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Polarization sensitivity in two species of cuttlefish – *Sepia plangon* (Gray 1849) and *Sepia mestus* (Gray 1849) – demonstrated with polarized optomotor stimuli

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SUMMARY

The existence of polarization sensitivity (PS), most likely resulting from the orthogonal arrangement of microvilli in photoreceptors, has been proposed in cephalopods for some time, although it has rarely been examined behaviourally. Here, we tested the mourning cuttlefish, *Sepia plangon*, and the reaper cuttlefish, *Sepia mestus*, for polarization sensitivity using a large-field optomotor stimulus containing polarization contrast. Polaroid filter drums with stripes producing alternating e-vectors were rotated around free-moving animals. Polarized optomotor responses were displayed, and these responses were similar to those performed in response to a black-and-white, vertically-striped drum, whereas no responses were displayed to a plain polarizing control drum producing just a vertical e-vector. This indicates that the animals are able to see the contrast between adjacent stripes in the polarizing drum. To our knowledge, this is the first demonstration of functional polarization sensitivity in cuttlefish.

Key words: *Sepia plangon*, *Sepia mestus*, optomotor response, optomotor apparatus, Polaroid, polarization sensitivity.

INTRODUCTION

The coleoid cephalopods (octopus, cuttlefish and squid) are a highly advanced group of marine molluscs, possessing a remarkable and complex visual system sensitive to the e-vector of polarized light (Moody and Parriss, 1961; Shashar et al., 1996; Shashar et al., 2000; Shashar et al., 2001b). Their eyes are strikingly similar in structure to the vertebrate teleost eye – an example of convergent evolution despite the two groups possessing no common ancestors (Muntz, 1999). These voracious predators rely substantially on their keen sense of vision to perform accurate predatory behaviours and predator-avoidance tactics, including their famous ability for camouflage (Hanlon and Messenger, 1988; Chiao and Hanlon, 2001).

Polarized light

Multidirectional e-vectors of light from the sun can become orientated, or polarized, into a single vibrational plane when they are reflected, refracted or scattered off or through certain objects (Nilsson and Warrant, 1999; Cronin and Shashar, 2001; Wehner, 2001; Sabbah et al., 2005). Such objects can include the ocean surface, the scales of fish or transparent zooplankton such as jellyfish and larvae (Cronin and Shashar, 2001; Marshall et al., 1999). The orientation of the resulting vibrational plane is referred to as the e-vector of polarization (Wehner, 2001).

Most coleoid cephalopods so far examined by the authors possess the structures necessary for polarization sensitivity (PS) within their retinae (C.M.T. and J.M., unpublished observations). Photoreceptor cells possess two sets of microvilli on opposite sides, called rhabdomeres. The rhabdomeres on one photoreceptor sit orthogonally to the rhabdomeres on adjacent photoreceptors. This arrangement allows sensitivity to e-vectors vibrating on axes parallel to those of the microvilli, and most likely parallel to the rhodopsin photopigment molecules within the microvillar membranes (Moody and Parriss, 1960; Young, 1960; Moody and Parriss, 1961; Saidel et al., 1983; Saibil et al., 1995; Nilsson and Warrant, 1999; Shashar et al., 2001b; Yamamoto et al., 1965). The array of orthogonal microvilli is arranged primarily along horizontal and vertical axes, suggesting strongest sensitivity to horizontal and vertical e-vectors (Young, 1962).

Polarization-sensitive animals such as some fish (Hawryshyn et al., 2002), crustaceans (Marshall et al., 1999) and cephalopods (Young, 1960; Saibil, 1982; Hanlon and Messenger, 1996) might use PS to break the camouflage of transparent objects (Shashar et al., 1998; Shashar et al., 2000; Shashar et al., 2001b), navigate throughout the ocean (Jander et al., 1963; Waterman, 1988; Wehner, 2001) and communicate with conspecifics (Shashar et al., 1996; Shashar et al., 2001a; Shashar et al., 2001b; Boal et al., 2004; Mäthger and Hanlon, 2006). A polarization-sensitive visual system can decrease the confounding effects of light scattering that occurs between an individual and another object and between that object and its surroundings (Cronin and Shashar, 2001). Furthermore, some animals possess body parts capable of reflecting polarized light, which could be a mode of communication with intra-specifics and other polarization-sensitive species (Shashar et al., 1996; Shashar et al., 2001a; Mäthger and Hanlon, 2006). For example, the antennae and telson of stomatopod crustaceans can reflect polarized light (Marshall et al., 1999; Cronin et al., 2003), as can the iridescent iridophores in the skin of the arms, head and body of some cephalopods (Shashar et al., 1996; Shashar and Hanlon, 1997).

Visual responses to large-field stimuli

Visual acuity, light/dark-adapted vision and responses to large-field stimuli have been tested previously in many animals, including cuttlefish, using an optomotor apparatus (Collewijn, 1970; Messenger, 1970; Groeger et al., 2005). The innate tendency to stabilize a moving image on the retina elicits a visual response, such as tracking or nystagmus (Walls, 1962; Carpenter, 1988; Land, 1999). This is usually

achieved by rotating a black-and-white, vertically striped drum around a free-moving or fixed animal. The high level of contrast between adjacent stripes on the drum elicits a visual response as the animal perceives movement of its whole or extended visual field. Test subjects can respond by: performing an optomotor response (OMR), whereby first the eyes, head and then the body follow the movement of the rotating visual field (Messenger, 1970) when the animal is allowed to move freely (Groeger et al., 2005); alternatively, they can display an optokinetic response (OKR) – a movement typical of animals that sit (or are held) stationary. A common OKR is nystagmus, whereby the eyes repeatedly follow the movement of the stimulus in the same direction at about the same speed (slow phase), then snap back in the opposite direction (fast phase), momentarily blurring the image (Walls, 1962; Horridge and Sanderman, 1964; Collewijn, 1970; Fritsches and Marshall, 2002). Using this technique, the acuity limits of the visual system of an animal can be tested by narrowing the width of, or decreasing the contrast between, adjacent stripes, altering the lighting/visibility conditions and changing the angular velocity of drum rotation.

Based on this idea, we created a drum to test for PS using a polarizing filter that produced contrasting e-vectors only detectable by a polarization-sensitive visual system. Similar tests have been conducted on some arthropod species, including some crustaceans and insects, yielding mixed results [for a full list, see Waterman (Waterman, 1981)]. Maximum contrast was obtained by having stripes of Polaroid, with alternating e-vectors set at 90 deg to one another. Thus, if the test animal was polarization sensitive, a rotating, cross-polarizing visual field should produce the same stimulus as a rotating black-and-white visual field, eliciting an OMR. Although past studies have conducted OMR tests on some species of cuttlefish, these tests used either just black-and-white stimuli (Collewijn, 1970; Groeger et al., 2005) to elicit OMRs or obtained no responses to polarizing stimuli (Darmaillacq and Shashar, 2008). Here, we show for the first time a positive OMR to polarized stimuli from two species of cuttlefish.

MATERIALS AND METHODS

All experiments were performed in accordance with: the University of Queensland Animal Ethics Committee, permit number SBS/738/08/ARC; Moreton Bay Marine Parks Regulation Permit, permit number QS2008/CVL625; and Queensland Government Department of Primary Industries and Fisheries, permit number 55604.

Test species

The species used in this study were the mourning cuttlefish, *Sepia plangon*, and the reaper cuttlefish, *Sepia mestus* (Fig. 1A,B), obtained from both a commercial supplier and private capture using sein nets in Moreton Bay, Queensland, Australia, between March 2007 and July 2008. Three specimens of each species were used. Both of these species inhabit shallow inter-tidal seagrass beds and mudflats (Norman and Debelius, 2000). Animals were kept at Moreton Bay Research Station at Dunwich, North Stradbroke Island, Queensland, Australia, in covered tanks with segregated circulation, and they were fed small crustaceans and pilchard pieces. The specimens used had mantle lengths of 8–15 cm. This size ensured that the animals could fit comfortably inside the optomotor apparatus.

Optomotor measuring apparatus

Three drums were used in this study (Fig. 2).

Control Drum 1

This was a black-and-white, vertically striped drum. The stripes were 2.5 cm in thickness [a width similar to that which has been used previously to elicit OKRs in other cephalopod species (Groeger et al., 2005)]. Black stripes were printed onto white paper, which was laminated for waterproofing and, using clear sticky tape, folded into a drum of height 30 cm and diameter 36 cm. This drum was used to demonstrate the classic OMR, as previously shown in cephalopods in studies by Collewijn (Collewijn, 1970), Messenger (Messenger, 1970) and Groeger and colleagues (Groeger et al., 2005).

Control Drum 2

This drum was constructed using a sheet of plain linear Polaroid filter of transmission 38% for wavelengths between 400 and 760 nm, with at least 99% transmission efficiency (American Polarizers, Reading, PA, USA) and produced only a vertical (0°) e-vector. This filter was suitable as it transmits light in a range that is detectable by the coleoid visual system, which peaks in sensitivity to light in the range 470–500 nm. Using clear sticky tape, it was folded into a drum of height 43 cm and diameter 36 cm. A layer of white paper was also used to line the back of this drum to act as a diffuser for light entering the drum from external sources, helping to provide a constant level of illumination in the background. The purpose of Control 2 was to ensure that animals were not responding to any imperfections in the test drum that might evoke an OMR during drum rotation, such as the edges of the Polaroid stripes and the joint in the drum.

Test Drum

This drum was constructed using a sheet of 'Polarmotion' linear Polaroid filter containing 2.5 cm thick, alternating, vertical stripes with e-vector angles set at 0 deg, 45 deg, 90 deg and 135 deg, respectively (American Polarizers). Using clear sticky tape, the sheet, which was lined with white paper from the manufacturer and thus acted as a diffuser, was folded into a drum of height 43 cm and diameter 36 cm. If animals did not respond to Control Drum 2 but responded positively to the Test drum, it could be concluded that an OMR was elicited in response to the contrast produced by the alternating e-vectors in this drum.

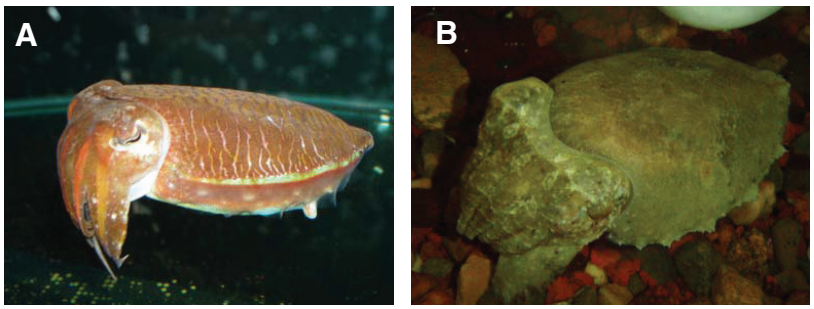

Fig. 1. (A) The study species *S. plangon* and (B) *S. mestus*, caught in seagrass beds and mudflats in Moreton Bay, Queensland, Australia.

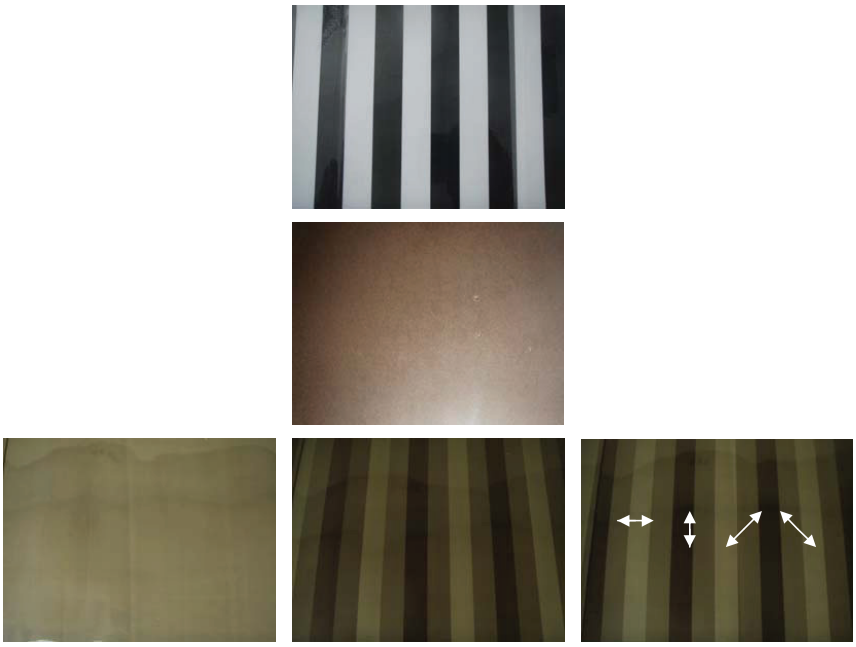

Fig. 2. The three drums used in this study: Control Drum 1 (top), Control Drum 2 (middle) and Test Drum (bottom row). These pictures show the drums as they would appear when looking with nonpolarization sensitivity (top, middle and bottom left), looking through a piece of Polaroid filter (orientated vertically – bottom middle, and orientated horizontally – bottom right). The contrast made between adjacent stripes in the test drum can be seen looking through a Polaroid filter. The e-vectors produced by each stripe in the test drum are 0 deg, 45 deg, 90 deg and 135 deg, indicated by the arrows.

The apparatus (Fig. 3) was constructed using a clear, Plexiglas cylindrical tank (height 24 cm, diameter 30 cm) containing a thin layer of sand, set atop a stationary disc. Below this sat a rotating disc with a frame mounted to its edge – this frame held each drum in place as it rotated around the tank. This rotating disc was powered by a 12 V motor through a rubber ring conveyer belt wrapped around its edge.

External light sources (EK-1 Fibre Optic Light, Euromex, Arnhem, The Netherlands) provided extra illumination through the drums to maximise the apparent contrast between the stripes. A hand-held video camcorder (Sony HDR-SR11) was mounted onto a tripod and positioned directly above the apparatus to capture the responses of the animals at 25 frames s^{-1}.

An animal was placed into the apparatus and allowed to settle for up to 5 min (indicated by cessation of movement). The external lights were then switched on. Drums were presented to each animal in random order. Each drum was rotated in one direction for 1 min, then reversed for 1 min, then reversed again for 1 min. The same process was repeated for the other two drums, which were used immediately one after the other. The drum was rotated at an angular velocity of 12 deg s^{-1}. This speed is known to elicit visual responses in *S. officinalis* using black-and-white striped drums (Collewijn, 1970).

OMR analysis

Video footage was analysed using Windows Movie Maker (Microsoft) and Adobe Premiere Elements (Adobe), which allowed footage to be viewed frame-by-frame. A positive OMR was one in which the animal moved in the same direction as the drum over at least a 90 deg turn. One sequence of a positive response was selected from each animal's time in the apparatus for use in this paper. The angular velocity of rotation of the drum was measured against the movement of the long axis of each animal in degrees (Fig. 4) by using a protractor placed over the computer screen. A vertical line was used as a standard reference against which all measurements were recorded. One measurement for the animal and the drum was taken every five frames for the duration of the OMR movement (five measurements per second). These values were then used to obtain the gain of each response.

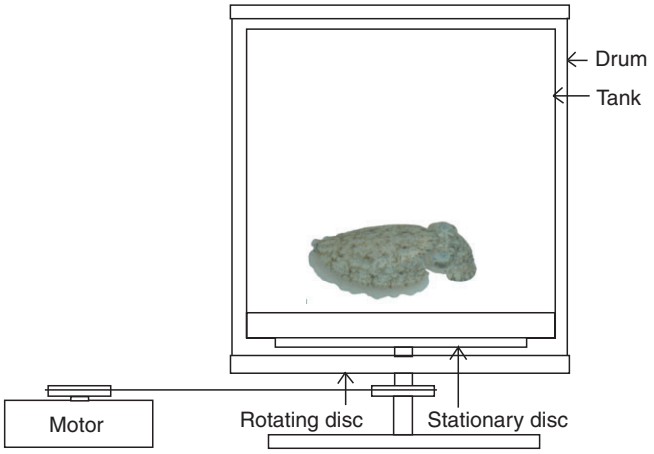

Fig. 3. A schematic diagram of the optomotor apparatus.

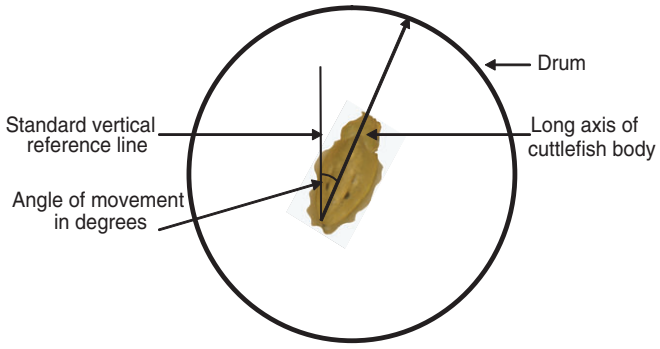

Fig. 4. The method for calculating each OMR: the long axis of each cuttlefish was used to measure its movement, in degrees, against a standard vertical reference.

Table 1. Summary of OMRs for each animal in response to each stimulus drum

	Black-and-white Control Drum 1		Plain linear Polaroid Control Drum 2		Polarizing-striped Test Drum	
	Response	Time spent (s) responding positively out of 180 s	Response	Time spent (s) responding positively out of 180 s	Response	Time spent (s) responding positively out of 180 s
S. plangon 1	Yes	45	No	0	Yes	40
S. plangon 2	Yes	10	No	0	No	0
S. plangon 3	Yes	26	No	0	Yes	51
S. mestus 1	Yes	130	No	0	Yes	53
S. mestus 2	No	0	No	0	Yes	90
S. mestus 3	Yes	67	No	0	Yes	30

It should be noted that each animal was tested once per stimulus in the apparatus to avoid habituation, and, despite multiple positive responses during each trial, only one positive response was selected per animal per trial to display in the results. These animals tend to be somewhat 'moody' in their behaviour and do not always respond to even the most basic stimuli. Thus, the following criteria were used to judge responses for analysis: whether the animal responded to the stimulus, and, if so, how long they spent responding positively to the stimulus (over at least a 90 deg turn in the same direction as the stimulus).

Gain

The gain [movement of animal/movement of drum in degrees per second – adapted from Collewijn (Collewijn, 1970)] was calculated for the response of each animal to each drum. A strong, positive OMR produces a gain value close to one (1), indicating that the animal is moving at about the same angular velocity as the drum (Horridge and Sandeman, 1964). The highest and lowest values from the OMRs of each animal (in degrees) were used to calculate the gain.

RESULTS

The results are summarized in Table 1 and show whether each animal responded to the stimulus, and, if so, how long they spent responding positively.

Two of the three *S. mestus* and two of the three *S. plangon* performed strong OMRs to Control 1. The third *S. plangon* performed one weak OMR, although it did not fit the criteria of at least a 90 deg rotation in the same direction as the drum. An example of an OMR performed by one representative of each species in response to Control 1 is shown in Fig. 5. Here, *S. mestus* responds to the drum as it goes from a stationary position, to rotating, followed by a change in direction. *S. plangon* can be seen responding to the drum just after a change in direction.

No animal responded to Control 2. Examples of this lack of response by one representative of each species are shown in Fig. 6. Although each of the six animals sat stationary, or moved randomly during drum rotation, no animals followed the movement of the drum over at least a 90 deg turn. Further to this, no whole-body optomotor nystagmic responses were observed either.

All *S. mestus* and two of the three *S. plangon* responded to the polarizing stimulus. Examples of an OMR performed by one representative of each species are shown in Fig. 7. This figure shows *S. mestus* following the movement of the drum in one direction, then changing direction following a short delay after the drum changed direction. *S. plangon* performed similarly, although interestingly there are three shorter OMRs separated by small movements in the opposite direction to drum rotation. This response is termed whole-body optomotor nystagmus, and each movement in the same direction to that of the stimulus was used to calculate the gain. The OMRs observed for the Test drum were not found to be statistically significantly different to those obtained in response to Control 1 [Welch two-sample *t*-test, P=0.944, CI=95% (R Development Core Team, 2010)].

Gains were calculated to compare the speed of movement of the animals with that of the drums (Table 2). These values were obtained from the results in Figs 5–7, whereby the average of each OMR was taken. Values approaching one (1) indicate a positive OMR in which the animal is moving slightly slower than the rotating drum. Here, *S. mestus* performed OMRs slightly slower than the speed of Control 1 and the Test Drum, whereas *S. plangon* performed OMRs slightly faster than the speed of the same drums.

DISCUSSION

All *S. mestus* and two of the three *S. plangon* displayed an OMR when presented with the polarizing stimulus. These responses were similar to those performed in response to Control 1 – a black-and-white striped stimulus. No response was performed in response to Control 2 – a plain Polaroid stimulus – thus it was concluded that *S. plangon* and *S. mestus* were responding to the alternating 0 deg,

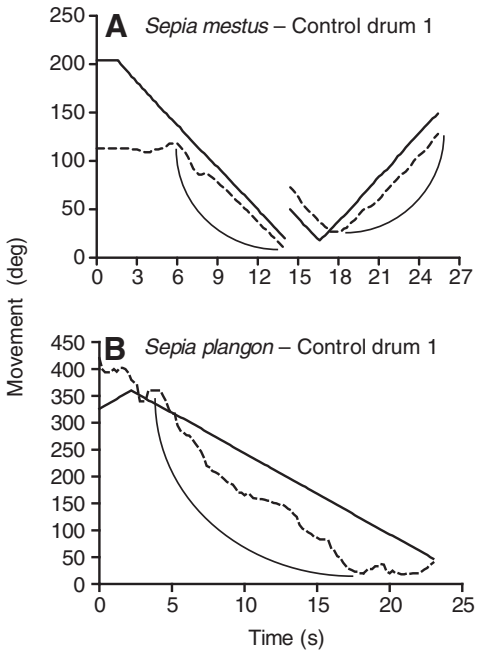

Fig. 5. The OMRs that (A) one *S. mestus* and (B) one *S. plangon* performed in response to Control 1 – a black-and-white vertically striped visual field. The dashed lines represent the movement of the animals; the solid lines represent the movement of the drum. The arc(s) encompass the OMR(s) used to calculate the gain. The gains of multiple OMRs were averaged.

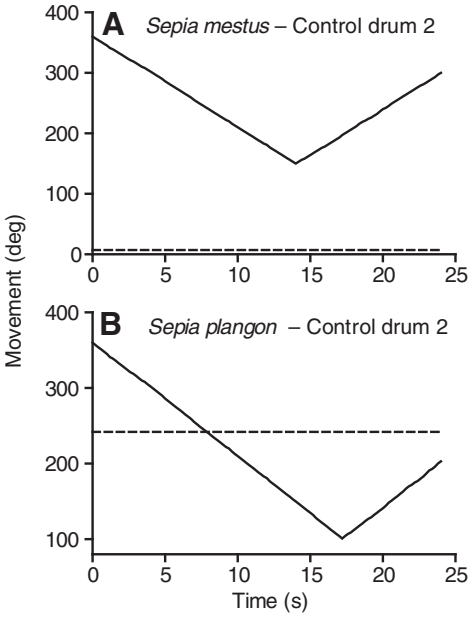

Fig. 6. No animal responded to Control 2 – a plain linear Polaroid filter. (A) and (B) show an example of the lack of response. The dashed lines represent the movement of the animals; the solid lines represent the movement of the drum.

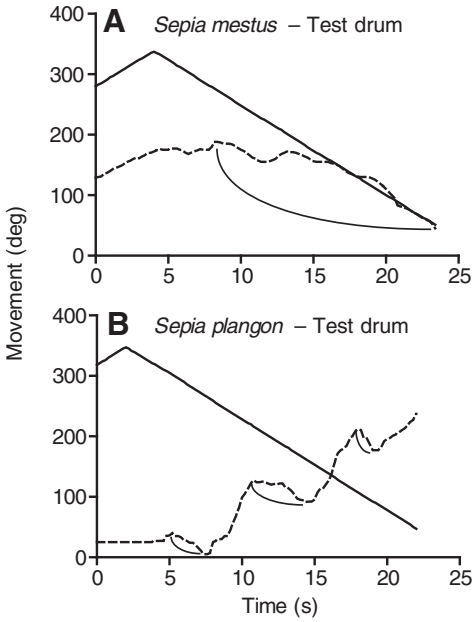

Fig. 7. The response of (A) one *S. mestus* and (B) one *S. plangon* to the test drum comprising cross-polarizing stripes. Note that the OMR from *S. plangon* is an example of whole-body optomotor nystagmus. The dashed lines represent the movement of the animals; the solid lines represent the movement of the drum. The arc(s) encompass the OMR(s) used to calculate the gain. The gains of multiple OMRs were averaged.

45 deg, 90 deg and 135 deg e-vectors in the Test drum. To our knowledge, this is the first demonstration of functional PS in any species of coleoid cephalopod using the OMR technique.

Interestingly, a similar study conducted by Darmaillacq and Shashar (Darmaillacq and Shashar, 2008) observed no OMR in the cuttlefish *S. elongata* using the same 0 deg, 45 deg, 90 deg and 135 deg polarizing striped drum. Although *S. elongata* did perform OMRs to black-and-white and grey-scale striped drums, these authors concluded that a lack of OMR to their polarizing drum was either an indication of an absence of PS or an indication that polarized signals are processed differently, and perhaps separately, to contrast signals and do not elicit OMRs. Thus, combining both signals into one polarized stimulus yielded no results.

In this study, *S. plangon* and *S. mestus* both responded positively to the test drum. This suggests that there is either an inter-species discrepancy in behavioural responses to large-field stimuli or it might simply be a result of *S. elongata* becoming stressed from being placed into the experimental apparatus, despite being given time to acclimatize in both studies. All three species possess the structures necessary for PS, and therefore these confounding results imply a behavioural or physiological difference that will have to be investigated in further studies.

It has also been suggested that there are ontogenetic differences in visual responses to large-field movements. It is probably more important for juveniles to maintain a state of crypsis during environmental disturbances compared with larger, mature individuals (Hanlon and Messenger, 1996; Barbosa et al., 2007). Perhaps there exists a threshold beyond which an OMR response is elicited, depending on the age and/or size of the individual, or level of disturbance. This was evident here when juvenile *S. mestus* gave no response to any optomotor drum in this study, instead maintaining a state of camouflage against the sandy substrate (C.M.T. and J.M., unpublished observations). This characteristic will also be investigated in future studies.

The strong OMRs observed in this study are typical of active, free-swimming animals such as fish (Walls, 1962) and cuttlefish. OKRs have also been observed in some species of cephalopod, such as *S. officinalis* (Collewijn, 1970), *Octopus tetricus* and *Sepioloidea lineolata* (C.M.T. and J.M., unpublished observations). They are also commonly seen in some teleost fish that exhibit independent eye movements, such as the sandperch and pipefish (Fritsches, 1999). Animals that tend to remain stationary for long periods of time, such as during periods of camouflage or crypsis, probably rely more on eye movements than whole-body movements and thus are likely to perform OKRs and not OMRs. This has been observed in *O. tetricus* and other octopuses, and *S. lineolata*, which typically buries itself in the substrate, leaving just the eyes exposed (C.M.T. and J.M., unpublished observations). Restriction of body movement of more active species might result in OKRs, and this has been demonstrated in *Sepia officinalis* (Collewijn, 1970). In Fig. 7B, *S. plangon* makes short movements in the opposite direction in between OMRs, referred to here as whole-body optomotor nystagmus. These responses, like typical OKRs, are artifacts of image slip on the retina. Where stationary or movement-restricted subjects perform anti-compensatory eye movements in the opposite

Table 2. Gain values of the OMRs of two animals from Figs 5 and 6

Test animal	Control Drum 1	Control Drum 2	Test Drum
S. plangon (*N*=1)	1.09	0	1.31
S. mestus (*N*=1)	0.9	0	0.7

Note that, as no responses were recorded for Control Drum 2, the gain for each is zero (0).

direction of stimulus movement to account for image slip, the free-moving subject here performed whole-body anti-compensatory movements in the opposite direction to the stimulus. Although the response shown in Fig. 7B was not a standard, criteria-based response compared with the others, it was an interesting result not observed in any other subject and is possibly a result of the vestibular sensory system overriding the optomotor system and responding to the moving large-field stimulus itself. Why the animal would do this when it could simply keep following the stimulus is not known; however, this response was still considered a positive OMR as the anti-compensatory movements in the reverse direction re-set the optomotor response system of the animal, resulting in movement in the same direction again (in the same way as the optokinetic response does).

In relation to the somewhat short and 'jittery' durations of some of the positive responses to the drums, it is worth noting that these animals, which are not necessarily hard-wired for consistent whole-field visual responses and can be periodic in their behaviour, did in fact spend considerable amounts of time not responding positively inside the apparatus. Instead, they appeared to spend time stabilizing themselves on the bottom of the tank, jetting backwards and forwards or fixating on other external stimuli, or, when they were responding, their movements were not always completely smooth. Such behaviour has been observed in similar tests on other animals (Horridge, 1966; Barnes and Horridge, 1969; Nalbach and Nalbach, 1987; Cronin et al., 1991; Mather, 2008). Thus, we have not measured or shown the angular results of these irrelevant movements. The durations of their positive responses were similar for both the black-and-white Control Drum and the striped-polarized Test Drum, and this was confirmed statistically. Here, the responses to the striped polarized drum do demonstrate a behavioural response to polarized light. However, to extrapolate on these findings and achieve a more detailed investigation into the mechanics behind this system, future tests using polarized stimuli with changing parameters should be conducted. Tests could include varying the stripe-width and rotational velocity of the drums and comparing those responses with nonpolarized controls.

Gain

The gains recorded from *S. mestus* in response to Control 1 and the Test drum were below one, indicating that the cuttlefish were following the rotating drums at a slightly slower speed. This is due to image slip on the retina, resulting in the animal lagging behind as it followed the moving stripes. Such gains of around 0.4 have also been observed in optokinetic tests on *S. officinalis* at similar speeds to this study – 12 deg s^{-1} (Collewijn, 1970) – and, in some cases, were even lower. Retinal slip is necessary in order to stimulate the eye and elicit a visual response (Horridge and Sandeman, 1964). *S. plangon* gave slightly faster gain values for Control 1 and the Test drum, indicating that it was moving slightly faster than the drums. This is possibly due to momentum generated while rotating around the tank. This anomaly can now be examined further by varying the angular velocity of drum rotation to determine whether these results were obtained owing to differences in how each species processes large-field stimuli or whether it was simply a result of momentum.

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LIST OF ABBREVIATIONS

OMR	optomotor response
OKR	optokinetic response
PS	polarization sensitivity

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