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<p>We are attempting to establish the possibility that the geometry of certain classes of vertebrate photoreceptors results in a birefringence that allows the animals to utilize the state of polarization of light striking their retinas as a meaningful stimulus parameter. We are simulating the photoreceptors as dielectric waveguides using a simple physical model, and we intend to augment this theoretical work with empirical measurements of the light guiding properties of photoreceptors in isolated pieces of retina from a green sunfish (<i>Lepomis cyanellus</i>). With a classical conditioning paradigm, we have discovered that this fish's sensitivity to light is modulated by the orientation of the plane of polarization of linearly polarized light. This functional dependence was predicted by a hypothetical antagonistic mechanism between twin cones of two orientations in the animal's retinal mosaic. We further plan to study the nature of the stimulus to which the fish is sensitive by creating a camera that will generate images based purely upon the contrast between orthogonal polarizations at each point in space.</p> <p style="text-align: right;"><i>Keywords:</i></p>					
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Annual Report

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Contract # N00014-89-J-1903

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Principal Investigator: Edward N. Pugh, Jr.

Contractor: University of Pennsylvania--Department of Psychology

Contract Title: Polarization Contrast Vision

Start Date: May, 1989

Research Objectives: We are currently studying how the visual systems of vertebrates can and do use the state of polarization of light as a meaningful cue. We are approaching the problem from four general directions: 1) We are attempting to apply waveguide models to double cones in order to demonstrate that they exhibit the geometrical birefringence necessary to extract the information inherent in the incident light's state of polarization. 2) We are attempting to reinforce that theoretical model with empirical evidence of the guiding properties of actual photoreceptors from the green sunfish (*Lepomis cyanellus*). 3) We are performing psychophysical tests with these fish to demonstrate that the animals' sensory systems do give them information about the state of polarization of perceived light, and 4) We are attempting to create a camera that will view a scene with alternate images taken through orthogonal plane polarizers. Once these images are generated we will digitally subtract successive frames to create a representation of the polarization contrast signal.

Progress:

I. Waveguide models

We began the year while attempting to model the photoreceptors as elliptically cross-sectioned infinitely long cylinders with an index of refraction of 1.36 embedded in an infinitely extended medium with an index of refraction of 1.33. The solution of such a problem involves a set of functions known as Mathieu functions (Stratton, 1941) after the person who discovered them while solving for the modes of vibration of a membrane with an elliptical boundary. We began with the intention of solving for the modes of this system because there is an analytical solution to this problem, and we felt that while developing models that were physically more realistic we could use these solutions as a test for later methods.

We attempted to follow the path set by Cavour Yeh (1962a-b), the first person to exhaustively study the propagation of electromagnetic waves in such a structure. Solving Maxwell's equations for such a geometry is relatively straightforward. The equations for the longitudinal components of the field are separable in the elliptical coordinate system, and it is easy to see by inspection which of the different types of solutions to the Mathieu equations must be utilized in each region. The problem suddenly becomes complicated when one attempts to match the fields at the boundary in order to produce solutions which are physically meaningful.

The solution of this boundary matching problem requires the construction of the fields from infinite sums of Mathieu and modified Mathieu functions (Yeh, 1962a). The problem may be somewhat simplified if one makes the assumption that the field on one side of the boundary may be constructed as a single Mathieu function while the field on the other is constructed from an infinite sum of such functions (Yeh, 1962b).



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In principle the generation of any of these Mathieu functions is fairly simple. For instance, if one assumes a solution of Mathieu's equation to be a Fourier series, substitution of this series into the equation will eventually lead to an infinite continued fraction the roots of which will allow for the determination of all of the Fourier coefficients except for a scaling multiple (McLachlan, 1947). In practice the generation of these solutions may be a fairly intractable computational problem. Qualitatively, a graph of the infinite continued fraction versus the separation constant resembles a graph of the tangent function. For certain parameters of Mathieu's equation, however, the regions where the singularities occur (and hence often the regions wherein the roots of the equation lie) are extremely narrow. This requires that the computations be carried out with extreme precision. In many cases of interest to us this requirement is too stringent to be met by conventional firmware.

After wrestling with this problem from a few different angles, we decided that our time would be better spent if we began to pursue a somewhat different geometry. Freeing ourselves from the requirement of obtaining a completely analytical solution left us with a great many options in terms of how we could approximate the geometry of the system, and how we could obtain approximately correct physical solutions once that geometry had been chosen. Since many approximations have been obtained for rectangular cross-sectioned (channel) waveguides (e.g. Marcatali, 1969, and Goell, 1969) we decided to focus on this type of geometry. In order to solve for the fields in this system, we have settled upon the technique developed by Haus et al (1987). This technique is different from most other approaches in that the field components in the search for solutions are never assumed to be polarized along any axis. Instead, the vector potential which is implied by the fact that the magnetic field is solenoidal (i.e. has no divergence) is assumed to be plane polarized leading to a scalar wave equation. Under these conditions, the solutions which are constructed never assume the existence of either TE or TM waves, and thus "hybrid" modes are solved for just as easily as the transverse cases.

There are two major steps in this method, solving the scalar wave equation to determine the dispersion relation in general, and determining the corrections that must be made to this relation in order to get more accurate results for the different cases of polarization of the vector potential. A variational analysis is employed to solve the scalar wave equation, and the solutions so obtained are in closed form. Unfortunately the minimization is extremely computer intensive and is taking quite some time. We began with the dominant mode and are plotting out its entire dispersion relationship from cutoff through the optical frequencies of interest. We have been using a computer in the electrical engineering department which is very fast but also very busy. Because of this the program is running rather slowly, and despite the fact that it has been running for nearly two months, it will probably be another month or so before it passes through the range of interest.

Results to date indicate that for the dominant mode, whether the vector potential is aligned along either the long or short axis of the waveguide's cross-section the polarization correction is such that the actual propagation constant is less than the propagation constant calculated by the scalar wave equation. However, the correction necessary for the potential aligned along the short axis is always larger (in magnitude) than the correction necessary for the potential aligned along the long axis. This means that the propagation constant when the vector potential is aligned along the long axis is larger than the propagation constant obtained when the potential is aligned along the short axis. Since the power propagating in a given mode is proportional to the propagation constant, this means that for a given input intensity, more power is

transmitted down the waveguide core if the vector potential is aligned with the long axis than if it is aligned with the short.

Although directing the vector potential is not the same as directing the electric field vector, for the dominant mode the component of the electric field parallel to the vector potential is three orders of magnitude larger than the orthogonal component. One would anticipate then that under these conditions the waveguide will propagate more power if the incident electric field is polarized along the long axis of the waveguide cross-section than if it is polarized along the short axis. Since we do not have the numbers for the frequencies of interest, we cannot yet calculate the magnitude of this effect, but it is certain that such an effect exists at least for this mode.

Since the mapping of the dispersion relation for the dominant mode is proceeding so slowly, we are concurrently searching for other modes but concentrating on the frequency range of interest. We have already found four modes (but not the dominant one) in this range. Due to the nature of the function that we are minimizing, the search is analogous to catching small fish with a big, coarse net. Judging from the appearance of the fields of some of these modes we fear that there will be many more propagating modes at these frequencies.

II. Empirical Measurements

In brief, the goal of these experiments is to shine light in the physiological direction through a piece of isolated retina and measure the intensity of light propagating through individual double cones for different orientations of the plane of polarization of the incident light. The best microscope that we have available for this task is a Zeiss IM 35 inverting microscope. Unfortunately, since humans are not sensitive to polarization cues, this microscope is not designed to maintain polarization faithfully (i.e. there are many mirrors in the optical path). In our preliminary experiments we attempted to compensate for this by inserting a polarizer after the tissue chamber so that all of the light going into the microscope was polarized at the same orientation regardless of the state of polarization of the light striking the sample. The major drawback to this was that we still had to be very careful about what orientations of polarization of the incident light that we used since the intensity (the signal that we were measuring) was a strong function of the angle of the incident polarization.

In order to circumvent this problem we have obtained a rotating stage, so that now we may maintain the incident beam at a fixed angle of polarization. We can determine the transmitting properties of the cells as a function of input polarization by rotating the tissue sample rather than by rotating the polarizer. When we began to perform these experiments we discovered that there was too much dirt in the light path, and that this must be taken care of if we are to obtain meaningful measurements. Some of the debris was found to be inside the lense housings, and we are currently getting these professionally cleaned. As soon as these lenses are returned to us, we plan to continue with this set of experiments.

III. Behavioral Experiments

The ultimate aim of these experiments is to demonstrate that the animals can detect objects based only on the local contrast in the state of polarization of perceived light. We have begun with the more straightforward task of demonstrating that the animals' (in this case green sunfish, *Lepomis cyanellus*) sensitivity to light is a function of the light's state of polarization. The animals are placed in a submerged box where they have almost no room to maneuver, and are thus forced to look in one direction. A

Maxwellian-view image is displayed for them in trials where the angle of polarization is varied randomly and they are conditioned with an electric shock applied to the water near their tails so that they respond when they detect the light. Cardiac and ventilatory rates are monitored with another set of electrodes placed near the animal. When a stimulus is detected, the animals cease both heart beat and respiration momentarily in anticipation of the mild shock.

Using this paradigm, the fish's threshold for detection has been mapped as a function of the angle of polarization. These fish are maximally sensitive to light which is polarized either along their superior-inferior or their medial-lateral axes. They are minimally sensitive (up to .8 log units less so in the animals studied so far) at angles at 45° away from these axes. This is exactly the type of function that we would predict

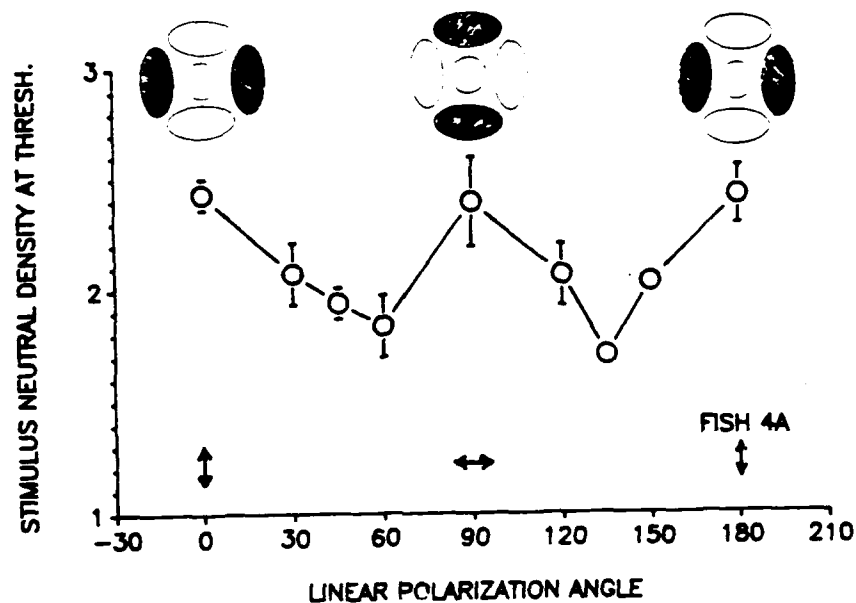


Figure 1. Threshold sensitivity of the Green Sunfish (*Lepomis cyanellus*) to lights plane polarized at the angles indicated by the abscissa. Stimuli were long wavelength (dominant wavelength, 610 nm) and 99% polarized, spatially homogeneous Maxwellian images of a ground-glass plate subtending 15° of visual angle at the fish's rostral cornea. Data are means \pm 1 sem, with $n=3$ at each angle. Insets show predicted anatomical organization of twin cone tetrads lying immediately under the area stimulated. Shading indicates cones predicted to exhibit greatest excitation at the underlying points.

based on the assumption that the animals subtract the signals obtained from two types of receptors whose maximal sensitivities are 90° apart from each other, and whose minimal sensitivities occur 90° away from their maxima. In such a scenario, there should be two orthogonal orientations at which the animals are maximally sensitive since in each case one class of photoreceptor is receiving a maximal signal while the other class is receiving a minimal one leading in either case to a large difference signal. 45° away from these places the two receptor types receive essentially the same signal, and although neither alone is receiving a minimal signal, the contrast signal is at a minimum since the two signals subtract each other out. This is analogous to the notch in sensitivity measurable

in humans when sensitivity is measured as a function of wavelength in the vicinity of unique yellow.

IV. Polarization Contrast Camera

As we have been focusing on the other aspects of this program, this aspect has unfortunately received little of our attention. At this point we have all of the components necessary for the system, but we have unfortunately just discovered that one of the major (and most difficult to obtain) elements may not serve our purposes. After we recently acquired the camera, we began to put all of the components together to test the system. At the heart of all of this is a plate similar to those used in electro-optic light valves that will rotate the plane of polarization of plane polarized light by 90° . Such devices have been developed for use in 3-D television viewing systems, which require that they switch between the on and off states (i.e. rotating or not) at 30 Hz. This particular device was custom built for us by Tektronix. Despite the fact that these devices are used in television imaging systems, this one seriously degrades the image forming light that passes through it. We will have to contact the company again in order to see if we can get this device replaced, or if there is some way that it can be fixed in such a way as to perform its function for us without stripping away our spatial resolution.

Future Plans:

I. Waveguide models

Although it is much too soon to tell, we fear that the model that we are currently using will not adequately explain the strength of the modulation that we have measured in the behavioural experiments. This seems true because the effect will probably be quite small even for the dominant mode at the frequencies of interest, and also because there will probably be a great number of propagating modes at these frequencies. Some higher order modes may propagate the same power when the electric fields are polarized along the short axis of the guide cross-section and cause the net effect to be essentially nullified in this particular model.

Although we will continue to characterize our current geometry and determine all of the applicable modes and the effects of polarization on their propagation, future work will begin to focus on what we feel are more realistic geometries. One of the advantages of the technique that we are currently using is that it can also be used for a model in which the index of refraction varies continuously across the waveguide cross-section rather than just as a step discontinuity at the interface. When we have examined this type of model, we will probably move on to an even more realistic one in which the index of refraction varies continuously in all three dimensions. Although we will not be able to use the current technique (we will probably turn to a finite element analysis e.g. Mariki and Yeh, 1985) to explore such a physical system, we will at least be able to test the newer technique by comparing its results for this geometry to the ones obtained with this analysis.

Future work is likely to continue to become even more computer intensive than that which is already in progress. For this reason it is becoming imperative that we obtain a machine that we can dedicate to this project. We hope to order a Sun work station in the near future, as this will greatly facilitate our efforts.

II. Empirical Measurements

All of the equipment except for clean lenses is currently in place. In preliminary experiments, since we were restricted to two orientations of incident light, we relied on subtraction of the intensities at these two polarizations in an attempt to extract the data in a meaningful way. With the current setup, we plan to measure the intensity of radiation emitted from the ends of individual double cones as a function of the orientation of the plane of polarization incident on the retinas. This will allow us to collect much more data per cell, so that we will not need to resort to any tricks in order to extract meaningful information. We predict that the guided power will vary as a function of orientation in a manner similar to the behavioural results discussed above, only the modulation will repeat every 180° rather than every 90° as it does in those experiments.

The behavioural evidence in conjunction with the waveguide model gives us the prediction that the orientation of the twin cone mosaic on the sunfish's temporal retina (where all stimuli fell) will be such that the rows will be aligned with the fish's medial-lateral, and superior-inferior axes. In concert with the above studies, we shall attempt to verify this prediction.

III. Behavioral Experiments

At this point, we have only demonstrated that the animal's sensitivity varies with the angle of polarization. The next logical step is to demonstrate that polarization is actually a signal that the animals can extract. In upcoming experiments we intend to condition the fish to respond to the light source only if it is polarized in a particular direction. If the fish can be trained to anticipate a tail shock when the light is polarized say horizontally, but not when it is polarized vertically, then we will have gone a long way towards demonstrating that this is a parameter to which the fish has access in ordinary life.

Upon completion of that, further studies will be aimed at measuring how well the fish can discriminate the orthogonal polarizations by using elliptically polarized light and perhaps by producing stimuli in which the state of polarization varies across the image. We hope that the fish can be conditioned to respond only when there is some component of the image that has polarization along a particular axis. We anticipate that these types of experiments will be analogous to those in which human observers are shown a stimulus and asked to respond only if the stimulus appears say reddish.

IV. Polarization Contrast Camera

As indicated above, our major goal for this aspect of the project is to put together all of the components in working order.

Publications

We have submitted an abstract to the Society for Neuroscience. We intend to present our results in a poster session at the annual meeting in St. Louis in November.

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