Research

Behavioural relevance of polarization sensitivity as a target detection mechanism in cephalopods and fishes

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Aquatic habitats are rich in polarized patterns that could provide valuable information about the environment to an animal with a visual system sensitive to polarization of light. Both cephalopods and fishes have been shown to behaviourally respond to polarized light cues, suggesting that polarization sensitivity (PS) may play a role in improving target detection and/or navigation/orientation. However, while there is general agreement concerning the presence of PS in cephalopods and some fish species, its functional significance remains uncertain. Testing the role of PS in predator or prey detection seems an excellent paradigm with which to study the contribution of PS to the sensory assets of both groups, because such behaviours are critical to survival. We developed a novel experimental set-up to deliver computer-generated, controllable, polarized stimuli to free-swimming cephalopods and fishes with which we tested the behavioural relevance of PS using stimuli that evoke innate responses (such as an escape response from a looming stimulus and a pursuing behaviour of a small prey-like stimulus). We report consistent responses of cephalopods to looming stimuli presented in polarization and luminance contrast; however, none of the fishes tested responded to either the looming or the prey-like stimuli when presented in polarization contrast.

Keywords: startle response; LCD; goldfish; zebrafish; squid; cuttlefish

1. INTRODUCTION

(a) *Polarization sensitivity as a sensory modality in the aquatic environment*

Aquatic environments are rich in polarized light patterns, which are the result of scattering within the water column, reflections from the body surface of many organisms and celestial light visible below the water's surface through Snell's window [1–3]. These patterns contain information regarding the position of the Sun and the presence of reflective objects, and create a background polarization field against which objects, which diffuse or differentially reflect polarized light, can be viewed. To an animal with a visual system sensitive to polarized light, these cues could provide valuable information about its environment and be useful for navigation and target detection [4,5].

The theoretical advantages of polarization sensitivity (PS) for target detection derive mainly from the potential of breaking the radiance matching-based camouflage that many marine organisms use to reduce their conspicuousness against the background illumination [6–8]. Fish scales have been shown to produce polarized reflections [9,10] and organisms with transparent bodies often refract/reflect the background light producing polarized patterns that could make them conspicuous against a uniformly polarized background. There are also circumstances under which luminosity and chromatic signals are unreliable, for example when surface waves focus and defocus the Sun's rays varying the light intensity both temporally and spatially, thereby reducing the effectiveness of discriminating objects on the basis of luminosity contrast [11]. Additionally, in many aquatic habitats, water and particulate matter filter the light, thus narrowing the range of wavelengths useful for vision and reducing the effectiveness of discriminating objects on the basis of hue [12]. Polarization patterns may therefore provide a more reliable channel for the detection of predators and prey in conditions where luminance or chromatic signals do not contain sufficient or reliable visual contrast.

PS has been found in both cephalopods and fishes, many of which share similar ecological niches and perform similar visual tasks. However, the mechanisms mediating PS in cephalopods and fishes differ. Cephalopods are known to be sensitive to linearly polarized light based on the orthogonal arrangement of microvilli in their photosensitive rhabdoms [13–15]. However, in fishes, with the exception of the anchovy (*Anchoa mitchilli*, Valenciennes, 1848) where the axial orientation of photoreceptor outer segment lamellae provide the basis for the detection of polarized light, PS is reported to be based on a complex interaction between ultraviolet (UV) cones and double cones that are organized in a regular square mosaic [16–20]. Both cephalopods and fishes have been shown behaviourally to respond to various types of polarized light cues, and it is thought that PS may play a role in improving the detection of small prey items, in navigation/orientation and in intraspecific communication [21–28]. However, while there is general agreement concerning the presence of PS in cephalopods and some species of fishes, its functional significance remains uncertain.

Testing the role of PS in predator or prey detection is an excellent paradigm in which to study the contribution of PS to the sensory armoury of both cephalopods and fishes, because such fundamental behaviours are critical to survival. However, creating dynamic polarized stimuli that are free of confounding luminance and chromatic cues has previously been a limiting factor. To overcome this problem, we have developed an experimental set-up based on the use of a modified liquid crystal display (LCD) monitor to deliver computer-generated, controlled polarized stimuli to free-swimming fishes and cephalopods and, as shown in previous literature, this system is intrinsically free from luminance bias [29]. We have tested the behavioural relevance of PS using stimuli that evoke innate responses such as an escape response from a looming (large rapidly approaching) stimulus and a pursuing behaviour of small moving (prey-like) stimulus. Our hypothesis is that if behaviourally appropriate innate responses can be evoked by stimuli that are produced using only polarization contrast in the laboratory, then PS might play a role in the detection of such stimuli in the wild.

Here, we report responses of cephalopods to a looming stimulus presented in polarization contrast that were comparable to their responses to the same stimulus presented in black and white (luminance contrast). However, none of the cephalopods showed any interest in the prey-like stimuli in either polarization or luminance contrast. All of the fishes tested responded to one or both of the looming and prey-like stimuli when presented in luminance contrast, but none responded to either stimulus when presented in polarization contrast.

2. MATERIAL AND METHODS
(a) *Animal management and care*
Three cephalopod species, mourning cuttlefish (*Sepia plangon*, Gray 1849*)*, striped pyjama squid

(*Sepioloidea lineolata*, Quoy and Gaimard 1832) and bigfin squid (*Sepioteuthis lessoniana*, Lesson 1830), were caught in shallow waters off the west coast of Stradbroke Island, near Brisbane, Queensland, Australia, and tested within 24 h of capture. At least three specimens (5–15 cm mantle length) for each species were tested. Four species of fishes, two saltwater: blue-green damselfish (*Chromis viridis*, Cuvier, 1830) and Ambon damselfish (*Pomacentrus amboinensis*, Bleeker 1868) and two freshwater: goldfish (*Carassius auratus*, Linnaeus 1758) and zebrafish (*Danio rerio*, Hamilton 1822) were purchased from local pet suppliers and used in experiments. These species were chosen because they all possess UV cones in their retinas, which are reportedly critical for PS in fishes [20,27,30–32]. Five *C. viridis* (8–12 cm in length) and two *P. amboinensis* (8–14 cm in length) were tested. *Chromis viridis* was chosen because behavioural and electrophysiological evidence indicates that it is polarization sensitive [27,33]. *Pomacentrus amboinensis* were selected on the basis of strong responses to prey-like and looming stimuli, presented in black and white, on an LCD monitor, as well as their phylogenetic proximity to other pomacentrids thought to have PS [34]. Five *C. auratus* (4–8 cm in length) and eight *D. rerio* (3–4 cm in length) were tested. *Carassius auratus* were chosen because behavioural responses to polarized light have been reported previously [26,35,36]. *Danio rerio* were chosen because of their phylogenetic proximity to goldfish and their strong response to the looming stimulus presented in black and white.

Animals were housed in species-specific tanks and tested individually, except for *D. rerio*, and both species of damselfish, which were also tested in small groups. Holding tanks were illuminated by full-spectrum fluorescent lights on a 12 h light/dark cycle.

(b) *Dynamic polarized stimulus production with modified liquid crystal display*
A 270 × 340 mm LCD monitor (Viewmaster JM777, Hallmark Computer International, Australia) was used to deliver both luminance contrast- and polarization contrast-based stimuli to cephalopods and fishes. The LCD was disassembled from its original chassis and polarizers on both surfaces of the LCD were removed. A UV transmissive, polarizing sheet (BVO, Boulder, CO, USA) with an extinction ratio greater than 1000 : 1 was positioned at 45° from the normal direction of the liquid crystal, on the back (non-viewing surface) of the panel; the polarized field produced by the system was close to 100 per cent as the components of the LCD display do not depolarize the light. LCD electronics were encased in a waterproof box and re-connected to the LCD. The LCD was controlled by a PC laptop computer and used as a second monitor (figure 1). Polarized stimuli were generated as black and white images on the laptop screen and displayed as polarized images through the modified LCD where luminance contrast was substituted for contrast in e-vector orientations. As liquid crystals do not posses intrinsic dichroic
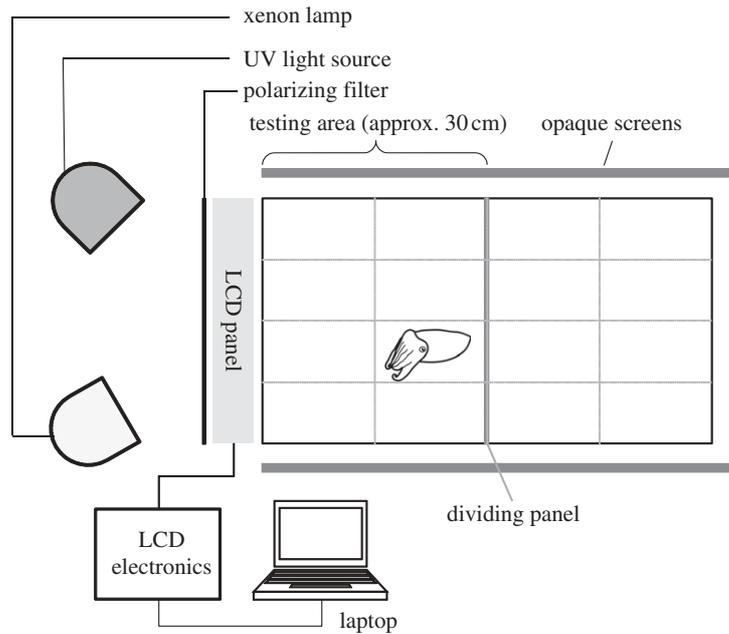
Figure 1. Overhead schematic diagram of the testing apparatus. Not to scale. Broad spectrum light is supplied as a combination of a xenon arc lamp and a UV fluorescent tube.

properties, the output of the LCD panel viewed without a polarizing filter appears as a homogeneously back-lit surface whose content is invisible to human eye.

To understand how we delivered polarized stimuli, it is helpful to briefly describe how the LCD functions. The LCD consists of a layer of twisted nematic liquid crystals that twist a quarter turn of a helix through the device. The liquid crystal layer is aligned between two orthogonal transparent substrates patterned with a thin-film transistor pixel array acting as the electrodes. Two linear polarizers are then attached to either side of the device at 90° orientation from each other. When diffuse light is passed through the back (first) polarizer, linearly polarized light enters the display. In the 'ON' bright state, the plane of polarization is rotated by 90° by the twisted nematic layer of the liquid crystal. In the 'OFF' dark state, an above-threshold voltage is applied to each pixel; the molecules then switch towards a homeotropic orientation reducing the guiding effect. The phase angle (e-vector orientation) of the transmitted polarization no longer matches the analyser orientation (positioned on the output/ viewing side of the screen) and less intensity is transmitted. Therefore, if the analyser is removed, the LCD can produce controllable variations in the angle of the plane of polarization (e-vector) detectable by a polarization-sensitive visual system.

We removed the standard fluorescent light source provided with the LCD and illuminated the device with a combination of a high-intensity discharge xenon arc lamp (3300 lm, 5000 K; Digitech) and UV fluorescent tubes (Philips PL-L 36W/O9N/4P behind a UV short-pass filter) projected onto a full-spectrum diffusing filter placed directly onto the initial polarizing filter. The combined light sources provided full-spectrum (350–800 nm) light (figure 2) and allowed

us to remove the UV component by switching off the UV light source independently from the xenon lamp.

(c) *Polarized output of the modified liquid crystal display*

We measured the linear contrast of the output of the modified LCD by comparing the 'black' with 'white' states. A portable fibre-optic spectrophotometer (S2000, Ocean Optics Inc., FL, USA) coupled with a rotatable linear polarizing filter was used to measure the normalized Stokes parameters, S_0, S_1, S_2 and S_3 as follows:

$$S_0, = 1;$$

$$S_1 = \frac{I(0^\circ) - I(90^\circ)}{I(0^\circ) + I(90^\circ)} \text{ and } S_2 = \frac{I(45^\circ) - I(135^\circ)}{I(45^\circ) + I(135^\circ)},$$

where $I(\theta^\circ)$ is the irradiance of the LCD measured through a polarizer oriented according the θ value; S_3 was calculated as the difference between $S_1^2 + S_2^2$ and S_0 assuming that

$$S_0 = \sqrt{S_1^2 + S_2^2 + S_3^2} = 1.$$

By choosing E_{0y} and E_{0x} as the respective perpendicular and parallel amplitude components of the e-vector in the plane perpendicular to the direction of light propagation, the angle α formed by the major axis of the ellipse and the (E_x, E_y)-coordinate system was calculated from the equation:

$$\tan 2\alpha = \frac{2E_{0x}E_{0y}}{E_{0x}^2 - E_{0y}^2}.$$

E_{0x} and E_{0y} can be expressed as a function of the Stokes parameters; therefore, we were able to estimate linear angular contrast between the black and white
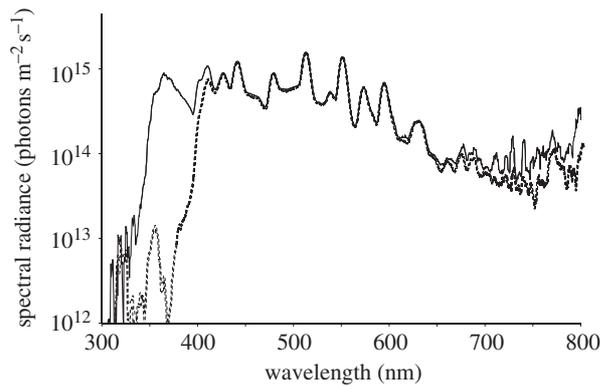
Figure 2. Spectral output of the modified LCD with UV (solid line) and without UV (dashed line) light source, measured through the UV transparent Plexiglas of the aquarium. The LCD was illuminated from behind with a high-intensity discharge (HID) arc lamp and a fluorescent UV light source (see text for details). Measurements were made using an Ocean Optics USB2000 spectrometer with a calibrated 400 μm, bare, UV + visible fibre (21° acceptance angle).

LCD states across all wavelengths used (figure 3). Linear polarization contrast averaged above $37.5°$ between 350 and 550 nm, which is as expected according to our set-up and the assumption that $S_0 = 1$.

The LCD monitor produces elliptically polarized light whose major axis is rotated according to the state of the LCD. The minor component of the signal that was not linear was not expected to be a problem since there is no evidence that fishes or cephalopods can discriminate handedness of circular/elliptical polarization. Mechanisms mediating PS in fishes and cephalopods are thought to provide a two-channel visual system with linear analysers capable of discriminating between different orientations of the major axes of different e-vectors; therefore, we characterized the polarization contrast of our LCD monitor as determined by the angular difference between the orientations of the major axes of the elliptical light.

(d) Stimuli

Two types of stimuli were produced (in Microsoft Office POWERPOINT 2003), a looming stimulus that was designed to simulate a rapidly approaching large object (predator), and a prey-like stimulus designed to simulate a small organism moving in a haphazard motion back and forth across the monitor. The looming stimulus consisted of a white screen in which a small black circle (2.0 cm diameter) appeared and rapidly expanded (in 0.5 s) to occupy half of the screen, and was intended to elicit a startle response. The prey-like stimulus consisted of a $0.5-2.0$ cm black circle (size covaried with animal size), on a white background, moving haphazardly across the screen and spanning it several times at a variable speed not exceeding 10 cm s^{-1}, and was meant to elicit a tracking/following response.

Stimuli were delivered as follows: all animals were first tested with black and white (luminance contrast) versions of the stimuli by placing a polarizer on the
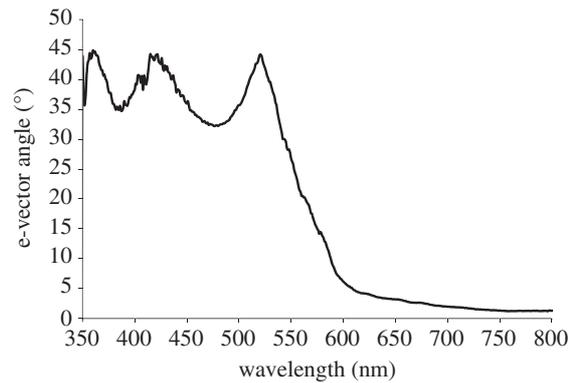

Figure 3. Maximum angular contrast produced by the LCD across the spectral output of the LCD. Contrast is estimated as the maximum angular difference between the major axes of the elliptical polarization produced by the LCD in the states 'white' and 'black'.

front, viewing side, of the modified LCD. When an animal responded to black and white versions of the stimuli, they were then tested using polarized-only versions (front polarizer removed). A blank screen was presented for at least 30 s before and after stimulus presentation. Stimulus delivery was automated to minimize external disturbance, and an interval of at least 2 min was left between test sessions.

(e) Experimental set-up

The experimental set-up comprised a rectangular tank (30 cm width, 60 cm length and 30 cm height) made of UV transparent Plexiglas, into which fishes were transferred and allowed to acclimatize for at least two days prior to testing (cephalopods were tested within 24 h of capture). The modified LCD was positioned on the narrow side of the tank, such that the modified LCD filled the entire field of view underwater (figure 1). Stimuli were presented when animals were approximately 20 cm from, and facing, the screen. Under these circumstances, the display occupied approximately 72° of the animal's visual field. Each animal was tested at least three times with each stimulus.

(i) Data scoring

Animal behaviours were recorded with digital video cameras in different configurations. Video footage was scored on a 21 inch CRT monitor using QUICKTIME (Apple). For each test session, the presence of the following behavioural variables was assessed at the onset of the stimuli for the cephalopods: (i) mantle pattern/texture change; ink release; swimming movement away from the screen; and for the fishes: (i) swimming movement away from the screen, (ii) swimming into the shelter, and (iii) following the moving target on screen. Scoring was done blind with respect to the type of stimuli (luminance contrast- or polarization contrast-based). In videos of the responses to the looming stimuli, the screen was not visible and stimulus onset was indicated by an acoustic signal recorded directly to the camera (not audible during trials). In videos of the responses to
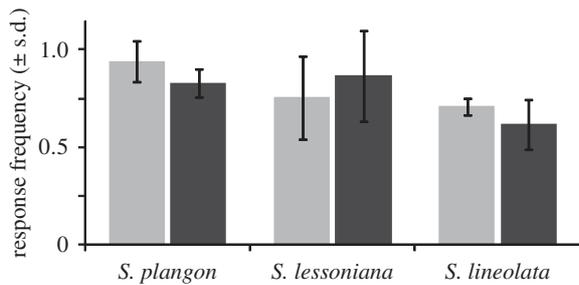
Figure 4. Frequency count of the behavioural responses of cephalopods to *stimulus* 1. Error bars represent 1 s.d. from the mean. Light grey bars represent the response frequency to luminance-based stimuli; dark grey bars represent response frequency to e-vector contrast-based stimuli.

the prey-like stimuli, the LCD panel was visible and the presence of a polarized filter on the camera lens permitted us to observe the location of the stimulus during movement. A positive response was recorded when animals presented one or a combination of the aforementioned behaviours. For prey-like stimuli, a positive response was reported when the animal closely followed the target movement on screen for at least 2 s. Response frequency to the various stimuli was recorded for each individual.

3. RESULTS

(a) *Cephalopods*

All three species of cephalopod responded strongly to a black and white version of the looming stimulus with a conspicuous change in body pattern/texture and/or a sudden movement away from the stimulus (figure 4). None of the subjects showed any interest in the black and white version of the prey-like stimulus (or to its polarization contrast equivalent).

When presented with a polarized version of the looming stimulus, all three species responded with a change in body pattern/texture and in a few occasions with a sudden movement away from the stimulus, similar to that observed for the black and white version (figure 4 and electronic supplementary material, video S1). On some occasions, *S. lessoniana* responded to the looming stimulus with an escape response that included all behavioural components of a natural response: quick movement, mantle coloration change and ink release (electronic supplementary material, video S2).

(b) *Fishes*

All experiments with fishes were repeated in the presence and absence of UV light; however, we observed no difference in the responses related to the presence or absence of UV light on the outcome of the tests.

Both *C. auratus* and *D. rerio* responded with a strong startle response, in the form of a rapid change in swimming direction and acceleration away from the LCD when presented with a black and white version of the looming stimulus. Neither of these two species showed any tracking or following behaviour towards the prey-like stimulus presented

in black and white. No responses were observed from either species to polarized versions of either stimulus (figure 5).

Both *C. viridis* and *P. amboinensis* responded with a strong startle response, in the form of a rapid change in swimming direction and acceleration away from the LCD when presented with a black and white version of the looming stimulus. Both species showed periodic tracking or following behaviour towards the prey-like stimulus presented in black and white. No responses were observed from either species to polarized versions of either stimuli (figure 5).

4. DISCUSSION

While sensitivity to the e-vector orientation of light has been demonstrated in many aquatic organisms [8,14,21,22,27,37–42], empirical evidence for its role in specific, untrained behaviour such as target detection are scant, and therefore the relevance of PS remains unclear. This study is the first to test for a direct link between PS, and its potential use in the context of fast-moving target detection using a video-based stimulus. In our tests, cephalopods responded to our looming stimulus, presented in polarization contrast, with a behaviour response that was typical of cephalopods startled in their natural environments. In particular, *S. lessoniana* often responded to the looming stimulus with a combination of rapid movement coupled with mantle coloration change and ink release. *Sepia plangon* typically responded with a body colour change or surface texture change to both luminance contrast- and polarization contrast-based stimuli, but on occasion these were combined with rapid movement. We were, however, unable to elicit a similar response from any of the fishes tested, which may indicate a difference between cephalopods and fishes in terms of the behavioural relevance of PS. While cephalopods may use polarized light cues in target detection and specifically detection of predators, it seems unlikely, based on our finding, that fishes do the same, especially given that the level of e-vector contrast provided in this study was within the range of contrast measured under natural conditions [1,2,43,44].

In cephalopods, responses to polarization contrast-based looming stimuli were qualitatively comparable to those obtained with luminance contrast-based stimuli, suggesting that PS might either work as self-sufficient detection mechanisms, when other visual cues are absent, or by enhancing the luminance contrast. Cephalopods did not respond to a full change of the polarized field delivered as a change of the LCD screen from black to white, corroborating that their responses were biologically relevant to an approaching/looming object.

None of the cephalopods responded to either the polarized or unpolarized version of the prey-like stimulus. We think this might be due to the particular design of the stimulus that may not have contained enough detail to be appealing to the animals. Presentation of an image of an actual prey item may have been more effective, in view of the fact that biologically relevant behaviours have been elicited from octopus (*Octopus*
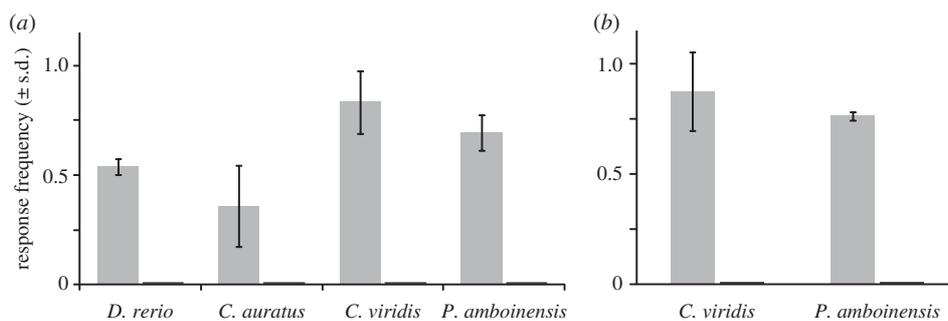
Figure 5. Frequency count of the behavioural response of fishes to (*a*) *stimulus* 1 and (*b*) *stimulus* 2 both with UV light present in the illuminant spectrum. Error bars represent 1 s.d. from the mean. Light grey bars represent the response frequency to luminance-based stimuli; dark grey bars represent response frequency to *e*-vector contrast-based stimuli. (*b*) Only two of the four fish species tested responded to *stimulus* 2.

tetricus Gould 1852) using colour video footage of real animals [45]. However, stereoscopic vision plays a more important role in prey targeting in Sepiida than in Octopoda [46,47] and the lack of depth of field in our display might have contributed to the negative outcome. Finally, behaviourally relevant responses from cephalopods provide proof of concept for our novel set-up and demonstrate that it is able to deliver detectable polarized stimuli to polarization-sensitive aquatic organisms. This result broadens what is known about the potential relevance of PS in cephalopods and is the first evidence for the use of polarized light in predator detection.

In fishes, our looming and prey-like stimuli presented in luminance contrast were highly effective at eliciting robust responses, indicating the low-activation threshold of such behaviours in nature. However, we observed no responses when stimuli were presented in polarized contrast. This result was unexpected, at least for *C. viridis* and *C. auratus*, which have been reported to respond behaviourally to local differences in e-vector contrast [26,27]. There are two alternative interpretations of this outcome. One possibility is that our set-up was inadequate to elicit behavioural responses in fishes. This seems unlikely for the following reasons: (i) our system provided a linear polarization contrast above $37.5°$ from 350 to 550 nm, which is higher than the threshold of detection for *C. viridis* ($10-25°$, [27]). (ii) The high per cent polarization produced by our system (close to 100%) rules out the possibility that this was a limiting factor in producing a detectable stimulus as linear polarization in natural systems tends to peak at 70 per cent [48,49]. (iii) Light levels in our system were within the range of values observed in natural environments for wavelengths from 350 to 800 nm [50].

The second possibility, reconciling our results with previous literature, is that the PS channel is not used in these animals for target detection (a function possibly dependent on luminance and chromatic contrast sensitivity), but mainly for the purpose of navigation and orientation [2]. This interpretation suggests that polarization cues would have been processed by the visual system but could not be used to trigger appropriate behavioural responses. Compartmentalization of sensory channels has been described previously, for example, in goldfish, where different spectral sensitivity functions measured behaviourally under different light adaptation levels indicate that L-cones are used for brightness but not for colour discrimination [51]; it is plausible that an analogous phenomenon of compartmentalization is the reason we did not see a behavioural response to polarized contrast in our fishes. However, it remains to be elucidated why an animal with sensitivity to e-vector contrast would not use it in the critical behavioural scenarios simulated by our experimental set-up.

In conclusion, polarized light cues are sufficient to elicit behaviourally relevant startle responses in cephalopods, suggesting that PS may play a role in predator detection under natural conditions. Conversely, the lack of responses to our polarization contrast-based stimuli by these species of fishes suggest that they may not use polarized light cues, analogous to what we used here, to aid in target detection and that PS may be restricted to behaviours, such as orientation or navigation, which might be triggered by gradual changes of one or more characteristics of the polarized light field.

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