THE ROYAL SOCIETY

Ultraviolet polarization vision in fishes: possible mechanisms for coding e-vector

Craig W. Hawryshyn

Department of Biology, University of Victoria, PO Box 3020 STN CSC, Victoria, British Columbia, Canada V8W 3N5
(chawrysh@uvic.ca)

Polarization vision in vertebrates has been marked with significant controversy over recent decades. In the last decade, however, models from two laboratories have indicated that the spatial arrangement of photoreceptors provides the basis for polarization sensitivity. Work in my laboratory, in collaboration with I. Novales Flamarique and F. I. Harosi, has shown that polarization sensitivity depends on a well-defined square cone mosaic pattern and that the biophysical properties of the square cone mosaic probably account for polarization vision in the ultraviolet spectrum. The biophysical mechanism appears to be based on the selective reflection of axial-polarized light by the partitioning membrane, formed along the contact zone between the members of the double cones, onto neighbouring ultraviolet-sensitive cones. In this short review, I discuss the historical development of this research problem.

Keywords: polarization vision; ultraviolet sensitivity; cone mosaic; ontogeny; neural coding; e-vector

1. INTRODUCTION

Animals often perceive the world in a manner quite different from the way humans see it. That animals may see things that we may not presents a paradox with respect to how scientists go about investigating the sensory world of any animal. These constraints were very much in evidence in the initial efforts concerning the research on ultraviolet (UV) photosensitivity in fishes. It is now common to see reports of UV sensitivity in a broad range of species.

Our current research effort on UV vision has shifted from cataloguing species of aquatic organisms exhibiting UV vision to examining the functional significance of UV vision in the aquatic ecosystem. While there are numerous possibilities, the focus of my research is on the role of UV vision in the detection of polarized light. Many invertebrates have UV polarization vision and this motivated us to test for polarization sensitivity in goldfish possessing UV sensitivity (Hawryshyn & McFarland 1987).

2. PHOTORECEPTOR MECHANISMS AND NEURONAL PROCESSING RELATED TO POLARIZATION SENSITIVITY

Our knowledge of the specific mechanisms mediating the process of polarization vision is more thoroughly understood in invertebrates and is based on the organization and orientation of visual pigment-bearing membrane in photoreceptors (Wehner *et al.* 1975). Visual pigment molecules, within a given rhadomeric microvillus, are aligned in one axis permitting preferential absorption of plane-polarized light.

Waterman and his associates (Waterman & Aoki 1974; Waterman & Hashimoto 1974) first examined the receptor mechanisms underlying polarization sensitivity in fishes. These studies revealed one class of polarization sensitivity in all single units recorded from the optic tectum, regardless of the test wavelengths of the polarized light stimuli. Our studies, on rainbow trout (Parkyn & Hawryshyn 1993) and goldfish (Hawryshyn & McFarland 1987), have since been extended into the UV part of the spectrum and have used chromatic adaptation to isolate the spectral sensitivity of individual cone mechanisms. Polarization sensitivity can then be evaluated with a polarized light stimulus, which is coincident with the spectral sensitivity peak of the isolated cone mechanism. Experiments that use white or spectral stimuli without chromatic adaptation offer questionable conclusions about the mechanisms of polarization sensitivity (Hawryshyn & McFarland 1987).

Our experimental results have identified the presence of two differentially sensitive classes of polarization-sensitive cone mechanisms in cyprinid and salmonid fishes. Like colour vision, polarization vision depends on the possession of at least two differentially sensitive receptor (cone) mechanisms (Bernard & Wehner 1977). Most research on invertebrate polarization systems has shown that differential polarization sensitivity is mediated by visual receptors possessing the same spectral sensitivity. However, our initial experiments, on goldfish and rainbow trout, have revealed that differential polarization sensitivity results from cone receptors that differ in spectral sensitivity, a scenario that would seem to suggest a confounding influence of colour. Nonetheless, both electrophysiological and behavioural experiments have demonstrated that polarization vision depends on the acquisition of UV polarized light stimuli (Coughlin & Hawryshyn 1995; Hawryshyn *et al.* 1990). So, while in theory spectral confounds are possible, functional polarization vision appears to operate only in the UV part of the spectrum.
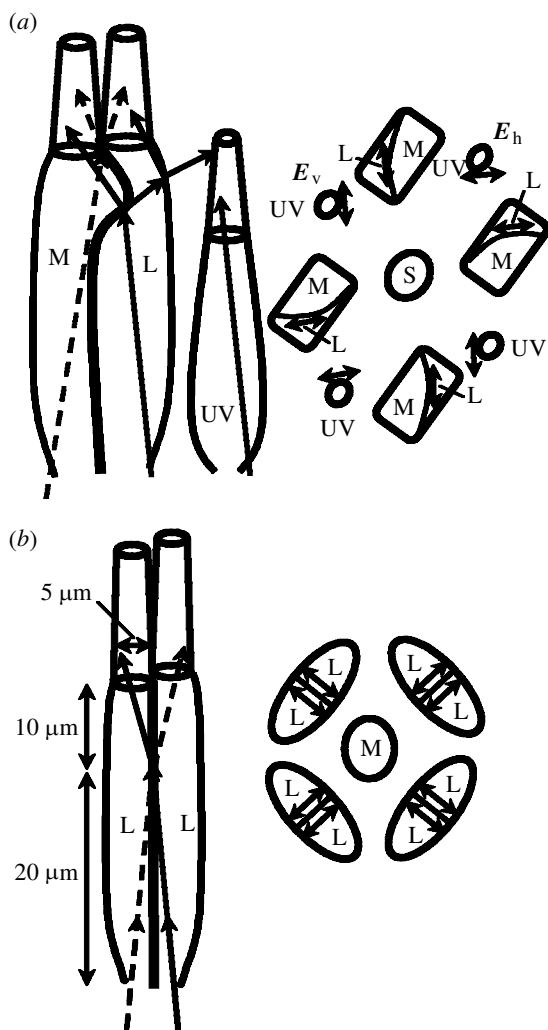
Figure 1. Schematic diagram showing the cone mosaics of rainbow trout and sunfish and the axial transmission of plane-polarized light. (*a*) Rainbow trout cone mosaic showing UV-, S-, M- and L-sensitive cones. E_h, horizontal e-vector; E_v, vertical e-vector.(*b*) Sunfish cone mosaic showing L-sensitive twin cones and M-sensitive single cones. Double-headed arrows, within the square mosaic, indicate the dominant plane of polarization. (Adapted from Novales Flamarique *et al*. (1998), which should be consulted for more details on this illustration.)

In both salmonids and cyprinids, the UV-sensitive cone mechanism exhibits maximum polarization sensitivity to the vertically orientated e-vector while the mid-wavelength-sensitive (M cones) and long-wavelength-sensitive (L cones) cone mechanisms show maximum sensitivity to the horizontally orientated e-vector (Hawryshyn & McFarland 1987). Further electrophysiological studies on rainbow trout, by Coughlin & Hawryshyn (1995), have shown that UV/L-sensitive colour-opponent neurons project primarily to the torus semicircularis in the central nervous system. There is good evidence that these neurons are specifically tuned to UV polarized stimuli as the capability of discriminating one plane of polarization from another is restricted to the UV part of the spectrum (α-band of UV cone mechanism and β-band of the L cone mechanism). This differential polarization sensitivity between cone mechanisms appears to

provide the potential for e-vector coding and hence polarization discrimination within the UV part of the spectrum.

3. ONTOGENETIC CHANGES IN THE SPATIAL PATTERN OF CONE MOSAICS AND POLARIZATION SENSITIVITY

Rainbow trout exhibit an ontogenetic loss of UV photosensitivity (Hawryshyn *et al*. 1989). Juvenile rainbow trout weighing less than 30 g displayed sensitivity to UV light with a peak sensitivity of 360 nm. Trout larger than 30 g exhibited a characteristic loss of UV sensitivity, both within individual trout and between fish measurements. It was inferred from these results that trout UV cones degenerated soon after transition to the adult stage (a similar conclusion was made by Bowmaker & Kunz (1987) for brown trout). This inference was further supported by the premature loss of UV sensitivity in rainbow trout treated with thyroxine (Browman & Hawryshyn 1994), a hormone known to play a key role in the development of all vertebrates. Although a square mosaic was found in the majority of the retinae examined, accessory corner cones (putative UV cones) were not present in the cone mosaic of trout treated with thyroxine (see figure 1*a* for spatial arrangement of cone mosaic in juvenile rainbow trout).

In a recent study, Beaudet *et al*. (1997) found that sexually mature salmonids possessed a cone mosaic with accessory corner cones, suggesting that there may be some potential for UV cone regeneration. The mechanism for the regeneration of UV cones is unknown. UV-sensitive accessory corner cones may regenerate from pluripotent cells within the retina or it is possible that rod precursor cells differentiate into accessory corner cones. Thus, in the life-history stage leading up to and during sexual maturity, salmonids may conceivably possess the capability of UV polarization vision. My laboratory is currently conducting research to address some of the unresolved issues concerning the ontogenetic changes in UV polarization in salmonids (Browman & Hawryshyn 1994; Beaudet *et al*. 1997).

4. BIOPHYSICAL MODEL OF CONE PHOTORECEPTOR POLARIZATION SENSITIVITY

Our observations that salmonids use different cone mechanisms to accomplish the task of polarization vision has presented an interesting challenge for determining the biophysical characteristics of photoreceptors necessary to generate cone-selective sensitivity to the e-vector. While Hawryshyn & McFarland (1987) showed that UV-sensitive cones have a preference for the vertical e-vector orientation and the M- and L-sensitive cones prefer the horizontal e-vector, single unit recordings have shown that e-vector coding occurs only in the UV part of the spectrum and only when UV-sensitive cones are expressed in the spectral sensitivity (Coughlin & Hawryshyn 1995). Therefore, despite the observation that different cone types have different polarization sensitivity, neuronal coding of the e-vector appears to occur as a result of differential polarization responses in UV cones within the cone mosaic. So how can spectrally different

cone types participate in polarization vision, yet e-vector coding occur only within the UV part of the spectrum?

The explanation for this paradox appears to be in the spatial pattern of cone photoreceptors within the cone mosaic and the ultrastructural properties of double cones. The polarization sensitivity observed in salmonids and cyprinids cannot be explained by other models of polarization sensitivity such as the elliptical-waveguide hypothesis since studies have shown there is little evidence for such biophysical mechanisms (Novales Flamarique *et al*. 1995). Rather, a recent study by Novales Flamarique *et al*. (1998) has shown that double cones possess a partitioning membrane that separates the two elements of the double cone. Furthermore, the partitioning membrane tilts at the distal end of the inner segments. The degree of tilt is *ca*. 10–25° and is orientated towards neighbouring UV cones. The cone of rays incident on this tilted surface is estimated to be about 20° and thus we hypothesize that the partitioning membrane reflects anisotropically polarized light onto neighbouring UV cones (i.e. transversely, at an angle of incidence facilitating dichroic absorption of polarized light). The tilted segment of the double cone partitioning membrane is orientated so that axial reflection of polarized light is directed onto adjacent UV cones (figure 1*a*, left panel). Thus, as the e-vector orientation of incident polarized light is rotated, anisotropic reflection from the double cone partitioning membrane would result and the UV cones would be transversely illuminated with a plane of polarization aligned parallel to the axis of the disk membranes. The tight spacing of cones in the trout retina would further facilitate this process. The right panel of figure 1*a* shows a tangential view of the cone mosaic and in this perspective it should be clear that axial reflection from tilted partitioning membrane surfaces is directed in two directions since double cones are arranged quadrilaterally in the square cone mosaic. The two directions of reflection are arranged orthogonally to one another. Hence, reflection in orthogonal directions would set up conditions for differential tuning of e-vector required for a two-detector polarization system. That is, within a square cone mosaic unit: (i) vertically orientated polarized light would transversely strike the outer segments of two corner UV cones, obliquely positioned in the corners of the cone mosaic; and (ii) horizontally orientated polarized light would strike the outer segments of the two other corner UV cones, obliquely positioned but in opposite corners of the cone mosaic.

Thus double cones could play an important role in the translation of polarization orientation information into intensity modulation that UV cones monitor. While the UV cones receive the transverse reflection, the outer segments of the double cones receive the residual polarization distal to the partition membrane reflection. Note also that blue-sensitive cones, which are the central cones in the square mosaic unit, do not receive transverse reflections from the double cone partitioning membranes and hence do not exhibit polarization sensitivity. This pattern of intensity variation over the cone mosaic permits the detection of polarization by comparing signals among different cones within the cone mosaic. Signal integration, by interneurons, within and across mosaic units would operate to amplify polarization sensitivity and conceivably provide a code for e-vector orientation.

Green sunfish, on the other hand, have been reported to possess polarization sensitivity (Cameron & Pugh 1991); however, these data have not been replicated despite the various attempts to do so (Novales Flamarique & Hawryshyn 1997). Figure 1*b* illustrates that the partitioning membrane between members of twin cones, in sunfish, do not exhibit tilt and hence cannot generate the transverse reflection onto neighbouring cones and thus there is no reflection of polarized light. Furthermore, attempts to identify birefringent inclusions in the inner segment of these cones have been unsuccessful (Novales Flamarique *et al*. 1995). Therefore it is not surprising that sunfish do not exhibit polarization sensitivity because they appear to lack the biophysical basis for it. There are species such as the common white sucker that possess UV photosensitivity yet lack polarization sensitivity. Histological examination of common white sucker photoreceptor organization shows a random mosaic of cone types and hence there is no geometric plan for the cone-specific reflection patterns observed in cyprinids and salmonids (Novales Flamarique & Hawryshyn 1998). Thus the critical factors determining polarization are the geometric pattern of the cone mosaic and the tilted partitioning membrane of the double cones.

5. CONCLUSION

My analysis of polarization vision in salmonid fishes indicates that a neural network for e-vector coding could occur at the level of the horizontal cells in the retina. Our future efforts should be concentrated on examining the polarization tuning of horizontal cells at multiple levels within the outer plexiform layer. This will provide valuable insights into the interneuronal interaction shaping the e-vector coding observed in central nervous system neurons.

REFERENCES

Beaudet, L., Novales Flamarique, I. & Hawryshyn, C. W. 1997 Cone photoreceptor topography in the retina of sexually mature Pacific salmonid fishes. *J. Comp. Neurol.* **383**, 49–59.

Bernard, G. D. & Wehner, R. 1977 Functional similarities between polarization and color vision. *Vision Res.* **17**, 1019–1028.

Bowmaker, J. K. & Kunz, Y. W. 1987 Ultraviolet receptors, tetrachromatic color vision and retinal mosaics in brown trout (*Salmo trutta*): age-dependent changes. *Vision Res.* **27**, 2101–2108.

Browman, H. I. & Hawryshyn, C. W. 1994 The developmental trajectory of ultraviolet photosensitivity in the rainbow trout is altered by thyroxine. *Vision Res.* **34**, 1397–1406.

Cameron, D. & Pugh, E. 1991 Double cones as a basis for a new type of polarisation vision in vertebrates. *Nature* **353**, 161–164.

Coughlin, D. J. & Hawryshyn, C. W. 1995 A cellular basis for polarized-light vision in rainbow trout. *J. Comp. Physiol.* A **176**, 261–272.

Hawryshyn, C. W. & McFarland, W. N. 1987 Cone mechanisms and the detection of polarized light in fish. *J. Comp. Physiol.* A **160**, 459–465.

Hawryshyn, C. W., Arnold, M. G., Chiasson, D. & Martin, P. C. 1989 The ontogeny of ultraviolet photosensitivity in rainbow trout (*Salmo gairdneri*). *Vis. Neurosci.* **2**, 247–254.

Hawryshyn, C. W., Arnold, M. G., Bowering, E. & Cole, R. C. 1990 Spatial orientation of rainbow trout to plane-polarized light: the ontogeny of E-vector discrimination and spectral sensitivity. *J. Comp. Physiol.* A **166**, 565–574.

Novales Flamarique, I. & Hawryshyn, C. W. 1997 No evidence for polarization sensitivity in for freshwater sunfish from multi-unit optic nerve recordings. *Vision Res.* **37**, 967–973.

Novales Flamarique, I. & Hawryshyn, C. W. 1998 The common white sucker: a fish with ultraviolet sensitivity that lacks polarization sensitivity. *J. Comp. Physiol.* A **182**, 331–341.

Novales Flamarique, I., Oldenbourg, R. & Harosi, F. I. 1995 Transmission of polarized light through sunfish double cones reveals minute optical anisotropies. *Biol. Bull.* **189**, 220–222.

Novales Flamarique, I., Hawryshyn, C. W. & Harosi, F. I. 1998 Double cone internal reflection as a basis for polarized light detection. *J. Opt. Soc. Am.* A **15**, 349–358.

Parkyn, D. C. & Hawryshyn, C. W. 1993 Polarized-light sensitivity in rainbow trout (*Oncorhynchus mykiss*): characterization from multi-unit responses in the optic nerve. *J. Comp. Physiol.* A **172**, 493–500.

Waterman, T. H. & Aoki, K. 1974 E-vector sensitivity patterns in the goldfish optic tectum. *J. Comp. Physiol.* **95**, 13–27.

Waterman, T. H. & Hashimoto, H. 1974 E-vector discrimination by the goldfish optic tectum. *J. Comp. Physiol.* **95**, 1–12.

Wehner, R., Bernard, G. & Gieger, E. 1975 Twisted and non-twisted rhabdoms and their significance for polarization detection in the bee. *J. Comp. Physiol.* A **104**, 225–245.