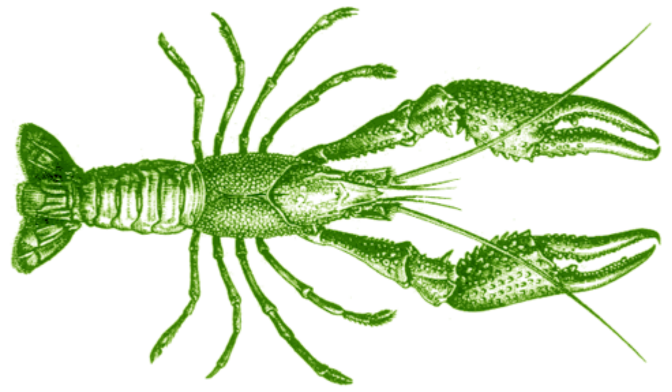

Polarization sensitivity enhances motion detection in the red swamp crayfish, *Procambarus clarkii*

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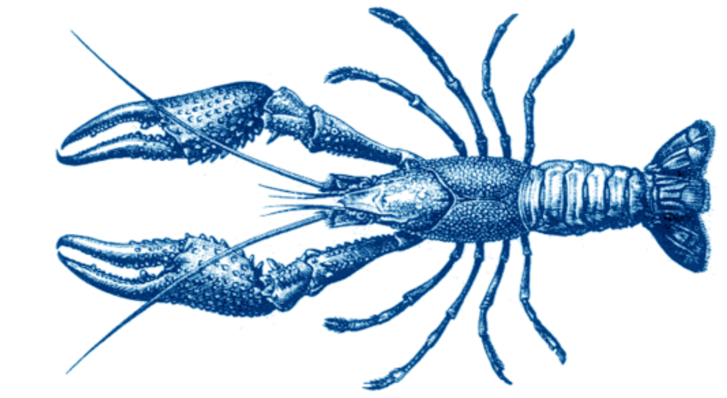

Introduction

Polarization sensitivity occurs in an eclectic variety of both terrestrial and aquatic vertebrates and invertebrates, and serves a variety of functions including orientation (1), navigation (2), intra-specific communication (3), camouflage-breaking (4), and contrast enhancement (5). The ommatidia of many crustacean compound eyes possess adjacent photoreceptors with orthogonally oriented microvilli, establishing the potential for discriminating the orientation of the plane in which the e-vector of light oscillates (6).

The red swamp crayfish, *Procambarus clarkii*, appears to have all the anatomical and neural structures required to distinguish differences in the dominant e-vector of polarized light. Inputs from photoreceptors and polarization-sensitive visual interneurons converge into two pathways with orthogonal e-vector sensitivity (7). Antagonistic inputs from these orthogonally oriented polarization analyzers project to the brain, where opponency may provide a mechanism for analyzing the polarization of the signal. In some of these cells, the response is enhanced by changes in e-vector over time, suggesting that polarization discrimination may enhance sensitivity to moving stimuli, a function that is particularly well-developed in crayfish (8).

In this study we test whether the neural evidence for polarization sensitivity in *P. clarkii* translates into a behavioral response. In particular, we test whether polarization information in an otherwise undetectable moving stimulus increases the ability of *P. clarkii* to detect it.

Materials and Methods

A longitudinal cut was made down the top of a half-section of PVC pipe, along which a transparent target could be advanced toward a chamber containing individual crayfish, *P. clarkii* (Fig. 1). The transparent target was made of a sandwich of clear acrylic and an optically anisotropic, colorless sheet of mylar. The mylar was aligned so that it rotated the e-vector of the light that passed through it (Fig. 2). Thus, while inconspicuous under transmitted unpolarized light, the target's optical properties rendered it highly visible when viewed under transmitted polarized light by a viewer with polarization sensitivity.

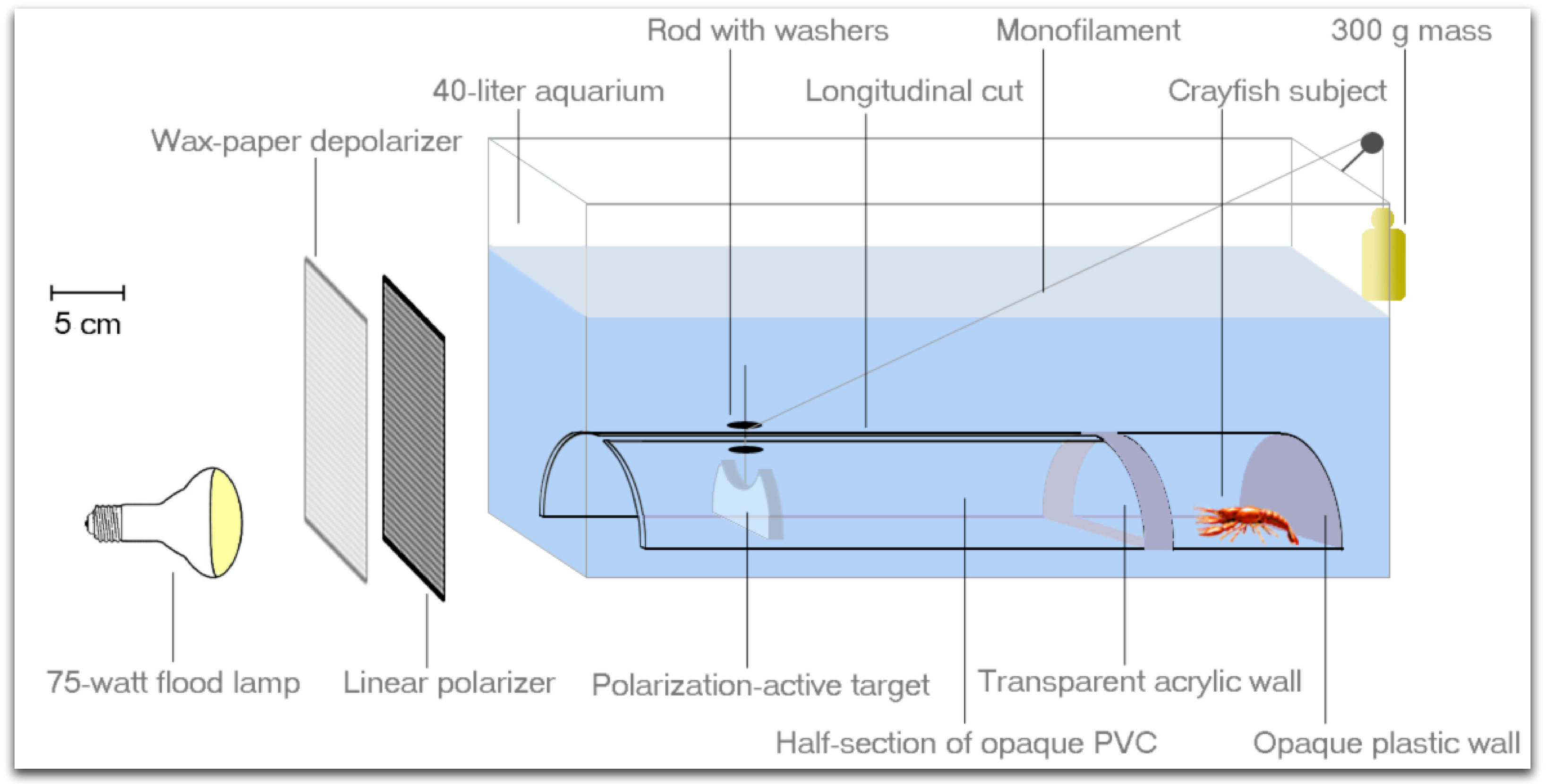

Figure 1. Schematic diagram of the experimental apparatus used in the study. The PVC half-section is transparent in this figure to show the inside of the device. In the actual device the polarizer/diffuser sheets were sandwiched together against the side of the tank.

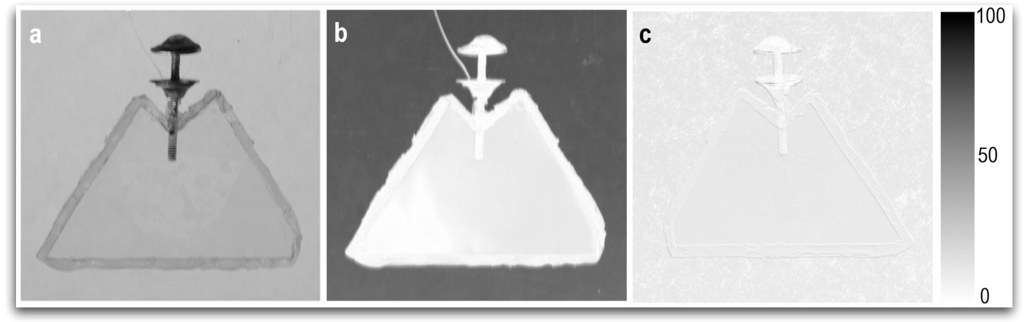

Figure 2. The target was constructed of clear acrylic covered with colorless, polarization-active mylar. (a) Unmodified photograph of the transparent target viewed under polarized light. (b) Difference image of the target generated by taking two photographs through a polarizing filter that was rotated by 90° between exposures. Black is maximum difference in intensity. (c) Same as in (b) but with wax-paper diffuser depolarizing the light.

The apparatus was illuminated through a sandwich of a linear polarizer and a wax-paper diffuser/depolarizer. For the polarized light trials, the polarizer followed the depolarizer. For the unpolarized light trials, the polarizer preceded the depolarizer. Thus, the two lighting conditions differed only in polarization and not in intensity or spectral distribution (Fig. 3).

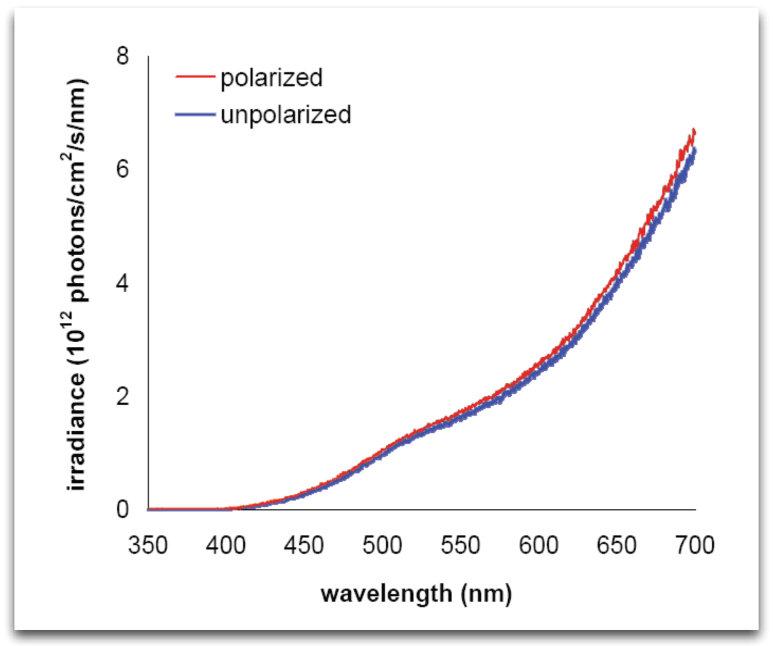

Figure 3. Spectral irradiance inside the crayfish chamber under both polarization conditions. The irradiance probe faced the light source.

The responses of the crayfish to the advancing target were recorded through the glass bottom of the aquarium. The presence or absence of a response was recorded by a blind (ignorant of light condition) examination of each experimental trial. Based on preliminary observations prior to testing, a positive response was defined as a retreat by the crayfish of >2 cm.

Results

Under partially linearly polarized light, P. clarkii were four times more likely to retreat from an advancing, transparent, polarization-active object than under unpolarized conditions ($\chi 2$ (1, N = 40) = 16.9, $p < 0.0001$; Figure 4). Out of 20 trials that took place under un-polarized light, 4 of the subjects retreated from the stimulus. Under polarized light, 17 out of 20 crayfish retreated. The retreat response generally consisted of the crayfish pushing off with the walking legs and chelipeds, and occasionally of a tail-flip escape response. Tail-flip escapes were observed only under polarized light conditions, in 4 out of the 20 trials.

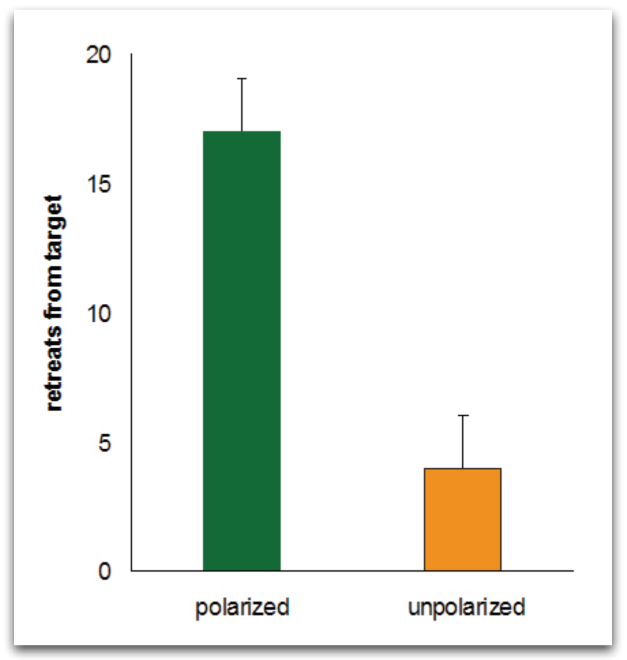

Figure 4. Response of Procambarus clarkii to the approach of the target under polarized and unpolarized conditions (n=20 for each treatment). Crayfish retreated from the target significantly more often in the polarized condition ($p < 0.0001$). Error bars show standard error.

Conclusions

The highly significant difference in response between treatments suggests that crayfish were able to perceive the advancing target more often under polarized light conditions. These results provide the first behavioral demonstration of polarization sensitivity in crayfish. They also demonstrate one effect of sensitivity to polarized light: enhanced detection of a moving polarization-active object against a linearly polarized background.

P. clarkii are sensitive to moving visual stimuli over a velocity range of at least four orders of magnitude (8), indicating that motion detection is a critical and acute component of the crayfish visual system. The results of this study are consistent with the hypothesis that crayfish use antagonistic inputs from orthogonally oriented polarization analyzers fibers to register the temporal changes in e-vector distribution detected by photoreceptors. This may provide *P. clarkii* with a mechanism to enhance motion detection.

P. clarkii is an abundant opportunistic omnivore in seasonally flooded wetlands, lakes, and streams throughout North America, often concealing itself in burrows or under rocks and logs. Camouflaged objects may produce polarization contrast that is discernible for organisms that have polarization opponency. For example, polarized reflection from mirror-like fish scales (9), and light scattering within the tissues of transparent animals creates polarization contrast by disrupting downwelling or sidewelling polarization backgrounds (4).

P. clarkii may use polarization-enhanced motion detection to avoid predators. Identification of the polarized reflections of approaching predators such as fish may alert the crayfish to retreat into the safety of its burrow. Polarization-enhanced motion detection would allow crayfish to effectively retreat from approaching predators in the absence of other contrast cues.

Polarization-enhanced motion detection may improve visual predation on mobile, transparent zooplankton, such as larvae of freshwater insects (e.g. *Chaoborus*), crustaceans (e.g. *Daphnia*), or other benthic invertebrates. Levels of polarization in the upper photic zone are highest during crepuscular periods (10) when crayfish are most active, indicating that crayfish forage when they are most visually prepared to detect moving prey and avoid potential predators.

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