

Optic Nerve Response and Retinal Structure in Rainbow Trout of Different Sizes

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This study presents evidence of ultraviolet (UV) sensitive, ON center ganglion cells in the fish retina. We determined the spectral sensitivity of ON and OFF responses from the optic nerve mass potential in small (18.0–28.5 g) and large (59.5–835 g) rainbow trout, with special reference to UV sensitivity. Under a mid + long-wavelength adapting background, the ON response of small fish revealed the presence of a UV cone mechanism (λ_{max} 390 nm) which was absent in large specimens. Under similar background conditions, the OFF response of both small and large fish showed one sensitivity peak, dominated by inputs from an M-cone mechanism. An almost complete absence of the accessory corner cones from the retinal mosaic was correlated with the loss of UV sensitivity.

Ultraviolet photosensitivity Ganglion cell Cone Development *Oncorhynchus mykiss* Retina

INTRODUCTION

Several studies have characterized the ultraviolet (UV) sensitivity in fish, using psychophysical techniques (Hawryshyn & Beauchamp, 1985; Neumeier, 1985; Douglas, 1986; Hawryshyn, Arnold, Chiasson & Martin, 1989; Hawryshyn & Harosi, 1991; Hawryshyn, 1991) and microspectrophotometry (Avery, Bowmaker, Djamgoz & Downing, 1983; Harosi & Hashimoto, 1983; Bowmaker & Kunz, 1987; Hawryshyn & Harosi, 1991; Bowmaker, Thorpe & Douglas, 1991). These studies describe a UV cone mechanism, and a photopigment maximally sensitive to 355–380 nm light. In addition, in some cyprinids, recordings have been made from tetraphasic horizontal cells, bipolar and amacrine cells, which are sensitive to UV light (Harosi & Fukurotani, 1986; Hashimoto, Harosi, Ueki & Fukurotani, 1988). To date, no study has examined the physiological response of retinal ganglion cells to UV light.

Retinal ganglion cells convey visual information to the brain. This information leaves the retina by two different functional pathways: ON- or OFF-type ganglion cells (Wheeler, 1979; DeMarco & Powers, 1991). The ON-type carries information relative to increments in light intensity, whereas the OFF ganglion cells carry information about decrements in light intensity. Compound action potentials (CAP) recorded from the optic nerve provide information on the spectral characteristics of these two information channels (Wheeler, 1979).

Juvenile rainbow trout (*Oncorhynchus mykiss*), experience a normal developmental loss of UV photosensitivity (Hawryshyn, Beaudet & Browman, 1989). In this paper, we used a combination of electrophysiology and light

microscopy to investigate this developmental event. We characterized the spectral sensitivity of ON and OFF responses recorded from the optic nerve CAP of small (18–28.5 g) rainbow trout, paying particular attention to UV sensitivity, and compared it to that of larger individuals (59.5–835.0 g). Examination of the retinal cone mosaic in small and large fish allowed us to correlate the observed loss of UV sensitivity with the disappearance of a class of cone photoreceptors.

MATERIALS AND METHODS

Rainbow trout (*O. mykiss*, Fraser Valley Trout Hatchery, Abbotsford, B.C.) were maintained at 15°C under a 12:12 hr light:dark photoperiod for at least 8 weeks prior to the experiments. Fish were fed daily with a constant ration of BioDiet Grower pellets (Bio-Products Inc., Warrenton, Ore.). The experiments were performed between 10:00 and 18:00 hr. Illumination in the holding facility was provided by fluorescent bulbs at an intensity of $33.54 \pm 14.39 \mu\text{W cm}^{-2}$ (integrated irradiance, 200–1100 nm, measured with a Photodyne Inc. radiometer). The small fish used in these experiments weighed between 18.0 and 28.5 g and the large ones between 59.5 and 914 g (Table 1).

Surgical procedures

Fish were anesthetized by immersion in MS-222 (tricaine methanesulfonate, 0.1 g/l), paralyzed by i.m. injection of Pavulon (pancuronium bromide, 0.038 mg/g body wt) and respired with water flow (400 ml/min, 15°C) over the gills. A local anesthetic was applied to the surgical area (tetracaine, 0.5%). The recording area was accessed by removing the tissues over the rostral optic tecta. During the surgery and the recording session, the physical condition of the fish could be monitored by

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direct observation of the regularity and strength of the tectal surface blood flow.

Recording technique

Compound action potentials were obtained by inserting a tapered Teflon-coated silver wire (0.38 mm dia) through the rostral optic tectum and into the lumen of the optic nerve, at the level of the optic chiasm. A reference electrode was inserted into the olfactory epithelium. The large size of the electrode allowed a direct visual evaluation of its position during preliminary studies. Subsequently, the electrode was positioned using stereotaxic reference points based on these initial assessments. The accuracy of electrode position was also evaluated by monitoring the configuration of the components of the response (see below). Signals were differentially amplified 50,000 times by a Grass preamplifier (P50 Series) with bandpass 0.3 Hz–0.1 kHz and displayed on an oscilloscope.

The compound action potential

The recording technique used in this paper monitors the activity of the major populations of fibers active within the optic nerve (Vanegas, 1974). The optic nerve compound action potential response is characterized by a sharp negative deflection of the baseline usually followed by a positive deflection, at the onset (ON) and at the termination (OFF) of the stimulus [Fig. 1(a)]. Its amplitude depends on the intensity of the stimulation. In addition, at certain wavelengths, we observed the presence of secondary negative peaks with longer latencies; either at the ON or at the OFF. This has also been observed by DeMarco and Powers (1991).

Stimulus and background conditions

A 150 W Xenon lamp was used as a light source for the stimulus. An Inconel coated neutral density wedge (nominal 4.0 neutral density) was used to control the stimulus intensity and a monochromator (ISA) to control its spectral characteristics. The stimulus consisted of a 750 msec square-wave pulse of given

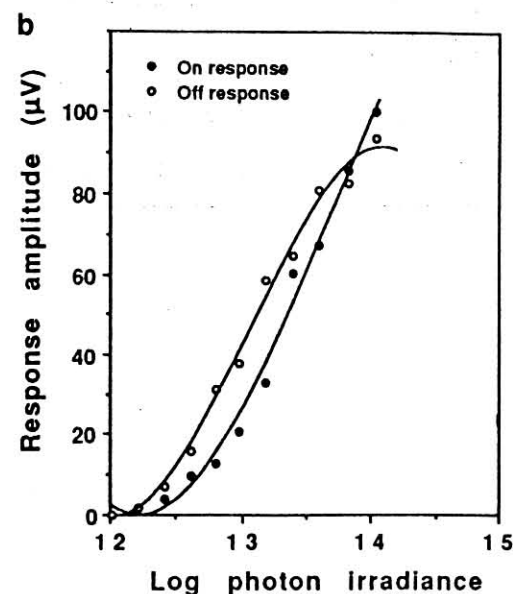
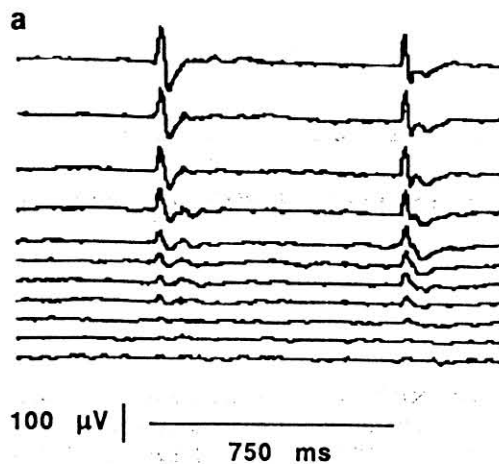


FIGURE 1. (a) Optic nerve compound action potentials in response to a 580 nm stimulus of increasing intensity (two responses averaged per trace). The intensity of the stimulation was increased by 0.1 log unit starting from the bottom. The amplitude measured was that of the first deflection (negative) for both ON and OFF responses. Negative upward. (b) Amplitude of the responses in (a) plotted against the intensity of the stimulations. A third-order polynomial function fitted to the data points was used to determine the criterion intensities.

TABLE 1. Weight and total length for the rainbow trout used in the experiments

Fish No.	Weight (g)	Total length (mm)
HC1	21.0	125
HC2	18.0	125
HC3	20.5	135
HC9	24.0	140
HC11	28.5	140
T1	59.5	185
L2	835.0	410
L4	756.0	370
L7	713.0	385
L9*	914.0	405
L10	85.0	210

*Not used in the electrophysiology experiments.

intensity and wavelength, generated by a shutter controlled by computer. Combinations of interference (500 nm long pass and 650 nm long pass, Oriel Corp.) and neutral density filters were used to produce an adapting background from two tungsten-halogen light sources. The colored background was used to selectively adapt the middle (M)- and long-wavelength (L) cone mechanisms, favoring expression of the short-wavelength (S) and, if present, the UV cone mechanisms. The stimulus and the background illumination were projected onto the fish's eye via UV-transmitting liquid light guides (Oriel Corp.), positioned to produce overlap of the illumination from all three optical channels onto the ventro-temporal quadrant of the retina. For each wavelength-intensity combination, the energy measured in W/cm^2 was converted to quantal irradiance.

Experimental procedures

Prior to each experiment, the fish were subjected to the adapting background for a minimum of 1 hr. Each test wavelength was presented in a series of increasing intensities (0.1 log unit steps), superimposed over the adapting background. In this way, a series of responses (ON and OFF) of increasing amplitude were generated for each test wavelength [Fig. 1(a)]. For each intensity, two or three responses were averaged, depending on the clarity of the signal, and the amplitude of ON and OFF first negative deflections measured. Usually, thirteen test wavelengths, covering the spectrum from 360 to 660 nm, were presented in an order preventing selective adaptation of any one cone mechanism. In some cases the amount of energy generated by the stimulus source was insufficient to allow testing wavelengths > 580 nm.

Analysis of the compound action potential responses and threshold determination

The amplified signal was digitized through an A/D board and analyzed by computer during the experiment. For each wavelength-intensity combination, the amplitude of the ON and OFF negative deflection was measured and the averaged prestimulus noise band (200 msec prestimulation) subtracted from it. At each wavelength, the amplitude of the ON and OFF responses was plotted against log photon irradiance [Fig. 1(b)]. A third order polynomial function was fitted to the ON and OFF amplitude-intensity data points [Fig. 1(b)]. Thresholds were calculated from the irradiance required to produce a criterion response of 30 μ V. The criterion response was selected at a relatively low level to ensure that the sensitivity of the RGCs receptive field center was measured (see Discussion).

The photopigment absorption curves fitted to our spectral sensitivity data were generated by an eighth-order polynomial template for vertebrate cone visual pigments (Bernard, 1987; Gary D. Bernard, personal communication). These absorption curves were corrected for the differential absorption of small and large fish ocular media, as determined by Hawryshyn *et al.* (1989).

Retinal histology

At the end of each experiment, fish were light adapted for 30 min, euthanized by decerebration and the retinae removed for histological study. Fixation, postfixation and embedding of retinae were performed following the protocol used by Ali and Anctil (1976). Tangential sections (1 μ m) at the level of the cone inner segments were made and stained with Richardson's stain. The stimulated area was examined to determine whether accessory corner cones were present. All of the procedures described in this paper were in accordance with the regulations of the Canadian Council for Animal Care.

RESULTS

Spectral sensitivity of the ON response

Small fish. In small fish subjected to an M + L adapting background, the ON response revealed the presence of a UV sensitivity peak [Fig. 2(a)]. This peak matched a photopigment absorption curve of λ_{\max} 390 nm. However, the sensitivity of the short wavelength limb of its action spectrum was slightly lower than predicted by the photopigment absorption curve. In addition to the UV peak, a short-wavelength sensitivity peak was present and matched best the absorption spectrum of a photopigment with a λ_{\max} at 420 nm [Fig. 2(a)]. Under these

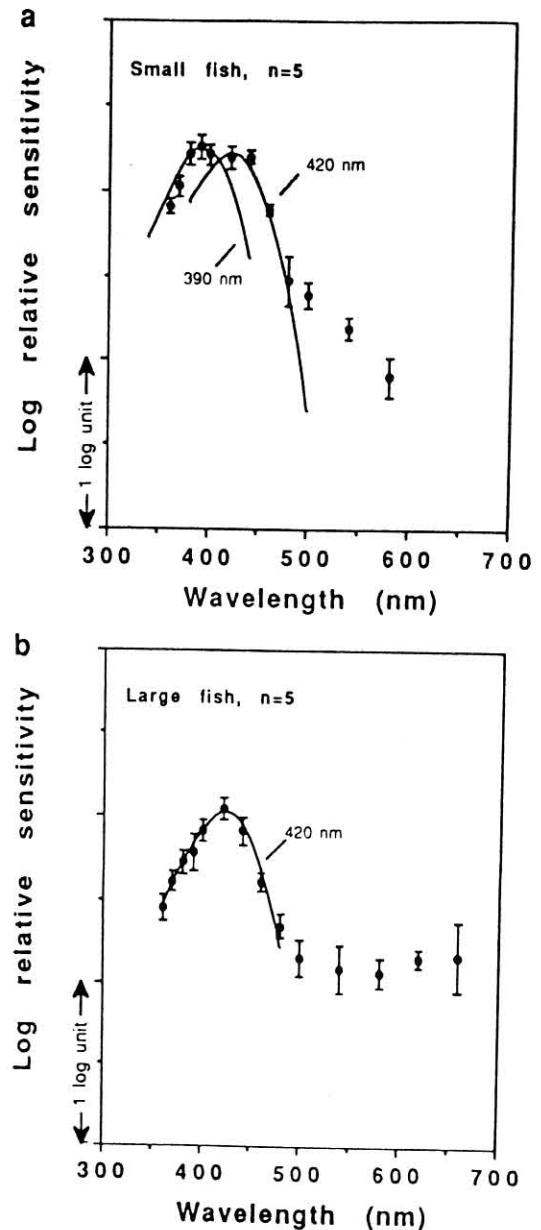


FIGURE 2. Spectral sensitivity of the optic nerve ON response in (a) small (<30 g) and (b) large (59.5–835 g) rainbow trout, under a mid + long-wavelength adapting background. 390 and 420 nm λ_{\max} photopigment absorption curves (solid lines), corrected for ocular media absorption, were compared to the sensitivity points in the small fish. A 420 nm λ_{\max} photopigment absorption curve, corrected for ocular media absorption, was compared to the sensitivity points in large fish. Bars represent one standard error of the mean.

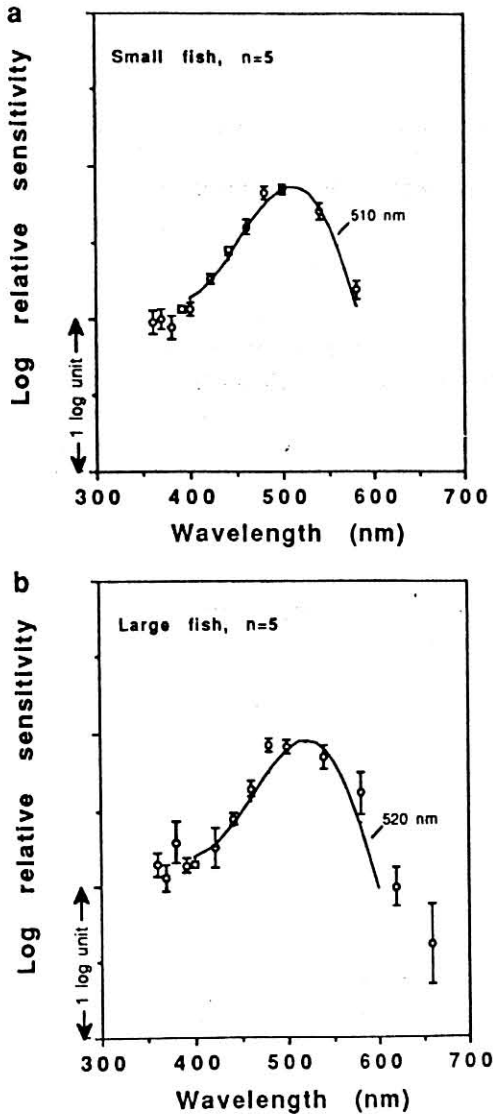


FIGURE 3. Spectral sensitivity of the optic nerve OFF response in (a) small (<30 g) and (b) large (59.5–835 g) rainbow trout under a mid + long-wavelength adapting background. 510 nm λ_{\max} and 520 nm λ_{\max} photopigment absorption curves (solid lines), corrected for ocular media absorption, were compared to the sensitivity points in small and large fish respectively. Bars represent one standard error of the mean.

background conditions, the relative sensitivity of the ON response to mid and long wavelengths was approx. 1 log unit lower than those of the UV and short [Fig. 2(a)].

Large fish. The spectral sensitivity of the ON response in large fish was characterized by a single peak with a λ_{\max} in the short-wavelength part of the spectrum [Fig. 2(b)]. The action spectrum of this cone mechanism matched the absorption curve of a photopigment with a λ_{\max} at 420 nm. The UV sensitivity peak was not present in these fish.

Spectral sensitivity of the OFF response

In both small and large fish, the spectral sensitivity of the OFF response was characterized by a single peak in the mid-wavelength part of the spectrum. In small fish, this peak matched closely the absorption curve of a photopigment with a λ_{\max} at 510 nm [Fig. 3(a)]. In large specimens, it matched the spectral absorption of a

photopigment with a 520 nm λ_{\max} . Furthermore, there was a discrepancy between the pigment absorption curve and the sensitivity points on the long-wavelength limb of the sensitivity peak. These points were more sensitive than predicted by the absorption curve [Fig. 3(b)].

Retinal histology

The ventro-temporal retina of the small fish from which the spectral sensitivity curves were obtained showed a square cone mosaic which included accessory single corner cones [Fig. 4(a)]. The square mosaic was composed of four double cones whose axes were directed toward a central single cone. The accessory single cones occupied the corners of a square having its sides running perpendicular to the double cones middle axes [Fig. 4(a)].

The retina of large fish exhibited a square cone mosaic lacking accessory corner cones [Fig. 4(c)]. However, the arrangement pattern of the cones showed heterogeneity, ranging from a square mosaic in the central retina to a row mosaic at the periphery. Furthermore, we found that the absence of a UV peak in the large fish is not correlated with a complete absence of the corner cones from the retinal mosaic: in two large fish (L10, 85 g and L9, 934 g), we found an area of the central retina, located near the optic nerve head and the embryonic fissure, where accessory corner cones were present [Fig. 5(a, b)].

DISCUSSION

The compound action potential response

Both the center and periphery of a large number of RGCs receptive fields are stimulated under broad field illumination. As a result, CAP recordings reflect the simultaneous activity of several classes of fibers which might differ in their spectral characteristics, absolute sensitivity, latencies etc. For example, a 400 nm light stimulus might trigger a response from the center and/or the periphery of UV- and/or S-wavelength-sensitive ganglion cells. Hence, care must be taken when interpreting this type of response and, especially, when trying to relate its characteristics to the activity of specific cells as is done with single unit recordings. However, if we operate under the following assumptions, information extracted from CAP recordings reveals characteristics of specific classes of retinal ganglion cells.

The first assumption is that at threshold, or slightly above it, the sensitivity of the RGCs center is higher than that of its periphery. In goldfish, the sensitivity of the receptive field center can be 10–20 times that of the periphery (Daw, 1968; Spekrijse, Wagner & Wolbarsht, 1972). The first assumption is that rainbow trout RGCs share more or less the same properties as the goldfish's, and that under stimulation of moderate intensity (up to about 1 log unit suprathreshold), the response recorded reflects the activity of receptive fields center. At higher intensities, the periphery may begin to inhibit response of the ON center as has been observed in single unit recording experiments (Spekrijse *et al.*, 1972).

The second assumption is that at low intensity, the contribution of the isolated cone mechanism to the response is predominant. Under this assumption, peaks of sensitivity represent the activity of discrete cone mechanisms. At higher intensities, more than one cone mechanism might be stimulated, especially at wavelengths located between the sensitivity peaks of two cone mechanisms. In such cases, the compound action potential response would represent the activity of a more or less heterogeneous population of optic fibers.

Optic nerve fibers sensitive to ultraviolet light

Our results show that under a UV isolating background, the UV cone mechanism mostly contribute to the ON response. We interpret the UV sensitivity peak as reflecting the activity of UV-sensitive, ON center ganglion cells within the retina of small rainbow trout. It is not possible to determine whether the UV input to

the center of these cells is the only one or one amongst several. The lack of an OFF response sensitivity peak in the UV and S wavelength part of the spectrum suggests an absent or reduced contribution of the UV cone mechanism to the OFF response. This also indicates an absence, or a greatly reduced number, of UV sensitive, OFF center retinal ganglion cells.

When a sensitivity peak is obtained in the UV part of the spectrum, there is the possibility that it results from β -band absorption by M or L photopigments. Under the background conditions used in this study, the relative sensitivity of the M and L cone mechanisms' ON response was 1.0–1.5 log unit lower than that of the UV and S cone mechanisms. Hence, β -band absorption cannot account for the presence of the UV peak since the relative sensitivity of the β -band of a photopigment is usually 0.5–0.8 log unit lower than that of the α -band (Beauchamp & Lovasik, 1973).

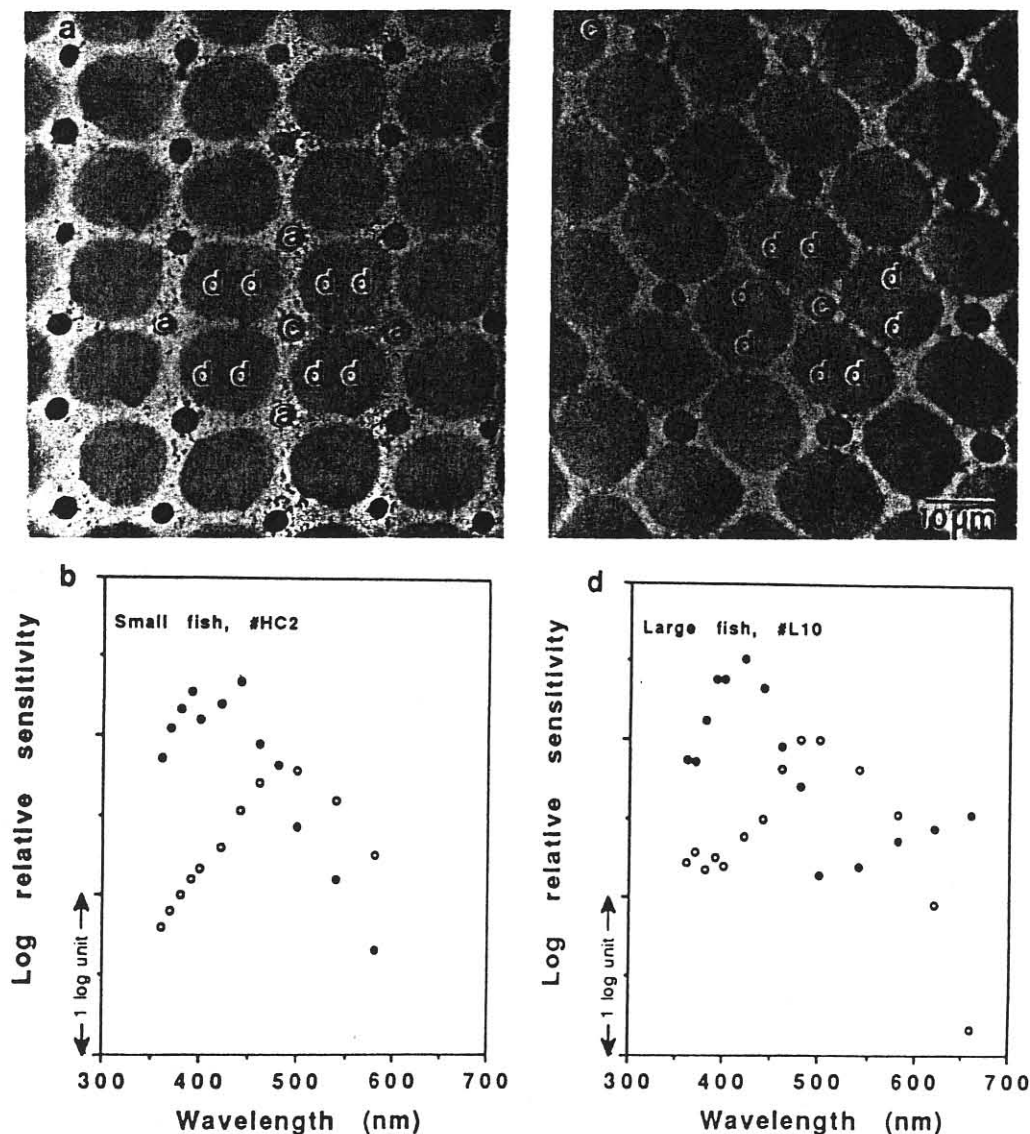


FIGURE 4. (a) Tangential section (1 μm thick) through the inner segments of photoreceptor cells in the temporo-ventral retina of a small rainbow trout (18 g) whose spectral sensitivity is illustrated in (b). (c) Tangential section (1 μm thick) through the inner segments of photoreceptor cells in the temporo-ventral retina of a large rainbow trout (85 g) whose spectral sensitivity is illustrated in (d). Spectral sensitivity curves were obtained under a UV-S wavelength isolating background. Solid circles, ON response; open circles, OFF response; d, double cone; c, central single cone; a, accessory corner cone; scale bar = 10 μm .

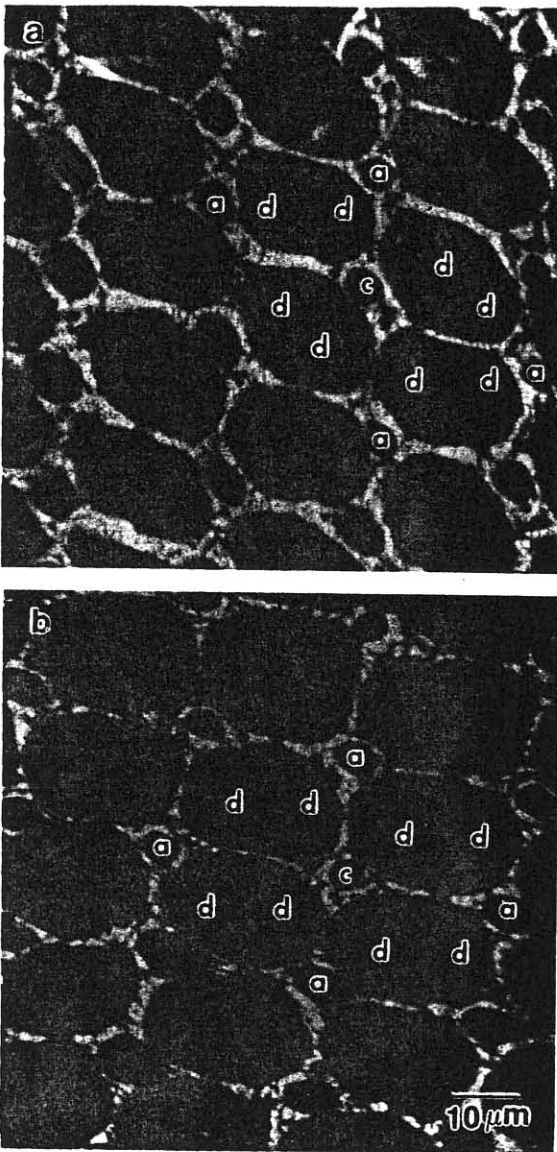


FIGURE 5. Tangential sections ($1\ \mu\text{m}$ thick) through the inner segments of photoreceptor cells in the vicinity of the optic nerve head of (a) rainbow trout No. L9 (914 g) and (b) rainbow trout No. L10 (85 g). d, Double cone; c, central single cone; a, accessory corner cone; scale bar = $10\ \mu\text{m}$.

Comparison of ON response spectral sensitivity with psychophysical data

The ON response action spectrum approximates the UV and S cone mechanisms action spectra as determined in small rainbow trout using a heart-rate conditioning protocol (Hawryshyn *et al.*, 1989; Browman & Hawryshyn, 1992). The ON spectral sensitivity curve in the UV–450 nm part of the spectrum is characterized by two maxima, indicating the presence of at least two cone mechanisms. However, the λ_{max} of the UV cone mechanism characterized here (390 nm) differs from that reported (360 nm) by Hawryshyn *et al.* (1989) and Browman and Hawryshyn (1992). These results indicate that the two techniques, although they yield similar results, are not directly comparable. That different techniques lead to somewhat different results has already been discussed (Neumeyer, 1984; Neumeyer & Arnold, 1989).

Loss of UV sensitivity and change in retinal photoreceptors mosaic

Our recordings showed the loss of a chromatic class of optic fibers: the UV sensitive, ON centers. Furthermore, the disappearance of the UV peak was correlated with the loss of the accessory corner cones from most of the retina. These findings support the contention that these cones contain a UV sensitive photopigment (Bowmaker & Kunz, 1987; Hawryshyn *et al.*, 1989; Browman & Hawryshyn, 1992).

The results presented here imply a developmental reorganization of the ganglion cell, as well as the photoreceptor cell layers. The reorganization resulting from the loss of UV sensitivity could follow at least two patterns. First, the disappearance of the corner cone from the photoreceptor mosaic could result solely in the removal of one class of inputs to the center-surround organization of the retinal ganglion cells. Hence, the neuronal elements responsible for carrying the information relative to UV stimuli would remain in place and continue to fill their functions with the remaining elements.

Alternately, the loss of UV-sensitive fibers could be accompanied by the degeneration of a class of retinal ganglion cells. Developmental degeneration of retinal ganglion cells has been reported in other species (Oppenheim, 1991; Wong & Hughes, 1987; Dunlop & Beazley, 1987; Young, 1984). Although Lyall (1957a) did not find any indication of accessory corner cone degeneration, this possibility cannot be discarded.

The disappearance of the accessory corner cones from the retina of growing trout is not an all or nothing event. In large fish, accessory corner cones are still present near the optic nerve head and embryonic fissure [Fig 5(a, b)]. These cones have also been found in 2 yr-old brown trout and Atlantic salmon (Kunz, 1987). Since the disappearance of the accessory corner cones is believed to proceed from the center toward the periphery of the retina (Lyall, 1957a, b), we suggest that they represent a population of “resident” corner cones, i.e. a population of corner cones which remain in the retina for the entire life of the animal. This proposal is supported by the observation that corner cones were found in individuals of very different size (85 and 914 g). We do not know if the small number of “resident” accessory cones present in the retina of large specimens are UV sensitive.

The OFF response: a shadow detecting mechanism

The spectral sensitivity of the OFF response in both small and large rainbow trout differed from that reported for the goldfish (Wheeler, 1979; DeMarco & Powers, 1991). These studies interpret the optic nerve OFF response as being dominated by a L-wavelength sensitive cone mechanism. Under our experimental conditions, the spectral sensitivity of the OFF response in rainbow trout appears to be dominated by input from a M-wavelength cone mechanism.

Wheeler (1979) suggests that the role of the L-wavelength-dominated OFF response of goldfish is to act as a predator- (or prey) detecting mechanism. We postulate that this system should be tuned to the prevailing wavelength, or the mid-spectrum of ambient light. The presence of a predator (or a prey) in the path of the downwelling light would produce a shadow, perceived at the optic nerve level as an OFF response. This shadow will generally be interrupting the illumination of the retina by the background light, making an OFF system optimally functional if tuned to this background.

This supposition is supported by the fact that rainbow trout, and the cichlid *H. burtoni*, whose natural photic environments are richer in wavelengths from the S-M part of the spectrum (Fernald & Hirata, 1977; Novales Flamarique, Hendry & Hawryshyn, 1992) have an OFF response dominated by input from the M-cone mechanism (Hawryshyn *et al.*, 1991; this study). Furthermore, juvenile rainbow trout eventually leave their native stream to enter a lake environment where they will spend their adult life until returning to spawn in the stream (Northcote, 1969). This migration is accompanied by a movement to greater depths where the mid-spectrum wavelengths of downwelling light field are shifted towards longer wavelengths (Loew & MacFarland, 1990; Novales Flamarique *et al.*, 1992). Our results show that the OFF response in large fish is relatively more sensitive to longer wavelengths than that of small fish.

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