Ultraviolet-polarization vision: it's role in salmon navigation.

Craig W. Hawryshyn

Department of Biology
University of Victoria
PO Box 3020
Victoria, British Columbia
CANADA V8W 3N5[1]

Abstract

Recent findings in a number of laboratories suggest that there are two classes of polarization sensitivity (PS) in fish, and perhaps in other vertebrates as well. One class shows orthogonal PS only in the UV spectrum (salmonids) while the other shows PS in the long-wavelength spectrum (sunfishes). Presumably, this diversity in PS systems implicates a more variable function of PS; such as contrast enhancement and spatial orientation. The work in my laboratory centers on the role of UV cones in PS and orientation behavior. Some salient findings include: (i) salmonids have four cone pigments which overlap in the UV spectrum. (ii) electrophysiological measurements of PS indicate the presence of orthogonal PS in the UV spectrum. (iii) spatial orientation behavior of salmonids requires UV light.

Single-unit recording in the CNS reveals that polarization sensitive ganglion cells project to the torus semicicularis not the optic tectum as indicated in the previous studies. I will present evidence that single neurons in the torus are capable of coding the e-vector of incident plane polarized light. Presumably, these neurons play a role in mediating polarized light guided behaviour in fish, like object detection/recognition and spatial orientation in the aquatic environment.

Keywords: Ultraviolet light, underwater polarized light, UV-polarization sensitivity, behavioral spatial orientation, extracellular recording, CNS processing, photoreceptor biophysics, Pacific Salmon.

......

General Description of Problem

Animals often perceive the world in a manner which is different than that of humans. Each sense an animal possesses contributes to mélange of sensations and overall perception that Niko Tinbergen described as the animal's *Merkvelt* or perceptual world[1]. Professor Tinbergen's observations were insightful for the time (1940-50) since this idea that animals may see or hear 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-polarization sensitivity in fishes. Indeed, the literature (1970-1980) at the time referred to ultraviolet sensitivity in vertebrate animals as "high blue aberrant sensitivity", a misuse of the concept *Merkvelt* to say the least. This motivated a series of experiments examining different hypotheses regarding the optical stimuli[2] to explain this unusually high sensitivity to near UV light, but this was to no avail. We considered what was thought to be the most unlikely possibility of them all; do fish possess the ability to detect UV light[2]? Further experiments and the efforts confirmed this suggestion that fish and other vertebrate animals can see UV optical stimuli and that fish have cone photoreceptors that are distinctly sensitive to UV light. Initially, ideas such as UV light not penetrating water and UV light being absorbed by the lens of fish eyes provided logical barriers that made UV vision, in any vertebrate, seem improbable. However, these logical barriers turned out to be nothing more than the human eye predicting what the fish eye could see. More recently, evidence has grown regarding the observation of ultraviolet visual sensitivity in vertebrate animals and the cone photoreceptors that mediate this aspect of vision, dissolving the issue of the scientist's bias.

---

[1]e-mail :chawryshy@uvic.ca
web site: http://darwin.ceh.uvic.ca/hawryshy.html
tel:250 721-7142 fax: 250 721-7120

SPIE Vol. 3120 • 0277-786X/97/$10.00

It is now common to see new reports of ultraviolet sensitivity in a broad range of species. In fact, it is currently difficult to find a vertebrate species that does not possess UV cones. Questions surrounding the possession of UV vision have shifted from looking at the organisms that possessed UV vision to what is the functional domain of UV vision might be in aquatic ecosystem. While numerous possibilities exist, the one most studied thus far is the role of UV vision in the dection of polarized light - yet another visual attribute that humans do not appreciate. Many invertebrates use UV receptors to detect plane-polarized light, so at Cornell University, William McFarland and I, tested for polarization sensitivity in fish possessing UV sensitivity. Our hypothesis was confirmed, namely that there was a link between polarization sensitivity and UV vision in fish. It is this link I would like to address in this paper; what is the role of UV-polarized light vision in the behaviour of fish?

Unpolarized solar radiation incident on the earth's atmosphere is scattered by very small particles (Rayleigh scattering) generating linearly (partially) polarized light. The question of the relevance of linearly polarized light as a behaviourla cue for animals has received much attention over the past 50 years. Most of the research effort has been concentrated on invertebrates with the seminal experiments performed by Karl von Frisch[3]. These studies demonstrated that honey bees detect polarized light and use this information as a compass cue. Our knowledge of the specific mechanisms mediating the process of polarization vision is more thoroughly understood for invertebrates than for vertebrates. The organization and orientation of visual pigment bearing membrane in photoreceptors is well known for invertebrates. Hence the biophysical basis for the preferential absorption of e-vector by invertebrate photoreceptors has been convincingly established[4]. The orientation of visual pigment molecules within a given rhadomeric microvillus are aligned in one axis permitting preferential absorption of plane-polarized light. The biophysical mechanisms for polarization sensitivity of different cone types in fish[5] remains unclear although a number of hypotheses have been suggested: intraphotoreceptor dichroic filter, chromophore alignment, light obliquely striking the outer segment, receptor wave-guiding and receptor oil droplet refraction. In a recent study by Cameron and Pugh[6] they hypothesize that double cones (twins) mediate polarization sensitivity through inner segment birefringence in the green sunfish. However, recent experiments by Novales Flamarique and Hawryshyn[7] have revealed a lack of evidence for polarization sensitivity in green sunfish and has shed some skepticism on the biophysical mechanism producing polarization in the eye of fishes.

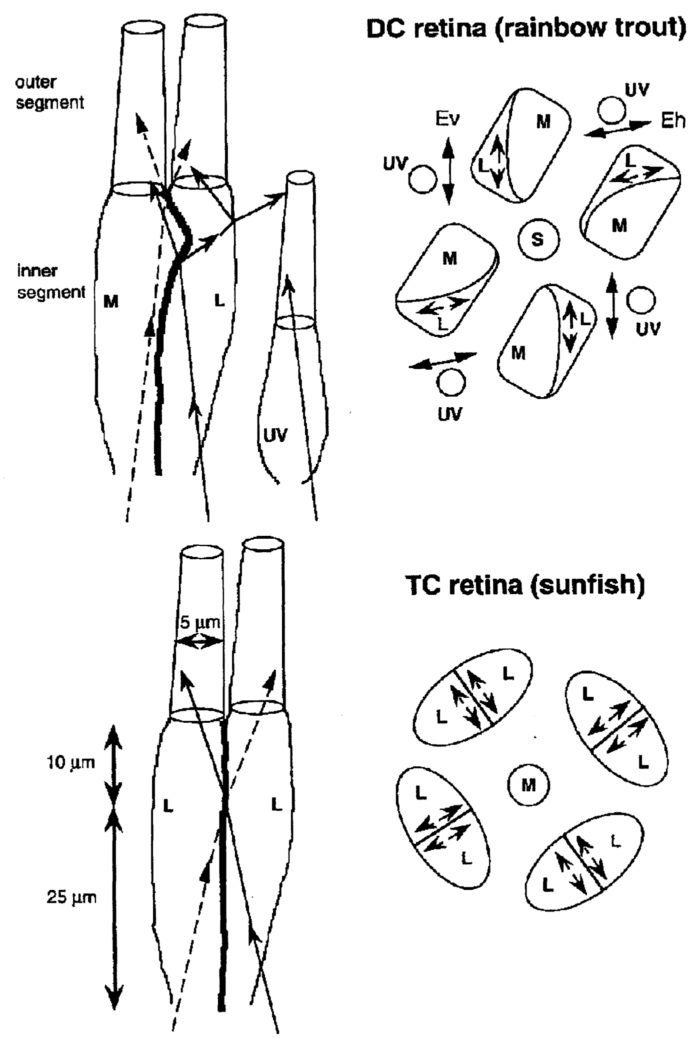

Figure 1: Examples of axial reflection in double cones.

The most recent observations regarding the biophysical mechanism of polarization comes from Novales Flamarique et al[8] where it has been hypothesized that light passing axially through double cones is reflected by the partitioning membrane and onto adjoining UV cone.

Notwithstanding the importance of biophysical, underwater light data, and electrophysiological processing mechanisms, this sensory capability and it's involvement in guiding the movement of salmon migratory behaviour ranks significantly amongst the most difficult biological problems of the day. Polarization vision provides animals with the potential to use spatial cues that may be used in direction finding. Migration is common among fishes and it is not inconceivable that some migratory movements such as those made by salmon range over 3,000 to 4,000 km. The use of a sun compass in migration has been demonstrated repeatedly, but it is during those segments of the journey when the sun is obscured, that polarization vision could play an important role in locating the position of the sun. To accomplish this hypothetical task the fish must be capable of scanning the polarized light field and further use this information for e-vector orientation. The experiments described below illustrate that such discriminations are possible through the UV, M and L (UV-, green- and red-sensitive) cones especially for polarized light in the UV spectrum where the cones have overlapping orthogonal polarization sensitivity.

This review will center on the role of polarization vision in orientation of salmonid fishes and will focus on several important facets of the problem including: underwater light field of fishes in the natural aquatic environment, receptor mechanisms mediating polarization sensitivity, orthogonal polarization sensitivity-rules for polarization discrimination, electrophysiology of polarization vision in fishes and behavioral orientation of fish to the polarized light field.

Underwater Light Field

To properly understand the role of polarization vision in orientation and navigation in fishes we must consider the characteristics of the light field in the aquatic environment. Celestial e-vector patterns have been extensively described by Wehner[9] and Brines and Gould[10]. Extensive measurements of the underwater polarized light fields have been described by Waterman (for review see Waterman[11]); and by Loew and McFarland[12]. The most striking finding was that, unlike the hemispherical field in the terrestrial situation, the polarization field underwater is spherical with respect to the observer's point in space. Most of the polarization of underwater light on cloudy days results from scattering by water molecules with little contribution from the sky light polarization[11]. The precise description of the polarized light field is based on three parameters: I, the intensity of the e-vector, p, the percent polarization of a point in the polarized light field and the e-vector orientation. These factors are highly dependent on the altitude of the sun as shown in Fig. 2.

Underwater polarization occurs through three processes: (i) direct transfer of sky born polarization, (ii) reflection at the air water interface[14], (iii) scattering by water molecules and very small particles in the water column. The degree of underwater polarization generated by these mechanisms is subject to variance in surface action and atmospheric conditions (cloud cover). The effect of solar altitude on the band of maximum polarization underwater. When the sun is at zenith the band of maximum polarization is arranged perpendicular to the solar beam but at dawn or dusk when the altitude of the sun is much lower the band of maximum polarization tilts and assumes an oblique orientation (mostly due to the refraction of the solar beam by the surface water).

A recent study has examined underwater polarized in a freshwater lake and in coastal marine habitats[15]. We measured the spectral distribution of underwater total and polarized light fields in the upper photic zone of moderately productive marine and freshwater. Percent polarization levels during the day were lower than 40 percent but during crepuscular periods rose to close to 70 percent. The spectral characteristics of underwater light are shown for a coastal marine habitat during the day and dusk[15]. When the sun is higher in the daylight sky the average percent polarization is much lower than when the sun is located lower in the sky such as at a time like dusk (Fig. 2)

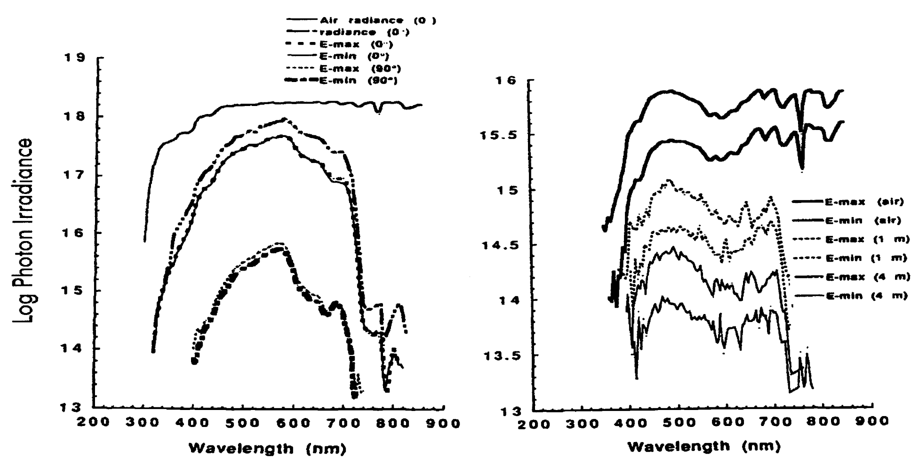

Figure 2 Radiance spectra measured at Ogden Point, Victoria, BC. Left panel: measurements made when the sun was roughly at zenith. Right panel: measurements made when sun was on the horizon, sunset. Note that the difference between the Emax and Emin was greatest at sunset thus providing the highest degree of polarization.

Retinal Mechanisms of Polarization Sensitivity

How vertebrate photoreceptors could be sensitive to polarized light has been the focus of much debate. For instance, what is the biophysical basis for the selective absorption of a plane of polarization by a photoreceptor? Moreover, what could be the biophysical basis for orthogonal polarization sensitivity in separate photoreceptors classes? Our knowledge of visual pigment molecule orientation in the receptor membrane is based on the rod receptor[16] and complimentary information for cones is limited but does indicate that cones show circular dichroism for end-on illumination[17]. Furthermore, in several species of anchovies[18] the cone outer segment discs are vertically oriented roughly analogous to the insect photoreceptors. Clearly, the issue of selective absorption of plane-polarized light remains equivocal at best.

Studies have demonstrated the presence of tectal cells sensitive to e-vector[19,20] in fish. Since this important first step, little additional information has been garnered from electrophysiological studies of polarization sensitivity in vertebrates. Investigators working with birds have used electroretinogram (ERG) recording to demonstrate polarized light discrimination[21]. However, these experiments do not clearly identify the receptor mechanism(s) that mediate polarization sensitivity.

Experiments by Waterman and Aoki[10] and Waterman and Hashimoto[20] looked for other receptor mechanisms by varying the test wavelength (λ) of the polarized light stimulus, but found no changes in polarization sensitivity. I would argue that although different test λ were not used. Not using chromatic adaptation and not using UV test λ (mainly because UV photoreception was unknown at the time of their studies) resulted in the observation of unimodal polarization sensitivity. More recent studies on rainbow trout[22] and goldfish[5] indicate that the UV-sensitive cone mechanism exhibits polarization sensitivity opposite to the mid wavelength- (M cones) and long wavelength (L cones)-sensitive cones[5] (Fig.3). Thus, differential polarization sensitivity between cone mechanisms appears to provide the potential for e-vector discrimination. The short wavelength (S cones)-sensitive cones do not exhibit polarization sensitivity; interestingly this is the part of the spectrum in which the underwater light field has the lowest degree of polarization underwater[23]. In addition, rod photoreceptors do not contribute to polarization sensitivity[16].

Like color vision, polarization vision depends on the possession of at least two differentially sensitive (with respect to e-vector) receptor (cone) mechanisms[24]. In addition, to enable between receptor comparisons the cone mechanisms must have overlapping regions of spectral sensitivity. For instance, in the case of the honey bee, those receptors that mediate polarization sensitivity are exclusively restricted to the UV spectrum [25] (three classes of UV receptors). In the case of fish all cone absorption spectra overlap in the UV spectrum. Without this capability, fish would not be able to make discriminations of e-vector independent of brightness or hue differences.

It has long been assumed the α - absorption band of a cone mechanism defines the range of the spectrum over which the cone mechanism is sensitive and the β - absorption band of the cone mechanism adds little utility to the responsivity of the cone mechanism. While this may be an acceptable assumption for most aspects of research carried out in color vision, it simply does not hold for other facets of vision mediated by cones such as polarization sensitivity. It has been estimated that the β - absorption band of the L cones, for instance, accounts for some 35 percent of the total absorption of the visual pigment. Figure 4 illustrates the degree of overlap of the visual pigment absorption spectra for the cones present in salmonids[26]. The β - absorption band of the L cones characteristically overlaps with theα - band of the UV sensitive cones. Not only do they overlap, but the β - absorption band of the L cones is capable of exhibiting the polarization sensitivity consistent with what is observed in the α - absorption band of the L cones.

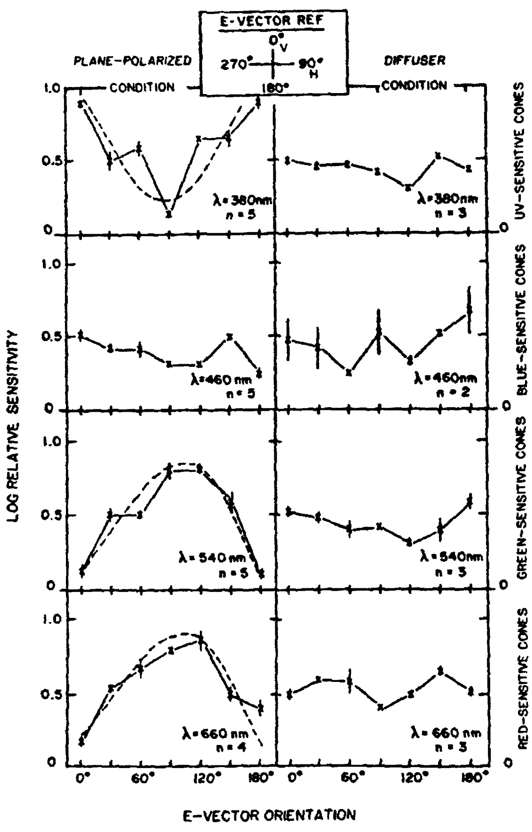

Figure 3 Polarization sensitivity curves for the cone mechanisms in trout.

Therefore, under the appropriate photic conditions, UV stimuli can stimulate both the UV and L cones (or M cones) producing orthogonal polarization sensitivity. Two differentially sensitive polarization cone mechanisms operating in the same spectral range (UV) provide a convincing basis for neural coding and hence the potential for discrimination of e-vector.

Coemans and his associates[27] were unable to show any convincing evidence that ERG responses varied with e-vector. While the ERG method is quick and easy in its application, relative to other modes of electrophysiological recording, there has been much discussion over interpretive problems of the changing nature of the waveform over varying conditions. Changes in amplitude alone do not necessarily explain most of the variance in response rather it appears the changing nature of the waveform plays a significant role in the response. New analytical strategies are required to more accurately assess if the ERG technique is reliable for polarization sensitivity measurements.

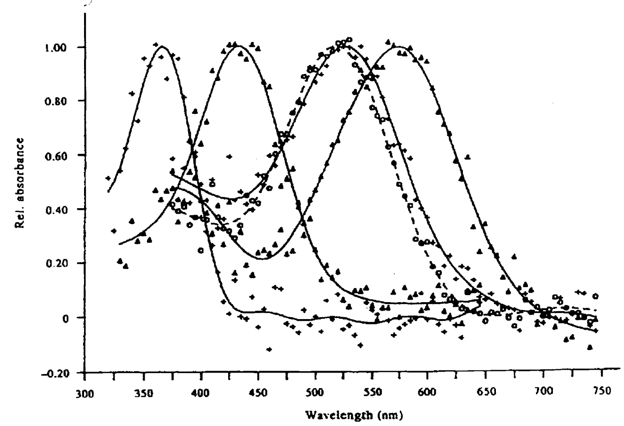

Figure 4 The absorption spectrum of the four cone pigments and rod pigment of rainbow trout.

Secondly, there are often problems related to the experimental design of polarization sensitivity experiments (electrophysiological or behavioral) which stem from failure to reveal the cone mechanisms which mediate polarization sensitivity. This can only be achieved through chromatic adaptation techniques (light adapting/selectively reducing the sensitivity of cone mechanisms with an intense color background) and using a polarized light stimulus which is spectrally coincident with the peak of the isolated cone mechanism[5]. Experiments that use white or spectral stimuli without chromatic adaptation can offer no conclusion(s) about the mechanisms that permit an animal to discriminate between different planes of polarization.

Central Nervous System Processing of UV-Polarized Light

Recent electrphysiological experiments have demonstrated neuronal processing underlying polarization vision[28]. Using extracellular recording techniques (tungsten electrode 5 µm, 10 MΩ), ganglion cell fibers were recorded in the optic nerve. The experiments involved a number of steps: (i) locate a color-coded ganglion cell. We have encountered numerous UV/L cone opponent units, the characteristics of such unit is shown in Fig. 5 (UV on and L off). Having identified the spectral sensitivity characteristics of the color opponent unit, one can correctly identify the origin of the cone mechanism

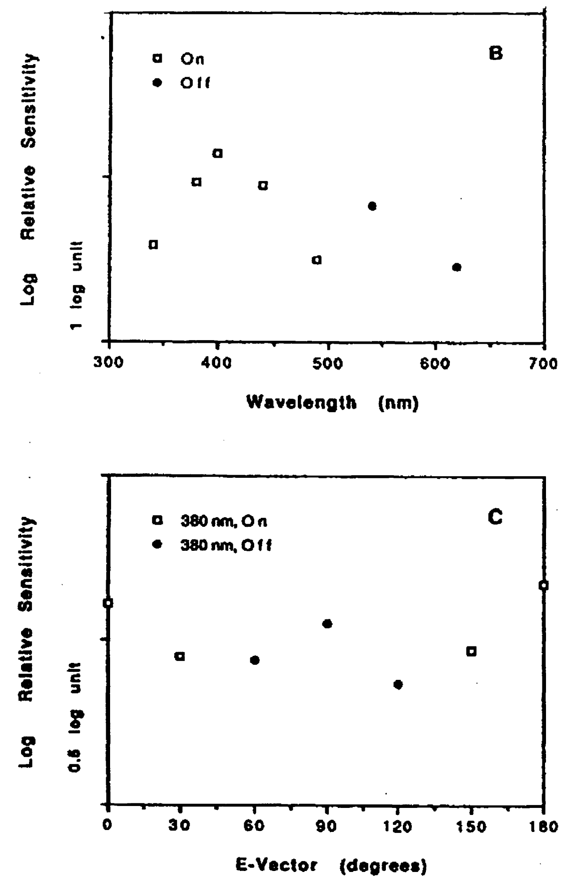

Figure 5 Single-unit electrophysiological recording: evidence of e-vector coding at the level of a single neuron.

response. (ii) show that the individual members (UV and L cones) of the opponent pair exhibit polarization sensitivity characteristics consistent with our observations in the heart - rate conditioning experiments[5]. For instance, a 380 nm linearly polarized stimulus was varied between the 0° and 90° e-vector orientations producing a 0.8 log unit modulation in sensitivity (0° maximum sensitivity). The same manipulation was used at 660 nm producing a modulation in sensitivity of the same magnitude (90° maximum sensitivity). (iii) show that the single-unit optic fiber is capable of exhibiting background and then a suprathreshold 380 nm polarized light stimulus was used to examine changes in nerve fiber coding with changes in the orientation of e-vector. When the 380 nm stimulus was presented in the 0° orientation an on response was evident indicating that the UV cones were being stimulated. When a 380 nm stimulus was presented in the 90° orientation an off response was evident indicating that the β - band of the L cones was being stimulated. The most important observation to consider is that a single-unit exhibits responses of opposite polarity for orthogonal presentations of the e-vector in the UV spectrum. This observation explains why fish fail to show correct behavioral orientation when the polarized light field does not contain UV light. Without two differentially sensitive polarization receptors, the potential for discrimination on the basis of e-vector orientation is not possible[28].

Behavioral evidence for polarization vision

Studies have shown that fish exhibit free-swimming spatial orientation to polarized light fields. Two behavioral techniques have been used to examine the response of fish to linearly polarized light: (i) Innate/unconditioned studies, whereby an e-vector field is imposed on a circular orientation tankand the angular orientation of the fish relative to the -vector orientation is scored. While data from these studies show considerable variability in angular response, they nonetheless exhibit statistically significant orientation to the e-vector[29,32]. Studies have established that this orientation results from the use of e-vector as a cue (i.e. polarotaxis) rather than from differential brightness patterns (i.e. phototaxis) generated from the polarized light reflecting off the internal surfaces of the test tank[32]. A completely different technique was used by Kawamura et al[33] in which innate responses to flashes of polarized light originating from above was monitored in terms of changes in heart rate activity (bradycardia). A number of species of fish were shown to exhibit innate cardiac responses to polarized light including cichlids and trout. (ii) Conditioned response studies whereby a fish is trained to swim to a particular location within a tank under a polarized light field. The fish is given food reward for swimming to a target location, and after a number of trials, the fish's movement to the target location is consistent. Once trained, the fish is released in the center of a test tank with a polarized light field present and the angular orientation of the fish's movement is scored (Fig. 5). The advantage of this technique is that it reduces the variance in angular orientation both within and between individuals and this in turn permits the investigator to reliably conduct longitudinal studies. A summary of the experiments that we have conducted on rainbow trout (*Onchoryncus mykiss*)[34,35] is given in Table 1. These experiments show a number of important features of the visually-mediated orientation behavior of trout: (i) The orientation accuracy of the test fish is highly dependent on the spectral composition of the polarized light field. A polarized light field containing UV radiation is necessary for orientation, since the angular orientation of trout is dramatically impaired when UV light is removed from the polarized light field. (ii) Partially polarized light can affect the orientation accuracy when the degree of polarization is less than 70% (recently confirmed by Novales Flamarique and Hawryshyn[15] using an electrophysiolgical technique). Because the degree of polarization in natural marine

Table 1 Summary of experiments on orientation of trout to polarized light.

photic conditions	proportion of trout statistically oriented to e-vector
(I) Spectral content	
(i) UV plus visible spectrum polarized light field	12/14
(ii) No UV only visible spectrum polarized light field	3/11
(iii) UV polarized light field	12/15
(II) Degree of polarization	
UV plus visible spectrum partially polarized light field	
(i) 90%	17/19
(ii) 83%	11/14
(iii) 77%	12/13
(iv) 75%	10/17
(v) 68%	3/13
(vi) 65%	2/17
(vii) 63%	0/15
(III) Ontogeny	
(i) Immature (possesses UV cones)	3/3
(ii) Mature (no UV cones present)	0/3

and freshwater ecosystems is variable, fish using the polarized light cues may require behavioural adjustments to posture and position (e.g. vertical position in the water column) to facilitate the acquisition of the polarized light cue. (iii) Some salmonids exhibit an ontogenetic loss of UV sensitivity [6,37] that can affect orientation accuracy (iv) Rainbow trout are capable of differentiating different orientations of the e-vector[34].

Future Directions

1. Neuronal Coding - Pathways in the Brain

Our research thus far has indicated that UV -polarization sensitive neurons are well represented in the mid-brain region of the central nervous system called the torus semicirularis located below the optic tectum. We also know that the optic tectum, an important visual processing center, does not appear to play a role in the processing of UV-polarized light information. How this particular visual information projects to different brain structures is a matter of current interest[38]. We would like to establish evidence for other higher order processing centers in the brain of salmonid fishes.

2. Life History Events

Rainbow trout (*Oncorhynchus mykiss*) belong to the Family Salmonidae. Pacific salmonids range from landlocked trout like rainbow trout to sockeye salmon, an anadromous migrating salmon that spends its life history in both freshwater and the marine environment. All salmonids have a keen sense of vision showing exceptional capabilities in detecting color, motion, spatially and temporally heterogeneous stimuli[2]. These attributes make rainbow trout a superb predator especially in foraging for plankton, insects and small fishes[39]. Rainbow trout have tetrachromatic vision possessing four spectrally distinct cone photoreceptors[26,28]. However, earlier studies in my laboratory revealed an ontogenetic loss of UV sensitivity and this observation has sparked a recent flurry of experiments in other laboratories to gain understanding into the mechanism(s) of loss of UV sensitivity in trout.

We chose rainbow trout as our model organism for our research on migratory Pacific Salmon for research since they exhibit natural plasticity at the level of the retina. The following changes occur during the development of trout : (i) From hatching to fry to juvenile stage trout possess UV cones and UV sensitivity. (ii) At the transition from juvenile to the adult the UV cones disappear from the cone mosaic[2]. Measurement of spectral sensitivity reveals that UV sensitivity also disappears. (iii) In the later stages of the adult phase UV cones regenerate back into the cone mosaic and UV sensitivity returns. Evidence from various studies shows that thyroxin and retinoic acid mediate changes in the pattern of the cone mosaic and its sensitivity to UV stimuli[40,41,36]. We will attempt to understand how environmental factors account for the varied pattern of development of the UV-polarization system in a wide range of Pacific Salmon species.

3. Open Ocean Tracking

This project would use a suite of ultrasonic tracking experiments to examine the migratory patterns and foraging behaviour of sockeye salmon (*Oncorhynchus nerka*) in relation to the biotic and biotic, basin-scale and mesoscale structure of the marine environment (e.g. prey, water masses, currents) and environmental stimuli that may be used by salmon to guide the spawning migrations from their foraging grounds in the Northeast Pacific Ocean to their natal streams in British Columbia (e.g. UV-polarized light, earth's magnetic field).

A towed hydrophone array and signal processing system would be developed to enhance the operational capabilities of ultrasonically tracking salmon. The tracking experiments would provide the migration paths of tagged salmon and time series of measurements from sensors from each tag (e.g. depth, temperature, heart rate). These experiments and the interpretation of the results would be conducted in collaboration with GLOBEC environmental observation and modeling programs in the Strait of Georgia, along the coast of British Columbia, and in the northeast pacific ocean. The intent is to conduct the ultrasonic tracking experiments with a multidisciplinary observation and modeling program (e.g. ocean physics, food web dynamics, sockeye salmon migration and foraging behaviors).

Sockeye salmon is the most important commercial fish in British Columbia and the Fraser River is the largest producer of this species within the province. As with all harvested species, a knowledge of the biophysical mechanisms that drive production is required to predict growth and return abundance (and to forecast the impacts of climate change on production); however, the Fraser River sockeye salmon fishery also requires pre-season predictions of stock-specific coastal migration routes and return times to meet complex escarpment and catch allocation goals. Migration and foraging behaviors affect growth, survival, and the distribution of fish

[2] A cone mosaic is a regular pattern of cone photoreceptors that repeats itself across the retinal hemisphere. A square mosaic pattern, characteristic of salmonids, consists of a central blue-sensitive cone quadralaterally surrounded by double cones (green- and red- sensitive pairs) with UV cones in the four corner positions.

in space and time, but these behaviors as yet can only be hypothesized. Understanding how productivity and distributions of sockeye salmon are affected by the complex marine environment, requires an understanding of how these fish respond to basin-scale and mesoscale variability and how they use oceanographic clues and other stimuli to guide their migrations.

Ultrasonic tags have been successfully used to track salmonids in the open-ocean and coastal environments; however, the technology currently available has restricted the number of fish that could be tracked at any given time and the duration that any salmon could be tracked. A towed array would permit the acquisition of a much greater volume of tracking data (i.e. more than one fish at a time, and for longer tracking periods), by placing the hydrophones at a greater depth, using array gain to increase the range at which fish can be tracked. It would be capable of receiving the ultrasonic telemetry simultaneously from several salmon, implanted with ULTRASONIC tags. The system would provide the horizontal position of each fish in addition to recording the time series of measurements from each tag (e.g. temperature, depth, heart rate).

Sockeye salmon would be caught off the coast of the Queen Charlotte Islands and in Queen Charlotte Sound (during their return migration along the coast of British Columbia to the Fraser River), tagged with ultrasonic transmitters and tracked at least as far south as Cape Cook on the west coast of Vancouver Island or the south end of Queen Charlotte Strait on the east coast of the island. It has been hypothesized that the mesoscale structure in queen Charlotte Sound, particularly immediately north of Vancouver Island affects the interannual variability of the Northern Diversion Rate (the percent of Fraser River sockeye salmon returning around the north end of the island). Concurrent observations of the abiotic and biotic characteristics of the mesocale structure would be required, as well as a multidisciplinary understanding of the processes which drive variability of these phenomena, to interpret the tracking results and predict future migration paths.

Our objective here is to evaluate the degree to which polarized light vision may be used in the marine environment to guide the migratory behaviour of salmon. Piloting, compass orientation and bi-coordinate navigation have been proposed as conceptual models for direction-finding, but the nature of the stimuli used by salmon is unknown. It has been established that salmon are capable of using polarized light to guide their orientation behaviour[2]. It is known that more than one sensory modality may be involved in guiding migratory behaviour[2], but the relative importance of these different stimuli under a variety of environmental conditions must be assessed. Sockeye salmon will be implanted with ultrasonic tags and released in Queen charlotte Sound, fitted with optically active eye covers modified degrade or maintain the polarization field incident on the eye. The relative movements of salmon that differ in the imposed optical characteristics of the eye, in relation to the local meteorological and oceanographic conditions will be used to assess the potential use of UV-polarized light clues as guidance mechanisms.

Acknowledgments

Professor Talbot Waterman and his associates have pursued the problem of polarization sensitivity for several decades and this has lead to the development of a rich library of information. For his contribution and insight into the study of underwater polarization vision, I think it is fitting to say that I owe Professor Waterman a debt of gratitude.

My research program is supported by a University Research Fellowship and an operating grant from the Natural Sciences and Engineering Research Council of Canada. I would like to thank my graduate students and postdoctoral fellows who have contributed to this research in many important ways.

References

1. N. Tinbergen. The Study of Instinct. Oxford University Press, New York. 1951.
2. C.W. Hawryshyn. Polarization vision in fish. Am. Sci. 80: 164-175, 1992.
3. K. Von Frisch. Die polarization des himmelscichtes als orientierender faktor bei den tanzen der bienen. Experimentia 4: 142-148, 1949.
4. R. Wehner, G. Bernard and E. Gieger. Twisted and non-twisted rhabdoms and their significance for polarization detection in the bee. J. Comp. Physiol. A 104: 225-245, 1975.
5. C.W. Hawryshyn and W.N. McFarland. Cone mechanisms and the detection of polarized light in fish. J. Comp. Physiol. 160: 459-465, 1987.
6. D. Cameron and E. Pugh. Double cones as a basis for a new type of polarization vision in vertebrates. Nature 353, 161-164, 1991.
7. I. Novales Flamarique and C.W. Hawryshyn. No evidence of polarization sensitivity in freshwater sunfish from multi-unit optic nerve recordings. Vision Res. 37, 967-973, 1997.
8. I. Novales Flamarique, C.W. Hawryshyn and F.I. Harosi. Double cone reflection as a basis for the polarized light detection in fish. J. Opt. Soc. Am., under review.
9 R. Wehner. Neurobiology of polarization vision. Trends in Neurosci. 12: 353-359, 1989.
10. M.L. Brines and J.L. Gould. Skylight polarization patterns and animal orientation. J. Exp. Biol. 96: 69-91, 1982.
11. T.H. Waterman. Polarization sensitivity: In Comparative physiology and evolution of vision in invertebrates. B:Invertebrate visual centers and behavior. Handbook of Sensory Physiology VII/6B. (J. Autrum, ed.). Springer, New York. pp. 281-469, 1981.

12. E.R. Loew and W.N. McFarland. The underwater visual environment. In Vision in Fishes. (R. Douglas and M.B.A. Djamgoz, eds.). Chapman and Hall, London. pp. 1-43, 1990.
13. T.H. Waterman. Polarization patterns in submarine illumination. Science 120: 927-932, 1954.
14. G. Horvàth and D. Varjú. Underwater refraction-polarization payyerns of skylight perceived by animals through Snell's window of the flat water surface. Vision Res. 35: 1651-1666, 1995.
15. I. Novales Flamarique and C.W. Hawryshyn. Is the use of underwater polarized light by fish restricted to crepuscular time periods? Vision Res. 37: 975-989, 1997.
16. R.A. Cone. Rotational diffusion of rhodopsin in the visual receptor membrane. Nature 236: 39-43, 1972.
17. B. Gupta and T.D. Williams. Lateral diffusion of visual pigment in toad (*Bufo marinus*) rods and in catfish (*Ictalurus punctatus*) cones. J. Physiol. 430: 483-496, 1990.
18. B.A. Fineran and J.J.A.C. Nicol. Studies on the photoreceptors of *Anchoa mitchilli* and *A. hepsetus* (Engraulidae) with particular references to the cones. Phil. Trans. Roy. Soc. Lond. B 283: 25-60, 1978.
19. T.H. Waterman and K. Aoki. E-vector sensitivity patterns in the goldfish optic tectum. J. Comp. Physiol. 95: 13-27, 1974.
20. T.H. Waterman and H. Hashimoto. E-vector discrimination by the goldfish optic tectum. J. Comp. Physiol. 95: 1-12, 1974.
21. J.D. Delius, R.J. Perchard and J.A. Emmerton. Polarized light discrimination by pigeons and an electroretinographic correlate. J. Comp. Physiol. Pychol. 70: 560-571, 1976.
22. D.C. Parkyn and C.W. Hawryshyn. Polarized-light sensitivity in rainbow trout (*Oncorhyncvhus mykiss*): characterization from multi-unit responses in the optic nerve. J. Comp. Physiol. A 172: 493-500, 1993.
23. A. Ivanoff and T.H. Waterman. Factors, mainly depth and wavelength, affecting the degree of underwater polarization. J. Mar. Res. 16: 283-307, 1958.
24. G.D. Bernard and R. Wehner. Functional similarities between polarization and color vision. Vision Res. 17: 1019-1028, 1977.
25. R. Wehner, G.D. Bernard and E. Geiger. Twisted and non-twisted rhabdoms and their significance for polarization detection in the bee. J. Comp. Physiol. 104: 225-245, 1975.
26. C.W. Hawryshyn and F.I. Harosi. Spectral characteristics of visual pigments in rainbow trout (*Oncorhynchus mykiss*). Vision Res. 34: 1385-1392, 1994.
27. J.J. Vos Hzn, M.A.J.A. Coemans and J.F.W. Nuboer. No evidence for polarization vision in the pigeon electroretinogram. J. exp. Biol. 198: 325-335, 1995.
28. D.J. Coughlin and C.W. Hawryshyn. A cellular basis for polarized-light vision in rainbow trout. J. Comp. Physiol. A 176: 261-272, 1994.
29. T.H. Waterman and R.B. Forward Jr. Field evidence for polarized light sensitivity of fish *Zenarchopterus.* Nature 228: 85-87, 1970.
30. R.B. Forward Jr, K.W. Horch and T.H. Waterman. Visual orientation at the water surface by the teleost *Zenarchopterus.* Biol. Bull. 143: 112-126, 1972.
31. H. Kleerekoper, J.M. Matis, A.M. Timms, P. Gensler. Locomotor response of the goldfish to polarized light and it's e-vector. J. Comp. Physiol. 86: 27-36, 1973.
32. R.B. Forward Jr. and T.H. Waterman. Evidence for E-vector and light intensity pattern discrimination by the teleost *Dermogenys.* J. Comp. Physiol. 87: 189-202, 1973.
33. G. Kawamura, A. Shigata and T. Yonemori. Response of teleost to the plane of polarized light as determined by the heartbeat rate. Bull. Jpn. Soc. Sci. Fish. 47: 727-729, 1981.
34. C.W. Hawryshyn, M.G. Arnold, E. Bowering and R.L. Cole. Spatial orientation of rainbow trout to plane-polarized light: The ontogeny of e-vector discrimination and spectral sensitivity characteristics. J. Comp. Physiol. A 166: 565-574, 1990.
35. C. W. Hawryshyn and A.E. Bolger. Spatial orientation of trout to partially polarized light. J. Comp. Physiol. 167: 691-697, 1991.
36. C.W. Hawryshyn, M.G. Arnold, D. Chiasson and P.C. Martin. The ontogeny of ultraviolet photosensitivity in rainbow trout (*Salmo gairdneri*). Vis. Neurosci. 2: 247-254, 1989.
37. J.K. Bowmaker and Y.W. Kunz. Ultraviolet receptors, tetrachromatic color vision and retinal mosaics in brown trout (*Salmo trutta*): age-dependent changes. Vision Res. 27: 2101-2108, 1987.
38. L. Beaudet. *Adaptation mechanisms in the Salmonid Visual System.* Ph. D. Thesis. University of Victoria, 1997.
39. H.I. Browman and C.W. Hawryshyn. Thyroxine induces a precocial loss of ultraviolet photosensitivity in rainbow trout (*Oncorhynchus mykiss*) Vision Res. 32, 2303, 1992.
40. H.I. Browman and C.W. Hawryshyn. The developmental trajectory of ultraviolet photosensitivity in the rainbow trout is altered by thyroxin. Vision Res. 34: 1397-1406, 1994.
41. L. Beaudet, H.I. Browman and C.W. Hawryshyn. Optic Nerve response and retinal structure in rainbow trout of different sizes. Vision Res. 33: 1739-1746, 1993.