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Report

Circular Polarization Vision in a Stomatopod Crustacean

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Summary

We describe the addition of a fourth visual modality in the animal kingdom, the perception of circular polarized light. Animals are sensitive to various characteristics of light, such as intensity, color, and linear polarization [1, 2]. This latter capability can be used for object identification, contrast enhancement, navigation, and communication through polarizing reflections [2–4]. Circularly polarized reflections from a few animal species have also been known for some time [5, 6]. Although optically interesting [7, 8], their signal function or use (if any) was obscure because no visual system was known to detect circularly polarized light. Here, in stomatopod crustaceans, we describe for the first time a visual system capable of detecting and analyzing circularly polarized light. Four lines of evidence—behavior, electrophysiology, optical anatomy, and details of signal design—are presented to describe this new visual function. We suggest that this remarkable ability mediates sexual signaling and mate choice, although other potential functions of circular polarization vision, such as enhanced contrast in turbid environments, are also possible [7, 8]. The ability to differentiate the handedness of circularly polarized light, a visual feat never expected in the animal kingdom, is demonstrated behaviorally here for the first time.

Results and Discussion

Stomatopod Visual Systems

Stomatopod crustaceans possess an unusual visual system, unlike that of any other animal yet described [9]. Their eyes possess extraordinary capabilities such as tunable, eight-channel color vision [10–12], complex linear polarization vision [13, 14], potential monocular stereopsis or range-finding [15], and luminance and form vision. Here, we add another visual capability to the repertoire of their astonishing eyes, circular polarization vision, a previously unrecognized visual modality. To detect these many channels of information, stomatopods employ a basic retinal design element consisting of eight cells (called the rhabdom) common to many crustaceans. Each rhabdom receives light through an individual set of optics: hexagonal lens elements and spacers called crystalline cones. The whole unit of photoreceptive rhabdom and optics combined is known as an ommatidium (Figure 1). Stomatopod ommatidia are highly modified and arranged into spatially discrete subsections within the eye [10, 13]. The six-row midband region of the eye (Figure 1) contains most of the unusual retinal specializations [10, 11, 13]. We now demonstrate that two ommatidial rows within this midband are specialized for circular polarization vision in some stomatopod species (Figures 1 and 2).

Circular Polarized Light: The Physical Basis

Before describing the sensory basis for circular polarization vision in stomatopods, we first revise the physics of linear and circular polarization of light. Although humans are normally unaware of any aspect of polarized light, we use linear polarizing filters in sunglasses or camera filters to reduce the inherently polarized glare from reflective surfaces such as water or glass [16]. Circular polarizing filters are also used, especially in photography, for related reasons [16]. Light that is linearly polarized has its electric vector (e-vector) confined to one orientation, e.g. vertical, and this vector is the result of having both x and y vibrational e-vector components in phase [17]. When these components are not in phase, the resultant e-vector projects an ellipse as the ray of polarized light travels through space. When the phase difference is ± 90°, the e-vector describes a circle. This is circularly polarized light. If the e-vector of circularly polarized light rotates in a counterclockwise direction as seen from the direction of the sensor, it is called right-handed circularly polarized light (R-CPL). If it rotates in a clockwise direction, it is left-handed circularly polarized light (L-CPL) (Figure 2; for a good description of this, see Chapter 33 in the Feynman *Lectures on Physics* [17]). One further detail of the physics needs mentioning here. If circularly polarized light is passed through transparent material that is birefringent (having nonisotropic refractive properties) with a thickness and refractive index such that light is slowed down (retarded) by ¼ of its wavelength in one e-vector orientation (this is called a ¼ wave plate or retarder), then the circularly polarized light becomes linearly polarized. Here, the 90° phase difference between x and y vectors in circularly polarized light is brought back into phase, and therefore linearly polarized light results [16, 17]. Importantly for the stomatopod story, the angle of the resultant e-vector for left-handed circularly polarized light is exactly orthogonal (at 90°) to that for right-handed circularly polarized light (Figure 2).

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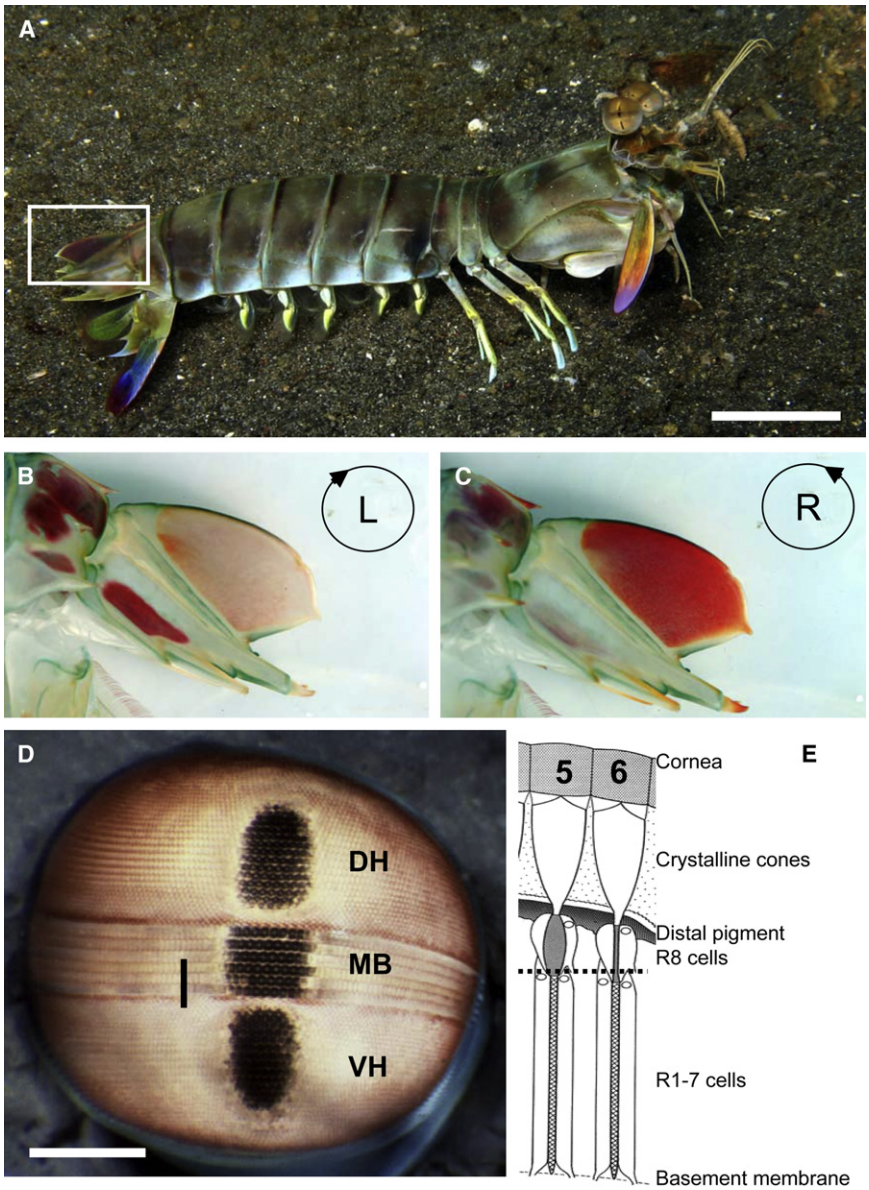

Figure 1. Circular Polarizing Signals and General Eye Anatomy in Stomatopods

(A) The stomatopod crustacean *Odontodactylus cultrifer* (male). The scale bar represents 1 cm. (Photograph by Chrissy Huffard.)

(B) Detail of telson keel (inset in [A]) photographed through a left-handed circular polarizing filter.

(C) As (B) except photographed through a right-handed circular polarizing filter. Note the striking contrast difference compared to (B).

(D) The eye of *Odontodactylus scyllarus*, a close relative of *O. cultrifer*, seen from the front. The vertical line is section direction and extent in (E). The following abbreviations are used: midband (MB), dorsal hemisphere (DH), and ventral hemisphere (VH). The scale bar represents 800 μm.

(E) Diagrammatic representation of a sagittal section (line in [D]) of rows five and six of the midband of the eye of a generalized gonodactyloid stomatopod (for full details, see [10, 13, 26]). The dotted line is approximate section level in Figure 2A.

Detection of Circularly Polarized Light: The Structural Basics

Photoreceptors, in both vertebrates and invertebrates, may be preferentially sensitive to a specific e-vector direction [1, 2]. In invertebrates such as stomatopods, this requires precise alignments of microvilli, the basic elements that construct the photoreceptive rhabdom. Maximum sensitivity to linearly polarized light in such a receptor occurs when the e-vector is parallel to the microvillar axis [18, 19]. Many insects, including desert ants, crickets, and bees, use receptors with specifically aligned microvilli to detect the natural e-vector variation in the sky, using this information for orientation and navigation [1, 2, 20]. Underwater, some crustaceans and cephalopods may employ linear-polarization-sensitive systems based on receptors with orthogonal microvilli. In crustaceans, this frequently results in square- or diamond-shaped rhabdom profiles in transverse section (Figure 2) [9]. This organization is seen in various areas of stomatopod compound eyes, most notably in the main rhabdoms of midband rows five and six, the R1–7 cells (see Figures 1 and 2 and [13] for cell nomenclature).

As occurs in many other crustaceans, in some stomatopods [14, 21, 22], these and other photoreceptors are capable of sensing the linear polarization of light.

In common with most malacostracan crustaceans [9], stomatopods have in each ommatidium a single retinular cell designated R8 with its centrally positioned rhabdom sitting on top of and optically coupled to seven retinular cells (R1–7) that between them make a single longer rhabdom (Figure 2). Cells are numbered by convention on the basis of their specific, asymmetrical position around the rhabdom (Figure 2) [13]. Cells 1, 4, and 5 make microvilli orthogonally oriented to those of cells 2, 3, 6, and 7, and these two cell populations normally provide opponent channels for linear polarized light discrimination [22–24]. This basic system, also present in the peripheral or hemispheric region outside the midband of stomatopod eyes (Figure 1) [10, 13], is modified in rows five and six of the midband in species of *Odontodactylus* for circular polarization vision, where the two cell populations (1, 4, and 5 versus 2, 3, 6, and 7) swap linear polarization discrimination for circular.

The R1–7 cells of *Odontodactylus sp*. rows five and six remain intrinsically linearly polarized light detectors, but only after light has been converted to this state from circularly polarized light by specialized overlying structures, formed by the rhabdomeres of the R8 photoreceptor cells (Figure 2). These photoreceptors are anatomically distinct from other R8s in the eye [10, 13] and act as ¼ wave plates with a fast axis parallel to their microvilli [13, 17]. This optical activity of the R8 rhabdom can be seen using polarization microscopy (Figure 3). Because of the specific orientation of the R8 rhabdomeres over the R1–7 cells (their microvilli are at 45° to those of R1–7 in both rows, Figure 2) the linear polarization directions resulting from conversion are orthogonal for L-CPL (+45°) and R-CPL (−45°, Figure 2) and are thus oriented precisely for the

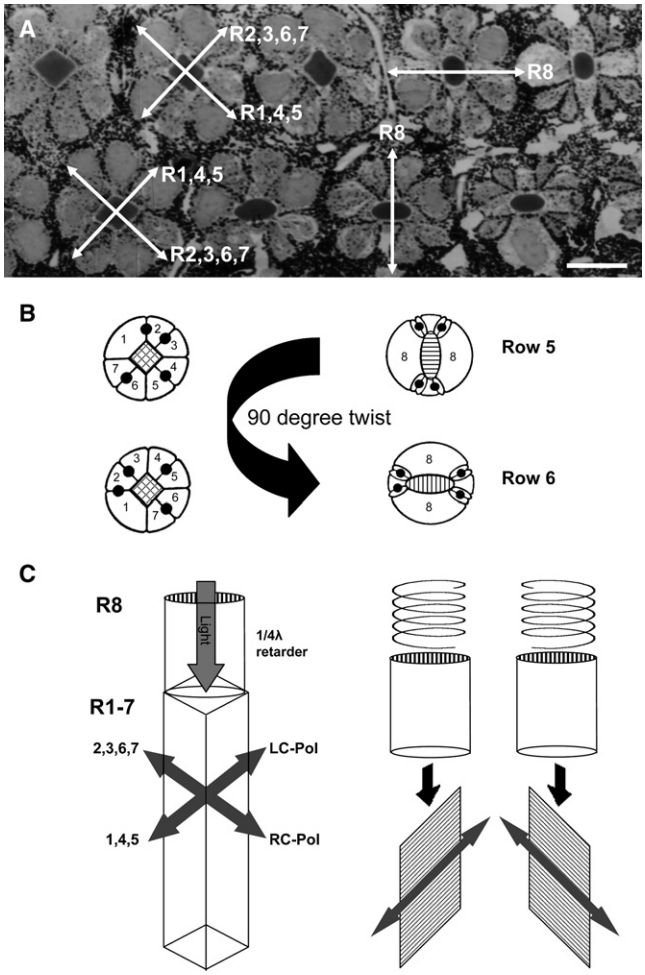

Figure 2. The Anatomy of ¼ Wave Retardation and Polarization Sensitivity

(A) Semithin toluidine-blue-stained (2 μm) transverse section through the rhabdoms of midband rows five and six at a level (indicated by dotted line in Figure 1E) to include both R8 and R1–7 rhabdoms. Cell numbering according to anatomical position is as previously published [13]. White arrows indicate both the microvillar direction and the resulting direction of linear polarization sensitivity. The scale bar represents 10 μm.

(B) Diagrammatic representations of transverse sections through the R8 and R1–7 rhabdomeres of rows five and six in (A) [13, 26]. Note the 90° twist between rows. The hatching shows microvillar direction in R8 (unidirectional) and R1–7 (orthogonal) rhabdoms.

(C) Three dimensional diagrammatic representation of row 6 R8 and R1–7 rhabdom (left) and how circular polarized light is changed and detected by this system (right). Arrows indicate three things: the direction of orthogonal microvillar layers in R1–7 cells, the cells producing these microvilli (1, 4, and 5 and 2, 3, 6, and 7), and the circular-polarization-sensitivity handedness that the R1–7 cells end up with as a result of the ¼ wave retardation of the overlying R8 cell.

most efficient stimulation of the underlying orthogonal R1–7 photoreceptor set. The overall result is an R-CPL- and L-CPL-detecting system in each ommatidium. There are actually two ommatidial rows containing units of this system, midband rows five and six; note that row six has all elements rotated 90° relative to row five (Figure 2) [10, 13].

Row Five and Six R8 Cells Are ¼ Wave Retarders

Typical R8 cells in stomatopods and other crustaceans have microvilli that are either bidirectional or random in orientation [9, 13]. However, the R8 cells of rows five and six of the midband of stomatopods are structurally unusual, being ovoid in transverse section, packed with very precisely aligned, unidirectional microvilli, and having substantially longer rhabdomeres than other R8 cells (Figures 1 and 2) [10, 13]. It is apparently this ultrastructural modification of the R8 cells that results in ¼ wave retardation of light passing through it's rhabdom in *Odontodactylus* species (Figure 3). Although all other gonodactyloid and lysiosquilloid stomatopods also possess R8 rhabdoms similar to this in structure [13], it is not known whether they have the same optical properties.

To estimate the R8 retardance, we measured the phase shift induced by the sections of the rhabdom with a polarization microscope. Here, the sample, in this case the frozen section containing the R8 rhabdom viewed on axis (that is, looking down the length of the photoreceptor), is placed between the two crossed polarizers of the polarization microscope. Light is polarized by the first polarizer and passes through the sample, and if the sample is birefringent, it becomes elliptical. The phase shift introduced by the sample that produces this elipticity can be obtained by analysis of its polarization state (e.g., elipticity) with measured rotations of the second polarizer in the light path. We then calculated the retardance on the basis of the approximate thickness of the section, around 10 μm, and the length of the whole rhabdom measured by tracking the number of sections one can get from an R8 cell. Figure 3D shows the phase shift (ϕ) of a whole length of the R8 rhabdom as a function of wavelength (see [25] for full method). Our results indicate that the retardance of the R8 is slightly lower but fairly close to ¼ of a wavelength from 400 nm to near 700 nm.

Microvilli in these R8 cells are oriented at 45° compared to the orthogonal microvilli in the R1–7 cells rhabdom below (Figures 2 and 3 see also [13]), and it was this angle, the exact conformation required for conversion of CPL, that first suggested the possibility for circular polarization sensitivity in this eye. Three lines of evidence supporting this optically and anatomically driven hypothesis are now presented: electrophysiological, behavioral, and signal design.

Electrophysiological Evidence for Circular Polarization Vision

If it is true that the structural design of row five and six ommatidia makes them sensitive to circularly polarized light, then intracellular electrophysiological recordings from the R1–7 cells should have the following properties. First, cells from the two orthogonal populations (1, 4, and 5 versus 2, 3, 6, and 7) should be sensitive only to either left- or right-handed circularly polarized light. Results shown in Figures 4A and 4C confirm this prediction. Because of the 90° rotation between rows five and six, the same receptor cell populations in rows five and six are sensitive to the same handed CPL; i.e., receptor cells 1, 4, and 5 in both rows five and six are sensitive to L-CPL but not to R-CPL, and receptor cells 2, 3, 6, and 7 in both rows five and six are sensitive to R-CPL but not to L-CPL. The identity of the cells was confirmed with intracellular staining after recordings were made (Figure 4D). In addition to this, all row five and six R1–7 receptor cells should be insensitive to the e-vector orientation of incoming linearly polarized light. That is, a light stimulus transmitted through a rotating linear polarizer should produce a constant response in these cells, independent of the angle of rotation (and the resultant e-vector angle) that they are exposed to. As shown in Figure 4B, this is what was found. The R8 rhabdomeres, acting as ¼ wave retarders, convert linearly polarized light into

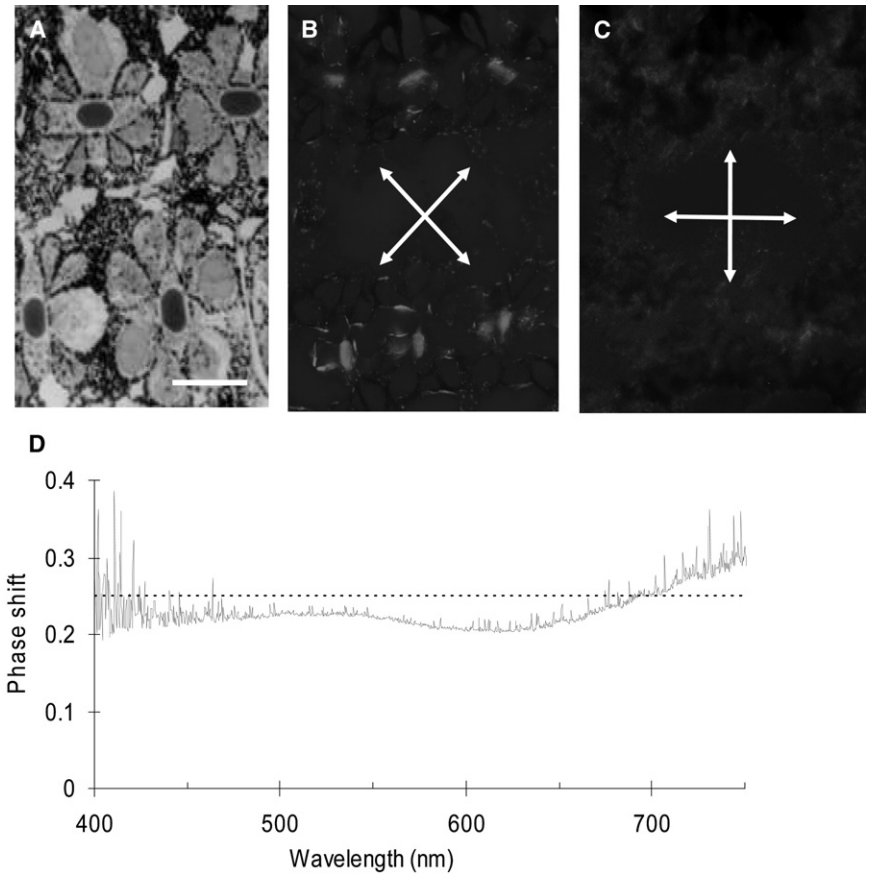

Figure 3. Description and Measurement of R8 Cell ¼ Wave Retardance

(A) Semithin section of the R8 cell rhabdoms in transverse section in rows five and six to show the orthogonal arrangement of the R8 cells and therefore their microvillar direction. The scale bar represents 10 μm.

(B and C) Equivalent retinal region to (A), 10 μm cryosection of row five and six R8 cell rhabdoms viewed with a polarizing microscope. In (B), the bright appearance of the R8 rhabdom eliptical transverse sections indicates they are birefringent or depolarizing. The crossed arrows indicate the microscope polarizer and analyzer direction, and the disappearance of the bright elipses in (C) when these are rotated 45° confirms birefringence as the property of the material rather than depolarization. This suggests but does not prove ¼ wave retardance in the R8 rhabdoms.

(D) The R8 retardance was measured by recording of the phase shift induced by the sections of the rhabdom with a polarization microscope in dark-field, or crossed-polarizer, configuration. We then calculated the retardance on the basis of the approximate thickness of the section and the length of the whole rhabdom. The phase shift (ϕ) of a whole length of the R8 rhabdom as a function of wavelength is shown here. Our results indicate that the retardance of the R8 is slightly lower but fairly close to ¼ of a wavelength from 400 nm to near 700 nm. See the main text and Supplemental Data available online for further details.

elliptically or circularly polarized light, depending on the angle of the linear polarization relative to the fast and slow axes of the retarder. The precise 45° angle of the R1–7 cell microtubules relative to the axes of the R8 ¼ wave retarder ensures that whatever the state of polarization transmitted, there is always equal absorption by a linear-polarization-sensitive cell. The receptor cell's response is therefore independent of the angle of e-vector entering the eye (Figures 2 and 3).

Behavioral Evidence for Circular Polarization Vision

Although our results demonstrate that these animals are sensitive to CPL, behavioral proof is needed to show that they actually make use of this ability [14]. In two-way choice tests with operant conditioning and food as a reward, stomatopods clearly learned to associate either L-CPL or R-CPL stimuli with the reward (Figure 5). As with their ability to distinguish colors or the e-vector orientation of linearly polarized light [14, 26] these animals can perceive and analyze the light's circular polarization. Four individuals were trained to associate L-CPL reflection with a food reward and three individuals to associate R-CPL with a food reward. During tests, when no food was present, animals were presented with two feeding tubes, identical to those used for training, one reflecting L-CPL and the other R-CPL. They chose the tube reflecting the CPL handedness to which they had originally been trained at levels significantly above chance (Figure 5).

Evidence for Circular Polarization Signals

How might the ability to discriminate CPL be useful for stomatopods? Humans use circular polarization filters (usually right-handed filters) in front of cameras, for example, to reduce glare from surfaces while not allowing linearly polarized light to adversely affect the camera's internal sensor systems. In certain circumstances where light is scattered, e.g., in turbid media or living tissue, the light can become circularly polarized, and in these instances, discriminating between R-CPL and L-CPL may be useful for enhancing the contrast between objects and their background [7, 8]. CPL exists in the marine environment [27], so CPL vision could be useful for stomatopods in this context. In addition to its potential for enhancing contrast, such vision could play a role in intraspecific signaling. Certain natural objects, including for example those with a helical layering of proteins, reflect circularly polarized light. The cuticles of scarab beetles provide the best known examples of this [5, 6], but it has also been noted previously in crustacean tissue [28] (where it occurs in areas not normally visible). Stomatopods use highly specialized color and linear polarization signals for complex social interactions [4, 26, 29, 30]. By using circular polarization imaging, we have identified three species of stomatopods within the genus *Odontodactus* where CPL is reflected from specific locations on the cuticles of males but not females (Figure 1). These sex-specific CPL-reflective areas are on parts of the body (uropods or telson) that are frequently used for behavioral displays by stomatopods [2, 8]. The precise role that these signals, visible to a CPL visual system, play in stomatopod sexual signaling is not yet known, but we speculate that these CPL reflections could act as a secret communication channel. Linear polarization signals, used by marine invertebrates [4, 30], are visible to animals like cephalopods that prey on stomatopods and are therefore open to exploitation [30]. Also, other genera of stomatopods that we have examined have variable CPL

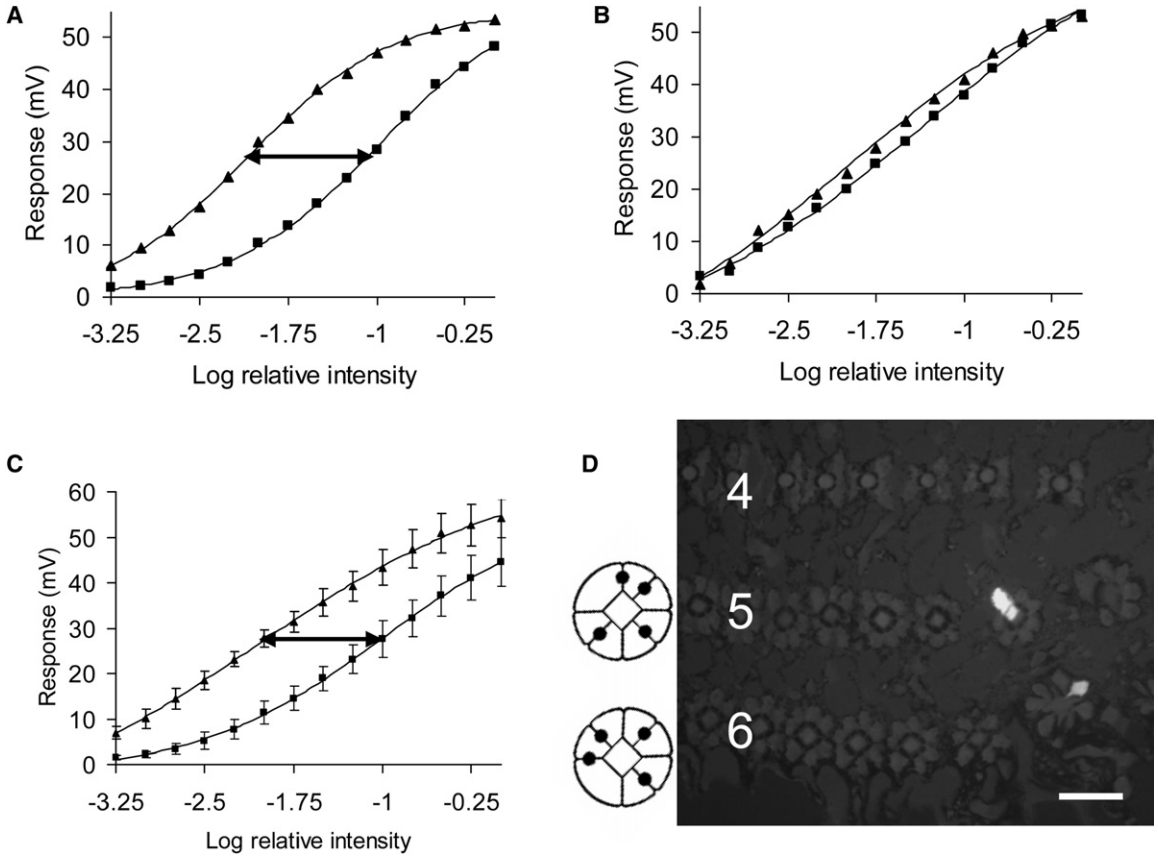

Figure 4. Electrophysiology of Circular-Polarization-Sensitive Photoreceptors

(A) Intensity-response curves (R-logI, normalized voltage response versus log intensity) of an R2 cell in row five to right- and left-handed circularly polarized white light. The cell is stimulated with increasing light intensity through a right-handed (triangles) and left-handed (squares) providing circular polarizing filter. Circular polarization sensitivity (CPS) is defined by the intensity shift (ΔS in log units—see arrow) between the two R-logI curves such that CPS = $10^{\Delta S}$. This cell is sensitive to right-handed circular polarized light with a CPS of 10.2.

(B) Similar recording as (A) but this shows the cells response to linear polarized light. A linear polarization filter was arranged with its axis at ± 45°, the angles that would theoretically elicit maximum and minimum response in row 5 R2 cell if it was sensitive to linear polarized light. Significantly, the cell shows very low (1.38) linear polarization sensitivity because of conversion of the incoming linear polarized light to circular polarized light that can not be detected by rhabdomeric photoreceptors.

(C) Average (10.4) of six intensity-response curves with ± standard deviation (SD) to left- and right-handed circular polarization flashes of increasing intensity. Symbols are as in (A).

(D) Dye-filled cells shown in 7 μm transverse sections of row five and six photoreceptors in the left eye (for orientation with such sections, see [13]). In row five, cell R1 is filled with Lucifer yellow, and in row six, cell R5 is filled with ethidium bromide. Each cell showed CPS similar to that in (A), although both cells here showed left-handed circular polarization sensitivity. The scale bar represents 10 μm.

sensitivity and may be unable to view the sexual displays of *Odontodactylus* species, making this a private channel of communication, unavailable to both predators and potential stomatopod competitors.

Whatever the use of CPL signals and CPL vision to stomatopods, comparing design features of their CPL reflectors and sensors to those of man-made systems will be interesting. Humans use CPL filters and imaging in everyday photography, medical photography, and object-detection systems in turbid environments [7, 8]. The reefs and waters that many stomatopods inhabit are often turbid, and it is no surprise that, perhaps as long as 400 million years ago (when stomatopod crustaceans first appeared), nature got there first.

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Supplemental Data

Experimental Procedures are available at http://www.current-biology.com/cgi/content/full/18/6/429/DC1/.

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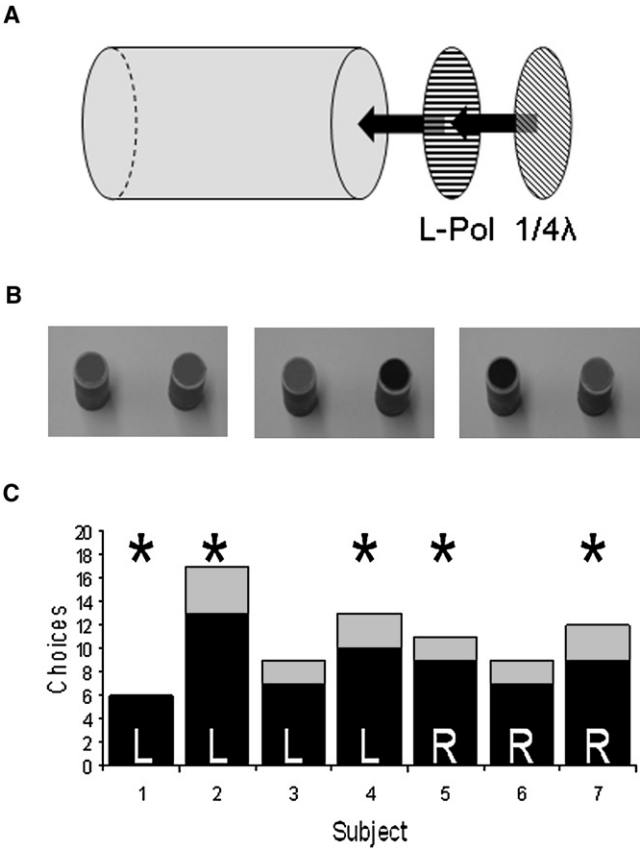

Figure 5. Behavioral Results, Discriminating Left- from Right-Circular-Polarization-Reflecting Feeding Tubes

(A) Diagrammatic representation of the construction of feeding tubes. The end of each tube is made to reflect either left-handed (L) or right-handed (R) circular polarized light. This is achieved by gluing of a laminate of two filters, a linear polarizing filter, and a ¼ wave retarder on top of a diffuse white reflective background disk (shown here as light gray for diagram clarity) that is in turn glued on one end of the feeding tube, blocking this end completely. During training, food is placed in the other, open end of the tube. In training and test situations, two tubes are presented to the animals, circular-polarizing-reflector-side first. Animals rapidly learn to pick up and feed from tubes and learn to discriminate L from R feeding tubes (see the Supplemental Data for more detailed description and [14] for similar experimental procedure).

(B) Photographs of the L- and R-circular-polarized-light-reflecting ends of feeding tubes: left, as seen through no filter; middle, through a right-handed circular polarizing filter analyzer; and right, through a left-handed circular polarizing filter analyzer. The tube on the left reflects left-handed circular polarizing light, and the one on the right reflects right-handed circular polarizing light. This "intensity difference" between tubes is therefore only seen by a system capable of circular polarization sensitivity.

(C) Operant condition training tests where individual stomatopods (*O. scyllarus*) were required to learn that food was present in either feeding tubes. Black bars are correct choices, and gray bars are incorrect choices. The chance level is half way up each combined bar. In a Fisher's exact test (one tailed), * indicates choices are made significantly more often than by chance; p values as follows: Individual 1, 0.045; 2, 0.034; 3, 0.072; 4, 0.040; 5, 0.049; 6, 0.072; and 7, 0.013.

References

1. Wehner, R. (1983). The perception of polarised light. In The Biology of Photoreception, D.J. Cosens and D. Vince-Prue, eds. (Cambridge, London: Cambridge University Press), pp. 331–369.
2. Horváth, G., and Varjú, D. (2004). Polarised Light in Animal Vision (New York: Springer).
3. Wehner, R., and Lanfranconi, B. (1981). What do ants know about the rotation of the sky? Nature *293*, 731–733.
4. Cronin, T.W., Shashar, N., Caldwell, R.L., Marshall, N., and Chiou, T.H. (2003). Polarization vision and its role in biological signaling. Integr. Comp. Biol. *43*, 549–558, Cheroske AG.
5. Neville, A.C., and Caveney, S. (1969). Scarabid beetle exocuticle as an optical analogue of cholesteric liquid crystals. Biol. Rev. Camb. Philos. Soc. *44*, 531–562.
6. Brink, D.J., van der Berg, N.J., Prinsloo, L.C., and Hodgkinson, I.C. (2007). Unusual colouration in scarabid beetles. J. Phys. D Appl. Phys. *40*, 2189–2196.
7. Yao, G., and Wang, L.V. (1999). Two-dimensional depth-resolved Mueller matrix characterization of biological tissue by optical coherence tomography. Opt. Lett. *24*, 537–539.
8. Rakovic, M.J., Kattawar, G.W., Mehrubeoglu, M., Cameron, B.D., Wang, L.V., Rastegar, S., and Coté, G.L. (1999). Light backscattering polarization patterns from turbid media: Theory and experiments. Appl. Opt. *38*, 3399–3408.
9. Marshall, N.J., Kent, J., and Cronin, T.W. (1999). Visual adaptations in crustaceans. In Adaptive Mechanisms in the Ecology of Vision, S. Archer, M. Djamgoz, E. Lowe, J.C. Partridge, and S. Vallerga, eds. (London: Kluwer), pp. 285–328.
10. Marshall, N.J. (1988). A unique colour and polarisation vision system in mantis shrimps. Nature *333*, 557–560.
11. Cronin, T.W., and Marshall, J. (1989). A retina with at least ten spectral types of photoreceptors in a mantis shrimp. Nature *339*, 137–140.
12. Cronin, T.W., Caldwell, R.L., and Marshall, N.J. (2001). Tunable colour vision in a mantis shrimp. Nature *411*, 547–548.
13. Marshall, N.J., Land, M.F., King, C.A., and Cronin, T.W. (1991). The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: The detection of polarised light. Philos. Trans. R. Soc. Lond. B Biol. Sci. *334*, 33–56.
14. Marshall, J., Cronin, T.W., Shashar, N., and Land, M. (1999). Behavioural evidence for polarisation vision in stomatopods reveals a potential channel for communication. Curr. Biol. *9*, 755–758.
15. Schiff, H., Abbott, B.C., and Manning, R.B. (1985). Possible monocular range-finding mechanisms in stomatopods from different environmental light conditions. Comp. Biochem. Physiol. A *80*, 271–280.
16. Goldstein, D. (2003). Polarised Light (New York: Marcel Dekker).
17. Feynman, R.P., Leighton, R.B., and Sands, M. (1971). Lectures on Physics (London: Addison-Westley).
18. Kirschfeld, K., and Snyder, A.W. (1975). Waveguide mode effects. birefringence and dichroism in fly photoreceptors. In Photoreceptor Optics, A.W. Snyder and R. Menzel, eds. (New York: Springer), pp. 56–77.
19. Snyder, A.W. (1973). Polarisation sensitivity of individual retinula cells. J. Comp. Physiol. [A] *83*, 331–360.
20. Labhart, T. (1999). How polarisation-sensitive interneurons of crickets see the polarisation pattern of the sky: A field study with an optoelectronic model neuron. J. Exp. Biol. *202*, 757–770.
21. Cronin, T.W., Marshall, N.J., Quinn, C.A., and King, C.A. (1994). Ultraviolet photoreception in mantis shrimp. Vision Res. *34*, 1443–1452.
22. Kleinlogel, S., and Marshall, J.N. (2006). Electrophysiological evidence for linear polarisation sensitivity in the compound eyes of the stomatopod crustacean Gonodactylus chiragra. J. Exp. Biol. *209*, 4262–4272.
23. Sabra, R., and Glantz, R.M. (1985). Polarisation sensitivity of crayfish photoreceptors is correlated with their termination sites in the lamina ganglionaris. J. Comp. Physiol. [A] *156*, 315–318.
24. Kleinlogel, S., Marshall, N.J., Horwood, L.M., and Land, M.F. (2003). Neuroarchitecture of the color and polarization vision system of the stomatopod Haptosquilla. J. Comp. Neurol. *467*, 326–342.
25. Huard, S. (1997). Polarization of Light (Paris: John Wiley and Sons).
26. Marshall, N.J., Cronin, T.W., and Kleinlogel, S. (2007). Stomatopod eye structure and function: A review. Arthropod Struct. Dev. *4*, 420–448.
27. Ivanoff, A., and Waterman, T.H. (1958). Elliptical polarisation of submarine illumination. J. Mar. Res. *16*, 255–282.
28. Neville, A.C., and Luke, B.M. (1971). Form optical activity in crustacean cuticle. J. Insect Physiol. *17*, 519–526.
29. Caldwell, R.L. (1991). Variation in reproductive behavior in stomatopod crustacea. In Crustacean Sexual Biology, R.T. Bauer and J.W. Martin, eds. (New York: Columbia University Press), pp. 67–90.
30. Chiou, T.-H., Cronin, T.W., Caldwell, R.L., and Marshall, N.J. (2005). Biological polarized light reflectors in stomatopod crustaceans. SPIE *5888*, 1–9.