

POLARIZATION CONTRAST VISION IN *OCTOPUS*

NADAV SHASHAR AND THOMAS W. CRONIN

Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21228, USA

Accepted 29 November 1995

Summary

While the ability to analyze polarized light is widespread among animals, its contribution to form vision has not yet been documented. We tested the hypothesis that polarization vision can be used for object discrimination, by training octopuses to distinguish between targets on the basis of the presence or absence of a pattern produced by a 90° polarization contrast within the target. Octopuses recognized a 90° contrast pattern within a single target, when presented either on a horizontal/vertical axis or on a 45°/135° axis. They were able to transfer their learning to

new situations and to detect a polarization contrast when the orientations of the *e*-vector of light passing through the target center and background differed by as little as 20°. Polarization vision may provide information similar to that available from color vision and thus serve to enhance the detection and recognition of objects.

Key words: *Octopus*, polarized light, vision, learning, cephalopods, sensory ecology.

Introduction

Unlike humans, numerous animals are differentially sensitive to the *e*-vector orientation of linearly polarized light; such a capability is known as 'polarization sensitivity'. These animals include various terrestrial and marine invertebrates (e.g. Bandai *et al.* 1992; Nilsson *et al.* 1987; Phillipsborn and Labhart, 1990; Schwind, 1984, 1991; Snyder and Laughlin, 1975; Rossel, 1993; see reviews by Waterman, 1981, 1984) as well as several species of fish (Cameron and Pugh, 1991; Hawryshyn, 1992), amphibians (Auburn and Taylor, 1979) and birds (Martin, 1991; Phillips and Moore, 1992). Animals use this sensitivity for navigation (Wehner, 1976; Waterman, 1981, 1984; Rossel, 1993), for spatial orientation (Hawryshyn, 1992; Waterman, 1988) and for finding large bodies of water (Schwind, 1991). Can polarization sensitivity be used for object detection or identification? This is a fundamental question regarding visual perception. Objects such as fish (Cameron and Pugh, 1991; Hawryshyn, 1992) and plants (Land, 1993; Wehner and Bernard, 1993) reflect partially linearly polarized light in a significantly different pattern from their depolarized light appearance. However, no animal has yet been shown to detect or recognize objects using polarization sensitivity.

Like other cephalopods (Jander *et al.* 1963; Saidel *et al.* 1983), octopuses are sensitive to the orientation of the *e*-vector of linearly polarized light and thus possess polarization sensitivity (Moody, 1962; Moody and Parriss, 1960, 1961; Rowell and Wells, 1961). The anatomical basis for this

sensitivity is the orthogonal arrangement of the microvilli in the photoreceptive rhabdoms throughout the retina (Moody, 1962; Moody and Parriss, 1961; Tasaki and Karita, 1966*a,b*). Nevertheless, the biological function of this sensitivity is as yet unknown.

While previous researchers (Moody, 1962; Moody and Parriss, 1960, 1961; Rowell and Wells, 1961) showed that octopuses are sensitive to the orientation of polarization of linearly polarized light coming from a single source, they did not determine whether these animals can detect and analyze polarization patterns within a single imaged object. The ability to analyze such polarization patterns is essential if polarization vision is to be used for object detection or recognition.

Octopuses can readily be trained to choose a target marked with a particular pattern (shape, brightness contrast, etc.) in preference to another, and are able to transfer this learning to select a target similar but not identical to the learned one (Wells, 1978). In this study, we made use of such learning to examine the ability of octopuses to discriminate between targets solely on the basis of polarization vision. This was performed by training them to select between targets differing only in the presence or absence of a polarization contrast within them.

Three questions were asked. (a) Can octopuses detect the contrast produced by variations in the orientation of polarization within an object? (b) Can octopuses recognize specific targets on the basis of their polarization patterns?

(c) What is the minimal polarization contrast that can be recognized by octopuses?

Materials and methods

Octopuses of two species, *Octopus vulgaris* Lamarck and *Octopus briareus* Robson, were obtained from a commercial supplier. Individual octopuses were maintained in 58 cm×30 cm×30 cm tanks, visually separated from each other, supplied with running, ultraviolet-sterilized sea water at 21 °C. Tanks were exposed to a 13h:11h light:dark cycle, provided through dim fluorescent illumination from above. As animals arrived in the laboratory at different times, individuals experienced varying numbers of target presentations.

Behavioral experiments involving training present a dilemma: because octopuses are very curious animals, they will behave ‘incorrectly’ every once in a while. Indeed, even after prolonged training, there may be a residual error rate of about 20% (Moody and Parris, 1961, 1962; Wells, 1978). Additionally, the response to training varies among individuals (Mather and Anderson, 1993) and the use of a strong punishment may cause them not to react at all. We chose not to punish negative behavior and therefore to accept a certain level of negative results.

Three *Octopus vulgaris* and one *Octopus briareus* were trained to select targets that lacked a polarization contrast pattern, and four *O. vulgaris* were trained to select contrast-containing targets. The targets presented were 4 cm×4 cm chromatically neutral, linearly polarizing dichroic sheet filters (Polaroid, HN38S), held in a probe made of two pieces of clear Plexiglas (which did not measurably affect the light polarization pattern) attached to a gray rod 40–50 cm long. A wax-paper depolarizer was attached to the back of each polarizing filter. A circle, 2 cm in diameter, was cut from the middle of each filter and was replaced either at the same orientation (creating no polarization contrast) or after rotation by 90° (creating a contrast of polarized light). This contrast could not be detected by a human eye unless the target was viewed through a linearly polarizing filter (Fig. 1). In order to prevent the animals from learning false cues, and to ensure that they reacted only to the polarization contrast, target position (left/right), the orientations (horizontal/vertical) of the center and background parts of the filter, and the probe in which each filter was presented were varied randomly, using a total of eight probes and more than 50 polarization filters, throughout training and experiments. Additionally, probes were washed after each presentation in 70% alcohol and afterwards in fresh water to remove any odor from previous presentations and to prevent transmission of naturally occurring diseases. Tanks were illuminated from above with dim fluorescent light. Prior to experimental sessions, a white plastic sheet was placed outside the front of the aquarium, diffusing incoming light, and an incandescent lamp was lit facing the front of the aquarium, where the targets were presented. Measurements using an imaging polarized light analyzer (Cronin *et al.* 1994; Shashar *et al.* 1995) revealed no residual polarization in the incoming light or in the underwater light field.

Since each aquarium was 58 cm in length, the central part of

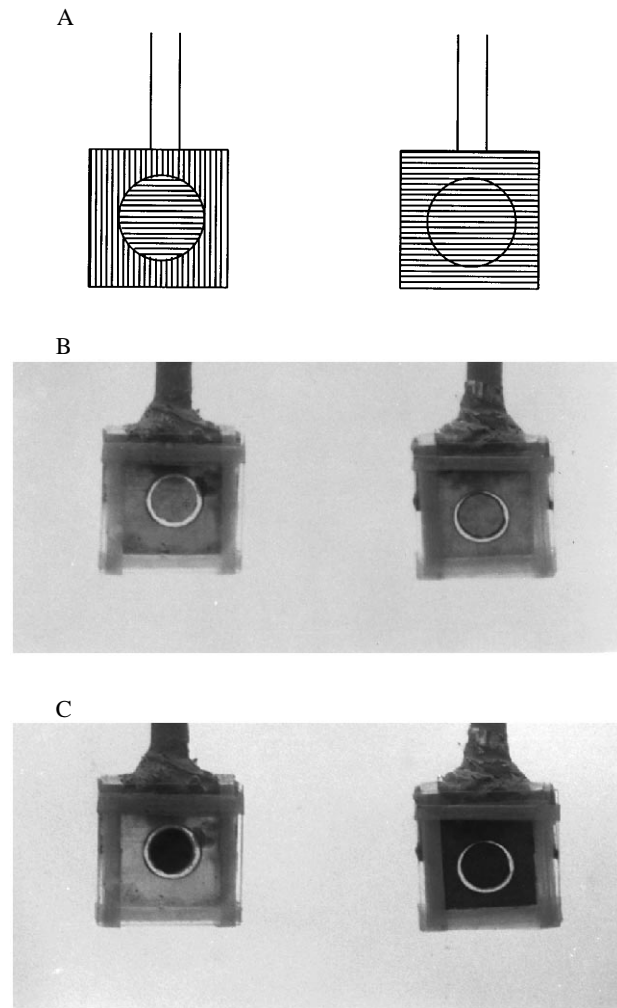
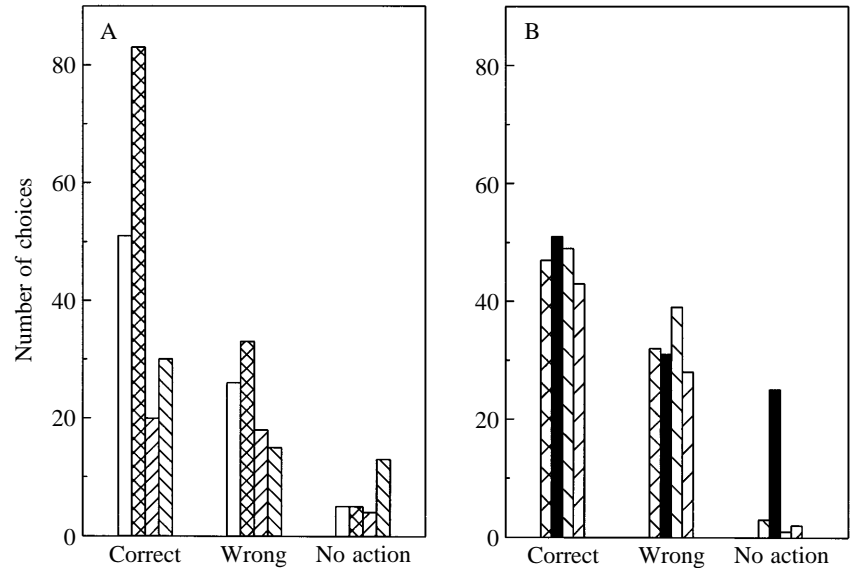


Fig. 1. Targets were constructed from 4 cm×4 cm linearly polarizing filters, with 2 cm diameter circles cut from the middle and replaced, either at the same orientation (creating no polarization contrast, right) or after a rotation of 90° (creating polarization contrast, left). In A, parallel lines illustrate the orientation of the transmitted *e*-vector. This contrast could not be detected by the human eye (photographs in B) unless viewed through a linearly polarizing filter (photographs in C, taken through a vertically oriented polarization filter).

each target, as viewed by the octopus, was at least 4° in diameter, and since the motion of the animals within the tanks was not restricted, this value was usually even greater (much larger than the 10–65′ minimal visual acuity angle typical of octopuses; Sutherland, 1963; Packard, 1969; Muntz and Gwyther, 1988).

The training and testing procedures were as follows. Each session consisted of five presentations separated by 5–10 min. For the first three training sessions, each animal was presented with only the positive target, which had a small piece of shrimp attached to its back as a reward. The subsequent three training sessions also involved only the positive target; however, the reward was not present on the target, but was given after the animal had selected the target. During all further tests, the animal was presented with both positive and negative targets

Fig. 2. Target choice by octopuses trained to select targets containing a 90° polarization contrast (A) or no contrast (B), when they were presented simultaneously with both types of targets. Target left/right position, polarization horizontal/vertical orientation and probes containing the polarizing filters were randomized. Each of eight individual animals is represented by a different bar pattern. Black bars represent data from the single *Octopus briareus*; all other individuals were *O. vulgaris*. In both groups of four animals, octopuses learned to choose the correct target on the basis of the presence or absence of polarization contrast. For animals trained to choose the contrast-bearing pattern (A), the overall results were as follows: correct choices 184, wrong choices 92, no action 29, $P < 0.001$. For those trained to choose the targets without a polarization contrast pattern (B), the results were: correct choices 190, wrong choices 130, no action 31, $P < 0.001$. Owing to variation in the times that the animals arrived at the laboratory, and to the death of two animals from causes unrelated to the experiments, the total number of presentations varied among animals.



simultaneously. If the animal selected the positive target, its choice was immediately reinforced with food; there was no punishment for a negative choice.

The selected target was defined as the first target contacted by the octopus. This definition was necessary since octopuses would occasionally persist in touching the other target. If a choice was not made within 5 min, both targets were removed. As controls, 38 presentations with both targets placed backwards in the probes (with the depolarizer facing the animals and the polarizing filter facing the aquarium wall) were randomly included among the test presentations.

To investigate whether the octopuses could transfer their learning to new situations, and as an additional control, two animals from each group were presented with targets containing filters polarizing light on $45^\circ/135^\circ$ axes, included randomly among horizontal/vertical targets. These targets also either contained or lacked a pattern of polarization contrast, and a human eye could not distinguish them from the 'regular' targets without the aid of an additional linear polarizing filter.

In the final set of experiments, we investigated the minimal detectable difference in polarization angle between the center and the background of the target. Three animals, from the group trained to choose contrast-containing targets, were presented with pairs of targets in which one did not contain a polarization contrast, while in the other the e -vector orientation of the target's center differed from that of the background by various angles (10° , 20° , 30° or 45°), and their choices were recorded. Presentations of the different angles (24 presentations for each angle) and the orientation of the background of both targets were randomized. In each session, two presentations involved targets with a 90° contrast and three included targets with smaller angles of contrast (10° , 20° , 30° or 45°), selected randomly.

Results were grouped according to the task under investigation and were analyzed, after excluding the cases where

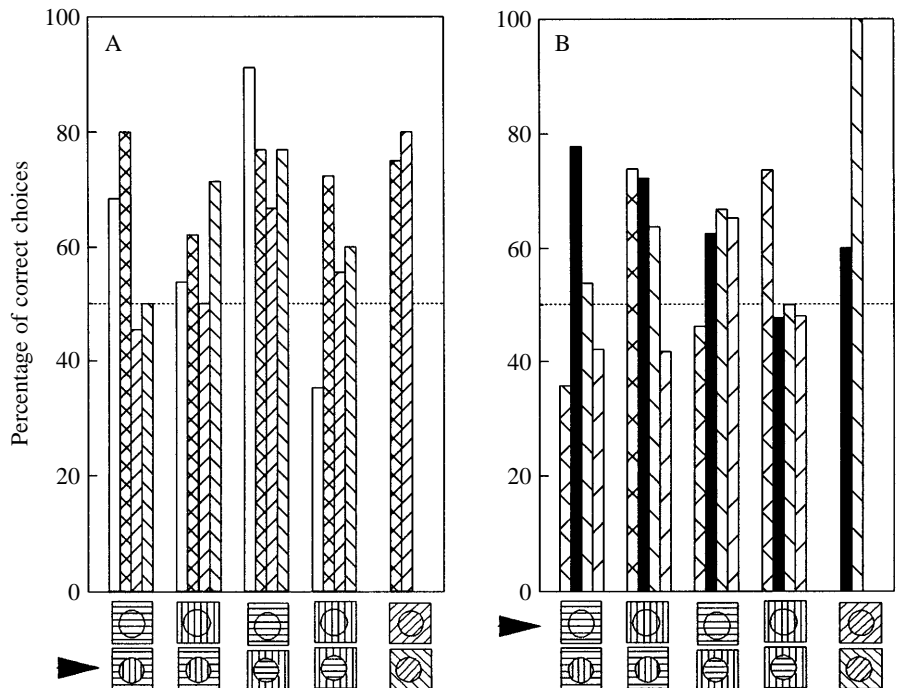
the animals did not select a target within 5 min, using a χ^2 goodness-to-fit test for two cells with equal expected frequency (Gibbons, 1976). For example, when examining the ability of octopuses to detect a polarization pattern on the $45^\circ/135^\circ$ axis, results from all animals presented with this task (animals trained either to prefer or to reject a polarization contrast) were grouped, cases where animals did not react to the targets were omitted, and then the results were analyzed using the χ^2 test.

Results

Octopuses could distinguish between targets on the basis of the presence or absence of polarization contrast. The overall results were: correct choices 374, wrong choices 222, no action 60, $P < 0.001$ (Fig. 2). Therefore, we conclude that octopuses can detect a pattern of polarization contrast within a single object.

The performance of the group trained to choose contrast-containing targets was not significantly different from that of the group trained to prefer targets without a polarization contrast ($P = 0.18$, Fig. 2). In these experiments, the octopuses did not consistently prefer any particular orientation of polarization in either part (center or background) of the targets presented, nor did they prefer a specific combination of center and background within a single target (Fig. 3). Additionally, animals did not discriminate between targets when the depolarizer side faced them (presented to five animals; correct choices 14, wrong choices 18, no action 6, $P = 0.335$). These results strongly suggest that discrimination between targets was based solely on the presence or absence of polarization contrast within each target. When targets which they had not previously encountered (with a polarization pattern on an axis of $45^\circ/135^\circ$) were presented to two animals from each group, they transferred their learning and continued to select the target type (patterned or patternless) to which they were trained

Fig. 3. Target choice by octopuses presented simultaneously with pairs of targets, illustrated by diagrams underneath each set of bars (parallel lines in diagrams indicate the e -vector pattern transmitted by each target). (A) Animals trained to select targets containing a polarization contrast pattern (four left-hand diagrams in the row indicated by an arrowhead). (B) Animals trained to select targets lacking a polarization contrast pattern (four left-hand diagrams in the row indicated by an arrowhead). Animals were not exposed during training to targets with their polarization on the $45^\circ/135^\circ$ axis (right-hand pair of diagrams). The dotted line at 50% shows the expected performance level if the animals had chosen randomly. Bar patterns identify the same eight animals as in Fig. 2. Although the animals did not perform equally well with all pairs of targets, there is no indication that selection may be based on features of the target other than polarization contrast.



(correct choices 14, wrong choices 4, no action 0, $P < 0.02$; Fig. 3). This transfer of learning indicates that octopuses can recognize objects on the basis of their polarization pattern.

Octopuses were able to transfer their learning to situations in which the contrast angle was less than 90° . In tests to determine the minimal detectable angle of contrast, octopuses could recognize a polarization contrast pattern at an e -vector difference as small as 20° ($P < 0.001$ for the presentations of 20° , 30° and 45° contrast combined, $P \leq 0.07$ for each of these angles separately), but apparently could not recognize a 10° difference (Table 1).

Discussion

The angular size of the targets' central region was much larger than the minimum visual acuity angle of the octopuses (Sutherland, 1963; Packard, 1969; Muntz and Gwyther, 1988). Therefore, we infer that the octopuses were capable of detecting the polarization variation within each target. Single photoreceptors of octopuses are unable to discriminate between lights polarized at 45° to the orientation of microvilli in the retina (Tasaki and Karita, 1961*a,b*). However, intact animals can discriminate behaviorally between lights polarized at 45° and 135° (Moody and Parris, 1961), and in our experiments octopuses were able to detect polarization contrast patterns on the $45^\circ/135^\circ$ as well as on the horizontal/vertical axes. Furthermore, they recognized a polarization contrast angle of 45° (on a vertical or horizontal background). We suggest that, in intact animals, discrimination of a 45° variation in polarization within a single target may be possible by using irregularities known to occur in the retinal array of rhabdomeres (Tasaki and Karita, 1961*b*) or by taking advantage of movements of the head or eyes.

Table 1. Target choice by *Octopus vulgaris* trained to take targets containing a 90° polarization contrast

Angle of polarization contrast (degrees)	Target choice			Statistical significance
	Correct	Wrong	No action	
45	13	5	6	$P=0.069$
30	16	7	1	$P=0.070$
20	16	5	3	$P=0.016$
10	9	11	4	$P=0.623$ (NS)

Three octopuses were tested, corresponding to the first, second and fourth bars of Figs 2A and 3A. Each individual was given eight presentations of pairs of targets, one containing a contrast pattern at the given e -vector angle between the inner part and background and the other target without a contrast. Target left/right position, horizontal/vertical orientation of background polarization and probes containing the polarizing filters were randomized. Octopuses recognized a contrast of at least 20° between the orientation of the polarizing filters in the center and background parts of the targets, but were apparently unable to detect a 10° contrast.

Statistical significance is based on a χ^2 goodness-to-fit test for two cells, both with an expected frequency of 0.5, with a continuity correction for small sample size, using only cases where a choice was made; NS, not significant.

In addition to transferring their learning of polarization contrast patterns on vertical/horizontal axes to the $45^\circ/135^\circ$ axes, octopuses recognized targets containing polarization contrasts at other e -vector angles, varying from 20° to 45° , which they had not encountered before. We therefore conclude that their choices were based solely on the presence or absence of differences in polarization between the center and outer

parts of the targets. This is the first demonstration of visual discrimination that is based solely on polarized light patterns.

Object detection based on polarization recognition may be the primary function of polarization vision in octopuses. Such a means of contrast enhancement could be used to detect and identify prey or to communicate with other octopuses. For example, our observations show that several species of crustaceans, which are preyed upon by octopuses, reflect light that is strongly polarized. The underwater polarized light field is only partially described (but see Waterman and Westell, 1956; Tyler, 1963; Horvath and Varju, 1995), and study of the polarization of light reflected from objects in the marine environment is just beginning (e.g. Cariou *et al.* 1990). Nevertheless, polarization-based object recognition could increase the range of detection compared with the use of unpolarized light cues alone (Lythgoe and Hemming, 1967). Polarization vision, like color vision, may also be used for enhancement of borders and for breaking camouflage (Bernard and Wehner, 1977). Under water, the wavelength spectrum reflected from an object varies with depth, while the reflected *e*-vector orientation remains relatively constant, and the percentage polarization of the background scattered light is high even at depths exceeding 50 m (Waterman, 1955; Tyler, 1963). Therefore, polarization sensitivity may serve as a reliable means of object identification.

Our experiments demonstrate one expression of sensitivity to linearly polarized light, namely sensitivity to features in the orientation of polarization. Polarization sensitivity, or polarization vision, is likely also to include the ability to discriminate between polarized and depolarized light, between differences in the partial polarization of the light arriving from different objects and, possibly, even the ability to integrate and compare these aspects of polarization.

We predict that the use of polarization sensitivity for object detection and identification will be found in other species of marine animals and possibly in terrestrial species as well.

We thank J. D. Robertson of the Department of Anatomy, Duke University and the Duke University Marine Laboratory Beaufort, NC, USA, for the use of his octopus maintenance and training facilities, and D. R. Murlless for his invaluable help throughout this study. G. D. Bernard, R. L. Caldwell, M. F. Land, J. B. Messenger and two anonymous referees all provided helpful comments on the manuscript. This study was supported by NSF grants no. BNS-8917183 and BIR-9317927.

References

- AUBURN, J. S. AND TAYLOR, D. J. (1979). Polarized light perception and orientation in larval bullfrogs *Rana catesbeiana*. *Anim. Behav.* **27**, 658–688.
- BANDAI, K., ARIKAWA, K. AND EGUCHI, E. (1992). Localization of spectral receptors in the ommatidium of a butterfly compound eye determined by polarization sensitivity. *J. comp. Physiol. A* **171**, 289–297.
- BERNARD, G. D. AND WEHNER, R. (1977). Functional similarities between polarization vision and color vision. *Vision Res.* **17**, 1019–1028.
- CAMERON, D. A. AND PUGH, E. N. (1991). Double cones as a basis for new type of polarization vision in vertebrates. *Nature* **353**, 161–164.
- CARIOU, J., JEUNE, B. L., LOTRIAN, J. AND GUERN, Y. (1990). Polarization effects of seawater and underwater targets. *Appl. Opt.* **29**, 1689–1695.
- CRONIN, T. W., SHASHAR, N. AND WOLFF, L. (1994). Portable imaging polarimeters. *Proceedings of the 12th International Congress on Pattern Recognition*. pp. 606–609.
- GIBBONS, J. D. (1976). *Nonparametric Methods for Quantitative Analysis*. New York: Holt, Rinehart and Winston.
- HAWRYSHYN, C. W. (1992). Polarization vision in fish. *Am. Sci.* **80**, 164–176.
- 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.
- JANDER, R., DAUMER, K. AND WATERMAN, T. H. (1963). Polarized light orientation in two Hawaiian cephalopods. *Z. vergl. Physiol.* **46**, 383–394.
- LAND, M. (1993). Old twist in a new tale. *Nature* **363**, 581–582.
- LYTHGOE, J. N. AND HEMMING, C. C. (1967). Polarized light and underwater vision. *Nature* **213**, 893–894.
- MARTIN, G. R. (1991). The question of polarization. *Nature* **350**, 194.
- MATHER, J. A. AND ANDERSON, R. C. (1993). Personalities of octopuses (*Octopus rubescens*). *J. comp. Psychol.* **107**, 336–340.
- 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.
- MUNTZ, W. R. A. AND GWYTHYR, J. (1988). Visual acuity in *Octopus pallidus* and *Octopus australis*. *J. exp. Biol.* **134**, 119–129.
- NILSSON, D. E., LABHART, T. AND MEYER, E. (1987). Photoreceptor design and optical properties affecting polarization sensitivity in ants and crickets. *J. comp. Physiol. A* **161**, 645–658.
- PACKARD, A. (1969). Visual acuity and eye growth in *Octopus vulgaris* (Lamarck). *Monitore zool. Ital.* **3**, 19–32.
- PHILLIPS, J. B. AND MOORE, F. R. (1992). Calibration of the sun compass by sunset polarized light patterns in a migratory bird. *Behav. Ecol. Sociobiol.* **31**, 189–193.
- PHILLIPSBORN, A. AND LABHART, T. (1990). A behavioral study of polarization vision in the fly *Musca domestica*. *J. comp. Physiol. A* **167**, 737–743.
- ROSSEL, S. (1993). Navigation by bees using polarized skylight. *Comp. Biochem. Physiol. A* **104**, 695–708.
- 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. (1984). Evidence for true polarization vision based on a two-channel analyzer system in the eye of the water bug *Notonecta glauca*. *J. comp. Physiol. A* **154**, 53–57.
- SCHWIND, R. (1991). Polarization vision in water insects and insects living on moist substrate. *J. comp. Physiol. A* **169**, 531–540.
- SHASHAR, N., CRONIN, T. W., JOHNSON, G. AND WOLFF, L. (1995).

- Portable imaging polarized light analyzer. *Proceedings of the 9th Meeting on Optical Engineering in Israel. SPIE* **2426**, 28–35.
- SNYDER, A. W. AND LAUGHLIN, S. B. (1975). Dichroism and absorption by photoreceptors. *J. comp. Physiol. A* **100**, 101–116.
- SUTHERLAND, N. S. (1963). Visual acuity and discrimination of stripe widths in *Octopus vulgaris* Lamarck. *Pubbl. Staz. zool., Napoli* **33**, 92–109.
- 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.
- TYLER, J. E. (1963). Estimation of per cent polarization in deep oceanic water. *J. mar. Res.* **21**, 102–109.
- WATERMAN, T. H. (1955). Polarization scattered sunlight in deep water. *Deep Sea Res.* **3**, 426–434.
- 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. (1984). Natural polarized light and vision. In *Photoreception and Vision in Invertebrates* (ed. M. A. Ali), pp. 63–114. New York: Plenum Press.
- WATERMAN, T. H. (1988). Polarization of marine light fields and animal orientation. *SPIE* **925**, 431–437.
- 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.
- WEHNER, R. AND BERNARD, G. D. (1993). Photoreceptor twist: A solution to the false-color problem. *Proc. natn. Acad. Sci. U.S.A.* **90**, 4132–4135.
- WELLS, M. J. (1978). *Octopus*. London: Chapman & Hall.