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Vision in the southern hemisphere lamprey *Mordacia mordax*: Spatial distribution, spectral absorption characteristics, and optical sensitivity of a single class of retinal photoreceptor

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#### Abstract

The dorso-laterally located eyes of the southern hemisphere lamprey *Mordacia mordax* (Agnatha) contain a single morphological type of retinal photoreceptor, which possesses ultrastructural characteristics of both rods and cones. This photoreceptor has a large refractile ellipsosome in the inner segment and a long cylindrical outer segment surrounded by a retinal pigment epithelium that contains two types of tapetal reflectors. The photoreceptors form a hexagonal array and attain their peak density (33,200 receptors/mm<sup>2</sup>) in the ventro-temporal retina. Using the size and spacing of the photoreceptors and direct measures of aperture size and eye dimensions, the peak spatial resolving power and optical sensitivity are estimated to be 1.7 cycles deg<sup>-1</sup> (minimum separable angle of 34'7") and 0.64  $\mu$ m<sup>2</sup> steradian (white light) and 1.38  $\mu$ m<sup>2</sup> steradian (preferred wavelength or  $\lambda_{max}$ ), respectively. Microspectrophotometry reveals that the visual pigment located within the outer segment is a rhodopsin with a wavelength of maximum absorbance ( $\lambda_{max}$ ) at 514 nm. The ellipsosome has very low absorptance (<0.05) across the measured spectrum (350–750 nm) and probably does not act as a spectral filter. In contrast to all other lampreys studied, the optimized receptor packing, the large width of the ellipsosome-bearing inner segment, together with the presence of a retinal tapetum in the photophobic *Mordacia*, all represent adaptations for low light vision and optimizing photon capture.

Keywords: Lamprey, Photoreceptor, Spectral sensitivity, Optical sensitivity, Tapetum

#### Introduction

Lampreys comprise three living families: the Petromyzontidae (northern hemisphere) and the Mordaciidae and Geotriidae (southern hemisphere). Although their eyes have several characteristics, that are primitive and not found in gnathostomatous (jawed) fishes, their structure still conforms to the basic vertebrate plan (Duke-Elder, 1958; Land & Nilsson 2002). Together with the hagfishes, this group (the Agnatha) represent an important stage in vertebrate evolution, which, based on recent fossils uncovered in China, inhabited shallow water environments in the early Cambrian at least 540 million years ago (Shu et al., 1999; Xian-guang et al., 2002).

To ascertain the evolutionary events leading up to the appearance of photoreception in the jawed vertebrates, many studies have been undertaken and have concentrated on the eyes of lampreys. However, the complement and morphological characteristics of the photoreceptors in representatives of the three lamprey families have been found to vary markedly, providing only limited clues to the visual capabilities in the ancestral vertebrates. Within the Petromyzontidae, *Petromyzon marinus* (Dickson & Graves, 1979, 1982), *Lampetra fluviatilis* (Öhman, 1971, 1976; Holmberg & Öhman, 1976; Holmberg, 1977), *L. japonica* (Yamada & Ishikawa, 1967; Tonosaki et al., 1989), *L. lamottenii* (Walls, 1928), *Entosphenus sp* (Stell, 1972), and *Ichthyomyzon unicuspis* (S. P. Collin, unpublished data) all appear to contain one type of cone (long) and one type of rod (short) photoreceptor in their retina,

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although debate still persists. Within the Geotriidae, Geotria australis, the sole member of the family, contains five types of cone photoreceptor based on morphological (Walls, 1942; Collin et al., 1999), spectral (Collin et al., 2003*a*), and molecular (Collin et al., 2003b; Collin & Trezise, 2004) criteria. The eyes of the southern hemisphere lamprey Mordacia mordax, the subject of this study and one of the two parasitic species in the third family of lampreys, the Mordaciidae, possesses only a single morphological type of photoreceptor with both rod- and cone-like characteristics (Collin & Potter, 2000). Based on the critical position of Mordacia in the phylogeny of lampreys (Gill et al., 2003) and its unique complement of photoreceptors, further study of photoreception in this species is likely to reveal important clues to the evolution of photoreception and visual plasticity, particularly given the range of visual demands placed on representatives of each of the three families and the different photic environments they inhabit.

The aims of the present study are to examine photoreception and vision in the southern hemisphere lamprey, *Mordacia mordax*. The spatial distribution of the single class of photoreceptor is examined in addition to the significance of a regional variation in receptor density in the context of previous findings that the eyes possess a ramped retina and a nonspherical lens (Collin & Potter, 2000). Photoreception is also assessed microspectrophotometrically by examining the spectral absorbance of the visual pigment located in the long outer segment and the spectral transmittance of the large ellipsosome located in the inner segment. Our measurements of spatial resolving power and optical sensitivity indicate that this photophobic species is adapted for vision in low light environments, and possesses a visual ecology very different from all other lampreys.

#### Materials and methods

#### Collection of animals

Sixteen metamorphosing representatives of *Mordacia mordax* (Mordaciidae, Agnatha) (2–3 g, 110–140 mm in total length, Figs. 1A & 1B) were collected from streams and rivers in south-western Australia using an electric fish shocker. All individuals were maintained in laboratories (Queensland Government Department of Primary Industries General Fisheries Permit, Stock Impoundment No: PRM01814G), in which temperature and light/dark regimes paralleled, as closely as possible, those in the field. These animals were used for experiments in spring, very soon after the time when, as young adults, they would otherwise have entered the sea (Potter et al., 1982).

#### Visualisation and spatial mapping of photoreceptors

Four animals were sacrificed using an overdose of methane tricaine sulfonate salt (MS 222, 1:2000) followed by decapitation, under the ethical guidelines of the National Health and Medical Research Council of Australia. The cornea and lens of each excised eye were removed and a lesion made in the dorsal retina for orientation. The eyecup was then fixed in 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2–7.4) for 1 h. The axial length of the unfixed, excised lens was measured with vernier calipers and used to calculate the spatial resolving power of the eye (see below). Following fixation, and while immersed in 0.1 M phosphate buffer, the retina was freed from the underlying retinal pigment epithelium (containing a tapetum) and the overlying vitreous humour. The retina (photoreceptor layer uppermost) was then flattened onto a gelatinized microscope slide by making several peripheral incisions. The retina was mounted in 100% glycerol under a raised coverslip, which was sealed with clear nail polish to prevent dehydration.

Using a slide projector, the outline of each retina was enlarged and traced onto 1-cm<sup>2</sup> graph paper, taking care to align the edge of the slide with the gridlines. The locations of major landmarks, including the position of the optic nerve head, were marked and used to orient the retinal map with the coordinates of the microscope stage when viewing the retina at high magnification. Photoreceptors were viewed using Normarski differential interference contrast (NDIC) optics with a Zeiss Axioplan microscope at a magnification of 1000×. The number of cells falling within a 10× 10 square grid (eyepiece graticule) were counted at intervals of 0.2 mm across each retina, with additional counts performed in areas of increased cell density. Cell densities were then converted to cells  $mm^{-2}$  and plotted on the retinal map. A composite map from eight retinae was constructed and mean cell densities ( $\pm$ standard deviations) were calculated. The method utilized to avoid double counting and the construction of isodensity contours followed Collin and Pettigrew (1988). The total number of photoreceptors across the retina was estimated by summing the product of the mean receptor density within each retinal area by the area of each isodensity contour. Counts were not corrected for shrinkage, which is known to be small (approximately 3% for free-floating retinae; Hart, 2002).

#### Estimation of spatial resolving power

Spatial resolution of the eye of *M. mordax* was estimated using the optical properties of the eye and the photoreceptor spacing. Although Matthiessen's ratio states that the distance from the lens center to the retina is 2.55 times the radius of the lens (Matthiessen, 1882), a ratio of 2.52 is used in this study following calculations made on frozen sections of the eye of a 110-mm-long individual (Collin & Potter, 2000). The focal length (*f*) is therefore 1.51 mm in an eye with a lens diameter of 2.19 mm on the visual axis. The minimum separable angle ( $\alpha$ ) was calculated using the focal length (*f*) and the photoreceptor separation (*cs*) in the formula,  $\alpha = \arcsin (2cs/f)$  (Tamura & Wisby, 1963). For a hexagonal photoreceptor array (as in *M. mordax*), *cs* can be replaced by v(3)cs/2 (Snyder & Miller, 1977). Therefore,  $\alpha = \arcsin 2 \cdot [(v(3)cs/2)/f]$ .

#### Estimation of optical sensitivity

The optical sensitivity was calculated using Land's equation (for the absorption of light at the absorbance peak wavelength, Land, 1981) and a modification of Land's equation derived by Warrant and Nilsson (1998) for the absorption of white light. Optical sensitivity  $(S) = (\pi/4)^2 \cdot A^2 \cdot (d/f)^2 \cdot F \ \mu m^2$  steradian, where A is the diameter of the circular pupil aperture ( $\mu$ m), d is the diameter of the photoreceptor outer segment  $(\mu m)$ , f is the focal length of the eye (in  $\mu$ m, calculated in mm above), and F is the fraction of incident light absorbed by each photoreceptor and can be calculated for both white light and the wavelength of peak absorption  $(\lambda_{\text{max}})$ . Although the visual ecology of *M. mordax* is unknown during its protracted marine phase, downstream migrants would be exposed predominantly to white light in their natal river although, in some areas, the rivers are stained with tannin and may transmit predominantly longer wavelength light. M. mordax are presumably exposed to attenuated light and exposed to wavelengths closer to

the photoreceptor peak absorption in deeper parts of the water column while at sea (Potter et al., 1968; Potter & Strahan, 1968). Therefore, *F* is calculated for both light conditions. In white light,  $F_w = kl/(2.3 + kl)$ , where *k* is the photoreceptor absorption coefficient (reported to be 0.035  $\mu$ m<sup>-1</sup> for teleosts, Land, 1981; Partridge, 1990; Warrant & Nilsson, 1998) and *l* is the outer segment length ( $\mu$ m). For monochromatic light at the preferred wavelength of the photoreceptor,  $F_{\lambda_{max}} = 1 - e^{-kl}$  (Land, 1981; Warrant & McIntyre, 1990). All calculations assume that the photoreceptors capture photons from an extended light source (Land, 1981; Warrant & Nilsson, 1998).

#### Microspectrophotometry

Four dark-adapted downstream migrants of M. mordax were euthanazed with an overdose of MS 222 (1:2000) and their eyes removed. Retinae were dissected out under infrared illumination, cut into small pieces, and mounted in a solution of 275 mosmol kg<sup>-1</sup> phosphate buffered saline containing 10% dextran. Absorbance spectra (350-750 nm) of individual photoreceptors were made using a single-beam, wavelength-scanning, computercontrolled microspectrophotometer (MSP), as described elsewhere (Shand et al., 2002; Collin et al., 2003a). Measured absorbance spectra were analyzed using the method of Govardovskii et al. (2000) to estimate the  $\lambda_{max}$  of the visual pigment. Spectra were fitted with both A1 and A2-based visual pigment templates (Govardovskii et al., 2000) to establish which type of chromophore was present. Outer segments were bleached with broadband white light from the monochromator at its blaze angle to confirm that the putative visual pigments were photolabile. The spectral absorptance of the large ellipsosome located within the inner segment was also measured to determine whether this intracellular structure has a spectral tuning function.

#### Predicting photoreceptor spectral sensitivity

The relative quantal spectral sensitivity of the single photoreceptor type was calculated from microspectrophotometric measurements of the visual pigment and ellipsosome. Visual pigment spectral absorptance was modeled using a mathematical template for a vitamin A<sub>1</sub>-based visual pigment of the appropriate  $\lambda_{max}$  (Govardovskii et al., 2000). Since microspectrophotometric measurements were made transversely and not axially, absorbance by the visual pigment and the ellipsosome was adjusted according to their respective dimensions (Collin & Potter, 2000 and this study). The photoreceptor absorption coefficient, *k*, used for this calculation was assumed to be 0.035  $\mu$ m<sup>-1</sup> (see above), which corresponds to a specific decadic absorbance of 0.015  $\mu$ m<sup>-1</sup>.

#### Results

The eyes of the southern hemisphere lamprey *Mordacia mordax* are located dorso-laterally in the head, subtending a large binocular overlap in the upper region of their visual field (Figs. 1A & 1B). Axial eye diameter is 2.2 mm. The pupillary aperture is circular and undergoes active constriction in response to light by reducing its area between 5% and 20% of the maximally dilated pupil area (measured from photographs at 10, 20, and 60 min after light exposure). The irideal pigmentation is predominantly brown, interrupted by golden yellow reflective material with the underlying fundus eliciting a clear, yellow/green eye shine (Fig. 1B). The ultrastructural characterization of both the photoreceptors and the



**Fig. 1.** A: A pair of adult southern hemisphere, *Mordacia mordax*. B: Close up of the head of *M. mordax* in lateral view showing the dorso-lateral position of the eyes and the upwardly orientated pupillary aperture. C: Light micrograph of the photoreceptor array and underlying retinal tapetum photographed using Nomarski differential interference contrast (NDIC) microscopy. Note the tightly packed inner segments arranged into an hexagonal array and the yellow/green reflex reflected from the tapetum located in the retinal pigment epithelium. Scale bars: 20 mm (A); 3 mm (B); and 20  $\mu$ m (C).

tapetal reflectors has been previously reported in Collin and Potter (2000).

#### Topographic analysis of the photoreceptor array

The photoreceptor array in the eye of *M. mordax* is predominantly hexagonal throughout the retina (Fig. 1C). However, in some regions, each receptor is bordered by either five or seven neighbors rather than six (Fig. 1C). This type of optimal packing is observed at the levels of the myoid and both the inner and outer segments.

The spatial distribution of photoreceptors in the dorsal and central regions of the retina (mean density  $\pm$  S.D. = 8870  $\pm$  3446 receptors/mm<sup>2</sup>; Fig. 2) is relatively uniform, and consistently lower than in the ventral retina, where the density of photoreceptors increases markedly towards the ventral periphery and attains a peak of 33,200 receptors per mm<sup>2</sup> (area centralis) in one small



**Fig. 2.** Spatial sampling by the photoreceptor array in the retina of *Mordacia mordax*. A: Iso-density contour map showing that receptor density increases in the ventro-temporal retina, which samples the upper frontal visual field with increased spatial resolving power. A sampling transect across the retina along the main visual axis reveals an almost uniform receptor density in dorsal retina, giving rise to a gradient (up to 3:1) that peaks at a maximum of 33,200 receptors/mm<sup>2</sup>. The optic nerve head is depicted by the circular black profile in central retina. Densities are ×10<sup>3</sup> photoreceptors/mm<sup>2</sup>. N: nasal; and V: ventral. B: Axial view of the photoreceptor array, without the underlying tapetum, imaged in retinal interference contrast optics. Note that the ellipsosomes appear clear in contrast to the yellow/green coloration observed when the retinal pigment epithelium is still in place (see Fig. 1C). Scale bar = 15  $\mu$ m.

region of the ventro-temporal quadrant of the retina (Fig. 2). A total of 104,830 photoreceptors occupy the photoreceptor layer.

#### Spatial resolving power

The minimum separable angle is calculated using the photoreceptor spacing of the single type of photoreceptor in the ventral region of the retina and is based on the angle subtended by the period of a grating twice the intercone separation, at the level of the inner segments. For an individual with a total length of 110 mm, the minimum separable angle (MSA) is 34'7'', based on a direct measure of the distance from the lens center to the retina made in

frozen sections of the eye along the visual axis (Collin & Potter, 2000). This low MSA value translates to a resolving power of 1.7 cycles/deg or 3.5 cells/deg.

#### Optical sensitivity

Optical sensitivity is the ratio of photons absorbed to the photons emitted per unit solid angle from an extended source (Warrant & Nilsson, 1998). Since the f-number (focal length/aperture diameter) is thought to be constant, at least for teleosts (Fernald, 1990), the length and diameter of the photoreceptor outer segments is critical in anatomically determining optical sensitivity. For the single class of photoreceptor in M. mordax, the optical sensitivity is found to be 0.64  $\mu$ m<sup>2</sup> steradian and 1.38  $\mu$ m<sup>2</sup> steradian for white light and the preferred wavelength  $(\lambda_{max})$  of the photoreceptor, respectively. The downstream migrants of M. mordax, which travel down their natal rivers toward the sea, will encounter predominantly white light (although some parts of the river may be stained with tannin and therefore may transmit predominantly long wavelength light). However, during their subsequent marine phase, these animals may encounter more attenuated light at depths, closer to their peak spectral sensitivity (see below).

The fraction (F) of incident light absorbed by this type of photoreceptor (absorptance), is based on the length of the outer segment (1) and the photoreceptor absorption coefficient (k = $0.035 \ \mu m^{-1}$  for bony fish, Land, 1981; Partridge, 1990; Warrant & Nilsson, 1998). Although the skate (Elasmobranchii) has a slightly different value for k (0.037  $\mu$ m-1, Cornwall et al., 1989), in the absence of empirical data on agnathans, the teleostean k value is used here. The fraction of light absorbed for white light and the preferred wavelength is 0.25 and 0.53, respectively. Based on the premise that a value of  $F = 1.0_{\lambda_{max}}$  is optimal for maximal light absorption (Fritsches et al., 2003), the mean outer segment length of 21.7  $\mu$ m in *M. mordax* is relatively short. However, when the length of the outer segment is doubled to account for the presence of a reflective retinal tapetum (E. J. Warrant, personal communication), where light will again pass through the photoreceptors, optical sensitivities reach 1.03  $\mu$ m<sup>2</sup> sr and 2.02  $\mu$ m<sup>2</sup> sr for white light and at the preferred wavelength, respectively (Table 1).

#### Microspectrophotometry

On the basis of the goodness-of-fit of the mean absorbance spectra to mathematical visual pigment templates (Govardovskii et al,. 2000), the visual pigment in the single photoreceptor type of Mordacia mordax is considered to be a vitamin A1-based rhodopsin (where the chromophore conjugated with the opsin protein is the aldehyde of vitamin A1, 11-cis retinal). The mean wavelength (± S.D.) of maximum absorbance ( $\lambda_{max}$ ) of the prebleach spectra is 514.4  $\pm$  1.68 nm prebleach (n = 20) (Figs. 3A, 3B and 3D). The mean  $\lambda_{\text{max}}$  of the difference spectra created by bleaching the outer segments with white light is  $517.8 \pm 5.68$  nm. The mean transverse measured absorbance at the  $\lambda_{max}$  of the difference spectrum is  $0.043 \pm 0.016$  nm. Microspectrophotometric analysis of the ellipsosomes (n = 10) revealed an absorptance of less than 0.05 across the measured spectrum (Fig. 3C), indicating that these large intracellular inclusions do not contain any pigment that causes spectral filtering of the incident light before it reaches the visual pigment in the outer segment. The slight increase in absorption at short wavelengths, evident in the mean spectrum in Fig. 3B, is probably an artefact due to increased scattering of the measuring beam at short wavelengths.

<b>TADIC 1.</b> MICUSAILES OF OPTICAL SCREENIVILY IN A PARTY OF VEHICUTALE PROTOTOLOGICOPTO	Table 1.	Measures	of o	ptical	sensitivity	in a	range	of v	vertebrate	photorece	ptor
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Species	Aperture diameter (mm)	Focal length (mm)	OS diameter (µm)	OS length (µm)	Fraction of light absorbed (white light)	Fraction of light absorbed (at $\lambda_{max}$ )	Sensitivity $(\mu m^2 sr,$ white light)	Sensitivity $(\mu m^2 sr, \lambda_{max})$	Reference(s)
Mordacia mordax	0.61	1.5	5.0	21.7	0.25 (0.40)	0.53 (0.78)	0.64 (1.03)	1.38 (2.02)	This study
Geotria australis (lamprey large cone)	0.63	1.2	2.2	10.0	0.13	0.30	0.12	0.26	Collin et al. (2003a)
<i>Geotria australis</i> (lamprey medium cone)	0.63	1.2	1.4	7.0	0.10	0.22	0.03	0.08	Collin et al. (2003a)
Geotria australis (lamprev small cone)	0.63	1.2	1.1	17.2	0.21	0.45	0.05	0.10	Collin & Trezise (2004)
Choerodon albigena (teleost double cone)	4.80	6.1	3.0	15.0	0.19	0.41	0.60	1.40	Collin & Pettigrew (1989), Fritsches et al. (2003)
Makaira nigricans (teleost double cone)	19.00	24.2	4.0	72.0	0.52	0.92	3.20	5.60	Fritsches et al. (2003)
Scopelarchus michaelsarsi (deep-sea teleost rod)	2.60	2.7	2.8	46.0	0.56	0.95	2.41	4.06	Collin et al. (1998)
Corythoichthyes paxtoni (teleost double cone)	0.40	0.6	2.6	9.3	0.12	0.28	0.20	0.44	Collin & Collin (1995; 1999)
Bufo americanus (amphibian rod)	5.60	4.7	2.5	54.0	0.48	0.88	2.60	4.79	Mathis et al. (1988)
Homo sapiens (human cone)	3.00	16.7	5.0	30.0	0.27	0.57	0.13	0.28	Land (1981), Warrant & Nilsson (1998)
Homo sapiens (human rod)	8.00	16.7	3.0	30.0	0.27	0.57	0.34	0.72	Land (1981), Warrant & Nilsson (1998)

<sup>a</sup>The fraction of light (white light and light at the preferred wavelength— $\lambda_{max}$ ) absorbed by a range of vertebrate photoreceptors and their corresponding optical sensitivities. The measurements used in calculations have been taken from the cited references and are predominantly from morphological data assessed in fixed tissue. The values in brackets for *Mordacia mordax* take into account the presence of a retinal tapetum, where the outer segment length has been doubled. The absorption coefficient ( $k = 0.035 \ \mu m^{-1}$ , Partridge, 1990) calculated for bony fishes is used for all species except for *S. michaelsarsi* (0.064  $\ \mu m^{-1}$ , Partridge et al., 1989), *B. americanus* (0.039  $\ \mu m^{-1}$ , Harosi, 1975), and *H. sapiens* (0.028  $\ \mu m^{-1}$ , Alpern and Pugh, 1974). OS: outer segment; and sr: steradian.

#### Discussion

### Spatial distribution of photoreceptors and spatial resolving power

In the retina of *M. mordax*, the density of photoreceptors is greatest in the ventro-temporal region. Uniquely among lampreys, the eyes of *M. mordax* are located dorso-laterally. Consequently, the temporoventral region of the retina will sample the upper frontal region of the visual field with high spatial resolving power (see Fritzsch & Collin, 1990 for alternative strategies in spatial sampling in the petromyzontid, *Ichthyomyzon unicuspis*). This specialization would be invaluable for detecting aerial predators and identifying hosts in its marine phase.

The lens of *M. mordax* is tapered posteriorly and may not provide a uniformly focused image across the retina. It has previously been proposed that the similarly tapered lens in other species of lampreys, for example, Ichthyomyzon unicuspis (Collin & Fritzsch, 1993) and Geotria australis (Collin et al., 1999), is multifocal or varifocal (Munk, 1986), and mediates near vision for objects viewed by the dorsal retina. However, in I. unicuspis and G. australis, the lens is displaced ventrally, where the distance between the lens center and the retina in the dorsal part of the eye would be greater than in the ventral part of the eye, thereby providing a blurred image of a distant object and a sharp image of a near object (or myopia). However, since the lens in M. mordax is dorsally displaced, the ventral hemiretina would be adapted for near vision and the remainder of the eye would be highly hypermetropic for off-axis rays and adapted for far vision. The possession of a ramped retina, a tapered lens, a small pupillary aperture (providing an increased depth of field through a stenopaic effect), and the specialized nature of the ventral retina for higher spatial resolving power all suggest that the eye of M. mordax has the ability to focus objects at different distances without the need for dynamic accommodation.

The estimate of spatial resolving power (1.7 cycles/deg) and minimum separable angle (34'7"), based on photoreceptor spacing, is lower than in teleosts such as the white crappie Pomoxis annularis (7'0", Browman et al., 1990), the convict fish Microcanthus strigatus (3'36", Yamanouchi, 1956; Nakamura, 1968), the bluegill sunfish Lepomis macrochirus (2'42", Williamson & Keast, 1988), the cichlid Haplochromis argens (11', van der Meer, 1995), and a range of marine species examined by Tamura (1957) who found acuities from 4'12" to 15'24". Considering that there is often an appreciable convergence of information onto the output or ganglion cells and that behavioral acuity is constrained by their spacing (Collin & Pettigrew, 1989), the spatial resolution of M. mordax may be even less. However, spatial resolving power based on ganglion cell spacing was not calculated given the high proportion of ganglion cells (74%) that reside within the inner nuclear layer in lampreys (Fritzsch & Collin, 1990) and the lack of any information regarding the convergence of photoreceptor signals.

#### Optical sensitivity

The low spatial resolving power of the eye and the large diameter of the photoreceptors suggest that the retina of *M. mordax* is specialized for increased sensitivity. The optical sensitivity for this photoreceptor type is calculated to be 0.642  $\mu$ m<sup>2</sup> sr for white light



Fig. 3. Spectral characterization of the single class of photoreceptor in the eye of *Mordacia mordax*. A: Prebleach and postbleach absorbance spectra. Filled squares indicate the mean prebleach absorbance spectrum fitted with the template spectrum (thick line) of Govardovskii et al. (2000). The open circles represent the mean postbleach absorbance spectrum fitted with an unweighted running average (thin line). B: Mean difference spectra (filled squares) fitted with a template spectrum of Govardovskii et al. (2000) (thick line). C: Trace of the mean absorptance of the ellipsosome within the inner segment fitted with an unweighted running average (smooth line). D: The relative quantal spectral sensitivity of the whole photoreceptor ( $\lambda_{max} = 514$  nm), based on both the visual pigment and ellipsosome spectra and the dimensions of the inner and outer segments.

and 1.375  $\mu$ m<sup>2</sup> sr for the preferred wavelength,  $\lambda_{max}$  (Table 1). In the sole representative of the other southern hemisphere family, Geotria australis, the retina contains 5 types of cones (Collin et al., 1999, 2003a,b; Collin & Trezise, 2004). The optical sensitivities (S) of the small cones (C5 of Collin & Trezise, 2004) are 0.046  $\mu$ m<sup>2</sup> sr (for white light) and 0.100  $\mu$ m<sup>2</sup> sr (for the preferred wavelength). For the medium cones (C3 and C4 of Collin & Trezise, 2004) S equals 0.034  $\mu m^2$  sr (for white light) and 0.078  $\mu$ m<sup>2</sup> sr (for the preferred wavelength), and for the large cone (C1 and C2 of Collin & Trezise, 2004) S equals 0.117  $\mu$ m<sup>2</sup> sr (for white light) and 0.260  $\mu$ m<sup>2</sup> sr (for the preferred wavelength). The single class of photoreceptor in M. mordax is therefore between 5 (large cone) and 18 (medium cone) times more sensitive than the photoreceptor types (based at least on morphological criteria) in the retina of G. australis. The values for the optical sensitivities of the photoreceptors in M. mordax and G. australis can be compared with calculations of 5.60  $\mu$ m<sup>2</sup> sr for the double cones in the blue marlin Makaira nigricans (Fritsches et al., 2003), 2.60  $\mu$ m<sup>2</sup> sr for the rod in the toad Bufo americanus (Mathis et al., 1988), and 0.13  $\mu$ m<sup>2</sup> sr and 0.34  $\mu$ m<sup>2</sup> sr for cone and rod in the human *Homo* sapiens (Land, 1981; Warrant & Nilsson, 1998), respectively, in white light.

However, another measure of the sensitivity of the photoreceptor population can be gauged from the fraction (F) of light absorbed. This is largely dependent on the length of the photoreceptor, where a value of  $F_{\lambda_{\text{max}}} = 1.0$  would reveal an optimal outer segment length (Fritsches et al., 2003). Wavelengths in white light, other than the  $\lambda_{max}$ , are absorbed at a lower rate, resulting in a reduced fraction of light absorbed and therefore reduced sensitivity (Warrant & Nilsson, 1998). In *M. mordax*,  $F_{\lambda_{\text{max}}} = 0.53$ , where only half of the available light at the preferred wavelength is being absorbed. However, this fraction may be increased substantially by the presence of both diffuse and spectral reflectors within the retinal pigment epithelium (Collin & Potter, 2000). Therefore, a more accurate measure of optical sensitivity should take into account the light passing back through the photoreceptors. When the effective length of the photoreceptor outer segment in M. mordax is doubled, the fraction of light absorbed increases to 0.40 (white light) and 0.78 (at the preferred wavelength), respectively, thereby optimizing light absorption and improving optical sensitivity (1.03  $\mu$ m<sup>2</sup> sr in white light and 2.02  $\mu$ m<sup>2</sup> sr at the preferred wavelength, Table 1). These values suggest that the retinal receptors of M. mordax are between 8 (large cone) and 35 (medium cone) times more sensitive than those in G. australis. An estimated optical sensitivity of 2.02  $\mu$ m<sup>2</sup> sr for *M. mordax* (at the preferred wavelength) is surpassed in aquatic vertebrates only by the receptors in the blue marlin, *Makaira nigricans* (5.60  $\mu$ m<sup>2</sup> sr) and the deep-sea pearleye *Scopelarchus michaelsarsi* (4.06  $\mu$ m<sup>2</sup> sr), which live in extremely low light levels (Table 1).

#### Spectral sensitivity

The 514 nm  $\lambda_{\text{max}}$  rhodopsin (vitamin A<sub>1</sub>-based visual pigment) of *M. mordax* is spectrally similar to that recorded for the short photoreceptors in the upstream migrants of two petromyzontid lamprey species, *Lampetra fluviatilis* (517 nm rhodopsin, Govard-ovskii & Lychakov, 1984) and *Petromyzon marinus* (525 nm porphyropsin (vitamin A<sub>2</sub>-based visual pigment, Hárosi & Kleinschmidt, 1993), and one of the two medium cones in the downstream and upstream migrant phases of *G. australis* (porphyropsins with  $\lambda_{\text{max}}$  at 506 nm and 500 nm, respectively; Collin et al., 2003*a*; Collin & Trezise, 2004). These  $\lambda_{\text{max}}$  values are similar to

those of the rod visual pigments found in a range of teleost fish species (e.g. Munz & McFarland, 1973). However, given that the true rod visual pigment (the opsin gene Rh1) has not been found in either of the two other families of lampreys (Petromyzontidae and Geotriidae) and that full scotopic (dim light, rod-based) vision is most likely only to have evolved after the separation of the jawed (gnathostomatous) vertebrates (Collin et al., 2003*b*; Collin & Trezise, 2004), the identity of the receptor type in *Mordacia* is still uncertain.

The ellipsosome located in the inner segment of *M. mordax* photoreceptors has a very low absorbance across the entire spectrum, suggesting that it does not have a spectral tuning/filtering function, unlike the yellow short-wavelength absorbing filters within the myoid regions of the photoreceptors in *G. australis* (Collin et al., 2003*a*). Given the other retinal adaptations for increasing photon capture in *M. mordax*, another possible function for the large ellipsosome is to focus light onto the visual pigment within the outer segment. This would parallel the role played by



Fig. 4. Schematic diagram summarizing the complement and morphology of the photoreceptors in downstream migrants of the northern hemisphere (holarctic) lampreys *Petromyzon marinus* and *Lampetra fluviatilis* (Holmberg & Öhman, 1976; Dickson & Graves, 1982, Petromyzontidae, A), the southern hemisphere lamprey *Geotria australis* (Collin et al., 1999, 2003*a*, Geotriidae, B) and *Mordacia mordax* (this study, Mordaciidae, C). The nomenclature for the five cone-like receptors (C1–C5) in *G. australis* follows that of Collin and Trezise (2004). Note the refractile bodies are the predominant feature characterizing the receptors in *G. australis*. These are yellow short-wavelength absorbing filters. OLM: outer limiting membrane. Scale bar = 3  $\mu$ m.

similar oil droplet-like structures in the cones of certain reptiles (Pedler & Tilly, 1964; Wong, 1989) and birds (Young & Martin, 1984). Since the ellipsoid region of the inner segment containing the ellipsosome is 25% wider than the outer segment in *M. mordax*, a proportion of the light striking the inner segment would fail to reach the visual pigments. We suggest that any focusing ability of the ellipsosome is mediated by an intracellular increase in refractive index and/or its elliptical shape (Young & Martin, 1984).

#### Optical adaptations for vision in low light environments

The downstream migrants of *M. mordax* burrow during the day and emerge at night and the same is also true for adults during their upstream migration, a situation which is unique amongst lampreys (Potter et al., 1968). The dorsal alignment of the two visual axes may also ensure that, by maximizing photon capture, the visual field is optimal for facilitating its migratory movements and/or detecting predators at night.

Photon capture, and thereby sensitivity, would be also greatly enhanced in this highly photophobic species by its possession both of large receptors, which are far greater in size than the photoreceptors of any other lamprey species examined, and of a prominent ellipsosome, whose function is presumably to focus light onto the outer segment. Furthermore, the outer segment in M. mordax is also twice as long as the photoreceptors of other lampreys (Fig. 4), which would greatly increase the amount of visual pigment exposed to the incoming light path. Other characteristics of the eye, which are unique amongst lampreys and would enhance sensitivity in low light intensities, include the presence of a retinal tapetum (Collin & Potter, 2000), the optimized orientation of the photoreceptor array towards the pupillary aperture (Collin & Potter, 2000), and a small mobile pupil which is thought to decrease optical aberrations and alter the depth of field for near objects (Lowenfeld, 1993; Douglas et al., 1998, 2002). Furthermore, Mordacia is one of only a few vertebrate species to contain a single type of retinal photoreceptor. These include deep-sea fishes, which possess rod-dominant retinae optimally adapted for vision beyond the penetration limits of sunlight (Munk, 1966; Locket, 1977; Fröhlich et al., 1995; Collin et al., 1998), and some species of skate (Dowling & Ripps, 1972) that live at considerable depth. Interestingly, like the short photoreceptors of Lampetra fluviatilis (Govardovskii & Lychakov, 1984), there is evidence that skate rods are capable of functioning over a broad range of light levels (Dowling & Ripps, 1972; Ripps & Dowling, 1991).

In summary, photoreception in *Mordacia mordax* is unique amongst the lampreys examined thus far. The possession of a single receptor type with both rod- and cone-like characteristics provides what might be a crucial key to the survival of these primitive vertebrates. Even at this early stage in vertebrate evolution, lampreys appear to be adapted to a range of visual environments, optimizing both spatial resolving power and sensitivity throughout their protracted lifecycle.

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