visual systems of species with a VS visual pigment are functioning over a narrower range of short wavelengths than those with a UVS visual pigment. However, it is not yet known if the spectral characteristics of the ocular media determine the λmax of the visual pigment in the single cone containing the T-type oil droplet or vice versa (Hart, 2001b).

Topography of the retinal ganglion cell layer

It is generally acknowledged that the topographic organisation of the retina represents an evolutionary adaptation...
to the habitat and life style of a given species, both in terms of
ganglion cell (e.g. Collin and Pettigrew, 1989; Hughes, 1977)
and photoreceptor (e.g. Ahnelt and Kolb, 2000; Hart, 2001a;
Partridge, 1989) distribution. The macroscopic topography of
the avian retina has been studied extensively using
ophthalmoscopy (e.g. Moroney and Pettigrew, 1987; Wood,
1917) and, to a lesser extent, using anatomical techniques (e.g.
Binggeli and Paule, 1969; Budnik et al., 1984; Chen and Naito,
1999; Hayes et al., 1991; Hayes and Brooke, 1990; Inzunza et
al., 1991; Wathey and Pettigrew, 1989), and a variety of
organizations are evident (for reviews, see Martin, 1985;

The Indian peafowl has a single, large, centrally located area
of increased ganglion cell density, the area centralis. In this
respect it differs from both the domestic chicken and the
Japanese quail Coturnix coturnix japonica, to which it is
closely related phylogenetically (Sibley and Monroe, 1990),
both of which have an area of increased ganglion cell density
in the dorso–temporal retina (area dorsalis) in addition to the
area centralis (Budnik et al., 1984; Chen and Naito, 1999). The
presence of only one area in the peafowl retina may reflect
differences in feeding behaviour of this species compared to
the chicken and quail. In the pigeon Columba livia, and
presumably other species with similar retinal specialisations,
the area dorsalis projects into a region of visual space in front
of and just below the beak, which corresponds to the region of
binocular overlap of the left and right visual fields, and is
thought to facilitate pecking at and grasping nearby objects,
especially food (Nalbach et al., 1993). The red jungle fowl
Gallus gallus, which is the ancestor of the domestic chicken,
and the Japanese quail, both feed predominantly on the seeds
of grasses and weeds and occasionally small invertebrates
(ants, beetles, termites). The peafowl, however, prefers slightly
more substantial items, including many green crops, insects,
small reptiles, mammals and even small snakes, berries, drupes
and figs (del Hoyo et al., 1994). These larger visual targets may
obviate the need for a specialized region of high spatial
resolution in the dorso–temporal retina. It is also possible that
the peafowl has a reduced binocular overlap in the anterior
sagittal plane compared to the chicken and quail.

The peafowl retina also displays a weakly defined visual
streak extending horizontally from the area centralis. Visual
streaks are common in mammals (Hughes, 1977) and birds
(Hayes and Brooke, 1990; Meyer, 1977) that inhabit open
environments where the visual horizon is largely unobstructed.
In this respect it is interesting to note that the peafowl spends
much of its time foraging on open plains and scrubland,
whereas the Japanese quail (which is only 17–19 cm tall)
prefers dense herbage less than 1 m tall and the red jungle fowl
favours the forest understorey (del Hoyo et al., 1994).

**Visual resolution**

The area centralis is used to view distant objects during
monocular fixation, and high spatial resolution is important
for both predator and prey detection (Pumphrey, 1948). The
calculated visual acuity for the lateral visual field of the peafowl
(20.6 cycles degrees–1) is better than that measured
behaviourally for the lateral visual field of the pigeon
(12.6 cycles degrees–1; Hahmann and Güntürkün, 1993) and the
chicken (7.1 cycles degrees–1; see Donner, 1951), largely due to
its relatively long PND. Of course, the visual acuity of the
peafowl might be considerably poorer if not all of the ganglion
cells in the area centralis contribute to spatial tasks. However,
estimates of visual acuity made on the basis of anatomy can be
remarkably similar to values measured behaviourally: assuming
a peak cell density of 31 500 cells mm–2 (42 000 cells mm–2
corrected for 25% shrinkage) in the area centralis of the pigeon
(Binggeli and Paule, 1969) and that about 85% of these are
ganglion cells (Hayes, 1984), and a PND of 7.9 mm (Marshall
et al., 1973), the calculated maximum visual acuity in the lateral
visual field of the pigeon would be 12.1 cycles degrees–1 (see
also Wathey and Pettigrew, 1989).

**Abbreviations**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>LWS</td>
<td>long wavelength sensitive</td>
</tr>
<tr>
<td>MSP</td>
<td>microspectrophotometer</td>
</tr>
<tr>
<td>MWS</td>
<td>medium wavelength sensitive</td>
</tr>
<tr>
<td>PBS</td>
<td>phosphate-buffered saline</td>
</tr>
<tr>
<td>PND</td>
<td>posterior nodal distance</td>
</tr>
<tr>
<td>SWS</td>
<td>short wavelength sensitive</td>
</tr>
<tr>
<td>UVS</td>
<td>ultraviolet sensitive</td>
</tr>
<tr>
<td>VS</td>
<td>violet sensitive</td>
</tr>
<tr>
<td>(\lambda_{cut})</td>
<td>cut-off wavelength</td>
</tr>
<tr>
<td>(\lambda_{max})</td>
<td>wavelength of maximum absorbance</td>
</tr>
<tr>
<td>(\lambda_{mid})</td>
<td>wavelength of half maximum-measured absorbance</td>
</tr>
<tr>
<td>(\lambda T_{0.5})</td>
<td>wavelength of 0.5 transmittance</td>
</tr>
</tbody>
</table>

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1985, of the National Institute of Health.

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Visual pigments and oil droplets from six classes of photoreceptor in the