

Article

A different view: sensory drive in the polarized-light realm

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Abstract

Sensory drive, the concept that sensory systems primarily evolve under the influence of environmental features and that animal signals are evolutionarily shaped and tuned by these previously existing sensory systems, has been thoroughly studied regarding visual signals across many animals. Much of this work has focused on spectral aspects of vision and signals. Here, I review work on polarized-light signals of animals and relate these to what is known of polarization visual systems, polarized-light aspects of visual scenes, and polarization-related behavior (e.g., orientation, habitat-finding, contrast enhancement). Other than the broad patterns of scattered polarized light in the sky, most polarization in both terrestrial and aquatic environments results from either reflection or scattering in the horizontal plane. With overhead illumination, horizontal features such as the surfaces of many leaves or of air: water interfaces reflect horizontal polarization, and water scatters horizontally polarized light under most conditions. Several animal species have been demonstrated to use horizontally polarized light fields or features in critical aspects of their biology. Significantly, most biological signals are also horizontally polarized. Here, I present relevant polarization-related behavior and discuss the hypothesis that sensory drive has evolutionarily influenced the structure of polarization signals. The paper also considers the evolutionary origin of circular polarization vision and circularly polarized signals. It appears that this class of signals did not evolve under the influence of sensory drive. The study of signals based on polarized light is becoming a mature field of research.

Key words: animal communication, polarized light, sensory drive, vision, visual signal

Introduction

When John Endler introduced the term “sensory drive” (Endler 1992), the idea encouraged the view that signals and the sensory systems of animals work together. The scheme he discussed was that sensory system evolution is heavily influenced by local environmental conditions, such as the sources of relevant stimuli, the characteristics of the transmission of stimuli in a particular environment, and the background features or ongoing irrelevant stimuli (“noise”) from which significant stimuli must be discriminated. Animal “signals,” stimuli significant for communication that originate from other animals, are in turn shaped—at least in part—by the properties of the sensory systems to which they are directed. Thus, environment shapes sensation, and sensation shapes signals.

Endler’s presentation seemed to invert the usual way in which signal and sensory evolution were assumed to evolve. But on thinking about the idea further (and as he discussed at some length), sensory systems must in some way be tuned to the environment for many reasons fundamentally associated with survival and successful reproduction. In fact, the ideas behind sensory drive were first articulated soon after the publication of *“The Origin of Species”*. In 1879, Grant Allen wrote “... almost all the colours of vegetal life, except the uniform green of the foliage, are ... due to the colour-sense of one or other of the great seeing classes, the vertebrate and the articulate”, adding “[Color vision has played a major role] in the moulding of organic forms (Allen 1879).” Effective signals must reach an intended receiver efficiently while being as

inconspicuous as possible to potential predators. Obviously, while there are many constraints on signal evolution (avoiding the presence of predators when possible, reducing interception by competitors or unintended receivers, and so forth), the signal must be perceptible to the receiver and clearly different from confounding stimuli. It must be structured to excite the appropriate sensory system of the receiver, and thus under the evolutionary influence of properties of this sensory system. Often, the reduction of predation and unintended interception are managed by the timing of signal production or by signaling mechanisms that direct it most effectively at the proper receiver.

Therefore, signals can represent an intriguing inversion of Wehner's (1987) "matched filter", where the features of a sensory system are shaped to detect a particular stimulus with high efficiency (see also von der Emde and Warrant [2016] for more about matched filters). In sensory drive, the stimulus is structured to be perceived by a sensory system. Nevertheless, there are a few cases in which sensory systems have converged onto signals which themselves have probably been shaped by environmental features. Perhaps the best example is found in the bioluminescent flashes of signaling fireflies. Here, it appears that the bioluminescent emission spectra of fireflies that are active at different times of the evening (early twilight, late twilight, or night) vary so as to be most effective in the illumination, and against the backgrounds, visible at that particular time and place (Seliger et al. 1982a, 1982b). In turn, the sensitivity spectra of receptors in their compound eyes are tuned to match almost perfectly these emission spectra across many species—perfect examples of matched filters (Lall et al. 1980, 1988; Cronin et al. 2000). This paper is not concerned with bioluminescence, but diverse bioluminescent signaling systems illustrate how sensory systems and signals coevolve in unexpected ways (see Haddock et al. 2010; Cronin et al. 2014).

Endler (1992) focused on sensory drive and visual signals in his presentation of the topic, and since then it's likely that a strong majority of studies of this process have concerned visual systems and visual signals (although there is no scarcity of other systems represented). Most of this work centers on spectral sensitivity tuning and color signals and patterns. However, a diverse assortment of animals uses an entirely different property of light for signals: its polarization.

Because humans are nearly insensitive to light's polarization and are incapable of resolving polarization patterns in nature or in animal signals, this aspect of visual signaling was ignored until Shashar et al. (1996) reported that cuttlefish produce rapidly varying patterns of polarized stripes that appear to act as visual signals. Since then, many examples of polarized-light signals (or potential signals) have been discovered (Cronin et al. 2003, 2014; Marshall et al. 2014). Here, we consider how sensory drive might have structured these polarization signals. We also report a type of polarized-light signal that appears to have evolved to a sensory modality that may have been lying dormant until an appropriate signal evolved.

Before proceeding further, I want to go into a bit of semantics. Sensory drive acts on signals, which are used in intraspecific or interspecific communication. When communicating with conspecifics, such signals may be directed at males, females, or both, and may be involved in mate selection, behavioral intent, competition, or agonistic behaviors. Signals directed at heterospecifics are often concerned with predator deterrence (agonistic or aposematic signals). "Biological communication" is very difficult to define, and definitions tend to center either on adaptiveness or on function (information content); see Scott-Phillips (2008) for a discussion of this dilemma. Bradbury and Vehrencamp (1998, p. 357) define

communication as "an exchange of a signal between a sender and a receiver to the benefit of both parties." This definition rules out camouflage or deceptive signals, such as bluffs or exaggerations (where only one party, the sender, benefits), even though such signals are obviously amenable to evolution via sensory drive. Owren et al.'s (2010) definition of communication focuses on a signal's influence on a receiver rather than on the information content of a signal; since the function of crypsis is to avoid detection by a receiver, it is not a signal under this definition, and we will not consider it here.

An excellent and approachable discussion of actual signals, including definitions, can be found in Maynard Smith and Harper's (2003) review, although they do not consider the sensory aspects of signaling. Still, defining (or even recognizing) a "signal" is sometimes problematic (Bradbury and Vehrencamp 1998). Just demonstrating that a particular action or marking is a signal can be challenging, since the generation of the signal, the behavior of both sender and receiver, and the benefits of such behavior are observed rarely or not at all under natural circumstances. This is particularly true of polarization markings and patterns, which certainly are strong candidates for signals. Most of these have never been observed in use in nature, and even under experimental conditions their validity as signals is only inferred, as will be noted later, when candidate signals are discussed. Nevertheless, there is compelling evidence that at least some polarization features are signals and that they are shaped by sensory drive. It is now time to turn to polarized light, its generation in nature, and its perception by animals.

Polarized Light

Properties and formation of polarized light

If you look up at a clear blue sky, you would never know that your eyes are being flooded with polarized light. Humans are essentially blind to this electromagnetic property, but many animals are as capable of seeing and analyzing light's polarization as we are of seeing and analyzing color. Here, we discuss the properties, sources, and distributions of polarized light in nature.

As it travels through space, each vibrating photon in a beam of light creates a wave of electromagnetic energy with 2 properties: wavelength and polarization. The wavelength is the distance in space between identical points, or phases, of the wave; in vision it ranges from ~300 to ~725 nm, varying with species. Polarization is a different property; it refers to the orientation of the wave. Single photons have a characteristic plane of vibration; the orientation of the electrical component of this vibration relative to the direction of travel is called the e-vector axis (or plane of polarization; measured clockwise relative to the detector's view, with 0°/180° being the vertical plane). By definition, each individual photon is polarized, but beams of light—such as light coming from a patch of the sky—contain countless photons, each vibrating with its individual wavelength on its individual e-vector axis. The mix of wavelengths determines the spectrum of the beam; to us and many other animals, it determines its color. The polarization of the beam as a whole similarly depends on the mix of e-vector axes of all the photons making it up. If the e-vectors are completely random, the beam is said to be unpolarized (0% polarized); if all are completely parallel, the beam is fully polarized (100% polarized). Much light contains photons with mixed axes and is partially polarized (see Johnsen 2012).

To this point, I have only covered a type of polarization properly called "linear polarization," since the e-vector, viewed along the axis of the polarized beam, is a straight line. In the laboratory, this

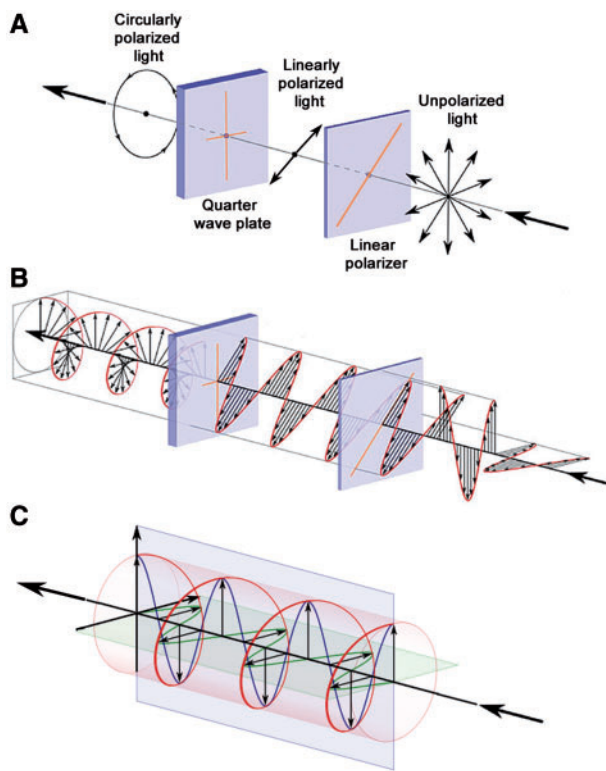


Figure 1. Diagrammatic representations of linearly and circularly polarized light as produced by an unpolarized light beam entering from the right and propagating through first a linear polarizer oriented at 45° and then a quarter wave plate with its fast axis oriented vertically. The linear polarizer transmits fully linearly polarized light, while the quarter wave plate delays the horizontal component of this light by $1/4$ wave relative to the vertical component, producing left-handed circularly polarized light. Panels **A** and **B** illustrate 2 ways of portraying polarization (as axes or vectors). Panel **C** shows the successive peaks of the horizontal (green) and vertical (blue) components of the same circularly polarized wave, as well as the helical path traced by their resultant vectors (red). (Figure modified from Wikipedia.)

light is usually produced by passing it through a linear polarizer (Figure 1A,B). However, light can also be circularly polarized, in which case the view along the beam axis is of an e-vector that rotates in a full circle, either clockwise or counterclockwise (Figure 1; see also Johnsen 2012). The e-vector makes this circle once for each wavelength travelled by the beam, so seen from the side the tip of the vector traces a helical path (Figure 1B,C). In the laboratory, circular polarization is produced by passing fully linearly polarized light through a quarter-wave plate (an optical device that delays one axis of linear polarization by $1/4$ of a wavelength relative to the orthogonal axis; Figure 1A,B). Much light in nature is elliptically polarized, having a mix of linear and circular components (Johnsen 2012; see also Cronin et al. 2014). In such cases, the long axis of the ellipse traced out by successive positions of the e-vector is at the e-vector angle of the linear component.

Most natural (and artificial) sources produce light that is either unpolarized or very weakly polarized. Still, the world is full of polarized light, because light's interaction with matter often favors one type of polarization over another. Scattering and reflection are the most common sources of linear polarization (Wehner 2001; Cronin and Marshall 2011; Marshall and Cronin 2011). That blue sky we looked at a little while ago has a prominent pattern of highly linearly polarized light caused by molecular scattering within the

atmosphere (Figure 2A). Such scattering is most effective for short-wavelength photons, which is why the sky is blue (as your mother explained to you; actually, it's even brighter in the ultraviolet). Scattering also favors photons with polarizations that are perpendicular both to the initial and to the final path of the photon, in other words, whose e-vectors are normal to the plane containing the incident and scattered ray. Scattering perpendicular to the axis of the incident ray is permitted *only* for such photons, so the degree of linear polarization (or percent polarization) varies from 0% for forward-scattered rays to 100% for rays scattered into the plane perpendicular to the incident path. Since essentially all light in the sky comes from the sun, the overall polarization pattern has a band of very highly linearly polarized light at 90° to the sun with diminished polarization at other angles. Celestial polarization never reaches exactly 100% because many photons reaching the earth's surface have been scattered more than once, somewhat scrambling their angles of polarization.

The second process that favors light of certain linear polarization planes is reflection. Light reflected from a non-metallic surface (such as leaves or the air: water interface) becomes enriched in photons with polarization planes parallel to the surface (Figure 2B). At an angle defined by the refractive indices of the materials on each side of the surface (e.g., air vs. water), called Brewster's angle, the reflected light is fully polarized. For water, Brewster's angle is about 53° . In other words, when looking down at a flat and calm pure water surface at an angle of 53° to the vertical, the reflected light you see is 100% polarized. Polarized sunglasses have their polarization transmission axes placed vertically, eliminating most horizontally reflected light, for example from wet surfaces, glass, or painted metal. Thus, they increase contrast; also, they allow the wearer to see through the attenuated shine of the water's surface into the water itself. Polarization filters on cameras may be used for the same purpose or to block polarization in the sky for dramatic images of clouds (which generally scatter little polarization) or skylscapes.

The very low refractive index of air ($n = 1.0$) compared with almost any solid or liquid material, together with the scattering of sunlight in the atmosphere, means that most terrestrial scenes have a complex pattern of polarized light, visible in almost any direction during the day. Underwater, the situation is much simpler. With water's elevated refractive index ($n=1.33$), there is far less reflection of light from submerged objects than there is in air. This leaves scattering as the primary means of producing polarization. Near the surface (perhaps to depths of 20 or 30 m in very clear water, less in turbid locations) the polarization pattern of the sky can be seen, although multiple-path scattering in water quickly obliterates it. On the other hand, water itself is a scattering medium. Since light generally enters water from nearly overhead, and becomes even more centered on the zenith as depth increases, the tendency to produce greatest polarization at scattering angles of 90° means that underwater scenes are dominated by a field of horizontally polarized light visible in all directions (Figure 2C; see also Ivanoff and Waterman 1958; Waterman 1981; Cronin and Shashar 2001; Cronin and Marshall 2011; Marshall and Cronin 2011; Cronin et al. 2014). If an animal is interested in seeing nearby objects or other creatures as silhouettes against this bright, horizontally polarized background, it is advantageous to view the world through a visual system that is able to detect this horizontal axis of polarization. On the other hand, animals may wish to penetrate this obscuring haze to see things that are further away and washed out by the intervening veil of horizontally polarized light. In this case, vision could favor enhancing vertical polarization sensitivity. Of course, depending on

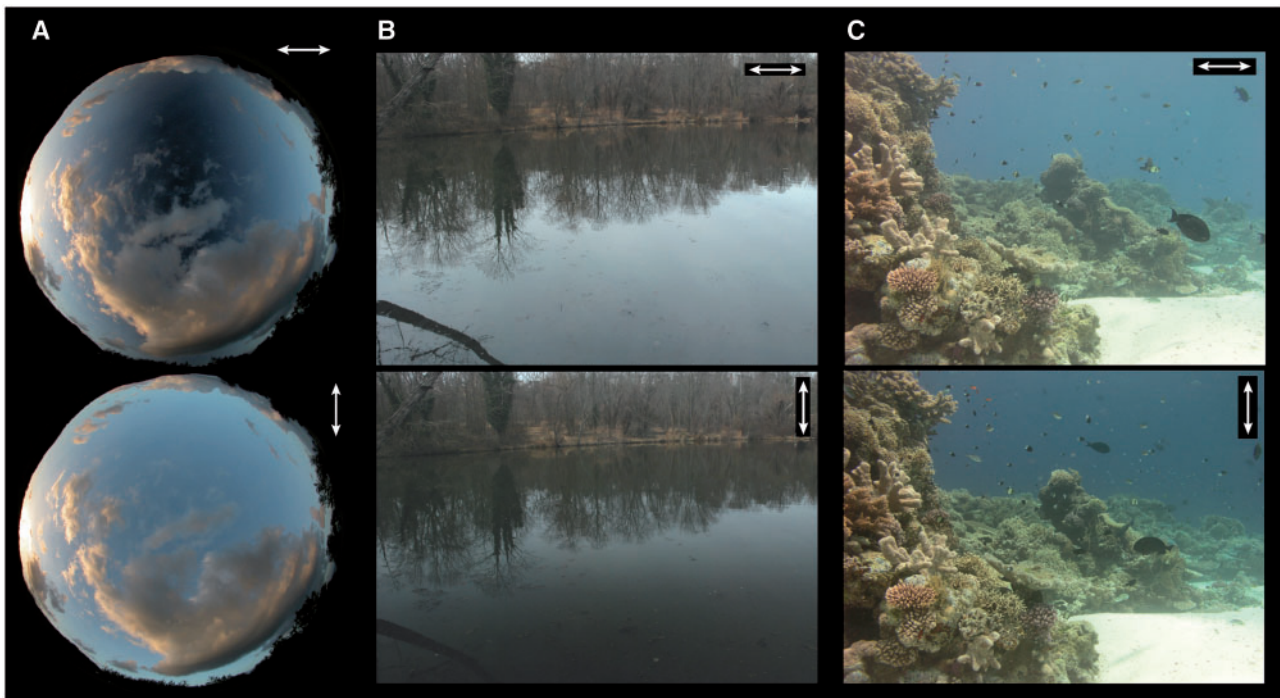


Figure 2. Polarized light fields in nature. In each pair of panels, the top view is photographed through a linear polarizer with its e-vector oriented horizontally and the bottom view through a vertical polarizer (also indicated by the 2-headed arrows). (A) Full-sky images taken using a fisheye lens viewing the entire celestial hemisphere, showing scattering in a partly cloudy sky at sunrise; North is to the top and East to the left. A band of polarization passing overhead with the e-vector polarized North: South is obvious. Even though the sky is partly covered with clouds, the pattern persists in open blue sky areas. (B) Reflective polarization from the surface of a pond. Note the strong horizontal polarization, especially in the lower part of the image which is viewed near Brewster's angle. (C) Scattering-induced polarization in the clear blue water over a coral reef. The light is ~50% polarized with a horizontal e-vector. When the horizontal polarization is removed there is greater contrast (lower panel), especially at longer viewing distances.

downstream neural processing, the same visual system could handle both vertically polarized and horizontally polarized objects or scenes.

Circular polarization is rare in nature; in fact, the only described case on earth is for linearly polarized light in aquatic habitats that becomes internally reflected from the air:water interface (Ivanoff and Waterman 1958). A few animals, however, create circularly polarized light by a variety of optical mechanisms that will be discussed in the section on circularly polarized signals (see also Johnsen 2012; Cronin et al. 2014). Because circularly polarized light is not common, most of the discussion here considers linear polarization. When writing about circular polarization, I note this specifically.

Many surfaces reflect polarized light, and some of these may be modified to form visual signals. Such modifications are only useful if they can be viewed and interpreted. As a consequence, the polarization vision systems of animals have the potential to drive the evolution of polarized-light signals. We now turn to the properties of such visual systems.

Polarized light photoreception and vision

With our very limited polarized-light sensitivity (Temple et al. 2015), humans probably have no natural behavior that involves using the polarization of light. Thus, we tend to discount the significance of polarization vision, but the huge majority of animals would disagree with us. In fact, linear polarization sensitivity is widespread among invertebrate phyla and is likely to be important in some vertebrates as well (Cronin et al. 2003, 2014; Marshall and Cronin 2011; Marshall et al. 2011). Detection of linearly polarized light is inherent to visual pigments of all animals, because the

chromophores of these molecules absorb photons most effectively when the e-vector of a given photon is parallel to the chromophore's long axis. To give an entire receptor cell linear polarization sensitivity, chromophores must therefore be aligned roughly in parallel throughout the receptive membranes of the cell (where the visual pigments are contained).

As it happens, when visual pigments sit in the plasma membrane, their chromophores are situated parallel to the plane of the membrane. The rod disks and cone lamellae of vertebrate photoreceptors have roughly planar membranes, and rhodopsin molecules apparently rotate rather freely in these membranes (Figure 3A); thus, the overall pattern of absorption is random, and these cells are expected to be polarization-insensitive. Nevertheless, because there is some evidence that vertebrates do use polarized-light analysis for orientation or migration, various mechanisms have been proposed that could give a limited polarization sense to rods or cones (Roberts et al. 2011). There is no convincing evidence, however, that vertebrates use polarized light for signaling. In photoreceptors where the membranes are organized into microvilli, as in arthropods or molluscs, the strong curvature of the microvillar membranes evidently restricts the rotational freedom of visual pigment molecules, giving the entire microvillus inbuilt linear polarization sensitivity (Figure 3B). To make an entire photoreceptor cell polarization-sensitive, all microvilli from that single cell must extend out parallel to each other. Most commonly, such cells are oriented so that microvilli of adjacent photoreceptors are oriented orthogonal to each other, an arrangement that fosters 2-axis polarization analysis (Marshall and Cronin 2011; Cronin et al. 2014; Marshall et al. 2014). All animals thought to use polarization signaling have such

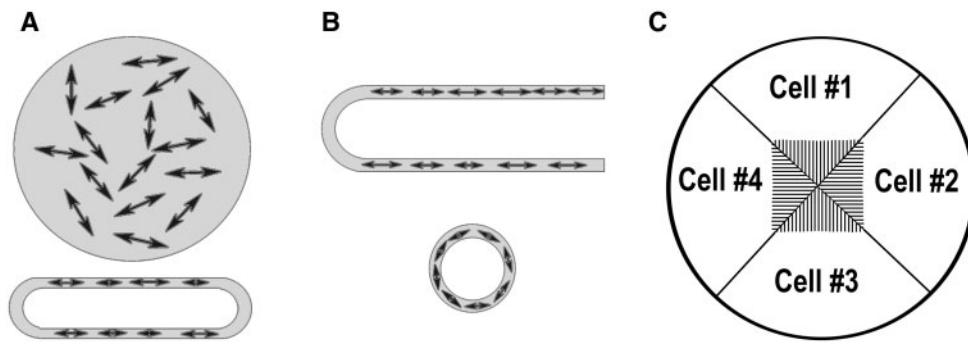


Figure 3. (A) Absorption of polarized light by vertebrate rod photoreceptors. Light arrives normal to the flat surfaces of rod disks and is absorbed by chromophores of visual pigment in the disk membranes (double-headed arrows show preferred e-vector orientations). Since the absorption preference is random, there is no overall polarization signal (top). Light aimed from the side of the disk encounters chromophores roughly parallel to the membrane, favoring the absorption of horizontally polarized light (bottom). (B) Absorption of polarized light by microvillar photoreceptors. Light arrives orthogonal to the long axis of each microvillus, and encounters visual pigment chromophores that are oriented roughly parallel to the axis of the microvillus (top). Thus, the microvillus as a whole preferentially absorbs light polarized parallel to its axis. If light were to arrive from the end of the microvillus (bottom), it would encounter chromophore orientations at all angles, so there would be no preferred polarization absorption. (C) Diagrammatic view of typical polarization-sensitive photoreceptors in compound eyes of insects, seen in cross section (crustaceans and cephalopods have analogous arrangements). Light arrives perpendicular to the plane of the page, and passes through many layers of microvilli. Cells on opposite sides of the receptor extend parallel microvilli toward the junction in the center, and thus have parallel polarization sensitivity. Two orthogonal sets of receptors (Cells 1 and 3 vs. Cells 2 and 4) can provide information for 2-axis polarization analysis.

2-axis analyzers, probably synapsing onto an opponent interneuron to enhance polarization sensitivity. A schematic example of such an arrangement, found in many arthropods and cephalopods, is illustrated in Figure 3C.

Perception of circularly polarized light seems to be very rare, and in fact is only described in a few species of stomatopod crustaceans (mantis shrimps). The mechanism used is the reverse of that used to create circularly polarized light in the laboratory (Figure 1), with the light entering the diagrams in Figure 1A,B from the left. Some mantis shrimp eyes contain structures that function as quarter-wave plates, and these recombine the out-of-phase circular components into a linearly polarized output (Chiou et al. 2008b; Roberts et al. 2009). This is then directed to underlying linear polarization receptors built from aligned microvilli, like those just described. The overall result is that these receptors respond differentially to circular polarization with clockwise or counterclockwise rotation.

Sensory Drive and the Evolution of Linearly Polarized-Light Signals

Production of linearly polarized light by animals

Animals use the same processes as environments to generate linearly polarized light from depolarized light sources. Most animals have surfaces that reflect polarized light, a process that is generally unavoidable in air. Some animals, such as many tropical butterflies (Figure 4A), have specialized features that enhance polarization reflections and use these to produce signals (Douglas et al. 2007). Butterflies use specially formed scales to produce bright, often spectrally narrow, reflections (Douglas et al. 2007; Vukusic and Stavenga 2009; Giraldo and Stavenga 2016). Linearly polarized reflections are also possible underwater, but because of the elevated refractive index of water, dense organic structures must be used. Cephalopod molluscs use specialized cells called iridophores containing a very high refractive-index protein, reflectin, to produce patterns of polarization on their bodies (Figure 4B; Shashar et al. 1996; Crookes et al. 2004; Chiou et al. 2007; Izumi et al. 2009).

Animals use 2 other optical mechanisms to generate linearly polarized light. Some species of stomatopod crustaceans employ a

special type of scattering to do this (Figure 4C; Chiou et al. 2008a; Jordan et al. 2016). Unlike the broad expanses of the sky or the surrounding light field in water, the polarization from some mantis shrimps' scattering structures has a constant e-vector angle, invariant with the angle of illumination, so clearly it is not due to symmetrical scattering as from a molecule. Instead, the mechanism is unique to stomatopods, being based on a rather exotic structure constructed from stacked, elongated, and precisely dimensioned and spaced photonic features that act as tuned scatterers favoring one axis of polarization (Jordan et al. 2016). Other stomatopods possess polarizing structures that use dichroic filters to polarize light, a mechanism thought to be unique to these animals. These filters, functionally analogous to polaroid film (basically, the same material used in polarized sunglasses), have long, aligned molecules that preferentially transmit polarized light having its e-vector plane perpendicular to the long axes of the molecules. The filters work because the long molecules absorb light polarized parallel to them, so light polarized in the orthogonal plane passes through. Stomatopods use the long keto-carotenoid astaxanthin to polarize via dichroism (Figure 4D), so the light that is transmitted is red (because astaxanthin absorbs shorter wavelengths of light). Species using this mechanism take advantage of the fact that astaxanthin's length is almost exactly equal to the distance between the layers of the plasma membrane's lipid bilayer. Consequently, the molecule spans the membranes of cells used in the polarizer, with its polarization axes perpendicular to these membranes. The transmitted horizontally polarized light is parallel to the plane of the plasma membrane, so such a polarizer is best seen when viewed at an angle. Stomatopods enhance the effect by placing membrane sheets containing the astaxanthin over a reflecting layer of cuticle (Chiou et al. 2012).

Polarized-light patterns as signals

While many surfaces of animals have the ability to reflect polarized light, the structures just described appear to be specialized to form visual signals. Understanding the nature (or even the presence) of polarized-light signals, not to mention their evolution, is very challenging. Marshall et al. (2014) strongly argued that the question has received "overenthusiastic optimism" in generating hypotheses and

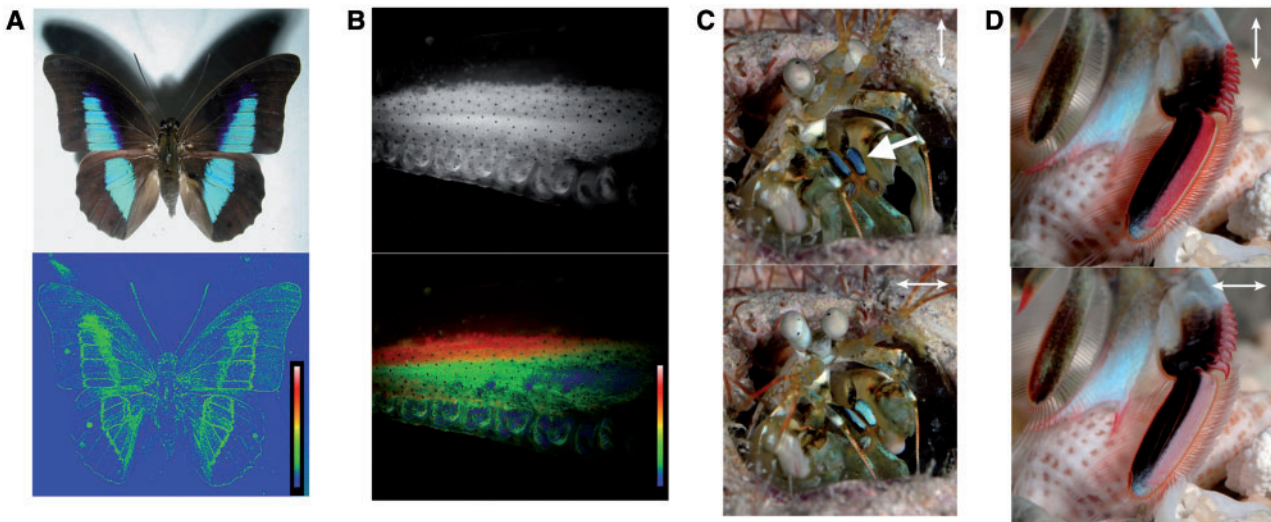


Figure 4. Examples of polarization reflections from animals thought to act as signals. **(A)** An individual of the Neotropical nymphalid butterfly, *Prepona pylene gnorima*, photographed in white light (top) and in a false-color polarization image (bottom). The color scale in the lower panel shows the percent of polarization from 0 to 100. The blue, iridescent patches act as reflective polarizers (credit: J. Douglas). **(B)** Intensity (top) and false-color polarization images (bottom) of the tentacle of a squid, *Doryteuthis pealeii*. As in **A**, the color scale shows the degree of polarization. The reflective iridophores in the skin strongly polarize light, especially on the upper curved surface of the tentacle (credit: T.-H. Chiou). **(C)** The blue maxilliped polarizer (arrow) of the mantis shrimp, *Haptosquilla trispinosa*, as the animal displays at the burrow entrance. This pair of photographs is taken through vertical or horizontal polarizers, as indicated by the 2-headed arrows. Scattering reflections from this structure are strongly horizontally polarized (credit: R.L. Caldwell). **(D)** Uropod of the mantis shrimp *Busquilla plantei*, illustrating a dichroic polarizer. The 2-headed arrows indicate the polarization axis of each image. The bright color seen when the white horizontal polarization is extinguished (top panel) is the red color typical of astaxanthin (credit: R.L. Caldwell).

interpreting results. The problem stems from the simple fact that animal surfaces naturally reflect all sorts of polarization patterns. We see none of these, so when careful polarimetry reveals a striking pattern in the polarization domain, it is natural to jump to the conclusion that it means something to a viewer with polarization vision. That these patterns are hidden to us then suggests that the signaling is “secret,” carrying privileged, encrypted intraspecific information. (Similar arguments were once advanced for patterns visible in ultraviolet light.) There are 2 types of problems with this kind of thinking. In the first place, knowing that an animal’s visual system responds to polarized light is no demonstration that it even is interested in polarized objects, much less that it is used in communication (see Cronin et al. 2014; Marshall et al. 2014). Also, impressive patterns of polarization reflection are likely to be a consequence of unusually shaped body features or of underlying structural elements, and thus may be unrelated to signal production. A final set of issues arises from the experimental challenges of polarization vision research in general, where it is very easy to misinterpret experimental results (Foster et al. 2018).

Given these limitations and biases, how do we decide that a polarization pattern is a signal? The minimal criteria are these: (1) the intended receiver must be capable of perceiving polarized objects; (2) the signal must be used on a body part or region prominently displayed when the sender is interacting with a conspecific; (3) the signal must be used in a behaviorally relevant context (e.g., aggression, deterrence, mate selection); (4) detection of the signal by the receiver must be associated with a clear response; and (5) the signaling should occur in a natural setting (particularly regarding lighting, polarization environment, and reasonable freedom of movement). In fact, no hypothetical polarization signal has ever met all 5 of these criteria. It is difficult to control the polarized-light environment (Foster et al. 2018), very difficult to separate the polarization content of a possible signal from other features (e.g., movement,

brightness, color), and hard to know whether a receiver’s subsequent behavior is a response or some irrelevant action. Nevertheless, there are some compelling cases that strongly suggest the use of polarization signaling.

The use of polarized-light reflections as potential signals was first reported in a cuttlefish, *Sepia officinalis* (Shashar et al. 1996). Cuttlefish produce highly polarized reflections, which can be switched on and off via neural regulation on timescales of seconds (Izumi et al. 2009), from iridophores in their arms; these reflections are horizontally polarized in typical underwater lighting conditions (Shashar et al. 1996; Chiou et al. 2007). The patterns are displayed in social interactions, and they differ in their frequency of use between males and females, suggesting that they play roles in communication (Shashar et al. 1996; Boal 1997; Boal et al. 2004). Similar reflections are found on the arms of squids (Chiou et al. 2007; see Figure 4B), where their biological significance is unknown. Given that cephalopods have large brains, good eyes with polarization sensitivity, and complex behavior, it is difficult to avoid concluding that their use of switchable polarization patterns is involved in signaling. Still, definitive proof that they are used in this way is lacking.

Probably the strongest case for the use of polarization signals is in the nymphalid butterfly *Heliconius cydno*. Sweeney et al. (2003) showed that this species reflects polarization patterns and that males of the species are far more likely to approach females viewed through windows that transmit polarized light than those viewed through depolarizing windows. Encouragingly, the congener *Heliconius melpomene*, which does not reflect such patterns, showed no differences in approach between the 2 types of windows. Overall, these results clearly suggest that *H. cydno* males indeed recognize the polarized-light reflections from females as signals. Taking these results further, Douglas et al. (2007) measured the polarization reflections from specimens of 144 nymphalid species, and found that about half (75) reflect polarized patterns (e.g., Figure 4A).

Species inhabiting dimly lit forest habitats were very likely to reflect these patterns (68% of these species), while species from bright, open habitats rarely used them (only 10% of species). Douglas et al. (2007) argued that polarization patterns are more likely than color patterns to stand out in a dim, achromatic world, and thus should make effective signals. Many other families of butterflies have iridescent, polarized reflections which could be important for signaling (see Marshall et al. [2014] for a review).

The animals that have the widest known diversity of intriguing polarization patterns are the mantis shrimps—stomatopod crustaceans. Mantis shrimp patterns are not produced by surface reflection (so far as is known), but by photonic, reflective scattering (Jordan et al. 2016) or by oriented, dichroic molecules (Chiou et al. 2012). To us, the photonic structures appear to be shiny blue (Figure 4C), so it is difficult to disentangle their signaling value as a color signal from their polarization features. Scattering polarizers are found on the anterior appendages of several stomatopod species (Cronin et al. 2003; Chiou et al. 2008a; How et al. 2014; Marshall et al. 2014), where they may be moved rapidly in a characteristic mating display (Chiou et al. 2011). In contrast to the relatively restricted locations of scattering polarizers, dichroic polarizers in mantis shrimps (Figure 4D) are found in many body structures, including antennal scales (the flaps that project laterally out from the base of the antennae), legs, carapace, telson, and uropods (Cronin et al. 2003, 2014; Chiou et al. 2008a, 2008b, 2012; Marshall et al. 2014). Because of the use of astaxanthin to produce the polarization (Chiou et al. 2012), this type of polarizer generally appears bright red, so again it is possible that polarized and colored signals are combined in such structures.

Evidence that stomatopod polarizers are used in signaling is suggestive, but not conclusive. The most solid case can be made for the blue polarizers of the Indopacific species, *Haptosquilla trispinosa* (the species illustrated in Figure 4C). Chiou et al. (2011) were able to destroy these devices by touching them briefly with a hot pin, a treatment that left the mobility of the appendage intact but which removed both the colored and polarized reflections (happily, the animals regenerated the device when they molted). After being so treated, courting males continued to display their appendages to females as before, and would eventually be accepted as partners, but their displays had to be extended longer, they had to endure more aggressive responses from females before being accepted, and they experienced shorter mating durations. These results strongly indicate that the polarizers are involved in signaling, but do not indicate whether the color, polarization, or both contain the important signal component. Evidence that the dichroic polarizers play a role in signaling is even more circumstantial. These devices, which are usually bright red or yellow in color, occur on parts of the body that are involved in agonistic displays, in defense postures, and in mating displays (Cronin et al. 2003; Marshall et al. 2014). For example, an individual *Odontodactylus havanensis* (a Caribbean species) will prominently display its polarized antennal scales to an intruder as it approaches the resident's burrow (Figure 5A). A different use of the same appendages has been seen in the Indospecific congener, *Odontodactylus scyllarus*. As a male approaches a female of this species from behind prior to mating, she will wobble her laterally extended antennal scales (Figure 5B). Since the degree of polarization reflected from the scale varies with the angle from which it is viewed (Chiou et al. 2012), this produces a display that should be very obvious to the approaching male.

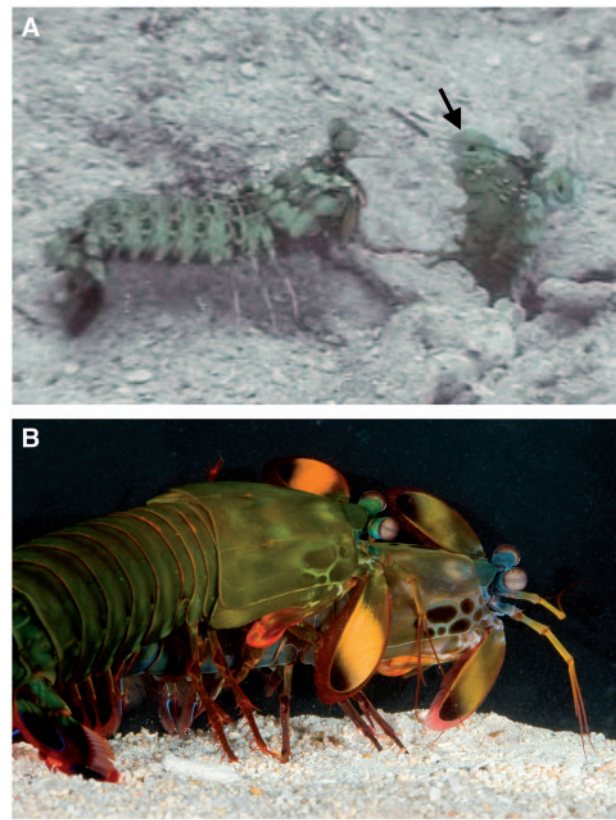


Figure 5. Apparent polarization signaling in stomatopod crustaceans. (A) Single frame from a video taken in the field showing 2 individuals of the Caribbean species *Odontodactylus havanensis* as they encounter each other at the burrow entrance of the animal to the right. This animal poses vertically above its burrow, extending the strongly polarizing antennal scales (black arrow) in a prominent lateral display. The animal on the left subsequently turns away and retreats (not shown). (Video recorded by A Cheroske; the background has been somewhat retouched to emphasize the 2 stomatopods.) (B) Two individuals of the Indopacific species *O. scyllarus* mating in the laboratory (the male is to the left, approaching and grasping the female from behind). The female angles her polarized antennal scales backward and waves them toward the male (credit: R.L. Caldwell).

Sensory drive and the evolution of polarized-light signals

Every signal described in this review is horizontally polarized in normal viewing conditions. In natural illumination in either terrestrial or aquatic environments, the geometry of the situation is such that reflective signals from horizontally oriented structures will mostly include horizontal polarization, so this might not be a surprise. Dichroic signals are also horizontally polarized for the same reason; the dichroism actually interacts with light reflected from an underlying layer (Chiou et al. 2012), so the signal is brightest and most polarized when lit from overhead (as is the case in most often encountered in nature) and viewed horizontally. Scattering polarizers, however, are not limited by the direction of illumination or view—they reflect horizontally polarized light regardless of how they are illuminated or seen (Chiou et al. 2008a; Jordan et al. 2016). If sensory drive is behind the evolution of polarization-based signals, is there a reason why signaling systems might favor horizontal polarization?

Because the overhead light field is bright during the day (especially on sunny days), the terrestrial environment provides an

abundance of horizontally polarized features (Horváth and Varjú 2003; Cronin and Marshall 2011; Marshall and Cronin 2011; Cronin et al. 2014; Horváth 2014). Insects, in particular, use horizontally polarized reflections from water surfaces (e.g., Figure 2B) to locate natural ponds and pools (Schwind 1984a, 1984b; Horváth and Varjú 2003; Horváth and Csabai 2014). In fact, the response is so widespread and invariant among aquatic insects that it has become a problem. These animals are fatally attracted to shiny artificial surfaces (Horváth et al. 2014b), and many human structures lure them in large numbers, where they perish. The sensory impact of horizontal polarization is illustrated in the oviposition behavior of an Australian swallowtail butterfly, *Papilio aegaeus* (Kelber 1999). Females of this species select horizontally polarized surfaces on which to oviposit. The choice is driven in part by the color of the substrate; green is preferred over both yellow and blue, but the butterflies will choose a horizontally polarized target of any color over a vertically polarized one of the same color. Furthermore, females prefer a horizontally polarized yellow surface over a vertically polarized green one, emphasizing the role of polarization in making a choice. Innate preferences like this easily could guide the evolution of horizontally polarized signals (like the patterns on butterfly wings; Figure 4A).

Underwater, the polarized world is much simpler than in air, since underwater surfaces are poorly reflective. This leaves the omnidirectional spacelight (which is horizontally polarized; Figure 2C) as the primary source of underwater polarization, against which objects (and signals) can be viewed. How et al. (2014) demonstrated that individuals of the protosquillid mantis shrimp *H. trispinosa* are significantly more likely to respond to a looming, horizontally polarized stimulus than to a vertically polarized one. This species and several close relatives have the bright blue scattering polarizers on their first maxillipeds (Figure 4C; see Cronin et al. 2003; Chiou et al. 2008a, 2011; How et al. 2014; Jordan et al. 2016). How et al. (2014) argue that the use of horizontal polarization in signaling evolved under the influence of the innate response to horizontally polarized objects. Significantly, the elevated responses to horizontally polarized looming stimuli are seen in several protosquillid stomatopods, including those lacking polarization signaling, which implies that the response is innate and available for signal evolution. Many aquatic animals, including crabs, crayfishes, and cephalopods, respond to polarized looming stimuli (Tuthill and Johnsen 2006; How et al. 2012; Temple et al. 2012), but biases toward particular e-vector angles have not yet been investigated.

Circularly Polarized Signal Evolution: Sensory Drive?

All signals discussed so far are linearly polarized, but a few animals reflect circularly polarized light. As mentioned before, most circularly polarized light includes a constantly oriented, linearly polarized component and is properly called “elliptically polarized light,” but here I’ll focus specifically on the circularly polarized component.

It has long been recognized that many scarab beetles reflect circularly polarized light (Figure 6A). Michelson (1911) first noted this, and the phenomenon has recently been described in some detail by Goldstein (2006). Brady and Cummings (2010) published results of spontaneous phototaxis experiments that suggested that one species of scarab beetles *Chrysina gloriosa* could discriminate vertical linearly polarized from left circularly polarized light, while another *C. woodi*, could not. Exhaustive tests with hundreds of beetles of 4 other scarab species by Horváth’s laboratory, however, found no

evidence that any of these beetles respond differentially to circularly polarized light of either handedness during feeding or when presented with individuals of their own species, whether walking or flying (Blahó et al. 2012; Horváth et al. 2014a; see also Foster et al. 2018). Since eyes of scarab beetles do not appear to have any optical specializations that would permit them to detect circular polarization, it now appears that their circularly polarized reflections are not involved in signaling behavior.

A more recent discovery is that some mantis shrimps actually have circularly polarized body parts and that they are capable of discriminating right from left circularly polarized light (Chiou et al. 2008b). An interesting structure, one that is very likely to be used in sexual signaling, is the “keel” on the median ridge of the telson of the stomatopod *Odontodactylus cultrifer* (Figure 6B,C). This feature is sexually dimorphic (being much larger in males than females), and reflects (and transmits) highly circularly polarized light. Amazingly, when seen from the right side, the polarization of the keel is right handed; the opposite is true on the left (Figure 6C). Mating behavior in this species has never been observed, but the sexual dimorphism strongly suggests that the keel is a sexual signal, and the unique presence of circular polarization vision in stomatopods may be critical in detecting and interpreting this signal.

Circularly polarized signals could also be useful in aggressive encounters. A different mantis shrimp species, *Gonodactylaceus falcatus*, displays highly circularly polarized markings on its legs and anterior body parts when it poses in its burrow entrance (Gagnon et al. 2015; Figure 6D). The polarization is left-handed, and *G. falcatus* can learn to discriminate circular polarization from depolarized light, although (unlike *Odontodactylus*) it seems not to discriminate right from left circular polarization. The circularly polarized markings displayed at the burrow entrance (as in Figure 6D) apparently act defensively, as naive individuals of this species avoid burrows with entrances marked with circularly polarized filters. Gagnon et al. (2015) suggest that the circular polarization can be considered a true “covert” signal, in that no animals besides stomatopod crustaceans would be able to recognize it. *Gonodactylaceus falcatus* is often sandy colored and thus well camouflaged against its coral sand or rock environment, but the circularly polarized reflections could be obvious to another mantis shrimp.

Unlike the evolution of putative linearly polarized signals, these circularly polarized ones seem not to have originated with a push from sensory drive. Except for rare and transient optical phenomena, such as internal reflection from the water’s surface (Ivanoff and Waterman 1958), the marine environment is thought to be devoid of circular polarization. Indeed, it is mystifying that mantis shrimps even are able to detect it, given the optical demands of constructing a circular polarization analyzer and the apparent inutility of sensing it in the first place. It now appears that circular polarization sensitivity exists because of an odd arrangement of receptor cells in a subset of receptors in the midband, a specialized region of mantis shrimp compound eyes. In 2 rows of ommatidia, excellent orthogonally arranged polarization receptors exist (similar in principle to Figure 3C). However, they are placed under a different receptor that absorbs ultraviolet light, but transmits longer-wavelength light that the polarization receptors absorb. Uniquely, this ultraviolet receptor is an optical, achromatic retarder, converting incoming circularly polarized light to linearly or elliptically polarized light that passes through to the underlying polarization receptors (Chiou et al. 2008b; Roberts et al. 2009). Simply put, it converts light that the polarization receptors would not normally discriminate from unpolarized light into discriminable light. The efficiency of the conversion

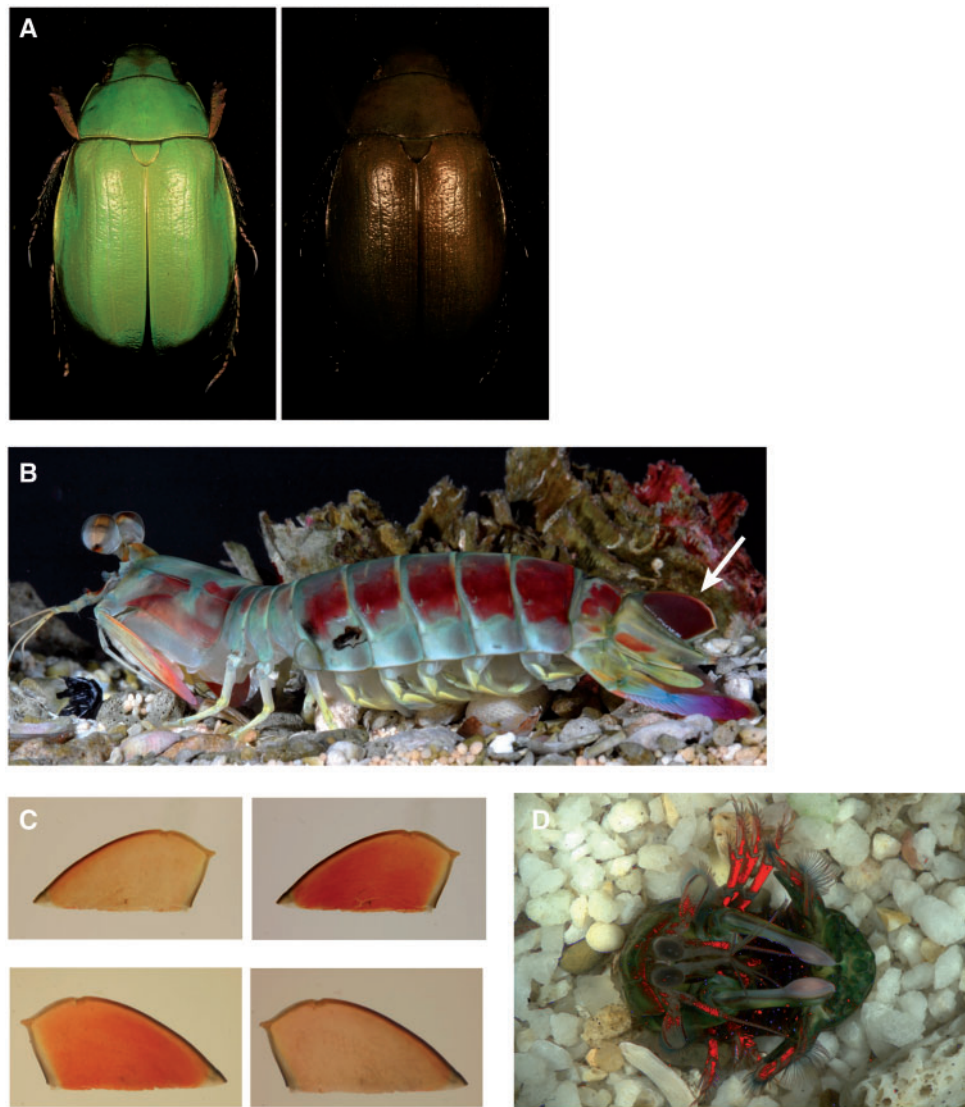


Figure 6. Circular polarization reflections from animals. (A) Scarab beetle *Chrysina beyeri*. Left panel: left circular polarization. Right panel: right circular polarization. Like many scarabs, the animal reflects left-handed highly polarized light, both by the green dorsal surface of the body (green) and by the purplish legs (credit: A. Harryman). (B) A male of the stomatopod *Odontodactylus cultrifer*. The white arrow shows the tall median keel of the animal's telson (credit: R.L. Caldwell). (C) Images of the keel in circularly polarized light. As in panel A, in each pair the image to the left is taken in left circular polarization, and the right image is taken in right circular polarization. From the left side (top pair), the keel preferentially reflects left circular polarization; from the right side (bottom pair), right circular polarization dominates (credit: T.-H. Chiou). (D) Circular polarization reflections from an individual of the Indopacific stomatopod *Gonodactylaceus falcatus* in a defensive pose at its burrow entrance. The bright red areas (on the legs and other appendages) are false-colored to show strong left circularly polarized reflections (from Gagnon et al. [2015]; used with permission).

depends on the length of the ultraviolet receptor, but at typical lengths the efficiency is fairly high (Roberts et al. 2009). The end result is a circular polarization analyzing system without a circularly polarized stimulus to analyze. Due to the often incomplete conversion of circular to linear polarization, the ellipticity of the light entering the linear polarization receptors is high enough to permit them to continue to detect its linear polarization content, while also responding to occasional circular polarization.

The circularly polarized signal is also not difficult to produce, as many arthropods besides mantis shrimps and dung beetles reflect circularly polarized light produced by several distinct mechanisms (Neville and Caveny 1969; Neville and Luke 1971). In the case of stomatopods, the chitin of the cuticle often is fortified with calcite, an optically active form of calcium carbonate. In combination with

the linear polarization passing through astaxanthin-based dichroic polarizers, this can form a circularly polarized signal. So it appears that the preconditions for circularly polarized signaling probably existed in these creatures, and signals evolved more or less by the fortuitous coincidence of there being an accidental sensory modality and a strange optical structure in the cuticle available to build a unique signaling system.

Summary and Conclusions

Animals convert depolarized environmental light to polarized light by a surprising diversity of optical mechanisms. Polarization patterns and polarized-light-producing structures are widespread and diverse among animals; many of these are likely to be used for

signaling. Most such structures provide horizontal polarization, which is consistent with the hypothesis of evolution by sensory drive since many polarization-related behaviors similarly involve horizontally polarized light. At this point, all examples of possible polarization signals are drawn from arthropods (butterflies and mantis shrimp) and cephalopods (primarily cuttlefish), and it will be important to extend the field to other taxa to know more about the biological extent of the use of polarization in communication. In addition, the huge majority of examples come from marine animals, specifically cephalopods and mantis shrimps. This suggests that polarization signaling is particularly useful in an environment that varies enormously in illumination and spectrum, but that has a fairly constant polarization content (Cronin et al. 2003). The connection to marine animals is particularly interesting because they do not normally reflect polarized light without specializations because of the weak specular reflectivity of surfaces in water, yet they have evolved exotic mechanisms to produce polarizations. The disproportionate expression of polarization reflective patterns in forest-dwelling nymphalid butterflies (Douglas et al. 2007) is consistent with the idea that polarization signaling is favored in dim environments.

The primary research tasks that demand attention now include the demonstration of polarization signaling in other kinds of animals besides butterflies, mantis shrimps, and cuttlefishes. Many insects, crustaceans, and cephalopods have polarization vision and might benefit from its use in communication. Further, we need rigorous demonstrations that the hypothesized signals are actually used to communicate and that their polarization content is a critical component of communication. A third avenue for research is a better understanding of the function and use of circularly polarized signals. In the future, signals based on polarized light may be equally fruitful subjects for study as color signals are today.

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References

- Allen G, 1879. *The Colour-Sense: Its Origin and Development*. London: Trübner & Co.
- Blahó M, Egri Á, Hegedüs R, Jósavai J, Tóth M et al., 2012. No evidence for behavioral responses to circularly polarized light in four scarab beetle species with circularly polarizing exocuticle. *Physiol Behav* 105:1067–1075.
- Boal JG, 1997. Female choice of males in cuttlefish (Mollusca: Cephalopoda). *Behaviour* 134:975–988.
- Boal JG, Shashar N, Grable MM, Vaughan KH, Loew ER et al., 2004. Behavioral evidence for intraspecific signaling with achromatic and polarized light by cuttlefish (Mollusca: Cephalopoda). *Behaviour* 141:837–861.
- Bradbury JW, Vehrencamp SL, 1998. *Principles of Animal Communication*. Sunderland (MA): Sinauer, 882 pp.
- Brady P, Cummings M, 2010. Differential response to circularly polarized light by the jewel scarab beetle *Chrysina gloriosa*. *Am Nat* 175:614–620.
- Chiou TH, Caldwell RL, Hanlon R, Cronin TW, 2008a. Fine structure and optical properties of biological polarizers in crustaceans and cephalopods. In: Chenault DB, Goldstein DL, editors. *Proceedings of SPIE* 6972. *Polarization: Measurement, Analysis, and Remote Sensing VIII*. Bellingham (WA): SPIE Press.
- Chiou TH, Kleinlogel S, Cronin TW, Caldwell RL, Loeffler B et al., 2008b. Circular polarization vision in a stomatopod crustacean. *Curr Biol* 18:429–434.
- Chiou TH, Marshall NJ, Caldwell RL, Cronin TW, 2011. Changes in light reflecting properties of signaling appendages alter mate choice behaviour in a stomatopod crustacean, *Haptosquilla trispinosa*. *Mar Freshw Behav Physiol* 44:1–11.
- Chiou TH, Mäthger LM, Hanlon RT, Cronin TW, 2007. Spectral and spatial properties of polarized light reflections from the arms of squid *Loligo pealeii* and cuttlefish (*Sepia officinalis* L.). *J Exp Biol* 210:3624–3635.
- Chiou TH, Place AR, Caldwell RL, Marshall NJ, Cronin TW, 2012. A novel function for a carotenoid: astaxanthin used as a polarizer for visual signaling in a mantis shrimp. *J Exp Biol* 215:584–589.
- Cronin TW, Marshall J, 2011. Patterns and properties of polarized light in air and water. *Phil Trans R Soc B* 366:619–626.
- Cronin TW, Järvilehto M, Weckström M, Lall AB, 2000. Tuning of photoreceptor spectral sensitivity in fireflies (Coleoptera: Lampyridae). *J Comp Physiol A* 186:1–12.
- Cronin TW, Johnsen S, Marshall NJ, Warrant EJ, 2014. *Visual Ecology*. Princeton: Princeton University Press, 405 pp.
- Cronin TW, Shashar N, 2001. The linearly polarized light field in clear, tropical marine waters: spatial and temporal variation of light intensity, degree of polarization, and *e*-vector angle. *J Exp Biol* 204:2461–2467.
- Cronin TW, Shashar N, Caldwell RL, Marshall H, Cheroske AG et al., 2003. Polarization vision and its role in biological signaling. *Integr Comp Biol* 43:549–558.
- Crookes WJ, Ding LL, Huan QL, Kimbell JR, Horwitz J et al., 2004. Reflectins: the unusual proteins of squid reflective tissues. *Science* 303:235–238.
- Douglas JM, Cronin TW, Chiou TH, Dominy NJ, 2007. Light habitats and the role of polarized iridescence in the sensory ecology of Neotropical nymphalid butterflies (Lepidoptera: Nymphalidae). *J Exp Biol* 210:788–799.
- von der Emde G, Warrant E, 2016. *The Ecology of Animal Senses*. Heidelberg (NY): Springer, 269 pp.
- Endler JA, 1992. Signals, signal conditions, and the direction of evolution. *Am Nat* 139:S125–S153.
- Foster JJ, Temple SE, How MJ, Daly IM, Sharkey CR et al., 2018. Polarisation vision: overcoming challenges of working with a property of light we barely see. *Sci Nat* 105:27.
- Gagnon YL, Templin RM, How MJ, Marshall NJ, 2015. Circularly polarized light as a communication signal in mantis shrimps. *Curr Biol* 25:1–5.
- Giraldo MA, Stavenga DG, 2016. Brilliant iridescence of Morpho butterfly wings due to both a thin film lower lamina and a multilayered upper lamina. *J Comp Physiol A* 202:381–388.
- Goldstein DH, 2006. Polarization properties of Scarabaeidae. *Appl Opt* 45:7944–7950.
- Haddock SHD, Moline MA, Case JF, 2010. Bioluminescence in the sea. *Ann Rev Mar Sci* 2:443–493.
- Horváth G, 2014. Polarization patterns of freshwater bodies with biological implications. In: G Horváth, editor. *Polarized Light and Polarization Vision in Animal Sciences*. Berlin: Springer, 333–344.
- Horváth G, Blahó M, Egri Á, Hegedüs R, Szél G, 2014a. Circular polarization vision of scarab beetles. In: G Horváth, editor. *Polarized Light and Polarization Vision in Animal Sciences*. Berlin: Springer, 147–170.
- Horváth G, Csabai Z, 2014. Polarization vision of aquatic insects. In: Horváth G, editor. *Polarized Light and Polarization Vision in Animal Sciences*. Berlin: Springer, 113–145.
- Horváth G, Kriska G, Robertson B, 2014b. Anthropogenic polarization and polarized light pollution inducing polarized ecological traps. In: G Horváth, editor. *Polarized Light and Polarization Vision in Animal Sciences*. Berlin: Springer, 443–513.
- Horváth G, Varjú D, 2003. *Polarized Light in Animal Vision*. Heidelberg (NY): Springer, 447 pp.
- How MJ, Pignatelli V, Temple SE, Marshall NJ, Hemmi JM, 2012. High *e*-vector acuity in the polarisation vision system of the fiddler crab *Uca vomeris*. *J Exp Biol* 215:2128–2134.

- How MJ, Porter ML, Radford A, Feller KD, Temple S et al., 2014. Out of the blue: the evolution of horizontally polarized signals in Haptosquilla (Crustacea, Stomatopoda, Protosquillidae). *J Exp Biol* **217**:3425–3431.
- Ivanoff A, Waterman TH, 1958. Factors, mainly depth and wavelength, affecting the degree of underwater light polarization. *J Mar Res* **16**:283–307.
- Izumi M, Sweeney AM, DeMartini D, Weaver JC, Powers ML et al., 2009. Changes in reflectin protein phosphorylation are associated with dynamic iridescence in squid. *J R Soc Interface* **10**:1098.
- Johnsen S, 2012. *The Optics of Life*. Princeton: Princeton University Press, 336 pp.
- Jordan TM, Wilby D, Chiou TH, Feller KD, Caldwell RL et al., 2016. A shape-anisotropic reflective polarizer in a stomatopod crustacean. *Sci Rep* **6**: 21744.
- Kelber A, 1999. Why “false” colours are seen by butterflies. *Nature* **402**:251.
- Lall AB, Seliger HH, Biggley WH, Lloyd JE, 1980. Ecology of colors of firefly bioluminescence. *Science* **210**:560–562.
- Lall AB, Strogher GK, Cronin TW, Seliger HH, 1988. Modification of spectral sensitivities by screening pigments in the compound eyes of twilight-active fireflies (Coleoptera: Lampyridae). *J Comp Physiol A* **162**:23–33.
- Marshall J, Cronin TW, 2011. Polarization vision. *Curr Biol* **21**:R101–R105.
- Marshall J, Cronin TW, Wehling MF, 2011. Introduction: new directions in the detection of polarized light. *Phil Trans R Soc B* **366**:615–616.
- Marshall J, Roberts N, Cronin T, 2014. Polarisation signals. In: Horváth G, editor. *Polarized Light and Polarization Vision in Animal Sciences*. Berlin: Springer, 407–442.
- Maynard Smith J, Harper D, 2003. *Animal Signals*. Oxford: Oxford University Press, 166 pp.
- Michelson AA, 1911. On metallic colouring in birds and insects. *Phil Mag* **21**: 554–567.
- Neville AC, Caveney S, 1969. Scarabaeid beetle exocuticle as an optical analogue of cholesteric liquid crystals. *Biol Rev* **44**:531–562.
- Neville AC, Luke BM, 1971. Form optical activity in crustacean cuticle. *J Insect Physiol* **17**:519–526.
- Owren MJ, Rendall D, Ryan MJ, 2010. Redefining animal signaling: influence versus information in communication. *Biol Philos* **25**:755–780.
- Roberts NW, Porter ML, Cronin TW, 2011. The molecular basis of mechanisms underlying polarization vision. *Phil Trans R Soc B* **366**:627–637.
- Roberts NW, Chiou TH, Marshall NJ, Cronin TW, 2009. A biological quarter-wave retarder with excellent achromaticity in the visible wavelength region. *Nat Photonics* **3**:641–644.
- Schwind R, 1984a. Evidence for true polarization vision based on a two-channel analyzer system in the eye of the water bug *Notonecta glauca*. *J Comp Physiol A* **154**:55–57.
- Schwind R, 1984b. The plunge reaction of the backswimmer *Notonecta glauca*. *J Comp Physiol A* **155**:319–321.
- Scott-Phillips TC, 2008. Defining biological communication. *J Evol Biol* **21**: 387–395.
- Seliger HH, Lall AB, Lloyd JE, Biggley WH, 1982a. e colors of firefly bioluminescence. I. An optimization model. *Photochem Photobiol* **36**: 673–680.
- Seliger HH, Lall AB, Lloyd JE, Biggley WH, 1982b. On the colors of firefly bioluminescence. II. Experimental evidence for the optimization model. *Photochem Photobiol* **36**:681–688.
- Shashar N, Rutledge PS, Cronin TW, 1996. Polarization vision in cuttlefish: a concealed communication channel? *J Exp Biol* **199**:2077–2084.
- Sweeney A, Jiggins C, Johnsen S, 2003. Polarized light as a butterfly mating signal. *Nature* **423**:31.
- Temple SE, McGregor JE, Miles C, Graham L, Miller J et al., 2015. Perceiving polarization with the naked eye: characterization of human polarization sensitivity. *Proc R Soc B* **282**:20150338.
- Temple SE, Pignatelli V, Cook T, How MJ, Chiou TH et al., 2012. High-resolution polarisation vision in a cuttlefish. *Curr Biol* **22**: R121–R122.
- Tuthill JC, Johnsen S, 2006. Polarization sensitivity in the red swamp crayfish *Procambarus clarkii* enhances the detection of moving transparent objects. *J Exp Biol* **209**:1612–1616.
- Vukusic P, Stavenga DG, 2009. Physical methods for investigating structural colours in biological systems. *J R Soc Interface* **6**:S133–S148.
- Waterman TH, 1981. Polarization sensitivity. In Autrum H, editor, *Handbook of Sensory Physiology, Vol. VIII/6B*. Berlin: Springer, 283–469.
- Wehner R, 1987. “Matched filters”: neural models of the external world. *J Comp Physiol A* **161**:511–531.
- Wehner R, 2001. Polarization vision: a uniform sensory capacity? *J Exp Biol* **204**:2589–2596.