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Visual sensitivity and spatial resolution of the planktivorous fish, *Atherinomorus forskalii* (Atherinidae; Rüppell, 1838), to a polarized grating

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ABSTRACT

Polarized light detection has been documented in only a small number of fish species. The benefit of polarization vision for fish is not fully understood, nor is the transduction mechanism that underlies it. Past studies proposed that one possible advantage of polarization vision is that it enhances the contrast of zooplankton targets by breaking their transparency. Here, we used an optomotor apparatus to test the responses of the planktivorous Hardyhead silverside fish *Atherinomorus forskalii* (Atherinidae) to vertical unpolarized (intensity) and polarized gratings. We also tested and compared the spatial and temporal resolutions of *A. forskalii* in the intensity and polarization domains. *A. forskalii* responded to the polarization pattern, but only under illumination that included ultraviolet-blue (λ > 380 nm) wavelengths. The spatial resolution of *A. forskalii* was measured as a minimum separable angle of 0.57° (a 1-mm prey viewed from 100-mm distance). The temporal resolution to unpolarized vs. polarized gratings was constant, at 33 and 10 Hz respectively at most of the stripe widths tested. At the smallest stripe width tested (1 mm = the minimal separable angle), which correlates with the size of prey typically consumed by these fish, the temporal resolution to the polarized grating increased to 42 Hz. We conclude that *A. forskalii* is polarization sensitive, may use polarization vision to improve detection of its planktonic prey, and that polarization may be perceived by the fish via a separate visual pathway than intensity.

1. Introduction

1.1. Polarization vision in the sea

Sea-water is rich in linearly polarized light generated by refraction at the water surface and scattering by the water molecules and suspended hydrosols in the water column (Kattawar, 2013; Lerner, 2014; Lerner, Shashar, & Haspel, 2012). Near the water surface, maximum partial polarization, can be as high as 60% (Sabbah, Lerner, Erlick, & Shashar, 2005; Tonizzo et al., 2009; Voss & Souaidia, 2010) and remains as high as 40% even at depths below 100-m, at least in some viewing directions (Ivanoff & Waterman, 1958, but see lower values in Johnsen, Marshall, & Widder, 2011). Of the >70 aquatic organisms that are known to be sensitive to linearly polarized light, about a dozen are fish, most of them planktivores. These include the rainbow trout, *Oncorhynchus mykiss*; Salmonidae (Hawryshyn & Bolger, 1990; Novales-Flamarique & Browman, 2001), three species of damselfish, *Dascyllus trimaculatus*, *D. melanurus*, and *Chromis viridis*; Pomacentridae (Hawryshyn, Moyer, Allison, Haimberger, & McFarland, 2003; Mussi, Haimberger, & Hawryshyn, 2005), two halfbeak garfish species, *Zenarchopterus dispar* and *Dermogenys pusilla*; Hemiramphidae (Forward, Horch, & Waterman, 1972, Forward & Waterman, 1973, Waterman & Forward , 1970, Waterman & Forward, 1972), and two species of anchovy, *Engraulis mordax*, and *Anchoa mitchilli*, Engraulidae (Fineran & Nicol, 1976; Novales-Flamarique & Harosi, 2002; Novales-Flamarique & Hawryshyn, 1998). Recently, an optomotor response to a polarized grating was reported in post-larvae of the anemone fish *Premnas biaculeatus*, Pomacentridae (Berenshtein et al., 2014). Polarization vision in sea-water has been hypothesized to serve several purposes, such as orientation and navigation (Berenshtein et al., 2014; Lerner, Sabbah, Erlick, & Shashar, 2011), communication and signaling (Boal et al., 2004;

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Marshall, Cronin, Shashar, & Land, 1999; Mathger, Shashar, & Hanlon, 2009; Shashar, Rutledge, & Cronin, 1996), and increasing detection distance through contrast enhancement (Novales-Flamarique & Browman, 2001; Sabbah & Shashar, 2006; Shashar, Hagan, Boal, & Hanlon, 2000; Shashar, Hanlon, & Petz, 1998).

1.2. Visual resolution in fish

The spatial resolution (minimum separable angle) of fish ranges between 0.07° and 0.94°, while the temporal resolution (critical flicker fusion frequency; CFF) of fish ranges between 5 and 100 Hz, but in most pelagic species between 20 and 60 Hz, depending on light intensity (Douglas & Hawryshyn, 1990; Sabbah & Hawryshyn, 2013). The temporal resolution of open water pelagic fish such as tuna and swordfish under optimal conditions (warm temperatures, high intensity) is roughly 40 Hz (Fritsches, Brill, & Warrant, 2005). In the polarization domain, information regarding the spatial and temporal resolution of fish is lacking, with the exception of Novales-Flamarique and Browman (2001) study on rainbow trout location (i.e. detection) distance to *Daphnia* against a polarized background. They reported (Fig. 2A therein) a maximum location distance of 60 mm to 0.89 mm prey, which corresponds to a minimum separable angle of ca. 0.85°.

The contradictory evidence about the role of polarization vision in fish, and the rarity of data available, contextualize the objectives of this study, which were to (a) test behaviorally for polarization sensitivity in the planktivorous Red Sea Hardyhead silverside (*Atherinomorus forskalii*; Atherinidae; Rüppell, 1838), and (b) compare its spatial and temporal resolution in the unpolarized and polarized domains. *A. forskalii* is an appropriate model species for this purpose because it is a shallow water pelagic planktivore that inhabits the upper 25 m of the water column, waters rich in polarized light, and visually searches for planktonic prey.

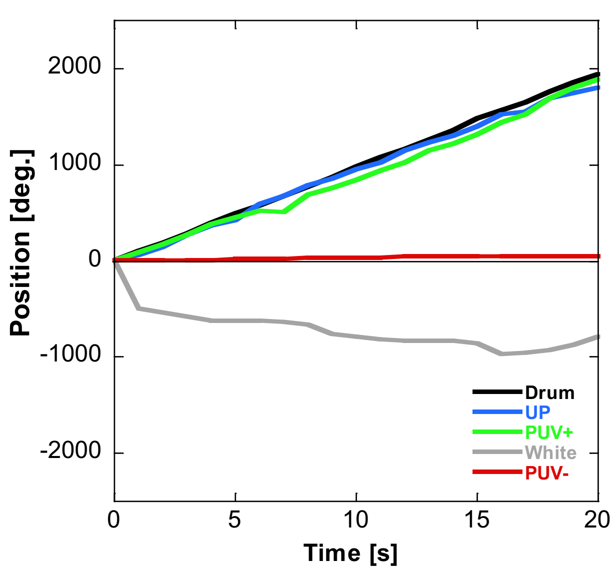

Fig. 1. Fish and drum position during 20 s of drum rotation of *Atherinomorus forskalii*. A positive position represents swimming with the drum rotation direction, while a negative position represents swimming against the direction of the drum rotation. The zero position represents no movement. Lines represent movement of the drum (black) and of the fish in response to unpolarized (UP, blue), white (W, no stripes, blank sheet, grey), and polarized patterns with (PUV+, green) and without (PUV−, red) UV illumination. Angular positions can exceed 360° because the fish could swim more than one circle during the 20 s observation period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Fish collection and maintenance

Individuals of *Atherinomorus forskalii* (mean ± sd total length = 55.6 ± 0.3 mm, weight = 3.4 ± 0.3 gr, n = 13 fish) were collected from shore and up to 1.5 m depth using a seine which covered an area of 1400 m^2 (for more details see Golani & Lerner, 2007), off the northern tip of the Gulf of Aqaba, Red Sea (N29°33′; E34°57′). The time of day during which *A. forskalii* feeds is poorly known, although it has been observed feeding during both day and night. It is mostly captured during crepuscular periods, when polarization cues are the strongest (Sabbah & Shashar, 2007). Although little is known about its diet, it is a planktivore that feeds on zooplankton. Individuals of the Gilthead seabream *Sparus aurata*; Linnaeus 1758; Sparidae (total length = 28.1 ± 0.3 mm, weight = 5.0 ± 0.2 gr, n = 13 fish), were provided by a local commercial supplier (Ardag Ltd, Eilat). The seabream share a similar shallow benthopelagic habitat with *A. forskalii.* In preliminary experiments, *S. aurata* did not response to a polarized grating. Therefore, it was used as a control to assure that the fish were not responding to any other cue but the polarized grating.

2.2. Optomotor apparatus

An optomotor response (OMR) apparatus, based on a rotating drum, was used to test responses to vertical gratings of different intensity and polarization. The same apparatus was used in previous studies on cuttlefish and fish and is described in detail by Berenshtein et al. (2014), Cartron, Dickel, Shashar, and Darmaillacq (2013), and Darmaillacq and Shashar (2008). Briefly, the method is based on evoking conditioned optomotor responses (body movement) of the fish as it swims with the rotating stripes to stabilize what it sees. Our apparatus included a round drum 39 cm in diameter which is rotated around a stable non-rotating round glass tank 19 cm in diameter filled with sea-water at room temperature (24 °C). Individual fish were placed, one at a time, inside the glass tank during the experiment, and the water was replaced with fresh aerated water between fish. The whole apparatus was placed in a dark chamber in which the only illumination available was from four pairs of UV fluorescent lamps (PHILIPS, ACTINIC BL 15 W, λ > 380 nm) and four incandescent light bulbs that emitted light in the human visual range and were positioned around the drum. The chamber was ventilated to prevent heating of the water by the incandescent bulbs. The spectral, intensity and polarization characteristics (380–700 nm) projected from the stripes were measured using a custom-made radiometer attached to an optical fiber (USB2000 and UV–VIS 600 μm respectively; Ocean Optics, Dunedin, Florida, USA), also used in a previous study (Lerner et al., 2008). To reduce the acceptance angle, a 5° restrictor was attached to the end of the optical fiber. To measure the polarization, a linear polarizer was placed on the restrictor, and three readings were taken at 0°, 45°, and 90° orientations of the transmitting axis of the polarizer. From these three readings, the partial polarization and the e-vector orientation of the stripes were calculated (for details see Sabbah & Shashar, 2006). The polarized pattern (by Frank Woolley & Co, Reading, PA, USA) that was presented to the fish included repeating sets of four vertical linearly polarized stripes offset by 45° (i.e. 0°, 45°, 90°, and 135° e-vector orientations, transmitting equal intensities). An example of the pattern used can be seen in Darmaillacq and Shashar (2008) (Fig. 2 therin). The stripes transmitted partial polarization between 60% and 85% across the 400–700 nm wavelength range. When UV light was applied, the partial polarization at wavelengths