

Polarization Vision and Its Role in Biological Signaling¹

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SYNOPSIS. Visual pigments, the molecules in photoreceptors that initiate the process of vision, are inherently dichroic, differentially absorbing light according to its axis of polarization. Many animals have taken advantage of this property to build receptor systems capable of analyzing the polarization of incoming light, as polarized light is abundant in natural scenes (commonly being produced by scattering or reflection). Such polarization sensitivity has long been associated with behavioral tasks like orientation or navigation. However, only recently have we become aware that it can be incorporated into a high-level visual perception akin to color vision, permitting segmentation of a viewed scene into regions that differ in their polarization. By analogy to color vision, we call this capacity polarization vision. It is apparently used for tasks like those that color vision specializes in: contrast enhancement, camouflage breaking, object recognition, and signal detection and discrimination. While color is very useful in terrestrial or shallow-water environments, it is an unreliable cue deeper in water due to the spectral modification of light as it travels through water of various depths or of varying optical quality. Here, polarization vision has special utility and consequently has evolved in numerous marine species, as well as at least one terrestrial animal. In this review, we consider recent findings concerning polarization vision and its significance in biological signaling.

INTRODUCTION

A critical biological requirement during interactions between animals, both interspecific and intraspecific, is that signals be sent and received clearly and unambiguously. Visual signals often use color patterns that may be displayed continuously, as in birds, transiently, as in certain “flash” patterns used by many animals (e.g., the display of colored spots on the wings of butterflies or appendages of mantis shrimps), or only in season, as is the case with many sexual signals. Other visual signals incorporate motion or particular postures or poses, well known in many animals. Visual signals like these have the advantages that they are easily detected and discriminated, often at long distance, and that the information they convey is available to the receiver almost instantly. On the other hand, they are available to any other appropriate visual system, which can be advantageous or disadvantageous, depending on the intended receiver.

A new class of visual signals, visible and virtually unambiguous to intended receivers, yet concealed or barely visible to others, has recently come to light. These signals are based on the controlled reflection of polarized light from the body surface. They are obviously targeted to receivers, generally of the same species, that have visual systems capable of analyzing light's polarization properties or of distinguishing among some aspects of it. Polarized-light patterns therefore carry privileged information, making them

quite different from other kinds of visual signals. Here, we survey the types of polarization signals that exist in nature, the environmental circumstances that make them useful to the tiny minority of animals known to use them, and the optical and structural properties that permit their formation and control.

POLARIZED LIGHT IN NATURE

Throughout this paper, unless specifically noted otherwise, the term “polarized light” refers to partially linearly polarized light. This can be regarded as a mixture of fully linearly polarized light with the plane of vibration of its electric vector (*e*-vector) at a fixed angle, called the *e*-vector angle, combined with fully depolarized light having random *e*-vector orientation. The fraction of photons contributing to the fully polarized component is the degree of polarization, often represented as a percentage (% polarization). Thus, partially linearly polarized light has 3 descriptors: overall intensity, degree of polarization, and *e*-vector angle. Later in this paper, we briefly refer to circularly polarized light. This is formed by two mutually perpendicular, linearly polarized components of equal amplitude but differing in phase by 90 degrees. The vector sum of the two components has fixed amplitude, but rotates by 360 degrees for each wavelength of propagation. Although it is relatively uncommon in nature, circular polarization may have biological significance, as will be discussed.

Even though the sun itself produces fully depolarized light, partially linearly polarized light is abundant in natural scenes (recent review: Wehner, 2001). In the sky and underwater, scattering of incoming light produces partial polarization that varies with solar position and direction of view, and reflection of light from

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the air-water interface or from shiny surfaces (*e.g.*, leaves, wet surfaces, animal skin, scales, or cuticle) produces strong polarization in geometrically favorable circumstances. For terrestrial animals with polarized-light vision (specifically arthropods), the sky presents a reliable pattern useful for navigation, but the more chaotic and unpredictable pattern of polarized-light reflection can mask or taint the “true” colors of objects (Wehner and Bernard, 1993; Kelber, 1999; Kelber *et al.*, 2001). Consequently, photoreceptors in some animals that would normally be sensitive to the polarization of light are structurally modified to destroy polarization sensitivity (Marshall *et al.*, 1991; Wehner and Bernard, 1993), while other animals may evaluate viewed objects using combined spectral and polarizational cues (Kelber, 1999; Kelber *et al.*, 2001). In this case, object identity must be a property of mixed visual cues, a situation somewhat analogous to sensor fusion in artificial systems.

The situation is almost always simpler in water than in air, particularly at depths greater than a few meters. Due to refraction at the air/water interface, illumination from the sun or moon is confined to within 46° of overhead. The resulting polarization field, while variable to some extent, is predictably near horizontal much of the time (Waterman, 1954; Wehner, 2001; Cronin and Shashar, 2001), and the degree of polarization is almost always lower than in air (Novales Flamarique and Hawryshyn, 1997; Cronin and Shashar, 2001). The “pointillistic” reflection of polarized light from objects is virtually gone underwater, as the refractive index gradient between water and most natural objects is much lower than in air, so there is little of the specular reflection of light that is required to produce polarization from dielectric surfaces. The predictable surround, typically low degree of polarization, and minimal polarized-light reflective “noise” favor polarization signaling. Indeed, most of the known biological signaling systems based on differential reflection of polarized light occur in the sea (Shashar *et al.*, 1996; Marshall *et al.*, 1999; see following sections). Nevertheless, other natural settings, for instance under dense forest canopy, may favor polarization signaling, and biological examples from terrestrial environments are beginning to emerge (Sweeney *et al.*, 2003).

BIOLOGICAL USES OF POLARIZED LIGHT

It is thought that the evolution of color vision was favored because of its huge utility in segregating scenes and in fostering the recognition of objects of special interest (*e.g.*, food items, individuals of the same species, etc.). The evolution of polarized-light sensitivity (one prerequisite for polarization vision, covered later) probably followed a different path, because most animal photoreceptors, no matter how they may contribute to a color-vision system, are inherently capable of responding differentially to partially linearly polarized light (reviews: Goldsmith, 1975; Nilsson and Warrant, 1999; Waterman, 1981; Wehner, 2001). This occurs because all visual pigment mole-

cules are based on a single molecular chromophore type (11-*cis* retinaldehyde and close chemical relatives), which has a linear absorption dipole and which therefore is maximally excited when the electrical vector (*e*-vector) axis is parallel to this dipole axis. Furthermore, visual pigment molecules are integral membrane proteins, and the chromophore dipole lies roughly parallel to the membrane surface (Goldsmith, 1975; Snyder and Laughlin, 1975). In vertebrate photoreceptors, the membrane surfaces generally are oriented perpendicular to the paths of incoming light rays, presenting a random array of chromophore axes and thus typically being insensitive to polarized light. Nevertheless, fish (review: Hawryshyn, 1992) and birds (Phillips and Waldvogel, 1988) do respond to polarized light patterns in nature, showing that at least some of their photoreceptors contribute to linear polarization analysis. Invertebrate photoreceptors are commonly built of huge numbers of microvilli, where the chromophore absorption axes are roughly parallel to the microvillar axis. If all microvilli of a single photoreceptor cell are parallel, the cell will respond most strongly to incoming polarized light with its *e*-vector aligned parallel to the microvillus. Invertebrate photoreceptors can enhance both polarization sensitivity and the ability to analyze polarized light with a number of further modifications to the microvillar array (see Nilsson *et al.*, 1987).

Until recently, researchers thought that polarization sensitivity throughout the animal kingdom was invariably associated with behavioral tasks like orientation or navigation. Honeybees have long been known to use polarization patterns in the sky for travel between the hive and foraging locations, and we now know that many insects orient using celestial polarization (reviews: Rossel, 1989; papers in *Journal of Experimental Biology*, 204(14), including Wehner, 2001). A similar capacity may exist in salmonid fishes (Hawryshyn, 1992), permitting them to orient in underwater light fields (Novales Flamarique and Hawryshyn, 1997), although the photoreceptor mechanisms underlying this remain obscure (Rowe *et al.*, 1994; Novales Flamarique *et al.*, 1998; Hawryshyn, 2000). A second class of polarization-controlled orientation behaviors relates to Schwind's (1983, 1984, 1991) discovery that water beetles and other insects orient to the horizontal polarization produced by light reflection from flat, water surfaces. This ability is now known to be present in many insect types, occasionally leading to disaster when the polarization comes from artificial or oily flat surfaces (Horvath and Zeil, 1996; Kriska *et al.*, 1998). On the other hand, flying insects can discriminate natural water surfaces from mirages or other “virtual” surfaces using polarization vision (Horvath *et al.*, 1997).

Lythgoe and Hemmings (1967) first proposed that polarization sensitivity could be used to enhance the visibility of transparent or well-camouflaged targets in water. Recent work by Shashar and others has proven that this is not only possible, but that squids and their

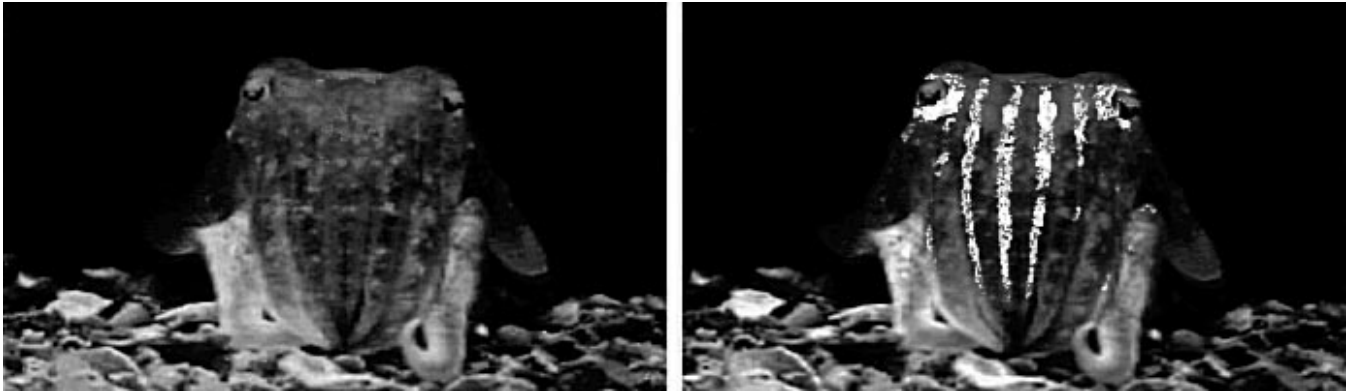


FIG. 1. Two views of a single video image of a cuttlefish, *Sepia officinalis*, showing its frontal display. The left panel shows the animal's usual normal black-and-white appearance (as it might appear to another cuttlefish's monochromatic visual system), while in the right panel, reflected polarized light with a horizontal e -vector angle is coded by bright white, illustrating its potential appearance to a polarization vision system. Note how much more prominent the facial stripes appear in the polarization view (modified from Shashar *et al.*, 1996).

relatives routinely use polarized light to see otherwise obscure objects (Shashar *et al.*, 1995, 1998b, 2000, 2002). These observations prove that some animals see patterns of polarized light in visual fields as image features within the field, not just as orienting stimuli having no particular role in image formation. But the finding that animals use polarization patterns for signaling was completely unexpected. Throughout the rest of this paper, we will cover this topic in detail.

BIOLOGICAL POLARIZED-LIGHT SIGNALS

The ability of cephalopod mollusks (squids, octopus, and cuttlefish) to see and analyze polarized light has been recognized for more than 40 years (Moody and Parriss, 1960, 1961; Rowell and Wells, 1961; Sidel *et al.*, 1983), but the biological function of this capacity was not demonstrated until about five years ago. Shashar and Cronin (1996) found that *Octopus* is able to discriminate polarization variation within a single object, in effect segregating it according to its polarization features. This sensory ability is analogous to color vision, whereby reflectances of similar brightness in a scene are discriminable because their spectral features differ, so we call it *polarization vision* by analogy to color vision (see also Bernard and Wehner, 1977; Nilsson and Warrant, 1999). Objects that look featureless to a human can have visual structure when viewed by an octopus. As mentioned in the previous section, octopuses and their relatives can use polarization analysis of a scene to pick out prey that would otherwise be invisible. The finding that *Octopus* sees polarization features of targets was followed closely by the surprising discovery that cuttlefish (*Sepia officinalis*) use controlled reflection of polarized light to produce species-specific signals (Shashar *et al.*, 1996). The signals (see Fig. 1 for an example) are frequently produced during aggressive or sexual encounters, although their intended meaning is still unclear. Squids produce analogous patterns of polarized light on their body surfaces; once more, the social significance is not known (Shashar and Hanlon, 1997; Shashar *et al.*, 2002;

Mäthger and Denton, 2001). The structural properties of the polarization reflector, and its ability to “turn on” or “off” polarization reflection on demand will be discussed later.

Cuttlefishes and other cephalopods have only one spectral photoreceptor class and are incapable of color vision (Messenger, 1981; Marshall and Messenger, 1996) so the replacement of color with polarization vision seems reasonable. However, the other marine animal group proven to use polarized-light signals has extraordinarily competent color vision. These are the mantis shrimps, or stomatopod crustaceans. They make up a unique crustacean group that (despite their common names) are not closely related to any other modern animals, having separated from the main line of crustacean evolution about 400 million years ago. Many species are brightly colored, and most use strongly colored markings and spots to communicate with each other and even with other stomatopod species. Understanding their polarized-light vision requires a brief discussion of retinal anatomy.

Mantis shrimps have compound eyes with a unique group of visual units (ommatidia) spread around the equator of the eye like a tire tread. These ommatidia form 6 parallel rows, jointly called the midband, and photoreceptors in each ommatidial row are uniquely specialized for ultraviolet, for color, or for polarization vision (see Fig. 2). The receptors at the top of each column of photoreceptors together make up six or more classes specialized for ultraviolet light detection, which does not concern us here (except for one class, see below). Receptors in the underlying tiers in each column in the four most dorsal ommatidial rows of the midband are specialized for color vision. Since each tier is divided into two levels, there are eight primary color receptor classes in addition to the ultraviolet types. All these are constructed so as to *destroy* their innate polarization sensitivity (Marshall *et al.*, 1991). The receptors of the midband which, based on structural evidence, are thought to be specialized to detect and analyze polarized light are in the two most ventral

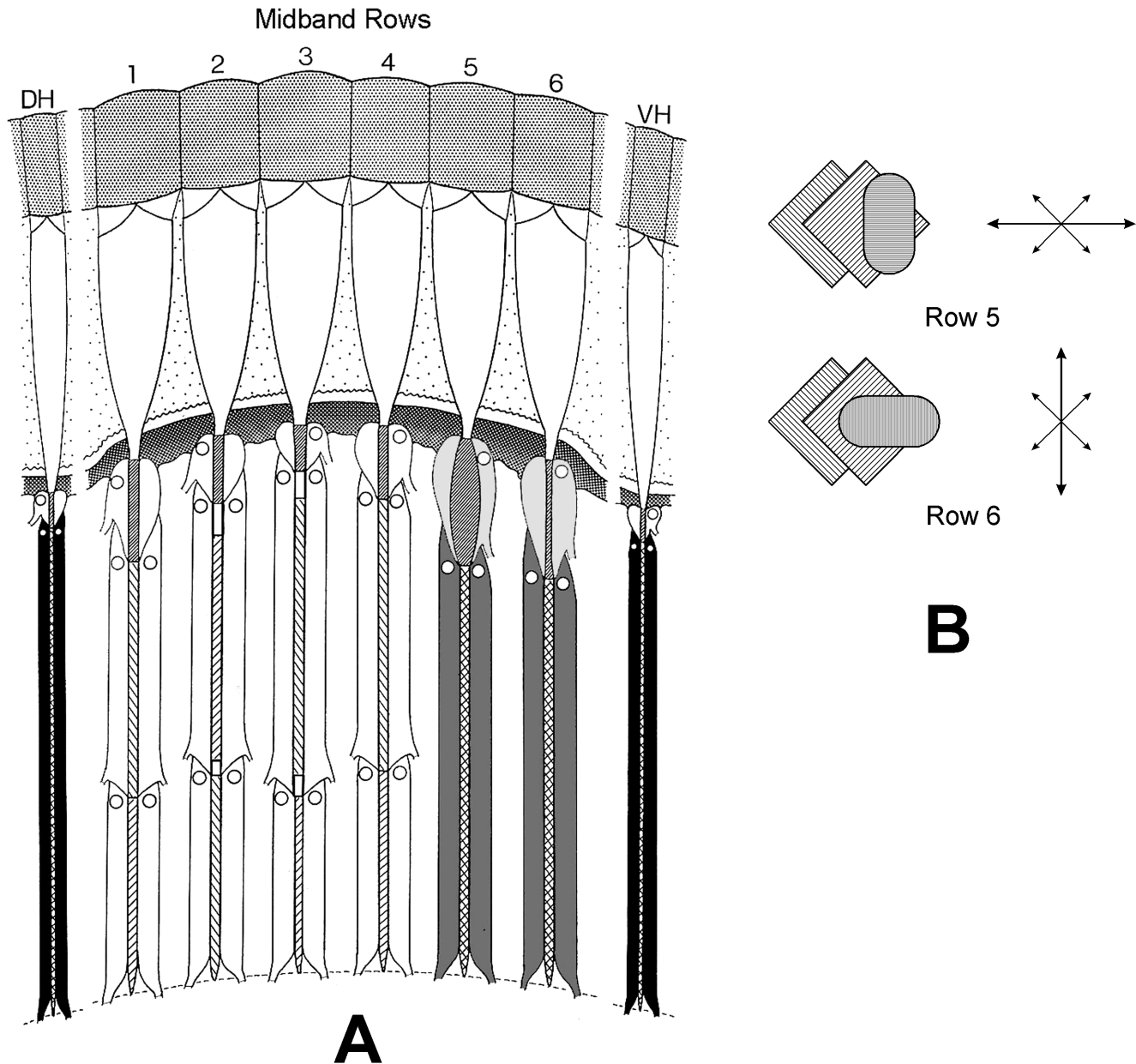


FIG. 2. (A) Diagrammatic view of the arrangements of photoreceptors in the eye of a typical gonodactyloid mantis shrimp, as seen in a vertical section through the cornea and retina. Most of the compound eye is like any other found throughout insects and crustaceans, having an extended array of ommatidia that sample visual space. These ommatidia are divided into two hemispheres by the midband, consisting of 6 parallel rows of ommatidia (indicated by the numbers 1 through 6). All receptors in the hemispheres are identical, and are diagrammed here as DH and VH (dorsal hemisphere and ventral hemisphere, respectively). The rows of the midband are numbered sequentially dorsal to ventral, 1 to 6. Polarization-sensitive receptors are indicated by shading: light gray for the ultraviolet-sensitive receptors of midband rows 5 and 6; medium gray for the middle-wavelength receptors of rows 5 and 6, and black for receptors throughout the dorsal and ventral hemispheres. (B) A schematic view of microvillar orientations (indicated by the direction of hatching and double-headed arrows) in photoreceptors in midband rows 5 and 6. The oval profile and long arrow indicates the ultraviolet-sensitive cell, while the 2 sets of square profiles and shorter arrows indicate the polarization-sensitive layers of the underlying middle-wavelength-sensitive cells. See text and references therein for further discussion (modified from Cronin and Marshall, 2004).

ommatidial rows (rows 5 and 6, Fig. 2). Here, the ultraviolet receptors on top (light gray in Fig. 2A) are rotated at 90° to each other, forming a pair of polarization-sensitive types specializing in very short wavelengths (near 360 nm). Under each of these is a group of large photoreceptors (dark gray in Fig. 2A) that performs 2-axis analysis of linearly polarized light in the

spectral band near 500 nm. Besides these highly specialized receptors of the midband, ommatidia throughout the rest of the eye (dorsal and ventral hemispheres; black in Fig. 2) are probably also polarization-sensitive, as are ommatidia in most crustaceans.

So, mantis shrimps see and analyze linearly polarized light (Yamaguchi *et al.*, 1976; Marshall, 1988;

Marshall *et al.*, 1991). In them, too, this ability was originally assigned to behavioral tasks like those of other arthropods or of salmonid fishes; *i.e.*, orientation and navigation in polarized-light fields (reviews: Waterman, 1981; Hawryshyn, 1992; Wehner, 2001). Thus, it was a real surprise to learn that stomatopods actually recognize polarized-light features of a visual stimulus (Marshall *et al.*, 1999). This finding opens up the possibility that, like the cephalopod mollusks just discussed, mantis shrimps use polarization of light analogously to color, fractionating images and seeing details of objects. Potentially, polarized-light signals may be just as significant as the color signals mentioned above. As just described, the polarization photoreceptors are located in the midband region of stomatopod compound eyes (Marshall, 1988; Marshall *et al.*, 1991). Receptors specialized for color analyses in this region of the eye have similar neural wiring (Marshall *et al.*, 1991; Cronin and Marshall, 2004; Kleinlogel *et al.*, 2003), suggesting that polarized-light and color stimuli are processed similarly. Thus, it is reasonable to infer that stomatopods may see polarized light in an analogous way to their perception of color.

Very recent research results, obtained over the last couple of years, demonstrate that mantis shrimps use polarized-light signals in much the same way that they do color signals. Indeed, signals based on controlled reflection of linearly polarized light should have advantages over color signals in certain circumstances. As mentioned above, few objects reflect strongly polarized light underwater (Cronin and Shashar, 2001; personal observations). Underwater spectral irradiance varies strongly with depth, but polarization is generally much more predictable and stable (Ivanoff and Waterman, 1958), making signal constancy a simpler problem. Many stomatopod species have body parts that are obviously specialized for the reflection of strongly polarized light, used in behavioral contexts that seem clearly linked to intraspecific communication (see Figs. 3 and 4 for striking examples). While our observations are still limited in ecological and phylogenetic coverage, we find that potential polarized-light signals generally become more common with increased habitat depth (both species in Figs. 3 and 4 live at depths >15 m). Therefore, polarization patterns may replace or augment color patterns when environmental light becomes spectrally restricted and polarizationally simple. Patterns based on differential reflection of partially linearly polarized light could be expressive of species-specific signals, and could be unusually direct and easy to interpret, since (unlike color) no other objects in the scene are likely to have similar appearance. They would also be “private,” to some extent, since they would be invisible to animals that do not have a polarization imaging visual system. The spectral properties of the polarization reflection appear to be very well suited to stomatopod communication. The maximum degree of polarization is near 500 nm (Figs. 3 and 4), which matches the polarization sensitivity peak of photoreceptors in midband rows 5 and 6 (as well

as in the dorsal and ventral hemispheres; see Cronin *et al.*, 2000), and is also nicely placed for transmission through natural waters.

One further example of polarized-light signaling has been found, and in this instance the system is designed to operate not in the depths of the sea, but instead deep in the rainforest. Butterflies in Panama, of the species *Heliconius cydno*, reflect iridescent colors from their wings. The reflected light is not only chromatically saturated, but is also ~90% polarized (Sweeney *et al.*, 2003). Males of this species appear to recognize females based on this polarization; when the reflected light from females is artificially depolarized, males approach them much less frequently. As in the examples from the marine environment, this polarization signaling system is found in a photic environment where natural polarization is limited because of the heavy screening of sunlight and sky by the rainforest canopy (see also Shashar *et al.*, 1998a).

CONTROLLING THE REFLECTION OF POLARIZED LIGHT

How are these polarized-light signals produced? Regarding cuttlefish (and probably squid), the signals arise from reflection from a cellular effector class called an *iridophore*, located under the surface of the skin (Shashar *et al.*, 1996). Iridophores contain flat platelets, probably of guanine, that should produce partial linear polarization by reflection. These iridophores are dynamic cells, capable of undergoing ultrastructural changes on neural command (Kawaguti and Ohgishi, 1962; Cooper and Hanlon, 1986; Cooper *et al.*, 1990). Such changes shift them between organized and disorganized forms and therefore almost certainly change their polarization reflectances on demand. The system permits signals to be regulated very rapidly, on time scales of a second or less (see Shashar *et al.*, 1996).

In contrast to the situation with the cephalopods, at present we know very little about how mantis shrimps produce their controlled reflection of polarized light. Preliminary measurements suggest that under diffuse or partly directional illumination (as would occur in water), the degree of polarization can be very high, as much as 75% at the peak, but varying strongly with wavelength (Figs. 3 and 4). Not only does the degree of polarization vary, but also (in some cases) the *e*-vector angle as well (Fig. 4), implying that a layered or helical structure may be involved. Only a few parts of the carapace produce the polarization, mainly the antennal scales, maxillipeds, and uropod scales (Figs. 3 and 4). The body parts used vary among species, creating many possible signal types.

The polarization must be produced structurally and internally in the carapace, for these reasons: (1) Reflection and polarization vary steeply with wavelength (Figs. 3 and 4), implying a precisely ordered structure. (2) Polarization properties change relatively little when the body part is observed in air, suggesting that the reflector is beneath the air/chitin (or water/chitin) interface. (3) In a given body part, the angle of polari-

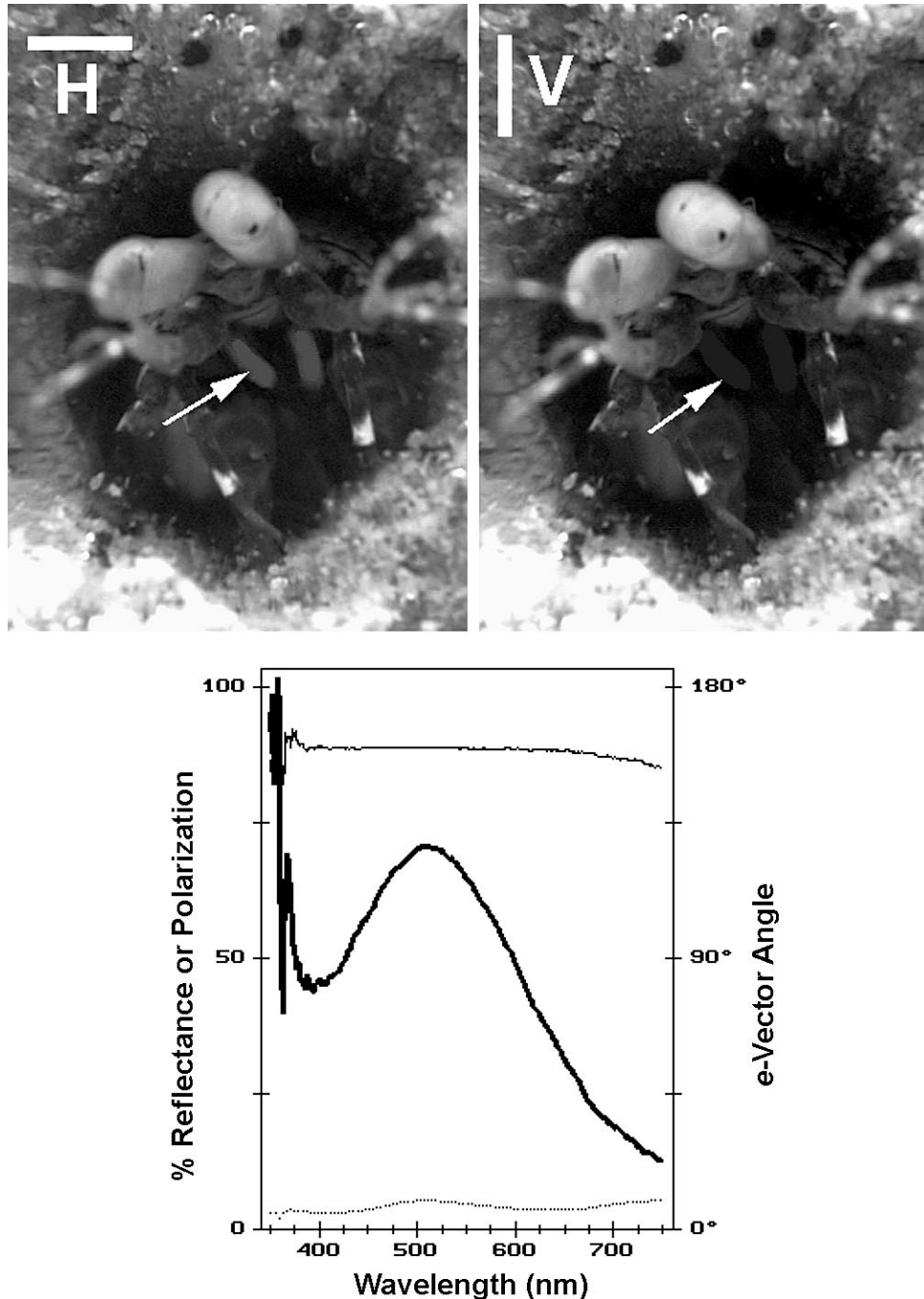


FIG. 3. Potential polarized-light signals used by the mantis shrimp species, *Haptosquilla trispinosa*. The pair of photographic images shows successive frames captured on digital video through a polarization-switching, liquid crystal filter that rotates the plane of a polarization analyzer 90° between frames; the *e*-vector plane transmitted by the filter in each frame is shown by the white line (H, horizontal; V, vertical). These images, taken in the lab, show an individual *H. trispinosa* at its burrow entrance displaying two brightly reflective patches (powder blue in life) on its 1st maxillipeds (arrows). These patches also reflect strongly horizontally polarized light. Notice that other body parts or objects in the video frames do *not* differentially reflect partially linearly polarized light (*i.e.*, do not vary in brightness between frames). The lower panel illustrates spectral properties of the reflected polarized light from these maxillipeds. The *dotted trace* plots overall reflectance, and is maximal at middle wavelengths, near 500 nm. The *dark trace* shows the degree (or percentage) of polarization, which peaks at $\sim 70\%$ polarization near 500 nm. The *light trace* shows the *e*-vector angle of the reflected polarization, which near 160° , or within 20° of horizontal, throughout.

zation preferentially reflected can vary from place to place in a smoothly changing pattern, implying local developmental control. (4) Molt casts retain polarization activity similar to that of live cuticle, although to

a lesser degree. Arthropod cuticle can produce unusual optical effects, analogous to solutions of liquid crystals, resulting from a layered, helicoid structure (Neville and Caveney, 1969; Neville and Luke, 1971). As

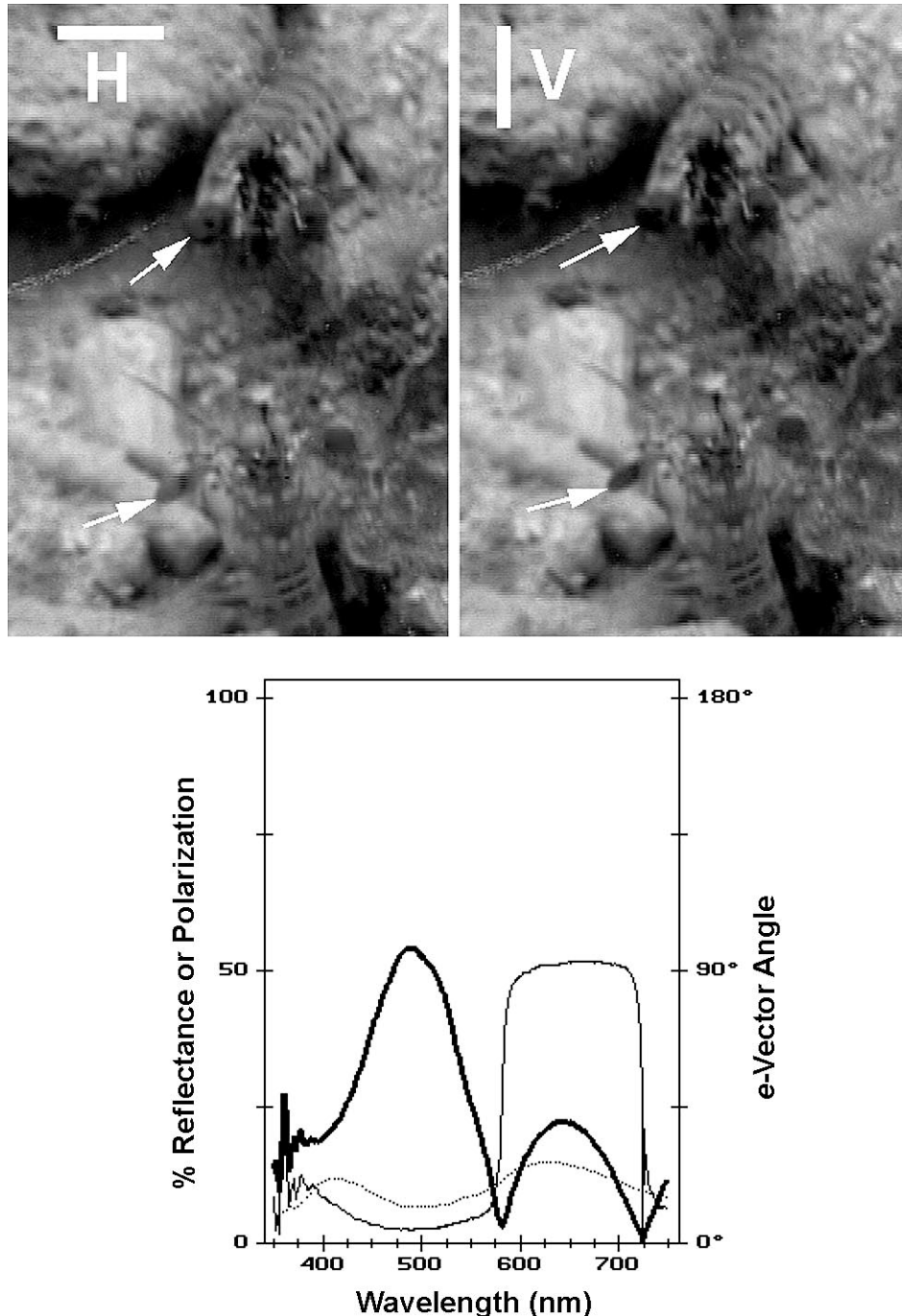


FIG. 4. This figure is like Fig. 3. The upper, photographic pair of images illustrate successive video frames taken at orthogonal planes of polarization (H, horizontal e -vector; V, vertical e -vector) showing interactions between two individuals of *O. havanensis* at the burrow entrance of the lower animal; the upper animal is an intruder. Both individuals have extended their antennal scales (the flap-like exopodites of the 2nd antenna, arrows), which preferentially reflect horizontally polarized light (appearing nearly black in vertical polarization). These images were obtained in the Florida Keys, in the field. The lower panel shows spectral properties of the reflected polarization from this species, as in Fig. 3. Note that there are two regions of maximal degree of polarization, near 500 nm ($\sim 60\%$) and 650 nm ($\sim 25\%$), with opposite e -vector angles. The main polarization band, near 500 nm, is nearly horizontally polarized but the secondary band is vertically polarized (near 90°).

Prum, Vukusic and others have demonstrated, other biological materials can also have unusual optical properties (Prum *et al.*, 1998; Vukusic *et al.*, 2000, 2001; Vukusic and Sambles, 2003). Our current work focuses on the structural and optical properties of sto-

matopod cuticle. We also plan to follow up our earlier work concerning the structure and optics of cephalopod polarizers, as their spectral reflectance properties are just beginning to be characterized (for two squid species; see Mäthger and Denton, 2001).

Reflection of polarized light from butterfly wings is optically simpler in some regards, as the reflection takes place in air. In fact, the iridescent scales of butterfly wings use alternating layers of chitin and air to produce their strong reflections (Vukusic *et al.*, 2000, 2001, 2002). It seems likely that insect iridescence is commonly polarized, and it is very likely that other forest species (and perhaps even open-air butterflies) use this polarization for species recognition and in mate selection.

THE BIOLOGICAL POTENTIAL OF CIRCULARLY POLARIZED LIGHT

No known visual functions involve circularly polarized light. Nevertheless, there are cases in which circular polarization may play a biologically meaningful role. One example, probably not significant, is the anecdotal report that firefly bioluminescence is circularly polarized. Circularly polarized emission occurs in biological systems (for instance, fluorescence from chlorophyll: Gafni *et al.*, 1975; scattering from phytoplankton: Shapiro *et al.*, 1991), but it is probable that the circular polarization of firefly light (if it exists) is incidental. Some biological structures, notably the cuticles of scarabaeid beetles, preferentially reflect left circularly polarized light, due to their unusual internal structure (Neville and Caveney, 1969; Neville and Luke, 1971), but there is no evidence concerning the biological significance (if any) of this feature.

The structure of polarization-sensitive ommatidia in mantis shrimp eyes presents a much stronger circumstantial case for the potential significance of circularly polarized light in vision. Photoreceptors of ommatidia in rows 5 and 6 (Fig. 2) are organized into two main tiers, an overlying single ultraviolet (UV) photoreceptor and an underlying set of middle-wavelength receptors. All receptors are polarization sensitive, and the two rows are twisted at 90° to each other. All microvilli in the ultraviolet receptors are parallel in every photoreceptor of this class in each row (*i.e.*, microvilli in all UV-sensitive cells are parallel to each other) and orthogonal to all homologous UV receptors in the other row. Significantly, microvillar receptors exhibit form birefringence, having a higher refractive index (*n*) for light polarized parallel to the microvillar axis than for that polarized on the orthogonal axis (Snyder and Laughlin, 1975). If the UV receptor were of the correct length, it would act as a quarter-wave retarder plate, converting circular polarization in its active spectral range to linear polarization. The resulting linear polarization would have its axis at either +45° or -45° to the microvillar axes of the UV receptor, depending of the direction of its original circularity, right or left. It is notable that this is the organization seen in receptors of rows 5 and 6; microvilli of the primary, underlying polarization receptors lie at ±45° to those of the UV receptor (Fig. 2B). The UV receptor's length (it is much longer than its homologues in almost all other rows; see Fig. 2A) is estimated to be correct for quarter-wave delay at ~500 nm—the sensitivity max-

imum of the underlying polarized-light-sensitive receptors. Therefore, it is possible that these receptor sets of mantis shrimps are organized to detect and analyze circularly polarized light. The presence of two receptor sets orthogonal to each other would permit the visual system to tease out the relative contributions of circularly and linearly polarized light to any stimulus. The existence of visual organization consistent with the perception of circularly polarized light encourages the search for its presence in natural situations, including signaling. Like the beetles mentioned earlier, mantis shrimp cuticle may have regions that preferentially reflect such a stimulus.

SUMMARY AND CONCLUSIONS

Most animal species have photoreceptors that are inherently polarization-sensitive, and many species use this sensitivity in their orientation and navigation behavior. A few of these polarization-sensitive animals have evolved a set of signals that are based on the controlled reflection of polarized light from parts of their bodies. Polarization signals have special properties that make them particularly suitable for use in photic environments where the natural polarization field is weak, stable, or highly predictable, as they will stand out against natural backgrounds. They have the additional potential advantage of being cryptic to some viewers (for instance, vertebrate predators) while being prominent to conspecifics or other intended recipients. The situations within which these signals are used, the messages that they communicate, and the biological structures that produce them demand further investigation.

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