Polarization signals in mantis shrimps

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ABSTRACT

While color signals are well known as a form of animal communication, a number of animals communicate using signals based on patterns of polarized light reflected from specialized body parts or structures. Mantis shrimps, a group of marine crustaceans, have evolved a great diversity of such signals, several of which are based on photonic structures. These include resonant scattering devices, structures based on layered dichroic molecules, and structures that use birefringent layers to produce circular polarization. Such biological polarizers operate in different spectral regions ranging from the near-UV to medium wavelengths of visible light. In addition to the structures that are specialized for signal production, the eyes of many species of mantis shrimp are adapted to detect linearly polarized light in the ultraviolet and in the green, using specialized sets of photoreceptors with oriented, dichroic visual pigments. Finally, a few mantis shrimp species produce biophotonic retarders within their photoreceptors that permit the detection of circularly polarized light and are thus the only animals known to sense this form of polarization. Mantis shrimps use polarized light in species-specific signals related to mating and territorial defense, and their means of manipulating light's polarization can inspire designs for artificial polarizers and achromatic retarders.

Keywords: biophotonic, biomimetic, polarizer, retarder, signal, mantis shrimp, stomatopod, dichroic, birefringent

1. INTRODUCTION

Almost all animals with well developed visual systems recognize and use visually-based signals in their communication systems. Such signals incorporate prominent pattern elements, most often based on intensity or color contrast. However, a few species of animals produce signals based on patterns of polarized light[1,2]. Such signals may be preferred in specific lighting or viewing conditions, when color-based signals would be unreliable, and are used for species identification and for aggressive or sexual communication. The circumstances that favor the use of polarization signals, the visual designs that are necessary to interpret them, and the very unusual biological structures that actually produce the polarized-light patterns are inherently interesting, but these aspects of polarization signaling are also of special interest to optical engineers because they suggest approaches to the use of polarization in communication and particularly because some of the biological designs are quite unlike those used in industry to produce and control light's polarization. In this paper, we will briefly review the contexts within which animals have evolved polarization-based visual signals and touch on the visual detectors they use. We will then discuss in detail a few of the biological polarizers and optical devices used in the production and control of polarized light.

1.1 Photic environments that favor the use of visual signals based on polarized light

Even though there are no natural light sources that produce significant amounts of polarized light visible at the earth's surface, linearly polarized light is abundant in natural scenes[3]. In terrestrial environments, the frequently complex appearance of polarization due to atmospheric scattering and the reflection from shiny surfaces of leaves and water limits the utility of polarization signaling. To date, the only terrestrial animals known to use polarization patterns for communication are a group of tropical butterflies[4]. These butterflies produce polarization reflections using oriented structures in their wing scales, and closely related species either possess or lack such reflections in correlation with their habitats. Butterflies that use polarization signals typically fly under the forest canopy, where polarization noise from local scattering or reflection is nearly absent, so the polarization signal is unique and prominent.

While it seems likely that other terrestrial animals have discovered polarizational signals, no examples besides butterflies have yet been identified. In the marine environment, however (but not yet in freshwater), two highly successful groups of marine invertebrates are known to use a diverse set of signals based on polarized light. These are the stomatopod crustaceans, or mantis shrimps[5], whose polarizers and optical retarders are described in this report, and the cephalopod molluscs (squids and cuttlefishes)[6,7]. The submarine environment is particularly favorable for the use of signals formed from polarized light for two reasons. First, as depth increases, the spectrum of light arriving from overhead increasingly narrows, making reflective color signals unreliable and at greater depths, useless. Second, there is a relatively weak linearly polarized-light field present, especially at greater depths, and at such depths the polarization pattern is quite constant[8,9]. Considering these advantages, it is likely that other animals living in the deep sea have evolved other forms of signals based on polarized light, potentially including bioluminescent signals.

1.2 Polarized-light photoreceptors

All known visual photoreceptors capture light using members of a single protein family, the opsins, and all opsins are located in photoreceptor membranes and use derivatives of molecules in the vitamin A family as chromophores to capture light. Because of their chemical structure, all such chromophores are naturally dichroic, and when joined to the opsin their absorption dipoles extend roughly parallel (within ±20º) to the membrane. Thus, single molecules of visual pigment respond differentially to polarized light, being stimulated most readily by photons whose electric field vectors (*e*-vectors) are parallel to the chromophore's preferred axis. Photoreceptor cells contain huge numbers of visual pigment molecules, so the only way for the entire cell to have polarization sensitivity (in the absence of external manipulation of polarized light in some way) is for there to be a non-random alignment of preferred absorption axes for the population of visual pigment molecules as a whole.

The polarized-light photoreceptors of cephalopods and stomatopods have similar adaptations that confer the desired alignment of visual pigment absorption dipoles. First, the visual pigments are located in the membranes of microvilli, minute cylinders that extend stiffly from the rest of the cell, held out by a central cytoskeletal axis, and their chromophores tend to be aligned roughly parallel to the microvillar axis[10]. It is not clear how this alignment is achieved or maintained, but the result is that each microvillus as a whole is dichroic, preferentially absorbing light polarized parallel to it. A second level of specialization is that, in cells that are specialized to detect polarized light, all microvilli of a single cell are themselves parallel. Most animals with polarized-light sensitivity have two populations of polarization receptors, with their microvilli extending orthogonal to each other. This two-axis organization cannot fully analyze light's polarization (linearly polarized light of a given wavelength has three components: overall intensity, degree of polarization, and angle of polarization, requiring three receptor classes for full analysis), but the arrangement is usually acceptable for analyzing linearly polarized-light signals because the signals commonly are strongly polarized and have a determined angle of polarization.

Until quite recently, the only type of polarization sensitivity recognized in animals was in response to linearly polarized light. However, a few species of mantis shrimps have been found to be capable of analyzing circularly polarized light as well[11]. Not surprisingly, the same species produce circularly polarized signals. As will be described below, the circular polarization signaling structures are built using one of the common types of biological linear polarizers in conjunction with a quarter-wave retarder layer. Similarly, the analyzing receptors are actually modified receptor types with the same organization used for two-axis linear polarization analysis. These are mated to a unique, biophotonic device that acts as an achromatic quarter-wave retarder, converting incoming circularly polarized light to linearly polarized and thereby enabling photoreceptors that would normally be insensitive to circular polarization to discriminate right-handed from left-handed types.

2. LINEAR POLARIZERS IN STOMATOPOD CRUSTACEANS

2.1 Polarizers based on the dichroic carotenoid molecule, astaxanthin

Two types of linear polarizers, based on quite different optical principles, have been found so far in stomatopod crustaceans. The first type, described in this section, is thought to use a naturally dichroic molecule in an ordered arrangement to produce partially linearly polarized light with its spectral peak slightly below 500 nm. An example of a

stomatopod appendage that contains this type of polarizer, together with typical polarization spectra of light reflected from it, is illustrated in Figure 1. A pair of these appendages, called antennal scales, project laterally from the anterior regions of most stomatopods, but the polarization is observed in only a few species – here, in *Odontodactylus scyllarus*. Note that the polarization of reflected light is very weak when the antennal scale is viewed on an axis normal to its surface, but that the polarization increases dramatically as the object tilts away and is viewed increasingly obliquely to the surface.
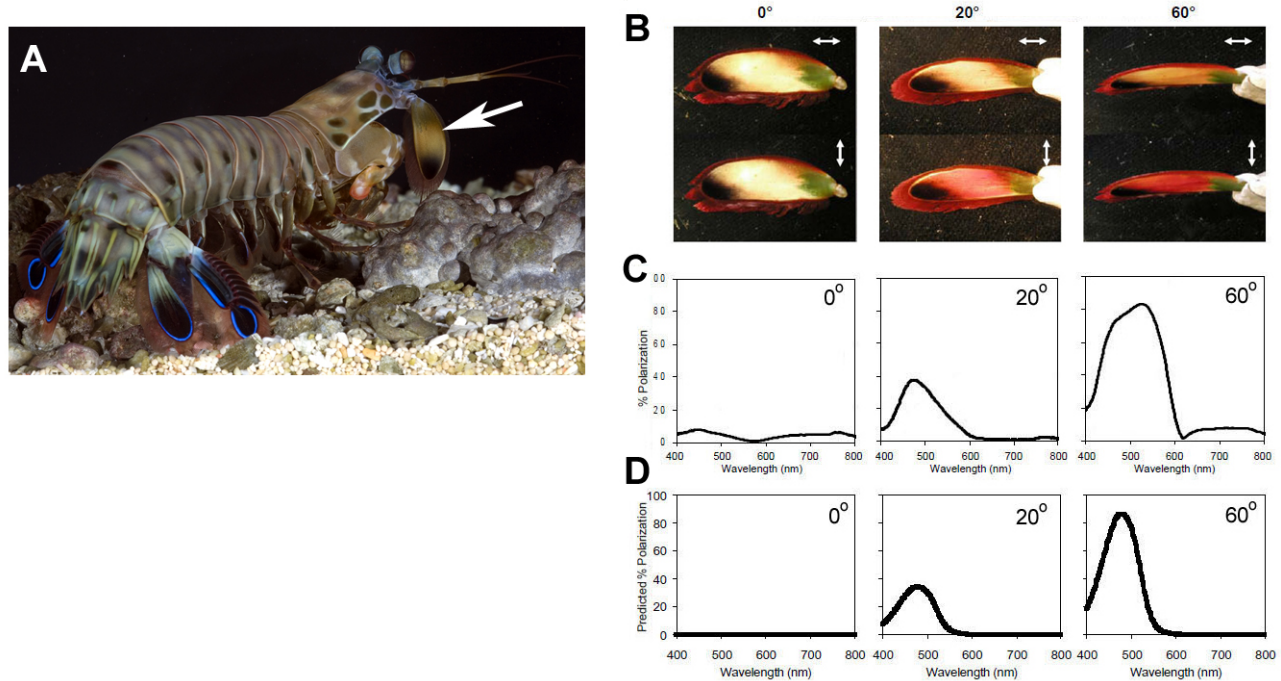

Figure 1. Polarization properties of the left antennal scale of the stomatopod crustacean *Odontodactylus scyllarus*. A. A photograph of a living animal showing the location of the right antennal scale. B. Image pairs obtained when viewing the left antennal scale under oblique illumination at various angles of tilt. The upper row shows the appearance in horizontal polarization and the lower row shows vertical polarization. Note how the scale looks darker and redder in vertical polarization as it is tilted. C. Linear polarization spectra obtained at these three tilt angles. Note that the polarization nas a relatively narrow peak near 500 nm. D. Modeled polarization spectra at the same angles based on the absorption spectrum of astaxanthin and assuming that the dipole axes of the astaxanthin molecules are all perpendicular to the surface.

Besides the obvious change in the degree of polarization, the reflected polarized light displays a strong spectral peak, suggesting that it is produced either by a strongly filtering substance or by a highly ordered structure. To discover how the polarization originates, we examined the internal structure of the *O. scyllarus* antennal scale. A vertical section of this structure (cut directly through the scale's thickness perpendicular to the long axis of the scale) is illustrated in Figure 2A. We found no evidence of multilayered structure of sufficient order to produce the polarization reflections. However, when the sectioned material was examined through a rotating linear polarizer, one region of the cross section, colored pink to our eyes, was found to be dichroic. This layer occurred just above the central core of the scale, which contains dense chitin and acts as a reflector of incident light coming from either side of the scale.

The pink color of the dichroic material suggested the presence of astaxanthin, a ketocarotenoid that is found in many crustacean tissues[12]. Astaxanthin is a long molecule, like other carotenoids consisting of a repeated chain of conjugated double bonds (see Figure 2C). This structure is strongly dichroic, because the linear chain readily interacts with light having an *e*-vector parallel to the chain's axis, but absorbs other planes of polarization more weakly. Astaxanthin actually forms three stereoisomers, based on the angle of the hydroxyl groups to the rings, but all are similarly dichroic to linearly polarized light (two of these stereoisomers also show circular dichroism, which is not relevant here). In biological membranes, molecules of astaxanthin are of the correct size to span the lipid bilayer, and thus sit vertically within the membrane with the hydrophilic ring structures embedded in the glycerol surfaces of biomembranes and the hydrophobic conjugated axis extending through the internal phospholipid tails[13,14]. Thus, in flat membrane layers, all

the dipole axes of the astaxanthin molecules are parallel but are perpendicular to the plane of the membrane. The dichroism of artificial lipid bilayers containing astaxanthin has been measured by Gruszecki[14], whose results suggest that the astaxanthin is oriented nearly perpendicular to the membrane plane, as predicted.
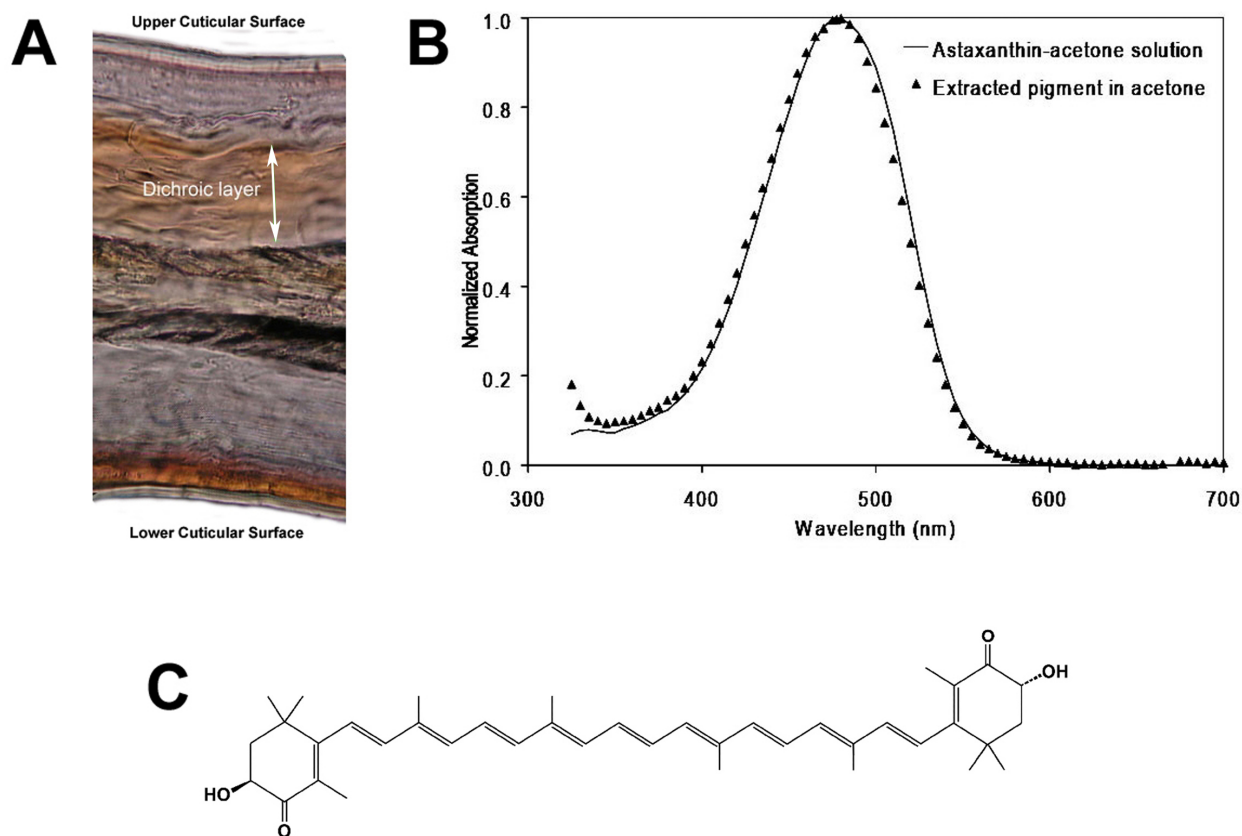

Figure 2. Astaxanthin in the antennal scale of *Odontodactylus scyllarus*. A. A natural-color photograph of a freshly sectioned scale of *O. scyllarus*, with the plane of section across the thickness of the scale and perpendicular to its long axis. A layer of pinkish dichroic material is located in the top half of the scale. B. The absorption spectrum of an acetone extract from a dried scale (triangles) compared to the absorption spectrum of pure astaxanthin (smooth line). The spectra are virtually identical. C. The molecular structure of astaxanthin. There are three stereoisomers of this compound (varying with the angles of the bonds of the OH groups relative to the plane of the rings), but all have the extended polyene chain connecting the rings and all are linearly dichroic.

The polarization spectrum of the intact scale is quite similar to the absorption spectrum of astaxanthin, further suggesting that this molecule could be producing the polarization by interacting with light entering the scale and reflecting from the central core layers. While each lipid bilayer absorbs light rather weakly, the thickness of the material in the scale, which presumably contains many layers (Fig. 2A) would produce much stronger overall absorption. A simple mathematical model of the changing degree of polarization with tilt, assuming that the dipoles are parallel to each other and perpendicular to the surface, predicts polarization spectra much like those of the intact scale (Fig. 1D). The spectra of the intact scale are somewhat broader than spectra produced by astaxanthin alone, suggesting that some of the polarization originates from dielectric reflection of light within the scale, or from its surface, as well. To identify the pigment within the scale, we extracted a dried scale with astaxanthin and compared the absorption spectrum of the extracted material with that of a sample of purified astaxanthin. As is evident in Figure 2B, the spectra are virtually identical, confirming the presence of this pigment in the scale. Furthermore, this extraction eliminated the ability of the scale to polarize light, strongly suggesting that the polarizer is indeed astaxanthin. To our knowledge, this is the first example of a biological signal based on linearly polarized light produced by transmission through an oriented dichroic organic molecule. These red-colored polarizers are widespread among species of mantis shrimps, and we

hypothesize that all are based on oriented arrays of astaxanthin molecules. This is the type of polarizer used with a delay plate to form the circular polarizers found in some stomatopod species as well, described below.

2.2 Polarizers thought to be based on scattering photonic structures

A second type of reflecting polarizer found in a number of mantis shrimp species is apparently based on resonant scattering from arrays of ovoid vesicles beneath the animals' cuticles. These polarizers tend to be relatively small compared to the dichroic type, forming bright blue-colored spots on the animal's body. They return highly polarized light with the *e*-vector orientation most commonly horizontal when the polarizer is displayed by the animal. A typical example, from *Haptosquilla trispinosa*, is illustrated in Figure 3A. Note the very bright pair of polarizers on a specific pair of cleaning appendages (the first maxillipeds) on the lower part the animal's anterior end. Interestingly, while this species has other blue-reflecting spots on its body, the only polarizers are the pair below the eyes.
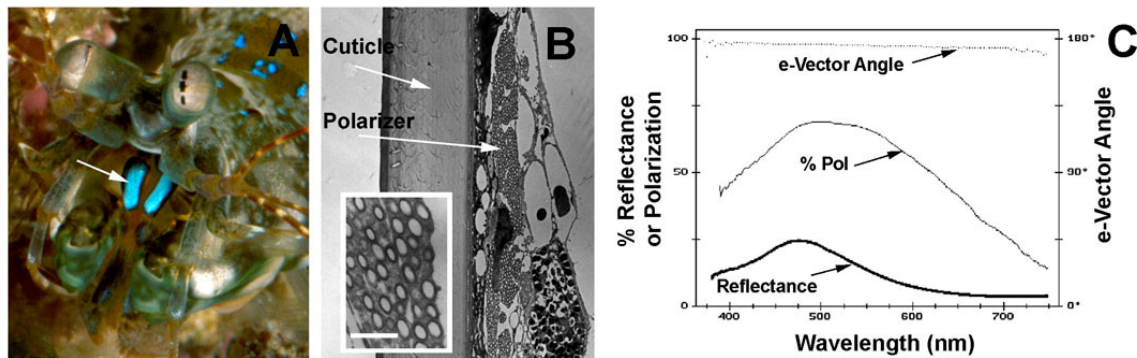

Figure 3. Scattering polarizers in stomatopod crustaceans. A. Anterior view of *Haptosquilla trispinosa,* showing the bright blue polarizers under the eyes (arrow). B. Electron micrograph to show the small vesicles that make up this type of polarizer. This image is from a section cut through the polarizer, parallel to its long axis and vertical to the cuticle. Inset: Vesicles at high magnification. Scale: 0.5 µm. C. Spectral features of the reflection and polarization.

Electron-microscopic examination of the polarizer reveals that it consists of several layers of parallel streams of vesicles backed with dark screening pigment and overlain by a transparent cuticle (Fig. 3B). These vesicles are arranged with their long axes parallel to the axis of the polarizer and perpendicular to the plane of polarization which it returns. The spectral features of the reflected light are graphed in Figure 3C, which shows that the polarization has a constant horizontal *e*-vector angle across the visible spectrum, with polarization reaching a maximum near 70% in the blue-green. Unlike the dichroic type of polarizer, in oblique lighting these scattering types reflect nearly constant polarization over a wide range of viewing angles.

If the polarizer is separated from its dark pigmentary backing, it reveals an unexpected property: the device acts as a polarizing beamsplitter, in its orientation in life transmitting vertically polarized light (relative to the long axes of the vesicles and of the blue polarizer as a whole) and reflecting horizontally polarized light (Fig. 4). This observation is consistent with a scattering system that is strongly dependent on the scale of the vesicles; in the shorter dimension presented in cross-section, the vesicles interact optimally with medium-wavelength light whose *e*-vector is parallel to the shorter cross-sectional radius, back-scattering it and thus, in its natural orientation, producing a horizontally polarized reflection (see Fig. 4B for measurements). If this hypothesis is correct, then longer-wavelength rays should interact with the vesicles in the opposite plane, encountering a properly scaled, longer, scattering system offered by the long axes of the vesicles. This would shift the plane of polarization from vertical to horizontal at longer wavelengths (Fig. 4C), with the point of the cross-over determined by the relative diameters and lengths of vesicles. Measurements of reflected polarization at longer wavelengths confirm this prediction, strongly suggesting that the polarization properties of this type of polarizer depend on the scale of the system.
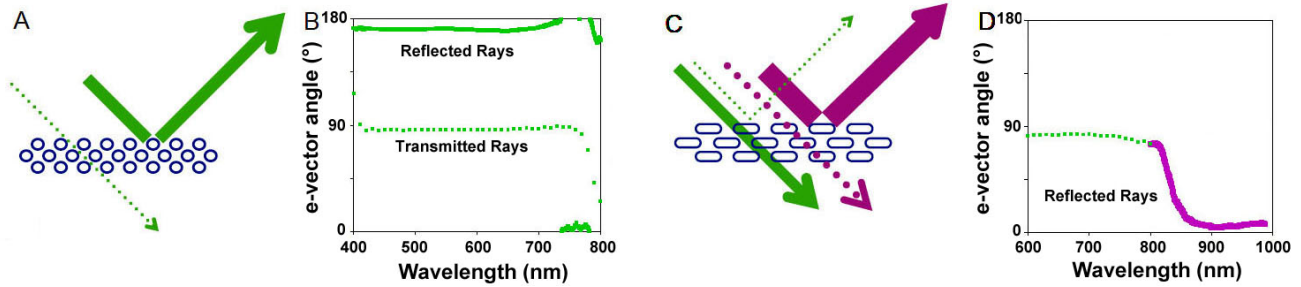
Figure 4. Schematics of the scattering polarizer of *Haptosquilla trispinosa*, together with measured *e*-vector orientations of polarization spectra. In parts A and C, dotted rays are polarized perpendicular to the plane of the page and thick lines are polarized parallel to this plane. A,B. Transmission and reflection of short-to-medium wavelength light. Here, the vesicles are viewed end-on, so the cross sections are circular. The polarizer separates vertically from horizontally polarized light, as illustrated by actual data in panel B. The *e*-vector angle is constant throughout the visible spectrum. C,D. Transmission and reflection of short-to-mediium wavelength light and long-wavelength light (>850 nm). The vesicles are viewed side-on, showing the oval section. The situation in panel C is the same for short-to-medium wavelengths as in panel A, but since the viewpoint is rotated by 90°, transmitted and reflected rays in C are orthogonal to what is illustrated in A. Long-wavelength rays encounter vesicles in a longer dimension, and are hypothesized to interact with them most effectively when the polarization is parallel to the vesicle's long axis. Panel D shows that, consistent with this hypothesis, the observed polarization of reflected long-wavelength rays is perpendicular to that of short-to-medium wavelength rays.

We are currently working to model theoretically the performance of this device, as it may serve to inspire artificial micropolarizers with the desirable ability to separate orthogonal planes of linearly polarized light as well as light within different spectral ranges. The device has the additional attraction of having relatively little angular variation, polarizing light arriving from over a broad angular range and returning polarization over a similarly wide angular coverage. The dimensions of the vesicles and of the array within which they occur have been measured, and we expect the refractive index of the ground material to be typical of cytoplasm, with n ~1.38 or so (see Figure 5). The major unconstrained parameter is the refractive index of the material within the vesicles, which is likely to be fairly high, as their contents are probably either lipids or a concentrated protein solution. However, the actual refractive index value of these materials can be allowed to vary freely in our theoretical model, with the expectation that only a limited range of values will produce the observed optical properties of the complete structure.
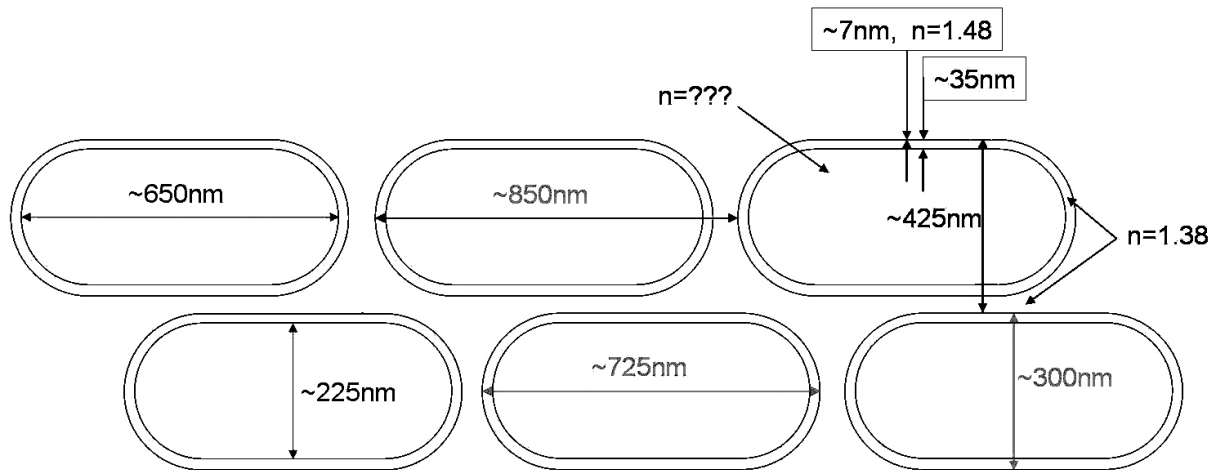

Figure 5. Schematic to represent the array of vesicles making up the polarizer of *H. trispinosa* and similar species of stomatopod crustaceans. The dimensions of the vesicles and their placement within the array are given, and the refractive index of the surrounding material is likely to be similar to that of cytoplasm in general (~1.38). The major unknown is the refractive index of the material within the vesicles. Note that the vesicles have a constant cross-sectional radius of ~300 μm and that the array extends indefinitely to the right and left and also out of the plane of the page. There are about six layers of vesicles stacked vertically, of which two are illustrated here.

3. A CIRCULAR POLARIZER IN ONE SPECIES OF MANTIS SHRIMP

Besides the two classes of linear polarizers discussed thus far, a few mantis shrimp species produce circularly polarized reflections, which appear to be used as sexual signals[11]. Surprisingly, the mechanism used to form these is unlike that described in the few other biological systems that reflect circularly polarized light. The previously best-described biological circular polarizers exist in the cuticles of scarab beetles, which usually reflect left-handed circularly polarized light through most of the spectrum[15]. The circular polarization is achieved by the passage of light through successive layers of material, each with its molecular axes slightly twisted relative its neighbors, giving an overall organization analogous to that of cholesteric liquid crystals[16,17,18]. There is no evidence that the beetles can visually analyze their circularly polarized-light reflections, so their function (if any) is unclear, although it is reasonable to hypothesize that the mechanism, which can produce nearly perfectly circularity[15], might have evolved to achieve a color signal free of potentially contaminating linear polarization. The only previous crustacean example of a circular polarizer, and indeed, the only well-described example of any kind outside the scarab beetles, is found in the inter-segmental membranes separating the abdominal segments of spiny lobsters. Here, reflection of circularly polarized light is achieved by layers of chitin microfibrils in the relatively transparent cuticle of these animals, by form optical rotary dispersion[19]. While this structure might have an adaptive mechanical function, it plays no known role in visual signaling.
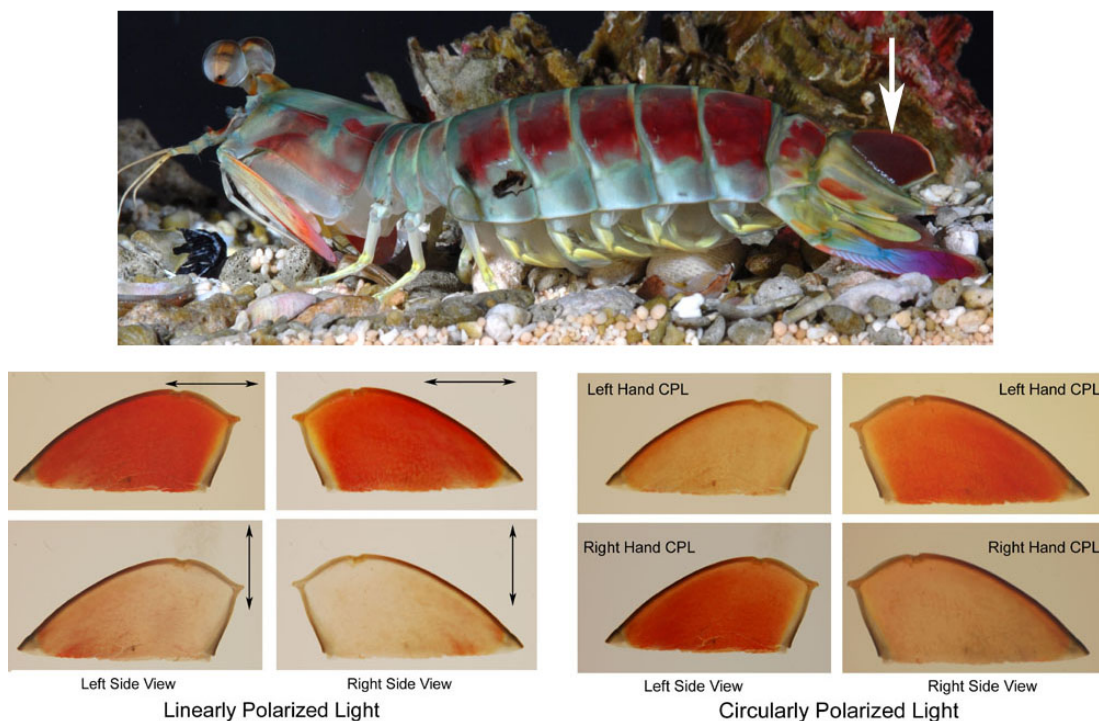

Figure 6. The keel of a male *Odontodactylus cultrifer*. The top photograph shows the location of this keel in a live animal (arrow). In the lower sets of images, the double-headed arrows show the plane of linear polarization transmitted by the polarizing filter (left), while the handedness of circularly polarized light (CPL) is indicated on each appropriate panel (right). Both sides of the keel transmit vertically polarized light, but the transmitted circularly polarized light has opposite handedness when viewed from the keel's right and left sides, favoring left handed CPL on the left and right handed CPL on the right.

The stomatopod crustaceans that use circularly polarized light in their signals adopt a technique commonly used in the optics laboratory, but not previously encountered in nature. They combine a linear polarizer (in this case, one based on dichroism as in Section 2.1, above) with a quarter-wave retarder. The overall result is illustrated in Figure 6, which shows the "keel" of a male stomatopod *Odontodactylus cultrifer* (this keel extends vertically from the telson, or tail plate, of the animal). The polarization is strongly elliptical, having major contributions of both circularly and linearly polarized components, but the circularity has the unexpected feature, not seen in other animals, of having opposite handedness depending on the side from which the structure is viewed. Acetone extraction of the keel shows that it

contains astaxanthin, and the removal of this pigment destroys the polarization, so in some ways this structure is similar to the polarizer of the antennal scale of the closely related *O. scyllarus*. However, in this case, the polarization is strongest when the keel is viewed orthogonally, not at glancing angles, suggesting that the astaxanthin must be oriented parallel to the surface of the structure, and thus that the membranes within which this pigment lies must extend somewhat perpendicular to this surface.
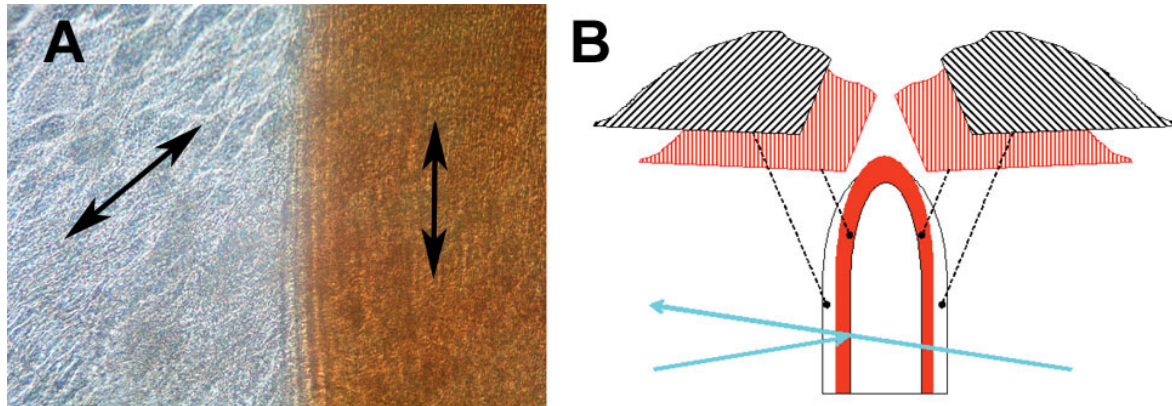

Figure 7. The circular polarizer in the keel of *Odontodactylus cultrifer*. A. A surface view of one-half of the keel, seen from the center of the vertical structure, which has been split so that the left half contains only the retarder layer and the right half has both the retarder and the dichroic polarizer. The double-headed arrows suggest the axis of the "grain" of each component. Note that the membranes in the polarizer run vertically in the image, while the general structure of the retarder is oriented at 45º to this, an ideal orientation to form a circular polarizer when light is transmitted through. B. A schematic to show the overall organization of the keel, with the polarizers placed medially and the retarders toward each surface on each face, illustrating how the structure would produce circularly or elliptically polarized light of opposite handedness on its two sides, whether the light is transmitted through it or reflected from it.

If the keel is split down its middle, and one half taken from this split is carefully separated into its layers, it becomes clear that the circular polarizer has a medial linearly polarizing layer overlain by a clear retarding layer at 45 degrees to it (Fig. 7A). We have found that the clear material, seen on the left half of Figure 7A, is birefringent, with the fast and slow axes at the proper 45º to the linear polarizer; this layer probably contains oriented crystals of calcite, a birefringent material commonly found in crustacean cuticle. With the polarizing material transmitting vertically polarized light (Fig. 6A) and the retarder's fast axis at 45º and parallel on both sides of the keel, the structure would produce elliptically polarized light of opposite handedness on either size, whether viewed in transmitted or reflected light (Fig. 7B). The keel is thought to serve in either species identification or sexual signaling (or both)[11].

4. QUARTER-WAVE RETARDERS IN MANTIS SHRIMP EYES

If circularly polarized light is to be useful as a visual signal, it must be detected, and presumably analyzed, by photoreceptors of the intended receiver. As described earlier, receptors sensitive to linearly polarized light are common in crustaceans. In the laboratory, a common technique used to convert a linear polarization detector to one responsive to circularly polarized light is to place a quarter-wave retarder in front of the linear polarizer with its fast and slow axes oriented at 45º to the preferred axis of the polarizer. The retarder converts circularly to linearly polarized light, which can then be analyzed by the polarization detector – typically, two detectors with orthogonal linear polarization axes are used to analyze the degree of left vs. right circular polarization for example, for measurements of the Stokes vector S3. By definition, quarter-wave retarders are designed for a single wavelength of light (because they are scaled to ¼ wavelength), so typical retarders are monochromatic. By combining materials with different dispersions, the spectral range can be extended to about 100 nm or so, and some man-made retarders based on sub-wavelength gratings are achromatic for about double this range at visible wavelengths[20].

We have located a quarter-wave retarder in polarization-sensitive ommatidia of the stomatopod *O. scyllarus*, and have found similar structures in the homologous ommatidia of many other stomatopod species. This retarder is built from a series of parallel microvilli, constructed from a photoreceptor cell that overlies other linear polarization receptors[11]. The

cell forming the retarder contains an ultraviolet-light-sensitive visual pigment, so it normally functions as an ultraviolet photoreceptor. However, its unidirectional microvilli are birefringent, as in typical arthropod photoreceptors[21], giving it an inbuilt ability to retard circularly polarized light (Fig. 8A,B); the degree of retardance thus depends on the length of the microvillar stack. Measurements of the optical properties of this cell show that it acts as a nearly perfect quarter-wave retarder (Fig. 8C).
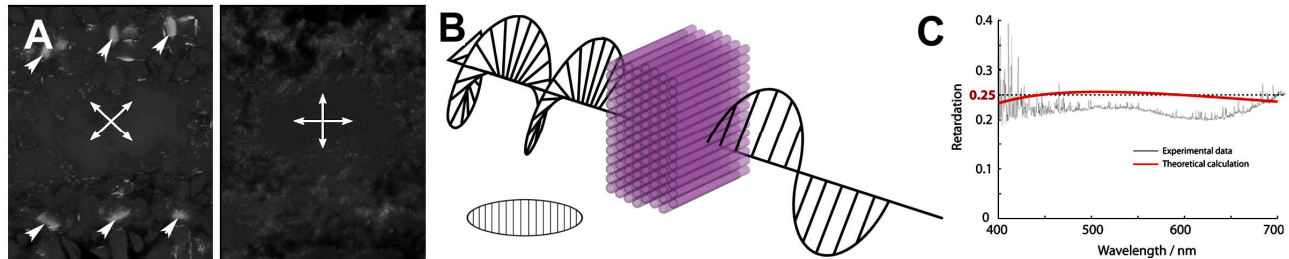

Figure 8. Retardation by the microvillar structures associated with circular-polarization-sensitive photoreceptors in mantis shrimp eyes. A. Transmission or extinction of light through crossed polaroids above and below the tissue sample, at two angles. Note that light is transmitted only when the polarizers are at 45° to the axes of the oval cross sections of the receptor cells (indicated by arrowheads), indicating that these are birefringent. B. Illustration of how this microvillar structure converts circularly polarized light to linearly polarized light with an *e*-vector angle at 45° to the microvillar axes. The inset indicates how the microvilli extend across the minor axis of the elliptical cross-section of the receptors. C. Graph illustrating a preliminary comparison between experimental and theoretical retardation calculated for the R8 cell structure.

A remarkable feature of this biological device is that it shows very little spectral variation in retardance over a range of wavelengths from 400 to 700 nm (Fig. 8C), quite unlike the man-made optical retarders described above. We have begun to explore the properties of the microvillar stack that confer this achromaticity. Our preliminary results suggest that in this periodic microvillous nanostructure, the intrinsic birefringence in the lipid membrane tubules and form birefringence of the packing offset each other to produce dispersion in the overall birefringence that cancels the changing wavelength effects, resulting in constant retardation. Unusually, both the absolute values of the intrinsic membrane refractive indices and the overall length of the structures determine the retardation for the broad range of wavelengths. In fact, the lengths of these cells vary among stomatopod species, which suggests that the relative sensitivities of the underlying photoreceptors to linearly vs. circularly polarized light also varies among species. Understanding this variation is important for working out how the stomatopod crustaceans use polarized light both for signaling and for other aspects of their visual ecology.

6. SUMMARY AND CONCLUSIONS

The mantis shrimps, or stomatopod crustaceans, have compound eyes with the most complicated sets of receptors yet described for any animal, including up to six receptor types specialized to detect ultraviolet light, eight used for color vision in the human "visible" spectrum, and four specialized for polarized-light analysis[22]. It is appropriate that in concert with their unusually well-developed polarization sense, they have evolved communication systems based on displays of patterns of polarized light. However, the optical mechanisms used to produce the polarization have not previously been described in living systems, and at least one mechanism they use (the putative resonant scattering mechanism) seems to have no counterpart in either natural or artificial systems. These animals are also unique in their ability to produce signals based on circularly polarized light of either rotational handedness. Not only is their circular-polarization vision apparently unique among animals, but the optical devices they have evolved that permit them to achieve this visual modality outperform the currently available artificial counterparts. These and potentially other features of the stomatopods serve as inspiration for new technical approaches for controlling polarized light.

ACKNOWLEDGEMENTS

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