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Target detection is enhanced by polarization vision in a fiddler crab

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Summary

We are constantly surprised by the ability of relatively simple animals to perform precise visually-guided movements within complex visual scenes, often using eyes with limited resolution. Exceptional examples include the capture of airborne prey by dragonflies [1], the learning flights of bees and wasps [2], and the tracking of conspecifics by crabs on intertidal mudflats [3-5]. Most studies have focussed on how animals do this using sensitivity to intensity or colour. However, it is increasingly evident that a third ability, polarization vision, may contribute to such tasks. In many insects, polarization-sensitive photoreceptors are confined within an area of the eye known as the dorsal rim [6], which detects the polarized sky pattern specifically for navigation [7]. However, some animals, including fiddler crabs, are sensitive to the polarization of light across the majority of their image-forming eyes [8, 9], potentially allowing them to use polarization information to increase perceived contrast for general visual tasks [10-13]. Investigations into the use of polarization image-parsing by animals have largely been confined to laboratory settings under artificial lighting [10, 13-18]. This approach can occasionally mislead if the lighting conditions are different from natural [19]. This study presents the first behavioural evidence from the natural context for a function of polarization image-parsing. Using experimental manipulations in wild populations of the fiddler crab Uca stenodactylus, we provide evidence that these animals use their polarization vision to enhance contrast in their visual environment, thereby increasing their ability to detect and respond to objects on the mudflat surface.

Results and Discussion

Crab polarization properties

Imaging polarimetry demonstrated that Uca stenodactylus, in their natural environment, generate two types of polarization contrast against the background (see also [20]). Firstly, the damp parts of the animal’s cuticle produce specular reflections that are polarized with e-vectors oriented parallel with the angle of the cuticle surface. For example, the sloped carapace of the crab in figure 1A-C reflects light with a similar degree of linear polarization (DoLP) to the light reflected from the mudflat, but with an e-vector axis (AoP) differing by
around 30°. Secondly, large parts of the crab appear unpolarized against the polarized background glare. In particular, the semi-transparent parts of the crab, such as the claws and upper legs, appear bright in intensity, but have little polarization (DoLP < 0.05). Here, the cuticle acts like a scattering diffuser, roughly analogous to a translucent lampshade that diffuses light, and so, when backlit by the sun, these structures do not appear silhouetted, but retain their bright intensity. This effect is most striking when we compare images taken through horizontal and vertical polarizing filters (fig 1E-F). In this case, the claw and legs continue to appear bright even when the background glare has been filtered out.

To further understand the relevance of the polarization properties of these natural scenes, we processed the images according to existing models of photoreceptor connectivity in crustaceans [21, 22]. Horizontal and vertical polarization images were used as two input channels to the model, and the ratio of activity between these two receptor channels, H and V, is displayed as a false colour image (fig 1D). Note that this measure ranges from -1 (H minimally active and V fully active) to +1 (H fully active and V minimally active). Values of 0 indicate that both receptor channels are equally active (i.e. there is no difference in activity between the receptor channels). This demonstrates that much of the polarization contrast discernible in the DoLP and AoP (angle of polarization) images also translates into a biologically-relevant estimate of visual contrast.

If we consider that the intensity and polarization components of the visual scene are likely to be synthesised into a single measure of contrast in the visual system of this species [23], then this semi-transparent leg and claw design may be the result of selection for signal efficacy. The perceived contrast of these structures, when viewed against polarized mudflat glare, is likely to be maximised by the additive effect of both intensity and polarization contrast. Several aspects of the crab's natural behaviour support this hypothesis. Firstly, the rhythmic, lateral claw waving pattern employed by this species to attract females maximises the visual exposure of the inner surface of the semi-transparent claw and legs to potential wandering females [24]. Secondly, when males are displaced from their burrows and attempt to avoid confrontation on the mudflat they will frequently tuck in their major claw close to, and occasionally beneath, the body thereby minimising the absorption and scattering of light by the claw, as well as its visible area. Further study is needed to determine whether these optical features of the claw enhance the signalling ability of males.

Response distance

We tested whether focal males, who were resident at and defending burrows, responded to approaching targets on the mudflat over distances proportional to the polarization contrast of the target. The targets consisted of a weighted sled pulled along the mudflat towards the focal males via a remotely operated pulley system. Attached to the sled was a 20mm square piece of polymer retarder film, which modified the transmitted polarized light to generate three types of polarization: 1) H (horizontal)- same as background, 2) U (unpolarized)- no linear polarization, and 3) V (vertical) – background e-vector axis rotated by 90 degrees. These generated a polarization contrast relative to the horizontally polarized mudflat background at naturally-occurring levels of DoLP < 0.4.
Male crabs responded to the approaching targets as if they were a threat, such as another crab seeking a burrow, or a predator. The response commenced with the male transitioning from waving its major claw (broadcast signalling) to a sequence of defensive behaviours: 1) ‘freeze’ - the male suddenly became stationary, often tucking its large claw in close to the body; 2) ‘home run’ - the male ran quickly back to its burrow and assumed a position of vigilance; and 3) ‘burrow descent’ – the male descended into its burrow out of sight. These are similar to behaviours observed in other fiddler crab species (both sexes) upon approach of objects, including other crabs and predators [5, 25]. On rare occasions, the focal male responded as if the target was a wandering female and directed courtship signalling towards it. In this species, courtship includes relatively slow lateral extension and contraction of the major claw while the male moves a short distance to-and-fro from the burrow. When in close proximity to a female, the male elevates its claw and performs rapid movements to intercept the female (‘herding’) as the male attempts to chivvy the female to his burrow [3, 4, 24]. In our study, experimentally induced courtship behaviours were only observed when the target was far away from the male. As the target approached, these males stopped courting and responded with evasive behaviours. In these cases, the courtship component was ignored and behaviours were scored beginning when the target elicited the ‘freeze’ response. Nevertheless, elicitation of courtship by the target supports the hypothesis that polarization cues are included in the set of features that males associate with other crabs.

‘Freeze’ responses occurred over distances 24.2% further away when the approaching target was vertically polarized (the target with the strongest contrast in AoP against the background) and 17.1% further away when the target was unpolarized (the target with the strongest contrast in DoLP against the background), when compared to horizontally polarized targets (fig 2A; p<0.001 for polarization contrast vs no contrast and based on random within-crab permutations with 10,000 repeats; see also fig 3B for dummy properties). Home run behaviour was affected in a similar way (p=0.013), but the final burrow descent behaviour showed no significant differences between target types (p=0.086; fig 2B-C). Burrow descent only occurred when the target was very close to the male (average < 15 cm) and may have been perceived using additional visual and seismic cues (see movie S1).

Our results provide one of the first examples for a function of polarization vision in object or target detection under natural lighting conditions. Despite a great deal of accumulated knowledge about polarization vision at the anatomical, physiological and behavioural levels, there are relatively few field studies demonstrating a clear functional advantage of this modality under natural illumination. Even those studies conducted in the field tend to use unnaturally elevated degrees of polarization to elicit behavioural responses in animals. We know, for example, that the natural flight or walking direction of many insects can be influenced by introducing highly polarized (DoLP >0.9) light fields above the animal, providing evidence that the polarized sky pattern can be used as part of a celestial compass cue [26-28]. Similarly, many insects associated with freshwater are known to be attracted to strongly polarized (DoLP >0.9) surfaces and light sources, providing evidence that they find water bodies using polarotaxis [29]. Again, few experiments have demonstrated such responses to naturalistic levels of polarization. A clear illustration of the possible pitfalls of
this approach is the debate over whether marine animals can use polarization vision to enhance the contrast of transparent (and often highly birefringent) zooplankton prey. Under unnatural lighting, including strongly polarized background lighting and minimal down-welling light, this does seem to be the case [14]. However, in the natural context, the small amount of polarization contrast generated by these transparent organisms is entirely swamped by reflections from down-welling light, implying that this proposed function is only relevant under a specific set of lighting conditions [19].

In our experiment, reflected glare on the damp intertidal mudflats rarely exceeded degrees of polarization of around 0.4. The background levels of polarization and the polarization contrasts induced by the targets were at naturally occurring levels of DoLP, and the animals themselves were behaving in their natural home environment. Our finding that response distance changed according to polarization contrast suggests that they use polarization information to enhance the perception of their visual scene, thereby increasing their ability to detect nearby objects of relevance. For male fiddler crabs, these objects can be broadly divided into 1) predators, 2) crabs posing a territorial threat, and 3) potential mates. Exactly how the polarization receptors contribute to enhancing image contrast, and hence detection, has yet to be demonstrated conclusively. However, there is evidence to suggest that intensity and polarization information conjoin early in visual processing to generate a single measure of contrast [23]. Future studies of this mechanism could lead to interesting technological applications in the field of digital image analysis, such as the development of contrast enhancement algorithms for polarization cameras [30, 31].

Conclusion
It is becoming increasingly evident that animals may use polarization reflections in the same way as colour, potentially contributing to sexual, territorial, and predator-prey interactions. For many crustaceans and the majority of cephalopod species, it may be that two-channel polarization vision is used in preference to colour vision [32, 33]. Fiddler crabs are highly social, live in a world full of background and object-based polarization [20, 34], and their enlarged claw has clearly evolved for communication [24]. Quantifying the relevance of colour vs polarization for conspecifics, prey, or eavesdropping predators remains a future challenge and part of a fascinating arms race that we are just beginning to explore.

Experimental procedure
The study site was located on an intertidal mudflat close to the Bridge of the Americas, Republic of Panama (8° 56’30.80”N; 79°34’17.92”W). Here, Uca stenodactylus occupy home burrows and spend the majority of each daytime low tide feeding on organic matter from the mud surface, defending their burrows from intruders, and engaging in territorial defence and courtship.

Photographic polarimetry
Measurements of the polarization properties of visual scenes were obtained using photographic polarimetry. Sets of four photographs were collected for each scene using a
digital SLR camera (EOS 7D with 15-85mm EFS lens, Canon, Tokyo, Japan), taken through a linear polarization filter (72CP, Tiffen, New York, USA) oriented at 0°, 45°, 90° and 135°. All camera settings were maintained constant for each image set to ensure that differences between images were a product of the visual scene and not of automated processes internal to the camera. Differences in intensity between the images were used to calculate the degree of linear polarization (DoLP) and e-vector axis (AoP) [35]. A third measure, receptor activity ratio, was calculated by treating horizontally and vertically polarized photographs as input channels to a polarization vision model [21, 22], assuming a polarization sensitivity of 10. This generated values for each image pixel that correspond to the relative activity of the two polarization channels, ranging from -1 (maximum vertical and minimum horizontal stimulation) to +1 (maximum horizontal and minimum vertical stimulation). This system is vulnerable to null points of discrimination that render some polarization contrasts indistinguishable, such as 45° polarized vs unpolarized light, and these are consistent with behavioural observations in fiddler crabs [36]. Polarization information was then collated into false-colour images to demonstrate its spatial distribution within the scene.

Target detection experiment

The movements of threatening crabs or small ground-based predators were simulated by dragging polarized targets along the mudflat surface (see movie S1). These targets directly approached a focal male (filmed from above using a digital video camera (Legria FS20, Canon, Tokyo, Japan) mounted on a tripod 1.5 m above the mudflat) and were controlled using fishing line coupled to a pulley system operated by an observer located 6 m away (Fig 3A). Target approaches came from the azimuthal direction of the sun (± 9.8° circular standard deviation [37]; fig S1C), ensuring that they were viewed against a background of horizontally polarized glare from the mudflat surface. The target consisted of a sled base, weighted with lead, and an interchangeable square of polymer retarder film (Edmund optics, Nether Poppleton, UK) mounted in a thin wire frame orthogonal to the direction of travel (inset fig 3C). 20 x 20 mm squares of retarder film were cut so that the fast axis was oriented to alter the background horizontally-polarized light in three different ways: 1 – [H] horizontal (or unmodified from the background); 2 – [U] unpolarized (i.e. with no linear polarization component), and 3 - [V] vertical (the e-vector axis of the background polarization is rotated by 90°) (fig 3B and S1A-B) [similar to 15]. For simplicity we refer to the second target type as ‘U’ or ‘unpolarized’, but it is, in fact, circularly polarized. From the perspective of the fiddler crab polarization vision system this circularly polarized retarder film is indistinguishable from unpolarized light.

Each of the three targets was presented to a focal male in randomised order, and the three following stages of response were scored manually, in a fully blind process, from the digital video: 1) ‘freeze’ - male stops feeding or signalling, and (usually) tucks its major claw close to the body; 2) ‘home run’; and 3) ‘burrow descent’. The position of the focal crab, home burrow and target were digitised for each of these events, and, in cases where the target was beyond the field of view of the camera, its position was extrapolated by tracking the
rotation of one of the marked pulley wheels. The image distortion caused by the camera lens was removed from the position data using an open source calibration system [38].

Data were only included if they met the following criteria: 1) the crab responded to all three target presentations; 2) all three presentations occurred under full sunlight; 3) the crab was not engaged in any behaviour that was directed towards, or in response to, other conspecifics on the mudflat or potential predators such as nearby birds; and 4) the focal crab was within the field of view of the camera during the response frame.

Statistics
To avoid assumptions about the underlying distribution of the data, a permutation approach was used for statistical inference. Under the null hypothesis there is no difference in the average response distance between the three experimental conditions (horizontal, unpolarized, and vertical). We therefore generated a distribution of the average difference in response distance between the three conditions by randomly permuting the condition vector and recalculating the average distances 10,000 times. To account for repeated measures effects, conditions were only permuted within crabs. The quantile of the experimentally determined difference in the distances is a direct measure of the one-sided probability that the null hypothesis cannot be rejected.

Author contributions
All authors contributed to conceptual development, experimental design, logistical support and editing the final manuscript. MJH conducted the fieldwork.

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References


Figure legends

Figure 1. Polarization images of male *U. stenodactylus* in an aggressive stance viewed in their natural environment. A) Original: unfiltered photograph; B) DoLP: degree of linear polarization; C) AoP: axis of polarization (black areas are below a 0.05 DoLP threshold); D) receptor activity ratio: relative level of activity of horizontally (H = 1) and vertically (V = -1) oriented receptor channels calculated using a visual model [22]. E) to G) Light diffusion in the claw and legs of *U. stenodactylus*. E) and F) Photographs taken through horizontal and vertical linear polarization filters respectively. G) Corresponding degree of linear polarization image.

Figure 2. Detection distances relative to the polarization of the target. Data are presented for three different sequential behaviours: A) ‘freeze’; B) ‘home run’; and C) ‘burrow descent’. Grey circles and connecting lines represent data for each individual. Black lines and error bars are the mean ± standard error. The three target types are, from left to right - H (horizontal); U (unpolarized); and V (vertical). Dotted lines represent the overall mean.

Figure 3. Experimental design. A) Top-view schematic of the experimental setup. Dashed rectangle represents the field-of-view of the downward-pointing camera. Inter-pulley distance is approximately 6 m (the illustration is not to scale). Inset photograph shows the target with retarder film mounted in place. B) Polarization images of each target type (H – horizontal; U – unpolarized; V – vertical) and a crab (from fig 1) viewed against the natural mudflat glare (see fig 1 for false colour image interpretation). Average values within dashed rectangle areas are presented for each measure.