

## POLARIZATION VISION IN CUTTLEFISH – A CONCEALED COMMUNICATION CHANNEL?

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### Summary

Polarization sensitivity is well documented in marine animals, but its function is not yet well understood. Of the cephalopods, squid and octopus are known to be sensitive to the orientation of polarization of incoming light. This sensitivity arises from the orthogonal orientation of neighboring photoreceptors. Electron microscopical examination of the retina of the cuttlefish *Sepia officinalis* L. revealed the same orthogonal structure, suggesting that cuttlefish are also sensitive to linearly polarized light. Viewing cuttlefish through an imaging polarized light analyzer revealed a prominent polarization pattern on the arms, around the eyes and on the forehead of the animals.

The polarization pattern disappeared when individuals lay camouflaged on the bottom and also during extreme aggression display, attacks on prey, copulation and egg-laying behavior in females. In behavioral experiments, the responses of cuttlefish to their images reflected from a mirror changed when the polarization patterns of the reflected images were distorted. These results suggest that cuttlefish use polarization vision and display for intraspecific recognition and communication.

Key words: polarized light, cephalopod, cuttlefish, *Sepia officinalis*, photoreceptor, vision, communication.

### Introduction

Like numerous other aquatic and terrestrial invertebrates, cephalopods, both octopods (Moody and Parriss, 1960, 1961; Rowell and Wells, 1961; Moody, 1962; Tasaki and Karita, 1966a) and decapods (Jander *et al.* 1963; Saidel *et al.* 1983), are sensitive to the orientation of the *e*-vector of linearly polarized light. This sensitivity arises from the structure of the photoreceptors in their retina, where neighboring rhabdomeres are positioned at orthogonal orientations to each other (Moody and Parriss, 1960, 1961; Snyder, 1973; Goldsmith, 1977, 1991; Waterman, 1981). This orthogonal structure of the photoreceptors in the cephalopod retina creates a polarization sensor with maximal sensitivity to two orientations of polarization (Moody and Parriss, 1961). However, it is possible that irregularities in the retina (Tasaki and Karita, 1966b) or movements of the eye enable cephalopods to sense any polarization orientation (Shashar and Cronin, 1996).

The function of polarization sensitivity in navigation, body orientation and the location of large bodies of water is well established (Wehner, 1976; Waterman, 1981; Goddard and Forward, 1991; Schwind, 1991, 1995). However, the function of polarization sensitivity in marine animals that do not migrate or forage over long distances is not yet fully understood. Messenger (1991) suggested that polarization sensitivity can be used for breaking camouflage of fish. Shashar and Cronin (1996) demonstrated that octopus can recognize polarization

contrast within small objects, suggesting that polarization vision is used in contrast enhancement and target recognition.

To better understand this type of visual sensitivity and its functions in marine animals, we examined the polarized appearance, the retina and skin structure and the behavior of the cuttlefish *Sepia officinalis* L.

### Materials and methods

Experiments were conducted at the National Zoological Park (NZIP) in Washington, DC, USA, and at the National Resource Center for Cephalopods (NRCC) at Galveston, TX, USA. At NZIP, 8–12 animals were kept in artificial sea water within a cylindrical tank (225 cm in diameter and 75 cm in depth) with a gravel-covered bottom and opaque white sides, under artificial illumination with a light cycle of 10 h:14 h light:darkness. At NRCC, animals were kept in two rectangular tanks (183 cm×366 cm×40 cm deep) with opaque light-blue bottom and sides. Each tank contained five or six animals. In both tanks, several of the animals occasionally engaged in mating or laying eggs.

### Polarization imaging

Using an imaging polarimeter capable of analyzing partial polarization (also termed degree or percentage of polarization) and orientation of linear polarization throughout an image on

a single pixel basis, we examined the appearance of cuttlefish. The polarimeter is described fully elsewhere (Cronin *et al.* 1994; Shashar *et al.* 1995). In short, two twisted nematic liquid crystals are placed in series with a linear polarizing filter fixed at the horizontal ( $0^\circ$ ) orientation. By controlling the voltage applied to these crystals, the plane of polarization of the light is rotated by  $0^\circ$ ,  $45^\circ$  or  $90^\circ$ . The polarizing filter only transmits light that is polarized parallel to its own orientation. The transmitted images were recorded with a Hi-8 handycam video recorder. Images (single fields) were digitized in the laboratory, *via* a frame grabber, onto a computer as  $320$  (horizontal)  $\times$   $240$  (vertical) pixel arrays, where they were analyzed on a single pixel basis. From consecutive images collected at the three orientations, we calculated the partial polarization and orientation of polarization.

Animals were viewed through this video-based polarimeter (which was placed in an underwater housing) while engaged in activities such as cruising in the tank, feeding, laying eggs, resting on the bottom, interacting with other individuals of the same or opposite gender and closely examining the instrument.

For display, polarization information was color-coded using the cylindrical HSL (hue, saturation, lightness) map (Hall, 1988; Wolff and Mancini, 1992). Orientation of polarization, which varies from  $0^\circ$  to  $180^\circ$ , was coded as hue by multiplying the orientation angle by two. In this coding, red represents horizontal polarization. Partial polarization was coded as saturation, where full saturation represents total polarization and depolarized light is represented by achromatic gray shades. Lightness remains unaffected and is proportional to the intensity of the light reflected from the object. This display method enables quick assessment of polarization information throughout an image that is intuitively understandable. However, we must emphasize that

we do not imply that any animal actually perceives polarization information in this fashion.

#### *Electron microscopical examination*

To understand the structures involved in polarization sensitivity and display, retinal and skin tissues of cuttlefish were examined by transmission electron microscopy. Tissue was fixed, shortly after death, for 24 h in 2.5% glutaraldehyde in Sorenson's phosphate buffer made using artificial sea water at pH 7.6. Tissue preparation for electron microscopy followed a protocol, modified after Bozzola and Russell (1991), where tissue was washed in Sorenson's phosphate buffer (pH 7.6) made using artificial sea water. Thin sections (60 nm) were cut using a Sorvall MT2-B ultramicrotome with a MicroStar diamond knife, stained in lead citrate and uranyl acetate, and examined with a JEOL 100CX transmission electron microscope.

#### *Behavioral experiments*

Cuttlefish respond to their mirror images (Hanlon and Messenger, 1988). We utilized this behavior to examine the role of polarization vision in intraspecific interactions. This was performed by presenting cuttlefish with their full reflected image and with a reflection in which the polarization component was distorted, and recording the animals' reactions.

Seven *S. officinalis* cuttlefish (three or four animals in each rectangular tank, performed at NRCC) viewed their own reflection in a mirror ( $21.5\text{ cm} \times 13\text{ cm}$ ), one animal at a time. The mirror accurately reflected the polarization pattern of the cuttlefish. Each animal viewed its reflection in the mirror through one of two transparent filters made of Pyrex glass. One filter was of high-quality Pyrex, which had no detectable effect

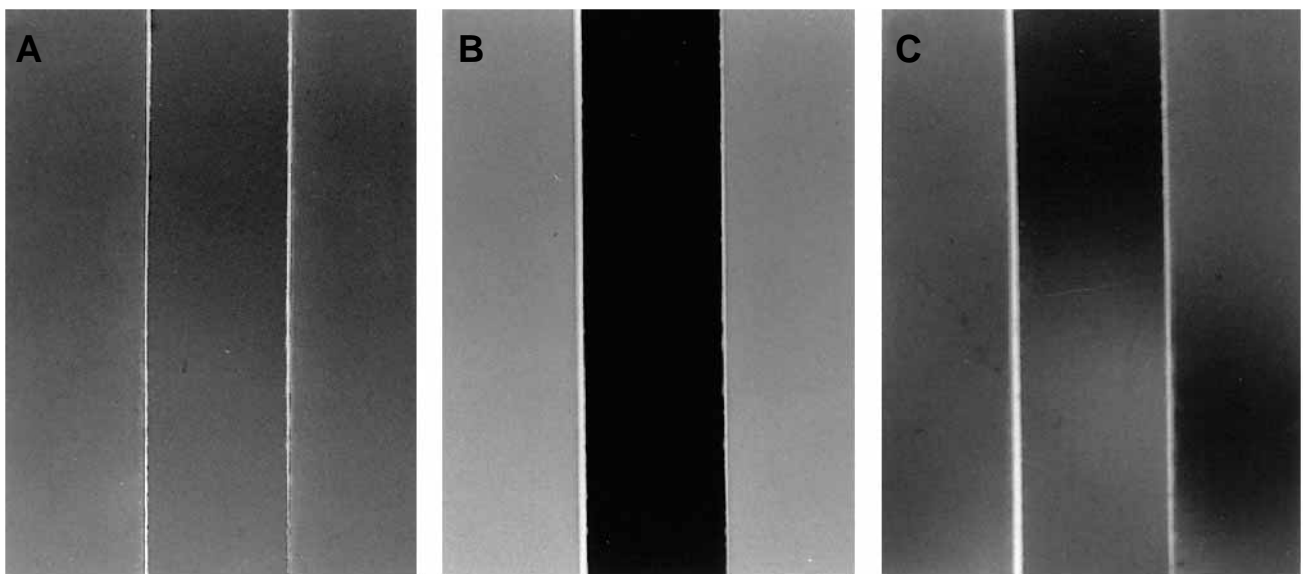


Fig. 1. Three linear polarizing filters (at orientations of  $0^\circ$ ,  $90^\circ$  and  $0^\circ$ ) creating a polarization pattern viewed directly (A), or through another linear polarizing filter (set at the horizontal orientation) plus one of two Pyrex glass filters (B,C). The polarization pattern cannot be seen by the unaided human eye (A), but appears when viewed through another polarizer (B). The glass filter in B does not affect polarization. The glass filter used in C was heated and cooled several times to induce stress in it. This stress alters the polarization characteristics of the light passing through the glass and therefore the polarization pattern is distorted.

on polarization. The other had been heated and cooled several times to create stress within it. This stress distorted any polarization pattern (Fig. 1) but otherwise did not affect the transparency of the filter, nor did it cause chromatic or pattern changes in the animals, and it was indistinguishable to naive observers from the untreated filter. Each animal viewed its reflection through each filter 10 times.

The mirror with the glass filter attached directly in front of it was presented to a cuttlefish, when it was at least 75 cm away from any other animal, at a distance of approximately 50 cm from and at the same height as the animal. The order in which the filters were presented and the animal to which they were presented were randomized. Each presentation lasted 30 s, unless the animal approached the glass filter to within touching distance, in which case the mirror and filter were taken out of the tank. These cases were also recorded.

The reactions of the cuttlefish were noted by one of three

naive observers. Observers were unaware of the purpose of the experiment, of the differences between the filters, and of previous responses by the animals, and were instructed to describe only the animal's action and not its possible meaning/motivation. As animals could carry out several types of behavioral acts, the number of behavioral responses exceeds the number of presentations. For example, in a single presentation, a cuttlefish could react by changing color, approaching the mirror and extending an arm. Results were analyzed at each level, testing for bimodal distribution with equal frequency, and the totals were analyzed using a multi-level  $\chi^2$  goodness-to-fit test, for two cells with equal expected frequency (Gibbons, 1976).

### Results

Cuttlefish displayed a striking polarization pattern (Fig. 2):

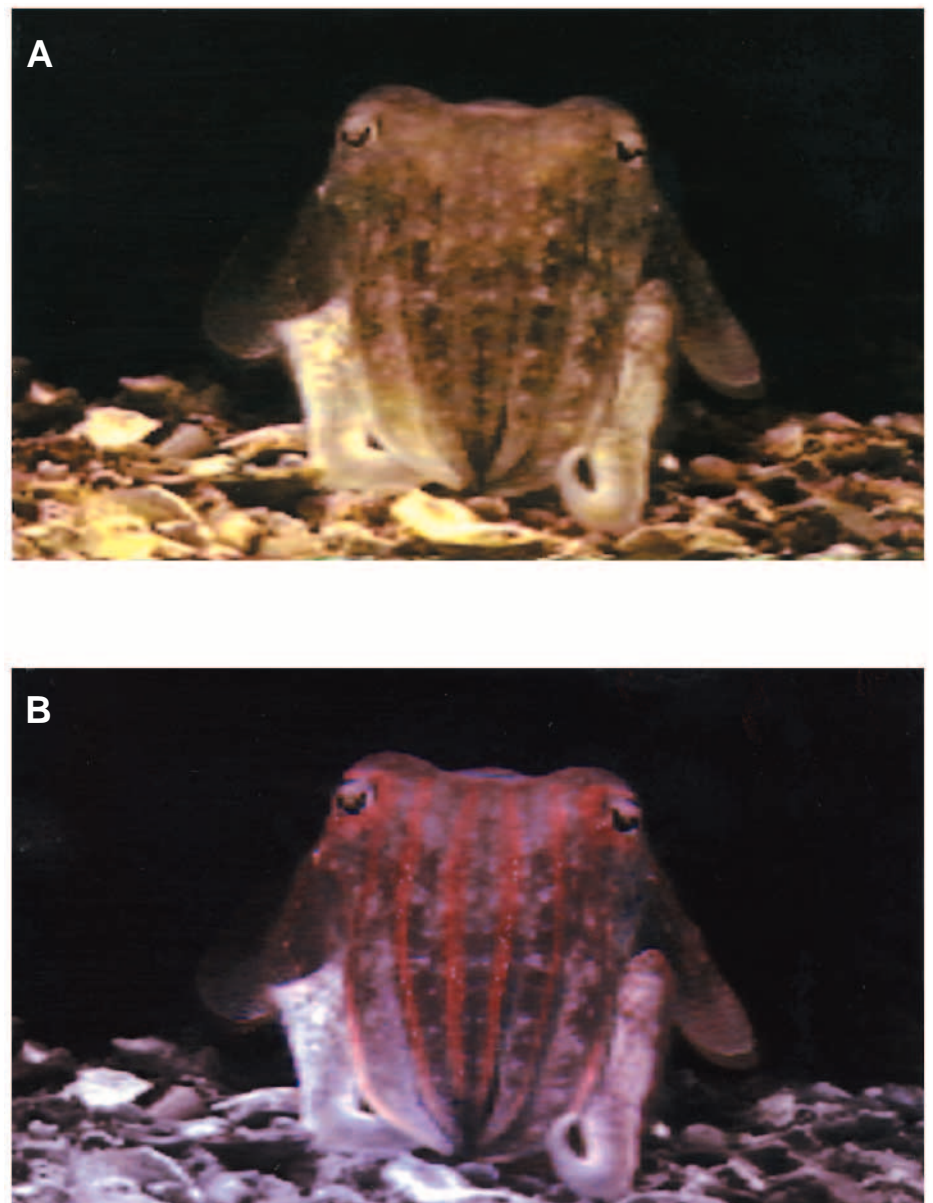


Fig. 2. A full color image (A) and false color polarization image (B) of a cuttlefish, *Sepia officinalis*. In the false color image, the polarization information is color-coded using the HSL (hue, saturation, lightness) map. Orientation of polarization is coded to hue (horizontal polarization is coded to red) and percentage of polarization is coded as saturation, where full saturation represents total polarization and gray shades indicate depolarized light. Lightness is proportional to the intensity of the light reflected from the object. A pattern of stripes reflecting horizontally polarized light is seen on the arms and the forehead of the animal.

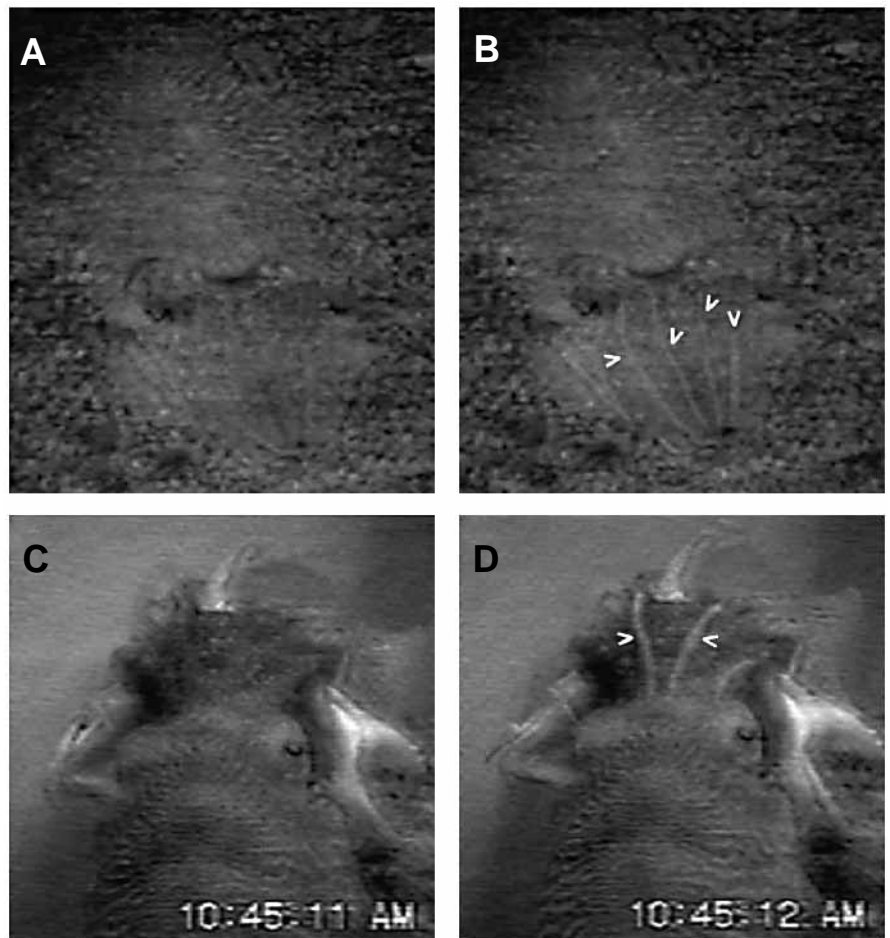


Fig. 3. *Sepia officinalis* cuttlefish, photographed through a filter transmitting horizontally polarized light, while lying on the substratum (A,B) and during mating (C,D, a male holding a female while copulating). Animals could display the polarization pattern (arrowheads in B,D), which appears as bright stripes in the middle of the arms, or conceal it (A,C). The polarization pattern could be fully expressed within 1 s (C,D).

a strip down the middle of each of the six central arms, the top of the front of the head and the region around the eyes all reflected polarized light. In all cases, this polarization had a horizontal orientation. The polarizing regions correspond to the 'pink iridophore arm stripes', the 'eye ring' and the 'posterior head bar' described by Hanlon and Messenger (1988). The polarization pattern was visible from the horizontal plane up to a viewing angle of  $45^\circ$  above the animals but, owing to the position of the arms, could not be seen from below. The strongest and clearest signal could be seen at viewing angles of less than  $20^\circ$ . Here, the polarization pattern of the arms was visible for up to  $100^\circ$  to each side, and that of the eye could be observed even from behind the animal.

The polarization pattern was most obvious while animals were cruising or hovering in the tank and when they lay alert on the bottom. When animals were camouflaged on the bottom, the polarization was not detectable (Fig. 3A), but it appeared as soon as the animal became alert (Fig. 3B), even when no noticeable movement of the body was performed (alertness was indicated by the tracking of the polarimeter by the cuttlefish's eye). During mating behavior, the male's polarization pattern was diminished during copulation (Fig. 3C), but reappeared just before the two animals separated (Fig. 3D). Other occasions when the polarization pattern was not visible occurred when a female was laying eggs, prior to

and during attacks on prey, and during extreme aggression between two males (see Hanlon and Messenger, 1988, for further description of cuttlefish behavior).

Electron microscopical examination of retinas of *S. officinalis* revealed the typical (Moody and Parriss, 1960, 1961) cephalopod orthogonal structure (Fig. 4A) in which the microvilli of each photoreceptor cell are aligned parallel to each other and orthogonally to the microvilli of neighboring receptor cells (Fig. 4B). This structure suggests that cuttlefish, like octopus and squid, possess polarization sensitivity.

Electron microscopical examination of the central strip of skin of the arms of cuttlefish showed that, like other cephalopod decapods (Kawaguti and Ohgishi, 1962; Hanlon, 1982; Cooper and Hanlon, 1986), the iridophores present throughout the skin of *S. officinalis* contain reflecting platelets positioned parallel to each other (Fig. 5). Such an arrangement is expected to induce partial linear polarization of the reflected light. Cephalopods are known to be able to alter their ultrastructure of their iridophores (Kawaguti and Ohgishi, 1962; Cooper *et al.* 1990) and may therefore control the reflectance of polarized light in this way.

In behavioral experiments addressing the role of the polarization pattern in intraspecific recognition, cuttlefish reactions to their reflected image altered significantly ( $P < 0.001$ ; multi level  $\chi^2$  goodness-to-fit test) when the linear

polarization component of the normal reflected image was distorted (Table 1). While animals tended to retreat from their normal reflected image, they more often stayed in place without a noticeable response when the polarization component of the reflected image was distorted.

### Discussion

In the complex underwater polarized light environment (Waterman, 1954, 1981; Waterman and Westell, 1956; Ivanoff and Waterman, 1958; Horvath and Varju, 1995), polarization sensitivity may be used not only for navigation (Goddard and Forward, 1991) but also for target recognition (Moody and

Parriss, 1960, 1961; Rowell and Wells, 1961; Moody, 1962; Shashar and Cronin, 1996), breaking camouflage (Messenger, 1991), increasing detection range (Lythgoe and Hemming, 1967), enhancing contrast (Budelmann, 1994) and detecting transparent objects (E. Lowe, personal communication). Can polarization vision be used by some animals for communication?

As we show here, cuttlefish can display a polarization pattern which changes with their behavior. Additionally, the animals' reactions to their reflected image change depending on the existence or absence of this polarization pattern. Cuttlefish display a variety of body colors and patterns (Holmes, 1940; Hanlon and Messenger, 1988). These patterns are used as visual signals for intraspecific communication and

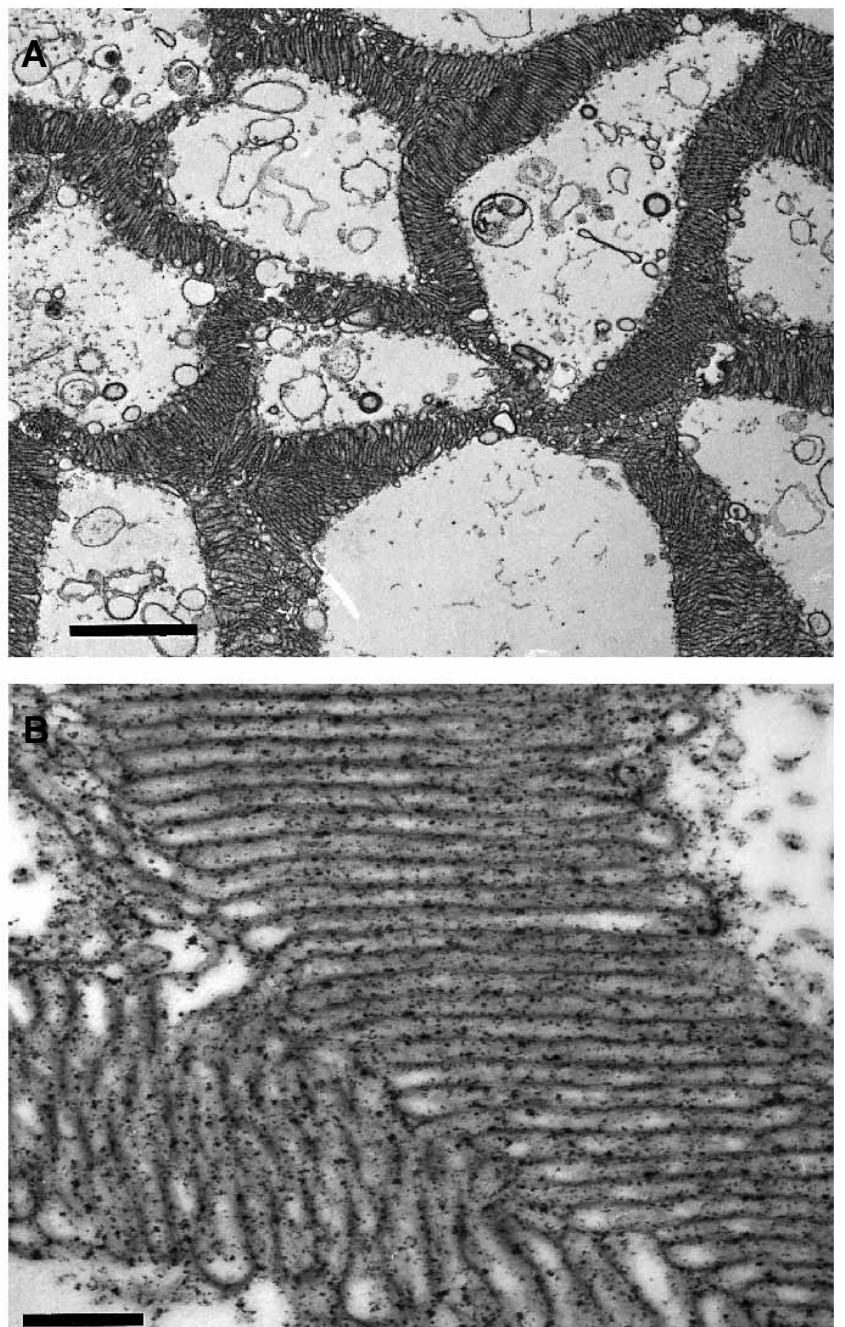


Fig. 4. Transmission electron micrographs of cross sections of photoreceptor cells from retinas of *Sepia officinalis*. (A) A low-magnification micrograph (scale bar, 5  $\mu\text{m}$ ) showing the overall arrangement of photoreceptors in the retina. (B) A high-magnification micrograph (scale bar, 0.2  $\mu\text{m}$ ) of the intersection of microvilli from neighboring photoreceptors. Neighboring photoreceptors are arranged orthogonally to each other, in a pattern similar to that described for octopus and squid. As the rhabdomeres of each single photoreceptor are aligned parallel to each other, the photoreceptor will possess preferential sensitivity to light polarized parallel to the microvilli. Therefore, the orthogonally arranged photoreceptors can serve as the basis for a polarization analyzing system.

for camouflage against various types of backgrounds, such as sand, rubble and corals (Holmes, 1940; Corner and Moore, 1980; Hanlon and Messenger, 1988). Our results suggest that polarization sensitivity and polarization display also play a role in cuttlefish recognition and communication.

Sharks, cetaceans and seals are known predators of adult cuttlefish (Clarke and Stevens, 1974; Lane, 1974; Clarke and Pascoe, 1985). It is likely that none of these vertebrates possesses polarization sensitivity. Cuttlefish base their defense on predator avoidance or camouflage (Holmes, 1940; Hanlon and Messenger, 1988). Polarization-based communication may provide cuttlefish with a channel concealed from some of their predators.

In conclusion, the work reported here demonstrates the following. (1) Cuttlefish can display a prominent pattern of reflected polarized light, which alters predictably with behavioral context. (2) The polarization pattern appears on regions of the skin containing iridophores, organized dielectric structures capable of inducing linear polarization by reflection. (3) The retinas of cuttlefish have an arrangement of photoreceptive microvilli consistent with polarization vision in other cephalopods. (4) The responses of cuttlefish to their own reflected image differ depending on whether the polarization structure of the image is altered. Taken as a whole, our observations are fully consistent with the hypothesis that cuttlefish use controllable polarization patterns for intraspecific

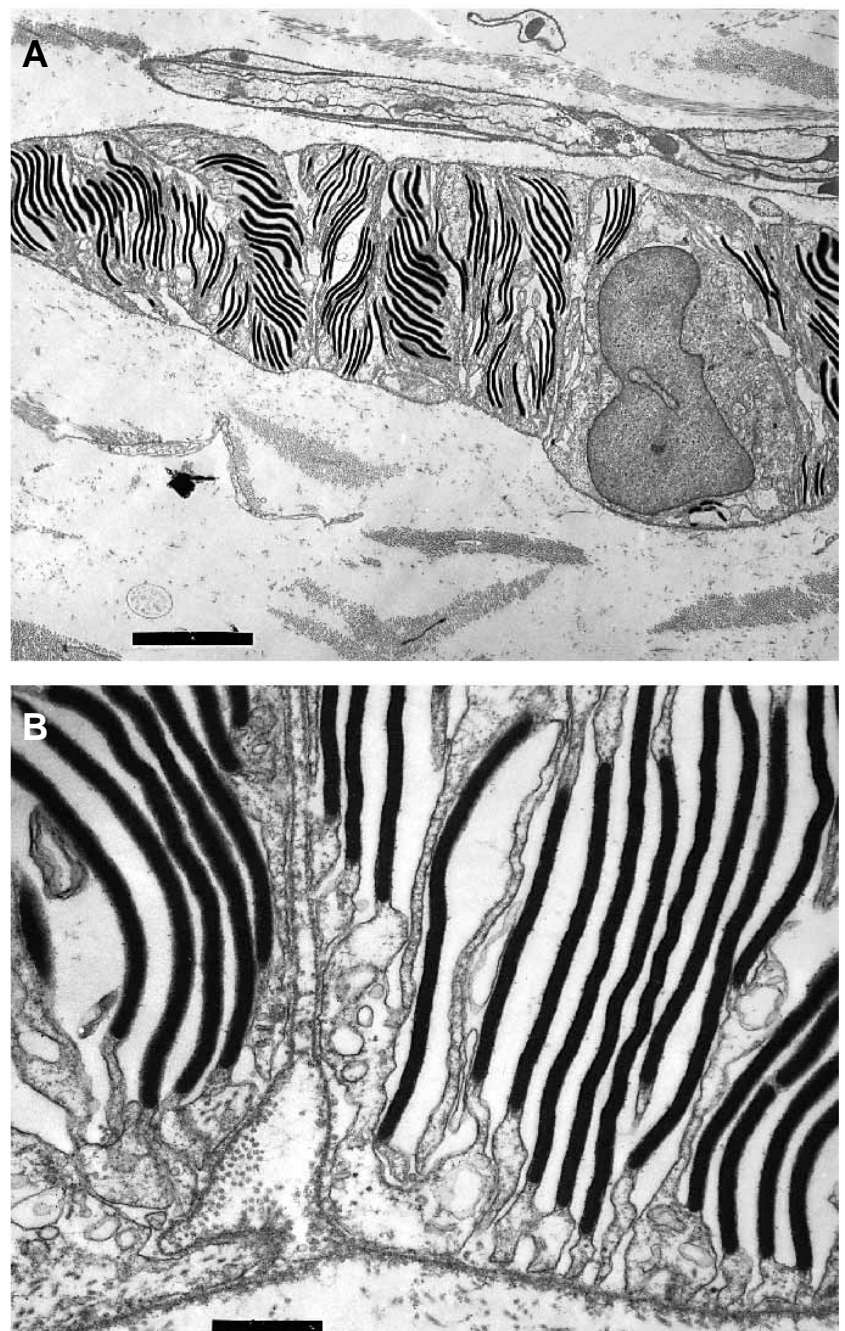


Fig. 5. Transmission electron micrographs of a cross section of an iridophore from the skin of the center of an arm of a cuttlefish *Sepia officinalis*. (A) Low-magnification (scale bar, 5  $\mu$ m) micrograph showing the iridophore containing darkly stained platelets and neighboring collagen fibers. (B) High-magnification (scale bar, 0.5  $\mu$ m) micrograph showing the parallel organization of neighboring reflecting platelets. Such a structure is expected to induce linear polarization of the light reflected from the platelets.

Table 1. Responses of *Sepia officinalis* to their reflected images viewed through a transparent filter or a filter that distorted polarization

Animal number	Filter type	Behavior						
		Moved towards mirror	Moved away from mirror	Darkened skin color	Extended arm	Flashed color display	No response	Other
F1	T	5	6	6	1	0	0	0
	D	4	1	4	0	0	3	0
F2	T	5	7	5	2	0	0	1
	D	4	1	5	1	0	2	0
F3	T	2	8	8	1	0	0	0
	D	2	1	3	0	0	6	0
F11	T	0	7	3	1	0	2	0
	D	0	2	3	0	0	5	1
F12	T	1	10	4	2	1	0	0
	D	2	2	5	1	0	4	0
M11	T	1	8	4	1	1	1	0
	D	2	2	5	1	0	4	1
M12	T	1	9	3	2	2	0	0
	D	0	0	4	3	0	5	1
Total	T	15	55	33	10	4	3	1
	D	14	9	29	6	0	29	3

T, transparent filter; D, filter that distorted polarization; F, female; M, male.

Responses that varied significantly between the two filters are indicated with asterisks; \* $0.05 < P < 0.1$  (based on bimodal distribution); \*\* $0.01 < P < 0.05$  (based on bimodal distribution); \*\*\* $P < 0.001$  (based on multi-level  $\chi^2$  goodness-to-fit).

communication. The ultimate proof of this hypothesis awaits a thorough investigation of the sensory, motor and behavioral components of this novel signalling system.

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### References

- BOZZOLA, J. J. AND RUSSELL, L. D. (1991). *Electron Microscopy*. Boston: Jones and Bartlett Publ. 542pp.
- BUDELMANN, B. U. (1994). Cephalopod sense organs, nerves and the brain: adaptations for high performance and life style. *Mar. fresh. Behav. Physiol.* **25**, 13–33.
- CLARKE, M. R. AND PASCOE, P. L. (1985). The stomach content of a Risso's dolphin (*Grampus griseus*) stranded at Thurlestone, South Devon. *J. mar. biol. Ass. U.K.* **65**, 663–665.
- CLARKE, M. R. AND STEVENS, J. D. (1974). Cephalopods, blue sharks and migration. *J. mar. biol. Ass. U.K.* **54**, 949–957.
- COOPER, K. M. AND HANLON, R. T. (1986). Correlation of iridescence with changes in iridophore platelet ultrastructure in the squid *Lolloguncula brevis*. *J. exp. Biol.* **121**, 451–455.
- COOPER, K. M., HANLON, R. T. AND BUDELMANN, B. U. (1990). Physiological color change in squid iridophores. II. Ultrastructural mechanisms in *Lolloguncula brevis*. *Cell Tissue Res.* **259**, 15–24.
- CORNER, B. D. AND MOORE, H. T. (1980). Field observations on the reproductive behavior of *Sepia latimanus*. *Micronesica* **16**, 235–260.
- CRONIN, T. W., SHASHAR, N. AND WOLFF, L. (1994). Portable imaging polarimeters. *Proceedings of the Twelfth International Conference on Pattern Recognition*, pp. 606–609.
- GIBBONS, J. D. (1976). *Nonparametric Methods for Quantitative Analysis*. New York: Holt, Rinehart and Winston. 481pp.
- GODDARD, S. M. AND FORWARD, R. B. (1991). The role of underwater polarized light pattern in sun compass navigation of the grass shrimp, *Palaemonetes vulgaris*. *J. comp. Physiol. A* **169**, 479–491.

- GOLDSMITH, T. H. (1977). Membrane adaptations of visual photoreceptors for the analysis of plane polarized light. In *Research in Photobiology* (ed. A. Castellani), pp. 651–658. New York: Plenum Publ.
- GOLDSMITH, T. H. (1991). Photoreception and vision. In *Neural and Integrative Animal Physiology* (ed. C. L. Prosser), pp. 171–245. New York: Wiley-Liss.
- HALL, R. (1988). *Illumination and Color in Computer Generated Imagery*. New York: Springer-Verlag. 282pp.
- HANLON, R. T. (1982). The functional organization of chromatophores and iridescent cells in the body patterning of *Loligo plei* (Cephalopoda: myopsida). *Malacologia* **23**, 89–119.
- HANLON, R. T. AND MESSENGER, J. B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behavior. *Phil. Trans. zool. Soc. Lond. A* **110**, 17–35.
- HOLMES, W. (1940). The colour changes and color patterns of *Sepia officinalis* L. *Proc. zool. Soc. Lond. A* **110**, 17–35.
- HORVATH, G. AND VARJU, D. (1995). Underwater refraction–polarization patterns of skylight perceived by aquatic animals through Snell's window of a flat water surface. *Vision Res.* **35**, 1651–1666.
- IVANOFF, A. AND WATERMAN, T. H. (1958). Factors, mainly depth and wavelength, affecting the degree of underwater light polarization. *J. mar. Res.* **16**, 283–307.
- JANDER, R., DAUMER, K. AND WATERMAN, T. H. (1963). Polarized light orientation in two Hawaiian cephalopods. *Z. vergl. Physiol.* **46**, 383–394.
- KAWAGUTI, S. AND OHGISHI, S. (1962). Electron microscopic study on iridophores of a cuttlefish, *Sepia esculent*. *Biol. J. Okayama Univ.* **8**, 115–129.
- LANE, F. W. (1974). *Kingdom of the Octopus*. New York: Sheridan House. 300pp.
- LYTHGOE, J. N. AND HEMMING, C. C. (1967). Polarized light and underwater vision. *Nature* **213**, 893–894.
- MESSENGER, J. B. (1991). Photoreception and vision in molluscs. In *Evolution of the Eye and Visual System* (ed. J. R. Cronly-Dillon and R. L. Gregory), pp. 364–397. Boca Raton, FL: CRC Press.
- MOODY, M. F. (1962). Evidence for the intraocular discrimination of vertically and horizontally polarized light by *Octopus*. *J. exp. Biol.* **39**, 21–30.
- MOODY, M. F. AND PARRISS, J. R. (1960). Discrimination of polarized light by *Octopus*. *Nature* **186**, 839–840.
- MOODY, M. F. AND PARRISS, J. R. (1961). Discrimination of polarized light by *Octopus*: a behavioral and morphological study. *Z. vergl. Physiol.* **44**, 268–291.
- ROWELL, C. H. F. AND WELLS, M. J. (1961). Retinal orientation and the discrimination of polarized light by octopuses. *J. exp. Biol.* **38**, 827–831.
- SAIDEL, W. M., LETTVIN, J. Y. AND MCNICHOL, E. F. (1983). Processing of polarized light by squid photoreceptors. *Nature* **304**, 534–536.
- SCHWIND, R. (1991). Polarization vision in water insects and insects living on moist substrate. *J. comp. Physiol. A* **169**, 531–540.
- SCHWIND, R. (1995). Spectral regions in which aquatic insects see reflected polarized light. *J. comp. Physiol. A* **177**, 439–448.
- SHASHAR, N. AND CRONIN, T. W. (1996). Polarization contrast vision in octopus. *J. exp. Biol.* **199**, 999–1004.
- SHASHAR, N., CRONIN, T. W., JOHNSON, G. AND WOLFF, L. (1995). Portable imaging polarized light analyzer. *Proceedings of the Ninth Meeting on Optical Engineering in Israel. SPIE* **2426**, 28–35.
- SNYDER, A. W. (1973). Polarization sensitivity of individual retinula cells. *J. comp. Physiol. A* **83**, 331–360.
- TASAKI, K. AND KARITA, K. (1966a). Intraretinal discrimination of horizontal and vertical planes of polarized light by octopus. *Nature* **209**, 934–935.
- TASAKI, K. AND KARITA, K. (1966b). Discrimination of horizontal and vertical planes of polarized light by cephalopod retina. *Jap. J. Physiol.* **16**, 205–216.
- WATERMAN, T. H. (1954). Polarization patterns in submarine illumination. *Science* **120**, 927–932.
- WATERMAN, T. H. (1981). Polarization sensitivity. In *Comparative Physiology and Evolution of Vision in Invertebrates* (ed. H. Autrum), pp. 281–463. Berlin: Springer-Verlag.
- WATERMAN, T. H. AND WESTELL, W. E. (1956). Quantitative effects of the sun's position on submarine light polarization. *J. mar. Res.* **15**, 149–169.
- WEHNER, R. (1976). Polarized-light navigation by insects. *Scient. Am.* **238**, 106–115.
- WOLFF, L. B. AND MANCINI, T. A. (1992). Liquid crystal polarization camera. *IEEE Workshop on Applications of Computer Vision*, pp. 120–127.