Commentary

Do cephalopods communicate using polarized light reflections from their skin?

Lydia M. Mäthger[1,*], Nadav Shashar[2] and Roger T. Hanlon[1]

[1]Marine Resources Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA and [2]Department of Life Sciences, Eilat Campus, Ben Gurion University, Beer Sheva, 84105, Israel

*Author for correspondence (email: lmathger@mbl.edu)

Summary

Cephalopods (squid, cuttlefish and octopus) are probably best known for their ability to change color and pattern for camouflage and communication. This is made possible by their complex skin, which contains pigmented chromatophore organs and structural light reflectors (iridophores and leucophores). Iridophores create colorful and linearly polarized reflective patterns. Equally interesting, the photoreceptors of cephalopod eyes are arranged in a way to give these animals the ability to detect the linear polarization of incoming light. The capacity to detect polarized light may have a variety of functions, such as prey detection, navigation, orientation and contrast enhancement. Because the skin of cephalopods can produce polarized reflective patterns, it has been postulated that cephalopods could communicate intraspecifically through this visual system. The term 'hidden' or 'private' communication channel has been given to this concept because many cephalopod predators may not be able to see their polarized reflective patterns. We review the evidence for polarization vision as well as polarization signaling in some cephalopod species and provide examples that tend to support the notion – currently unproven – that some cephalopods communicate using polarized light signals.

Key words: chromatophore, iridophore, camouflage, signaling, polarization vision.

Introduction

Cephalopods (squid, cuttlefish, octopus) can produce a variety of body patterns for camouflage and signaling using their optically changeable skin, which contains neurally controlled pigmented chromatophores as well as structural light reflectors (Hanlon and Messenger, 1996). For example, squid generally have two distinct layers in their skin: (i) superficially located chromatophores, which are organs that consist of a red, yellow or brown pigment sac, attached to which are radial muscle fibers that are innervated directly by the brain, and (ii) underlying structural reflector cells called iridophores. Chromatophores can expand and retract over the iridophores, and thus influence both the light that reaches the iridophores and the light reflected from the iridophores before it exits the skin (Hanlon, 1982; Mäthger and Hanlon, 2007; Williams, 1909). Iridophores are composed of stacks of protein plates interspersed by spaces of cytoplasm, each differing in refractive index (Denton and Land, 1971; Kramer et al., 2007). The series of plates and spaces acts as a multilayer interference reflector (Land, 1972), which reflects specific wavelengths depending on the thickness of the plates and spaces. Furthermore, the wavelengths of light reflected by such a reflector move towards the shorter (blue/UV) end of the spectrum with increasing angles of incidence, and the reflected light becomes linearly polarized.

The body pattern repertoires of some cephalopod species are impressive (e.g. Fig. 1). Detailed body patterning ethograms (defined as a catalog of discrete body patterns typically shown) have been developed for approximately 20 cephalopod species [(e.g. Hanlon and Messenger, 1996) and citations therein]. Many cephalopod species (studied using SCUBA, as well as in the laboratory) seem to be able to camouflage themselves on almost any natural habitat they encounter, and they can change from one

pattern to another within a fraction of a second (Hanlon, 2007). The body pattern repertoire used in communication (intraspecific and interspecific) is equally impressive, such as the zebra display in cuttlefish and the passing cloud display of various cephalopods (Hall and Hanlon, 2002; Mather and Mather, 2004).

Cephalopods are visually oriented. The optic lobes are larger than other regions of the brain, indicating the importance of visual information to the behavior of these animals (Young, 1971). Indeed, *Octopus vulgaris* can quickly learn to visually discriminate between a series of objects (Boycott and Young, 1955; Messenger and Sanders, 1972). The cephalopod eye resembles a vertebrate eye in that it has a lens, pupil and retina containing photoreceptors. However, the retina does not contain rods and cones but is of the rhabdomeric kind typical of arthropods and other mollusks. The photoreceptors are long cells that contain only one visual pigment (Bellingham et al., 1998; Brown and Brown, 1958), making cephalopods almost certainly color blind, which has been confirmed in a number of behavioral studies (Marshall and Messenger, 1996; Mäthger et al., 2006; Messenger, 1977). There is one known exception: the firefly squid *Watasenia scintillans,* which has three visual pigments (Michinomae et al., 1994; Seidou et al., 1990).

Reflection of polarized light by the skin

Cephalopod skin produces polarized reflective patterns (Chiou et al., 2007; Mäthger and Denton, 2001; Mäthger and Hanlon, 2007; Shashar et al., 2001) (Fig. 2). The structures responsible for polarizing light are the structurally reflecting iridophore cells that contain stacks of protein plates interspersed by cytoplasm spaces. These types of reflector can produce a colorful appearance: the mechanism of reflectance is the same as that of colored soap
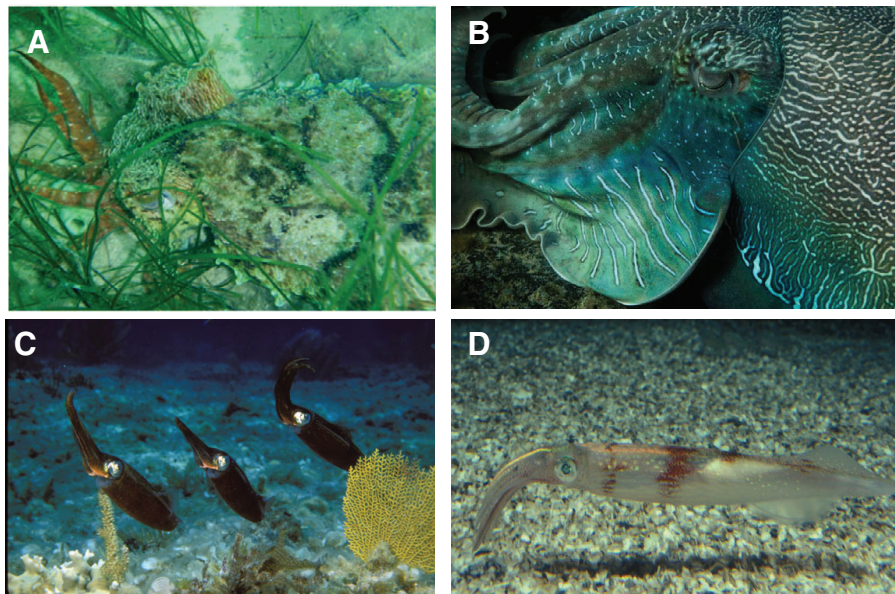
Fig. 1. Images show how pigmented chromatophores and structural light reflectors (iridophores and leucophores) act in concert to produce the final visual appearance. Iridophores produce colorful patterns that can be linearly polarized, whereas leucophores are responsible for producing white areas that can be used in high contrasting body patterns. (A,B) *Sepia apama*. Note camouflage in A but high contrasting pattern in B caused by white leucophores and blue-reflecting iridophores (Mäthger et al., 2009). (C) *Sepioteuthis lessoniana*. Dark patterning is caused by expansion of dark chromatophores. (D) *Loligo pealeii*, with conspicuous pink iridophores on the dorsal side of the mantle and arms.

bubbles. If the soap film (or multilayer plate) is very thin, shorter wavelengths are reflected, for example blue light; if it is thicker, longer wavelengths such as yellow and red are reflected (Boys, 1959; Huxley, 1968). Furthermore, at around Brewster's angle (the angle at which maximum linear polarization occurs), the reflected light is maximally and highly polarized. The angle of maximum polarization (μ) can easily be derived from Brewster's law ($\mu = \tan n_b/n_a$, where n_a and n_b are the refractive indices of a plate and space, respectively). For a squid multilayer reflector consisting of protein plates [n_a=1.59 (Kramer et al., 2007)] and cytoplasm spaces [n_b=1.33 (Denton and Land, 1971)], Brewster's angle is therefore 50.1 deg. Obviously, the direction in which polarized light is reflected depends critically on the orientation of the plates and

spaces of the multilayer reflector. For example, a number of loliginid squid [e.g. *Loligo vulgaris* and *L. pealeii*; see Mäthger et al. for more examples (Mäthger et al., 2009)] have a distinct stripe of iridophores along their dorso-lateral sides (called 'red' stripes). These iridophores have most of their reflective plates oriented parallel to the skin surface. At normal viewing angles, they reflect red light; at oblique angles, they reflect green light and the reflected light is polarized. A squid in a normal body position in the water column (NB the light intensity in the sea has an angular distribution) will reflect bright polarized light in a horizontal direction. In *L. pealeii* and *Sepia officinalis*, prominent polarization patterns can also be seen along the arms (Chiou et al., 2007; Shashar et al., 2001) (Fig. 2C). When the arms are held in a normal
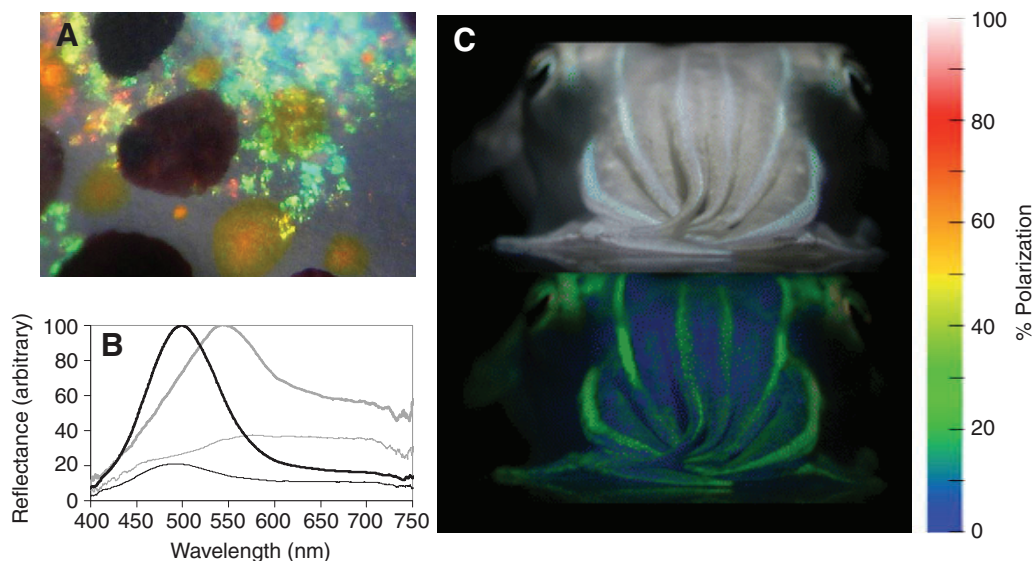

Fig. 2. (A) Close-up image of squid skin taken at an oblique viewing angle showing green iridescence as well as brown and yellow chromatophores. (B) Spectral reflectance measurements (in arbitrary units) at both planes of polarization for the green iridescence shown in A (black lines) and when a yellow chromatophore expands above the green iridescence (gray lines). The chromatophore shifts the spectrum of the reflected iridescence towards the longer wavebands but polarization is maintained (for details, see Mäthger and Hanlon, 2006). (C) The top image shows a frontal view of a cuttlefish *Sepia officinalis* with iridescent blue iridophore arm stripes (RGB image). The bottom image shows the degree of polarization coded in false color (see scale on right side for degree of polarization) [after Chiou et al. (Chiou et al., 2007)].

position in front of the head (i.e. no arm raising or arm curling underneath the head), the polarized reflective patterns are also best seen from a horizontal viewing position.

An interesting property that has received much interest from a variety of scientific fields (such as materials science and optical engineering) is that cephalopod iridophores, at least those of some squid, are physiologically active. Light reflectance from iridophores is changeable. This has been observed in living squid and can also be achieved by immersing a dissected skin preparation in a solution of acetylcholine, showing clearly that reflectance changes are under physiological control (Cooper and Hanlon, 1986; Cooper et al., 1990; Hanlon, 1982; Hanlon et al., 1990; Mäthger et al., 2004). This means that the degree of polarization can also be controlled and this has indeed been recorded for the arms of *L. pealeii.* Applications of acetylcholine to the arms of *L. pealeii* induced a change in the polarization reflection (Shashar et al., 2001). This finding is intriguing because it is at least conceivable that cephalopods could actively produce polarized light signals for communicative purposes (i.e. turn the signals on and off, as well as change their intensity). Iridophore reflectance changes generally take longer than chromatophores; however, we have observed fast changes in polarization patterns coming off iridophores (less than a second) (Shashar et al., 1996). Interestingly, although iridescence in cephalopods spans the entire visible spectrum (blue to near-IR), polarized reflections are strongest in the blue and green parts of the spectrum (Chiou et al., 2007; Mäthger and Denton, 2001; Mäthger and Hanlon, 2007; Shashar et al., 2001). That is, iridescence in other wavebands is generally not, or only weakly, polarized. Cephalopod vision is most sensitive in the blue–green parts of the spectrum [e.g. *S. officinalis*: 492 nm, *Loligo forbesi*: 494 nm, *Paroctopus defleini*: 480 nm (Bellingham et al., 1998; Brown and Brown, 1958; Marshall and Messenger, 1996; Mäthger et al., 2006)].

The production of polarized light signals by cephalopod skin has been thought of as a potential 'private', 'hidden' or 'secret' communication channel; that is, it is only visible to animals able to detect polarized light (Shashar et al., 1996).

Evidence for polarization vision in cephalopods

Visual pigment molecules are based on a single type of chromophore, whose highest absorption occurs when the molecule's dipole is aligned with the e-vector axis of the light, making visual pigment molecules naturally polarization sensitive (Goldsmith, 1975; Horváth and Varjú, 2004). However, in vertebrate rods and cones, the visual pigment is arranged in a semi-random array of axes, which makes the photoreceptor equally sensitive to any e-vector orientation when the light arrives parallel to the photoreceptor's long axis. This means that the typical vertebrate eye is mostly insensitive to polarized light.

There is a distinct difference between polarization sensitivity and polarization vision. Polarization vision can be defined as the ability to discriminate between two adjacent stimuli using e-vector orientation or percentage polarization alone, i.e. detecting a polarization contrast. Polarization sensitivity requires only sensitivity to polarization of a single object or area in the visual field (such as light reflected from water). Further, an animal can be sensitive only to a given e-vector orientation of polarization while insensitive to others.

Some vertebrates have been shown to respond to polarized light patterns (reviewed by Horváth and Varjú, 2004), such as several species of fish (Hawryshyn, 2000; Flamarique and Harosi, 2002), amphibians (Auburn and Taylor, 1979; Taylor and Adler, 1973) and birds (Kreithen and Keeton, 1974; Phillips and Waldvogel,

1988), although the question of polarization sensitivity or vision in birds is still a matter of controversy (Coemans and Vos, 1992; Hzn et al., 1995).

The rhabdomeric eyes of several invertebrate phyla are very different from vertebrate eyes: the visual pigments are contained in well-aligned microvilli that are arranged at well-defined and consistent angles (in cephalopods orthogonally) to each other, effectively functioning as an analyzer of linearly polarized light. Polarization sensitivity appears to be common in arthropods and cephalopods and was even recorded in echinoderms (e.g. Johnsen, 1994). Insects are known to use polarization patterns for navigation and orientation (Rossel, 1989; Rossel, 1993; Schwind, 1991; Shashar et al., 2005; Wehner, 1989; Wehner, 2001; Wehner and Labhart, 2006), as do several crustaceans (e.g. Goddard and Forward, 1991; Schwind, 1999). Kelber and colleagues suggest that some insects may evaluate objects using both spectral and polarization cues (Kelber et al., 2001). However, true polarization vision has so far only been shown for stomatopods that can also detect both linearly and circularly polarized light (Chiou et al., 2008; Marshall, 1988).

The microvilli of the polarization-sensitive photoreceptors in most cephalopods are highly organized: for example, in squid most neighboring photoreceptors vary less than 10 deg. from orthogonality, with a small percentage of receptors varying from their neighbors by 45 deg. (Shashar et al., 2002) (Fig. 3). However, no such orthogonal arrangement of the microvilli exists in the chambered nautilus, suggesting that it lacks polarization sensitivity (Muntz and Wentworth, 1987). The question of whether cephalopods have polarization sensitivity or polarization vision is still somewhat controversial. Polarization sensitivity in cephalopods has been demonstrated physiologically by recording from photoreceptors (Saidel et al., 1983; Saidel et al., 2005; Sugawara et al., 1971) (Fig. 4) as well as behaviorally. The first behavioral evidence came from discrimination studies on *Octopus vulgaris* (Moody and Parriss, 1960; Moody and Parriss, 1961). The octopus in Moody and Parriss' studies were shown to be able to discriminate between light sources that were covered with Polaroid filters aligned at different e-vector angles. Shashar and Cronin (Shashar and Cronin, 1996) modified the study method to ask whether octopus have polarization vision and these authors showed that octopus recognized a 90 deg. contrast pattern within a single target. The study by Shashar and Cronin (Shashar and Cronin, 1996) was criticized for not being sufficient proof of true polarization vision because the animals in their experiments were trained to recognize a pattern of pure polarization and they may have cued on the brightness contrast perceived by a single class of polarization-sensitive receptors (Nilsson and Warrant, 1999). A series of experiments (Shashar et al., 1998b; Shashar et al., 2000) demonstrated that squid and cuttlefish were able to detect prey items based on the existence of a polarization contrast or pattern, providing strong support for true polarization vision. There is definitive proof that stomatopods (mantis shrimp) have true polarization vision (Marshall, 1988; Marshall et al., 1999; Marshall et al., 1991; Yamaguchi et al., 1976). In Marshall and colleagues' experiments, stomatopods were trained to recognize an object that could only be identified by its e-vector angle. This experiment was carefully controlled to ensure that the animals only used polarization and not brightness as a visual cue. An experiment along these lines needs to be performed on cephalopods, although the combined evidence from the behavioral and morphological studies of Moody and Parriss as well as Shashar and colleagues suggests that cephalopods as a group do have polarization vision.
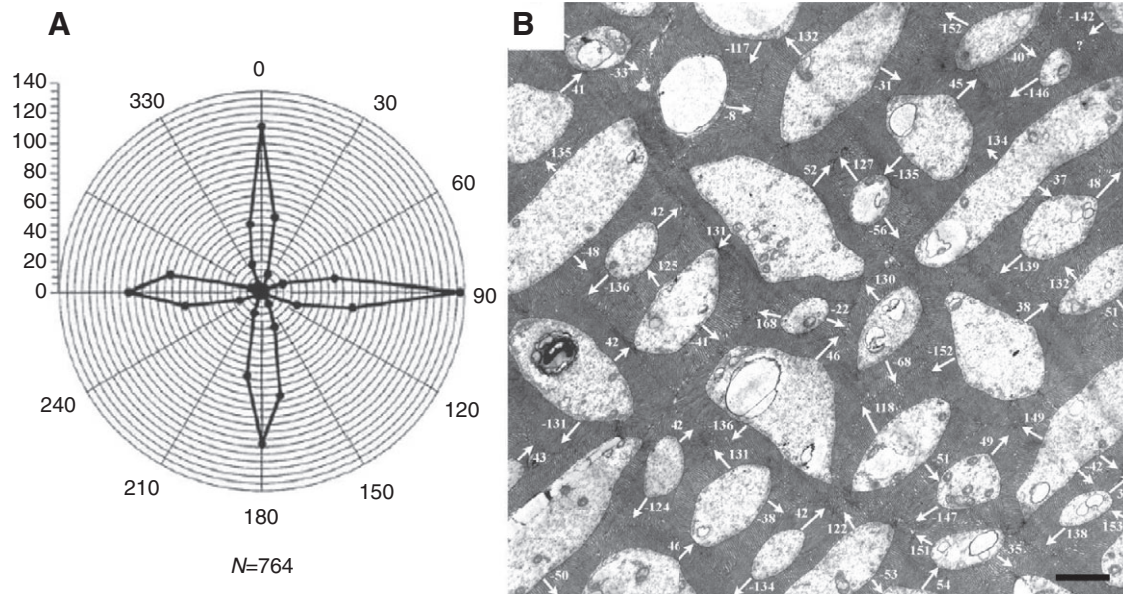
Fig. 3. (A) Measurements of the orientations of squid photoreceptors of one squid retina (a total of 764 photoreceptor orientations were measured). Diagram shows the number of photoreceptors (vertical axis; number increases from center towards periphery) that are oriented at specific angles (indicated in 30 deg. steps around periphery). This demonstrates the high degree of organization and orthogonality of the photoreceptors. (B) Light micrograph of a squid retina showing orthogonal arrangement of rhabdomeres (for details, see Shashar et al., 2002). Scale bar, 2 μm.

Functions of polarization vision in cephalopods

Given the evidence above, it seems likely that polarized light influences cephalopod behavior. Shashar and colleagues examined the preference of cuttlefish *S. officinalis* when presented with silvery fish whose polarization reflection was reduced *versus* silvery fish whose polarization reflection was not altered (Shashar et al., 2000). These authors showed that cuttlefish preferentially attacked fish with normal polarization reflection, suggesting that the detection of polarized light is useful during predation. Silvery fish take advantage of the angular distribution of daylight in the sea for camouflage. The reflectors on their scales are oriented towards the vertical, essentially acting like vertically suspended mirrors: they reflect the same amount of light as the light they are viewed against, making it extremely difficult to detect a silvery fish
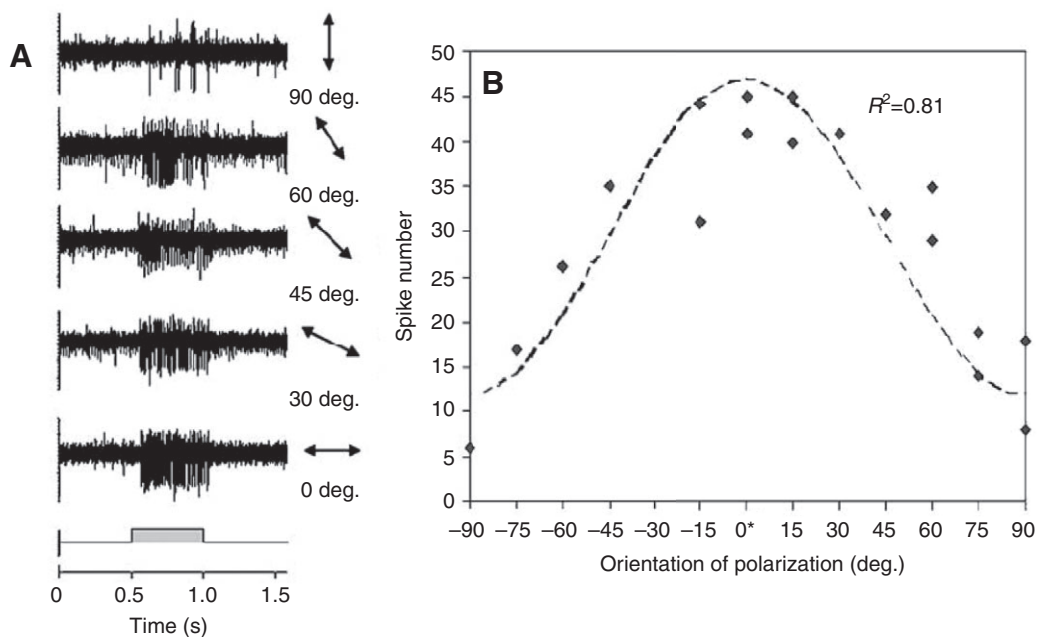

Fig. 4. Squid photoreceptor response to polarized light flashes. (A) Spike responses of nerve fibers to a 0.5 s light stimulus (bottom trace) of equal intensity, but polarized at different orientations (illustrated by double-headed arrows). Polarization orientations in this figure were set such that the horizontal orientation produced the maximal response and the vertical polarization provided the minimal response. (B) The nerve fiber illustrated in A correlates with a $\cos^2$ function of the orientation of polarization (dashed line). Angles were normalized, as in A, such that 0 deg. produces a maximal response and 90 deg. produces a minimal response [after Saidel et al. (Saidel et al., 2005)].

(Denton, 1970; Denton et al., 1972; Denton and Land, 1971). The only disadvantage is that silvery scales produce at least some polarization, which may be one of the few ways to detect such a fish.

Shashar and colleagues demonstrated that polarization vision may also be useful in detecting transparent prey (Shashar et al., 1998b). In all aquatic systems, many smaller organisms (or larval stages of large organisms) are transparent, which makes them difficult to detect (Sabbah and Shashar, 2006). However, some of these organisms contain tissues that change the polarization characteristics of light passing through them, and this 'polarization signature' may differ from the background polarization pattern against which the transparent animals are viewed, giving their camouflage away to predators with polarization sensitivity.

Several cephalopod species migrate to their feeding and spawning grounds (Hanlon and Messenger, 1996). Being able to detect polarized light may therefore also be useful for navigation. Just as the sky has a particular polarization pattern when the sun or moon is out (Gál et al., 2001), the underwater light field has distinct characteristics (Cronin and Shashar, 2001; Ivanoff, 1956; Ivanoff and Waterman, 1958; Jenkins and White, 1937; Jerlov, 1976; Sabbah et al., 2006; Sabbah et al., 2005; Tyler, 1960; Waterman, 1954; Waterman and Westell, 1956). However, owing to the complexity of the underwater polarized light field, this remains speculation. Very little is known about whether animals do indeed take advantage of underwater polarization patterns for long distance migration.

Do cephalopods communicate using polarized light signals?

The previous section gave some examples of how detecting polarized light can be useful. While there is experimental proof for some functions, such as breaking transparent camouflage and potentially detecting silvery fish, others remain speculative and require further study.

The fact that cephalopods can detect polarized light and can also produce changeable polarized light patterns in their skin begs the question whether cephalopods communicate using polarized light signals. The likely answer is that they do. Unfortunately, we have little evidence to support this statement. The difficulty in obtaining such data lies in the nature of the subject. Although the optical appearance (color, polarization patterns, etc.) of cephalopods is recordable using video imaging, spectrometers and polarimeters, it is much harder to define a specific appearance as a visual signal that is meant to convey a particular piece of information and harder yet to prove that the signal was received, especially if the behavioral signal carried the message to remain motionless and camouflaged.

It has long been known that cephalopods use their body patterning to communicate visually with conspecifics (Moynihan and Rodaniche, 1982; Wells, 1962). Perhaps the best-known example is the zebra display (created by scattering of light from leucophores) of male cuttlefish (e.g. *S. officinalis*). This display is an agonistic body pattern that is mostly shown by sexually mature males when sighting a rival male (Boal et al., 2004; Hanlon and Messenger, 1988; Tinbergen, 1939). The zebra display is an honest signal of fighting intent with contest winners having a stronger contrasting pattern than contest losers (Adamo and Hanlon, 1996; Boal et al., 2004).

Shashar and colleagues studied cuttlefish polarization patterns using an imaging polarimeter capable of analyzing partial polarization (Shashar et al., 1996). The polarimeter revealed prominent polarization patterns on the arms, around the eyes and on the head of the animals, in particular when the animal appeared alert. When animals were camouflaged on the substrate, or during aggression displays and prey attacks, the polarization patterns disappeared, and often re-appeared afterwards. Furthermore, cuttlefish changed their behavior in response to seeing themselves in a mirror when the polarization patterns of the reflected images were distorted. These authors concluded that cuttlefish may communicate using polarized patterns.

In a lengthy follow-up study by Boal and colleagues, no unequivocal evidence was found that cuttlefish modified the polarization of their body patterning in response to conspecifics, but tentative evidence was found to suggest that polarization information could be important to female receivers viewing both males and females (Boal et al., 2004). Their data showed that female receivers modified their behavior (e.g. activity levels, body pattern and body orientation) according to the polarization information they received.

In squid *Loligo plei* (DiMarco and Hanlon, 1997; Hanlon, 1982) it has been shown that iridescence changes during agonistic bouts. Furthermore, distinct polarization patterns were recorded in a range of behaviors in the squid *Loligo pealei* (Hanlon et al., 1999).

Conventionally speaking, polarization can be considered a 'by product' of iridescence, i.e. the animal cannot avoid polarized reflections when showing iridescent patterns; polarization is an integral part of the pattern. However, as squid are color blind, could the polarization within the pattern be the main communication signal, and the change in color be simply the 'by product'?

Another interesting finding is that the overlying pigmented chromatophores can be expanded to cover the polarized iridescence without extinguishing it. This reduces the conspicuousness of the iridescence while the polarization is maintained (Mäthger and Hanlon, 2006) (Fig. 2B). This could enable squid (and probably other cephalopods) to blend into their light field, while simultaneously sending polarized light signals to conspecifics.

Mäthger and Denton (Mäthger and Denton, 2001) speculated that the iridescent and polarization patterns of squid may function as visual signals in schools of squid (e.g. to communicate movements of individuals within a school). The iridophores are arranged in distinct stripes and spots and both the spectrum of the reflected iridescence (which will appear as changes in brightness because cephalopods are color blind) and the degree of polarization are affected by changes in viewing angle.

As we have pointed out, detection of polarized light may serve several functions such as enhancing contrast, breaking camouflage, recognizing objects, navigation, orientation and detecting signals. However, the behavioral and experimental evidence for these functions varies greatly.

Linearly polarized light signals could have advantages over color signals in certain light environments (Cronin et al., 2003). The underwater light field is partially polarized but only a few objects reflect strongly polarized light underwater, and while the spectral distribution of underwater light changes dramatically with depth, the polarization field is much more stable, making signal constancy less difficult to achieve (Cronin and Shashar, 2001; Cronin et al., 2003; Shashar et al., 2004). Cronin and colleagues (e.g. Cronin et al., 2003) have found that polarized light signals become more common with increased habitat depth. They suggest that polarization patterns may augment, or even replace, color patterns as the light field becomes more confined spectrally but in polarization terms becomes simpler with increasing depth. Polarized light signals could be easy to interpret because they can be strong and directional and would therefore stand out from the weakly polarized ambient light field. Cronin and colleagues

(Cronin et al., 2003) suggest that one can almost think of polarization vision as taking the place of color vision.

There are several reasons (even if there is no empirical evidence) for considering that polarization communication in cephalopods may act as a 'private' communication channel. Cephalopods have many predators: some are invertebrates (stomatopods, other cephalopods) but many are vertebrates (a wide variety of teleost fish, sharks, whales, dolphins, birds, etc.) (Boyle and Rodhouse, 2005). Polarization-analyzing visual systems appear to be more common in invertebrates than in vertebrates (at least, more invertebrate examples are known). Of the crustaceans, stomatopods are known to have advanced polarization vision and because they prey upon, and are themselves preyed upon by, cephalopods, they may use the polarization patterns of cephalopods for their detection. However, stomatopods are not the main predators of cephalopods. In vertebrates, polarization sensitivity has so far been found in only a limited number of species of teleost fish (Hawryshyn, 2000; Hawryshyn and McFarland, 1987; Parkyn and Hawryshyn, 1993). In fish, polarization sensitivity has often, although not always, been associated with UV vision (Hawryshyn, 2000). UV vision appears to be common amongst teleost fish (Losey et al., 1999) but polarization sensitivity has been suggested only for a few species, such as those of the families Pomacentridae and Salmonidae (Coughlin and Hawryshyn, 1995; Mussi et al., 2005). In other marine vertebrates, such as elasmobranchs, cetaceans and pinnipeds, no evidence for polarization sensitivity has been described.

When polarization sensitivity is confined to UV sensitivity, fish may be further limited in detecting polarization signals. (a) UV light does not penetrate far in water. This is true not only with depth but also in a horizontal plane, limiting the distribution of any UV signal both in depth and in distance. (b) The intensity of polarization signals in the UV range is most likely low. Although not specifically examined, there is strong supporting evidence for this claim (Chiou et al., 2007; Mäthger and Denton, 2001; Mäthger and Hanlon, 2006; Mäthger and Hanlon, 2007), showing that the per cent polarization of light reflected from cephalopod skin is very low at short wavelengths around 400 nm.

However, there have been suggestions that polarization sensitivity in fish may be independent of UV-sensitive cones, such as in anchovies (Fineran and Nicol, 1976; Fineran and Nicol, 1978). Double cones may also provide a method of polarization detection that would include wavebands in the visible part of the spectrum (Cameron and Pugh, 1991; Flamarique et al., 1998). Further work is needed to establish whether cephalopod predators are able to detect the polarized light signals produced by cephalopod skin and the extent to which the cephalopod system deserves to be called a 'private' communication channel.

Polarized light communication has been suggested for other animals besides cephalopods. Some light environments (in addition to the marine light field) may favor polarization signaling, such as dense forest canopies (Cronin et al., 2003; Shashar et al., 1998a). Indeed, one example of polarization communication has been found: the butterfly *Heliconius cydno* in Panama's rainforest. The wings of these butterflies are strongly iridescent and the reflected light is also highly polarized (up to 90%) (Sweeney et al., 2003). *Heliconius* males seem to recognize females using polarization as a cue. Females were approached less frequently by males when the polarization patterns were artificially depolarized.

Conclusions

The published evidence presented herein allows only speculation about whether polarized light signals are used for communicative purposes in cephalopods. Several aspects must be considered when studying this subject matter. Here we consider these and discuss some of the problems that researchers will encounter when addressing this question.

Recording polarized light signals requires precision. The iridophore cells in cephalopod skin that are responsible for reflectance of these signals are highly directional and often spectrally tuned. This means that the optical features of the light field (e.g. direction of highest intensity, spectral distribution, percentage polarization of light field) and the position of an observer (such as an imaging polarimeter) are crucial in detecting such signals. The small size of the structures producing polarized light signals makes such a study even more difficult to perform in a living animal that moves (and with movements come changes in the appearance of the signal).

Animal communication involves three steps: (1) the production of a signal by a sender, (2) sensing of this signal by a receiver and (3) a change in the receiver's behavior (Alcock, 1984; Hailman, 1977), and it must be beneficial to the sender or both the sender and receiver (Bradbury and Vehrencamp, 1998; McFarland, 1982). Testing this definition typically requires assigning a benefit to the change in the receiver's behavior. Note that this definition does not require conspicuous action by the sender (analogous examples are those of body posture or blushing in humans). When examining polarization signaling according to this definition, one finds that (a) cephalopods do produce polarization body patterns that change with their own behaviors (e.g. Boal et al., 2004; Hanlon, 1982; Shashar et al., 2001); (b) conspecifics have polarization sensitivity and can detect these polarization patterns; and (c) changes in polarization patterns – and more notably their elimination – cause a change in the behavior of the receiving conspecific (e.g. Boal et al., 2004). Whether such changes in behavior are of benefit to the sender or receiver of the signal remains to be examined. A problem that is commonly encountered in the field of sensory ethology is interpreting a sender's signal as such, especially when the receiver's behavior is not conspicuous or recordable.

Although the evidence is circumstantial, in sum it suggests that polarized light signals may be used for communication in cephalopods. In comparison, there is no doubt that many conspicuous signals of some animals, for example the colors of coral reef fish and some birds (Marshall, 2000; Shawkey et al., 2009) who have color vision, are used in visual communication. Animals communicate using a range of channels (chemical, visual, tactile, etc.), and polarized light communication may just be one of these specialized channels.

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