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RESEARCH ARTICLE

High e-vector acuity in the polarisation vision system of the fiddler crab *Uca vomeris*

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SUMMARY

Polarisation vision is used by a variety of species in many important tasks, including navigation and orientation (e.g. desert ant), communication and signalling (e.g. stomatopod crustaceans), and as a possible substitute for colour vision (e.g. cephalopod molluscs). Fiddler crabs are thought to possess the anatomical structures necessary to detect polarised light, and occupy environments rich in polarisation cues. Yet little is known about the capabilities of their polarisation sense. A modified polarisation-only liquid crystal display and a spherical rotating treadmill were combined to test the responses of fiddler crabs to moving polarisation stimuli. The species *Uca vomeris* was found to be highly sensitive to polarised light and detected stimuli differing in e-vector angle by as little as 3.2 deg. This represents the most acute behavioural sensitivity to polarised light yet measured for a crustacean. The occurrence of null points in their discrimination curve indicates that this species employs an orthogonal (horizontal/vertical) receptor array for the detection of polarised light.

Key words: e-vector discrimination, compound eye, predation.

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INTRODUCTION

Except for the weak phenomenon of Haidinger's brush (Haidinger, 1844; Le Floch et al., 2010), humans lack polarisation vision. Animals, however, are known to use polarised light for a range of tasks, including the detection of bodies of water by airborne insects using surface-reflected polarised light (Schwind, 1983; Schwind, 1991; Kriska et al., 1998; Horváth et al., 2011), intra-specific communication with inbuilt polarised body patterns (Shashar et al., 1996; Chiou et al., 2008; Chiou et al., 2011), and navigation and orientation using the pattern of celestial polarised light (von Frisch, 1949; Wehner, 1976; Dacke et al., 2003; Weir and Dickinson, 2012). Some animals, such as cephalopods, have apparently evolved an acute polarisation sense as a substitute for colour vision (Moody and Parriss, 1961; Messenger, 1981; Marshall et al., 1999; Temple et al., 2012). Much is now known about the structures involved in invertebrate polarisation vision (reviewed by Wehner and Labhart, 2006). However, the behavioural capabilities and functional significance of polarisation vision systems in crustaceans remain poorly understood.

Fiddler crabs (genus *Uca*) occupy tropical and semi-tropical inter-tidal mudflats around the world (Crane, 1975). They possess large apposition compound eyes mounted on stalks, high above the body. These turret-like eyes gather full panoramic visual information from their relatively flat, uncluttered environment (Zeil and Hemmi, 2006). The sampling array of their compound eyes reflects many details of the animals' environment and the behavioural tasks they have to perform (Smolka and Hemmi, 2009). Fiddler crabs are highly visual animals and visual information plays a major part in many behavioural tasks such as predator detection (Hemmi, 2005a; Smolka et al., 2011), territorial surveillance (Hemmi and Zeil, 2003), and conspecific identification and tracking (Detto et al., 2006; How and Hemmi, 2008a; How et al., 2008).

The mudflat environment that fiddler crabs occupy is rich in polarised light information (Zeil and Hofmann, 2001). For example, the relatively unobstructed sky provides strong celestial polarisation cues potentially useful for orientation and navigation (Wehner and Labhart, 2006), and the shiny cuticle of conspecifics provides reflected polarised light that may be useful for differentiating harmless neighbours from dangerous competitors (Zeil and Hofmann, 2001) (see Discussion). In common with many crustaceans, fiddler crabs are thought to be polarisation sensitive (Altevogt and von Hagen, 1964; Korte, 1965; Herrnkind, 1968; Zeil and Hofmann, 2001). Anatomical studies reveal that their eyes possess the typical crustacean organisation of eight light-sensitive retinula (R) cells, with cells R1–7 contributing stacked, orthogonally oriented microvillar layers, capped at the distal end with a single small R8 cell (Alkaladi, 2008). The microvillar arrangement of R1–7 strongly suggests polarisation sensitivity through optical dichroism (Snyder and Laughlin, 1975; Shaw and Stowe, 1982). Although electrophysiological studies of photoreceptor activity in *Uca* have yet to be completed, preliminary evidence is consistent with their possessing sensitivity to polarised light (Smolka, 2009) (M. Falkowski, unpublished data).

Except for some brief early behavioural studies (Altevogt and von Hagen, 1964; Korte, 1965; Herrnkind, 1968), there have been few investigations into polarisation vision in this genus and no attempt to measure the capabilities or limitations of this sensory modality. To address this, we used a liquid crystal display (LCD)

monitor, modified to present polarisation-only stimuli (Glantz and Schroeter, 2006; Pignatelli et al., 2011) to tethered fiddler crabs fixed in position over a freely moving treadmill (Buchner, 1976; Hedwig and Poulet, 2004; Oliva et al., 2007). By presenting stationary fiddler crabs with moving polarisation cues and monitoring their response, we were able to show that this species has a highly acute polarised vision system and is able to make use of differences in the electric vector (e-vector) of light to detect and escape from predators.

MATERIALS AND METHODS

Seven male and seven female fiddler crabs (*Uca vomeris* McNeill) were collected from the intertidal mudflats of Brisbane, Australia (27°31′27.28″S; 153°17′11.75″E) and transported by air freight to the Australian National University, Canberra. Animals were lodged individually in 500 ml plastic flasks (Corning, Corning, NY, USA) with a 1 cm depth of seawater and a folded paper towel substrate. Water was replaced daily and fish flake food (Marine Masters, tropical fish flakes, VitaPet Corp, Taiwan) added twice weekly. A natural day–night light cycle was maintained for the duration of the experiments.

A treadmill setup was used to test the response of fiddler crabs to polarisation stimuli (Fig. 1A) (Buchner, 1976; Hedwig and Poulet, 2004; Oliva et al., 2007). The treadmill consisted of a 13 cm diameter polystyrene ball balanced over a cushion of air flowing from a reservoir. The crabs were fixed in position on top of the treadmill by means of a hinged wire hanger attached with cyanoacrylate glue to the animal's dorsal carapace. The hanger allowed the fixed crab to rotate about the vertical axis and to walk freely in any direction along the surface of the treadmill, causing the polystyrene ball to rotate beneath it. The treadmill was placed in the middle of a testing arena (50×50 cm), the floor of which was level with the top of the treadmill and surrounded by four LCD screen monitors (37×30 cm; HP L1906, Hewlett-Packard, Singapore) (Fig. 1A).

Stimuli were presented on one of the four monitors, from which the outer-most polarising filter had been removed so that it produced polarisation-only images (Glantz and Schroeter, 2006; Pignatelli et al., 2011). The three other monitors showed a stationary image, simulating a mudflat with a dark ground and a bright sky, roughly matching the brightness of the polarisation monitor. Each animal was mounted over the treadmill and allowed 3–5 min to acclimatise. Stimuli were presented on the polarisation monitor at approximately 3 min intervals and crab behaviour was recorded using a digital HD video camera (Legria HF10, Canon, Tokyo, Japan) located directly above the testing arena.

The visual 'looming' stimulus consisted of a rapidly expanding disc, similar to that used in other experiments (Pignatelli et al., 2011; Temple et al., 2012). The stimulus simulated, in spatial terms, the direct approach of a spherical object towards the crab from either a height of 1.5 m and a distance of 6 m (visual angle: start 0.6 deg, end 82.4 deg) approaching with a speed of 41 cm s^{-1} (slow/small stimulus), or from a height of 1 m and a distance of 4 m (visual angle: start 1.7 deg, end 102.1 deg) approaching with a speed of 165 cm s^{-1} (fast/big stimulus). Stimuli were presented either in luminance intensity contrast only (in this case the polarising filter was replaced on the front side of the LCD to convert e-vector angle into luminance intensity contrast) or with polarisation contrast only. The luminance intensity stimulus was composed of a black looming circle on a white background. When presented as a purely polarised image the stimulus disc had an e-vector angle of –43 deg against a background of 32 deg (relative to horizontal), which is equivalent to an angular contrast of 75 deg. Subsequent variation of the monitor intensity input values produced a range of polarisation angles between –43 and 32 deg (Fig. 1B, solid line) [details of screen calibration are published elsewhere (Pignatelli et al., 2011; Temple et al., 2012)]. Associated with this change in e-vector angle was a change in ellipticity (Fig. 1B, dashed line), the implications of which for signal detection are taken into account in our analysis.

To ensure that changes in the polarisation stimulus were not accompanied by significant changes in radiant light intensity, the amount of light emitted by the HP L1906 monitor at three different stimulus/background settings and at three different viewing angles was quantified. Measurements were made using a high-sensitivity temperature-controlled spectrometer (Ocean Optics QE65000 cooled to –20°C; Dunedin, FL, USA) coupled to a cosine collector, sampling over 2 s integration periods. Changes in the input 8 bit unsigned integer (uint8) greyscale value of the monitor (and hence the e-vector of the polarisation stimulus) caused small, just-measurable changes in intensity (Table 1). From a normal (0 deg) viewing angle these changes in intensity were lower than 0.15% of total light intensity – more than 30 times lower than the estimated polarisation contrast of 4.6% for the 3 deg stimulus [$\cos(32\,\text{deg})^2$–$\cos(29\,\text{deg})^2$=4.6%]. From oblique viewing angles this increased to as high as 3.43%, demonstrating the importance of maintaining a near-normal (0 deg) viewing angle for such experiments.

In addition to quantifying changes in radiant light from the stimulus monitor, the light intensity from the other three surrounding monitors was also measured to check for polarisation-related reflection artefacts. There were no detectable changes associated with variations in stimulus e-vector angle.

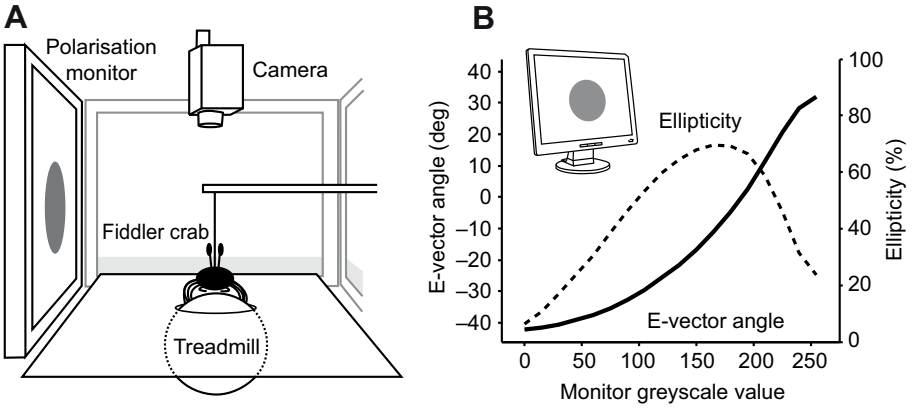

Fig. 1. Experimental methods. (A) Experimental design. The fiddler crab was held in position on top of a spherical polystyrene treadmill suspended on a cushion of free-flowing air. Intensity- and polarisation-based contrast stimuli were presented on a modified LCD monitor (left) and crab behaviour was filmed from above using a digital video camera (top). Three unmodified LCD monitors displaying a static sky/ground pattern formed the remaining walls of the arena (one and a half illustrated in light grey). (B) Polarisation properties of the monitor. Variations in the pixel greyscale signal sent to the modified monitor produce corresponding changes in e-vector angle and ellipticity of monitor output.

Table 1. Changes in radiant light intensity from the modified HPL1906 LCD monitor viewed from three different directions

Stimulus/background uint8 value	Equivalent e-vector angle (deg)	Radiance from three different viewing directions		
		0 deg	45 deg	70 deg
240/255	29/32	0.14%	0.06%	0.20%
125/255	–25/32	0.15%	0.73%	1.60%
0/255	–43/32	0.07%	0.54%	3.43%

In order to fully understand the properties of the polarisation monitor from the perspective of a fiddler crab, an artificial fiddler crab photoreceptor was constructed using horizontally and vertically oriented linear Polaroid filters coupled with a spectrophotometer. The contrast in intensity levels detected through these two filters when viewing the polarisation monitor was used to approximate the contrast in activity levels of the two sets of orthogonally oriented photoreceptors in the fiddler crab eye.

Video sequences were synchronised to stimulus events by means of an array of small LED bulbs mounted above the apparatus, such that they were outside the field of view of the test animal but inside the field of view of the camera. Changes in animal behaviour before and during stimulus presentations were then visually identified from video playback. These behaviours were divided into four categories: 'walk' – starts walking in any direction; 'stop' – stops moving; 'sprint' – rapid run in any direction (but generally away from the stimulus); and 'limb tuck' – the animal tucks its legs and/or claws close to the body.

Data were analysed using a generalised linear mixed model in R version 2.13 (CRAN, 2011), using the glmer function of the lme4 package. All models included crabs as random factors. This accounts for variance and possible biases due to response differences between crabs. For the analysis of response probabilities, we used the link function logit and family binomial. For response timing we used family gaussian. The significance of an explanatory variable was determined by comparing the model that included the variable of interest against the model without the variable of interest.

Absolute angles were all measured using the polar coordinate system (horizon=0 deg, measured counter-clockwise).

RESULTS

To identify which of the behaviours observed in this study occurred in response to our visual stimuli, the timing of all behavioural transitions was plotted relative to the timing of the stimulus, regardless of stimulus type. Sprint and limb tuck behaviours occurred only during the rapid expansion phase of the looming disc, when the stimulus had subtended approximately 4.5 deg of the visual field (Fig. 2A,B). This 4.5 deg angular size conforms with extensive field and laboratory studies investigating the response of crabs to approaching luminance-based predator-like objects (Hemmi, 2005b; Oliva et al., 2007; Hemmi and Tomsic, 2011; Smolka et al., 2011). The frequency of stop behaviour also increased in conjunction with sprint and limb tuck behaviours. Because of their tight correlation with the rapid expansion phase of the looming disc, these behaviours were considered to occur in response to the visual stimulus. Walk and stop behaviours occurred throughout stimulus presentation and were not limited to the period of rapid expansion of the looming stimulus, even occurring when the stimulus was absent or too small to be perceived by the animal (Fig. 2). The frequency of walk did not change relative to stimulus occurrence, and so walk was excluded from response behaviours in the subsequent analysis. All remaining behavioural transitions falling within a 1.5 s range around the peak level of behavioural transitions (–2.75 to –1.25 s for the slow/small stimulus and –1.25 to 0.25 s for the fast/big stimulus; Fig. 2, grey background) were labelled responses. This method leaves open the possibility of recording false positives, which may occur when, by chance, a non-responding crab initiates stop behaviour within the response time frame. The frequency of stop behaviour occurring before the response period was used to predict the expected proportion of these false positive responses. Because of the relatively low background frequency of this behaviour, the expected level of false positive responses was low (2.4% of categorised responses). No stop behaviours were recorded during any of the 27 control trials.

The travel direction of sprint behaviour was recorded each time it occurred in response to a polarisation stimulus. The distribution

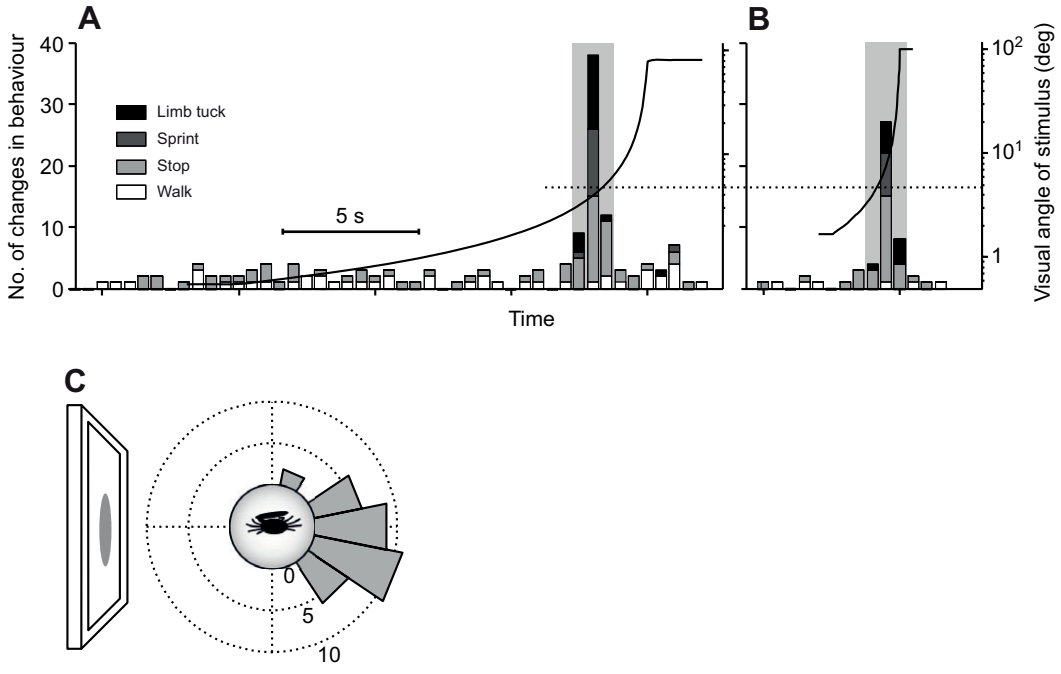

Fig. 2. Behavioural changes during looming stimulus presentations. The timing of four main behavioural transitions is plotted for both stimulus types: (A) a slow/small looming stimulus and (B) a fast/big stimulus. Bar height represents the total number for each behavioural transition occurring over all trials (left *y*-axis). Black curves represent the angular size of the stimuli (right *y*-axis, log scale). Grey background areas indicate the time interval within which behaviours were classified as responses to the stimuli. Horizontal dotted line indicates the approximate size of the stimulus during the response (visual angle of 4.5 deg). (C) Polar histogram demonstrating the direction of 'sprint' behaviour in response to polarisation stimuli. Gridline scale represents the number of responses for each direction bin.

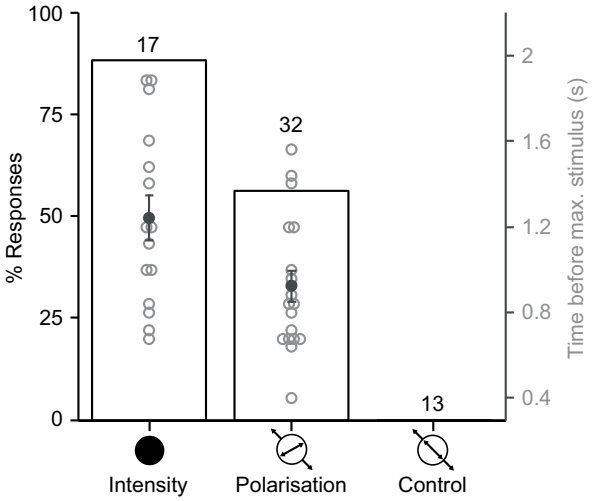

Fig. 3. Proportion of fiddler crab responses (white bars) to intensity, full-contrast polarisation (e-vector difference of 75 deg) and control stimuli (number of stimulus presentations is indicated). Overlayed is the timing of each response relative to the occurrence of maximum stimulus expansion (light grey open circles; right *y*-axis) and their mean (dark grey filled circle, ±s.e.m.). Eight fiddler crabs contributed to each bar.

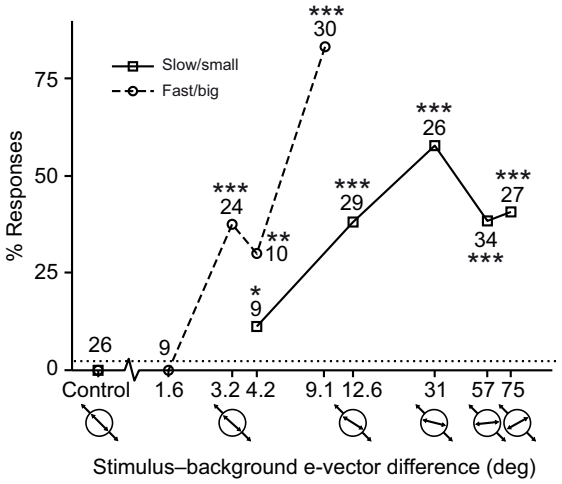

Fig. 4. E-vector acuity of fiddler crab polarisation vision. Proportion of responses to slow/small and fast/big polarised light stimuli. E-vector difference is measured as the angular difference between the stimulus e-vector and the background, ranging from 0 to 75 deg (plotted on a log scale). Number of stimulus presentations is indicated next to each data point. Significant differences from the control measurements are indicated as follows: **P*<0.05; ***P*<0.01; ****P*<0.001 (lmer, family 'gaussian'). The expected level of false positives of 2.4% predicted from the background distribution of 'stop' behaviour is indicated by the horizontal dotted line. Between 5 and 8 fiddler crabs contributed to each data point.

of sprint direction clearly demonstrates that the behaviour occurred as a direct response to the stimulus presented on the modified LCD screen, as opposed to any other intensity modulations resulting from reflections or refractions of the stimulus from the surrounding monitors (Fig. 2C).

To determine whether fiddler crabs are sensitive to polarised light, we compared the responses of eight animals to three versions of the slow/small looming stimulus: (1) intensity contrast (black stimulus on a white background), 17 presentations; (2) high polarisation contrast (e-vector difference of 75 deg), 32 presentations; and (3) control (no contrast of either kind between the stimulus and the background), 13 presentations. For the intensity, polarisation and control stimuli, 88%, 56% and 0% of trials generated responses, respectively (Fig. 3), and animals responded sooner to intensity than to polarisation stimuli (Fig. 3, grey circles; lmer, family gaussian, 33 presentations, d.f.=1, χ=8.2, P=0.0042).

The behavioural sensitivity of *U. vomeris* to the e-vector of polarised light was then analysed by presenting fiddler crabs with fast/big or slow/small looming stimuli of varying e-vector orientation against a constant background of 32 deg relative to horizontal. Responses to stimuli were observed for e-vector differences down to 3.2 deg (Fig. 4; for 3.2 deg: lmer, family gaussian, 50 presentations, d.f.=1, χ=12.0, P<0.0001). No animals responded to stimuli with e-vector differences of 1.6 deg or lower.

DISCUSSION

The fiddler crab *U. vomeris* responds to polarised light cues, and does so to a minimum e-vector discrimination threshold of at least 3.2 deg. This is the highest known behavioural polarisation sensitivity threshold recorded for a crustacean. Until recently, it was thought that the e-vector discrimination ability of full view (as opposed to dorsal rim area) polarisation vision systems was relatively poor [octopus ~20 deg (Shashar and Cronin, 1996); damselfish ~10–15 deg (Mussi et al., 2005); crayfish ~15 deg (Glantz and Schroeter, 2006)]. However, the recent use of modified LCD monitors to generate polarisation-only looming targets has begun to show that the e-vector acuity of some polarisation vision systems is much higher than previously assumed [e.g. cuttlefish ~1 deg (Temple et al., 2012)]. It is important to note, however, that the measured value of 3.2 deg is not a universal threshold for this species. Sensitivity to e-vector angle differences will vary according to the angle of the e-vectors relative to the orientation of the microvilli in the fiddler crab eye.

What functional implications might this level of polarisation sensitivity have for the everyday lives of fiddler crabs? Despite extensive research into fiddler crab visual ecology, the role of polarisation vision for these species remains poorly understood. Fiddler crabs have relatively poor visual acuity and so must rely largely on non-shape visual cues when making behavioural decisions. Despite this, they are able to perform apparently sophisticated visually guided behaviour, including escaping from airborne predators (Hemmi, 2005a), intercepting territorial intruders or potential mates (Hemmi and Zeil, 2003; How and Hemmi, 2008a), and herding mates to the home burrow (How and Hemmi, 2008b). Much of their visually guided behaviour can be divided into three important categories: (1) predator surveillance; (2) detection and identification of other crabs; and (3) orientation and navigation, all of which may be influenced in some way by polarised light.

Predator surveillance consists largely of monitoring the sky for airborne avian predators such as terns, and this behaviour is thought to rely mostly on detecting the movement of small differences in luminance intensity in the upper part of the visual field (Smolka and Hemmi, 2009). Fiddler crabs first respond to approaching birds when they subtend an angle of only 1–2 deg in the visual field (Smolka et al., 2011). At this point the crabs only see the birds with one or two of their ommatidia (Hemmi, 2005b; Smolka and Hemmi, 2009; Hemmi and Pfeil, 2010). Detection at these distances was thought to be limited by the luminance contrast sensitivity. However, it is possible that the ability to detect small differences in polarisation properties between the airborne predator and the background sky may assist an escape response, but this has not yet been investigated in detail. The stimuli used in this experiment were explicitly designed

to simulate predator approach visible in the upper part of the fiddler crab's visual field, and so it is probable that these animals can, and do, use polarisation cues to detect and respond to predators.

The identification of nearby crabs on the mudflat is a task of vital importance to fiddler crabs. These animals live in large, highly social, mixed-sex and often mixed-species colonies and must frequently distinguish between harmless neighbours, potential mates and dangerous competitors. Because of their relatively poor spatial acuity, fiddler crabs are likely to rely on non-shape visual cues, such as motion, colour or polarisation, to identify and track approaching crabs and decide whether they are harmless neighbours or intruding competitors. Resident, burrow-owning crabs regularly enter their burrows to submerge themselves in a reservoir of seawater in order to fill their branchial chambers, and as a consequence, tend to be covered in a thin film of water. However, wandering competitors do not own a burrow, and so often have a much drier carapace. Given that a damp cuticle produces higher levels of reflected polarised light than a dry cuticle, it is possible that polarisation vision in this part of the visual field would aid in the discrimination of 'damp', harmless resident neighbours from the potential threat of 'dry' wandering competitors (Zeil and Hofmann, 2001). Males of some fiddler crab species have been shown to use close-range, subtle visual cues to identify specific individuals with whom they form pair bonds (Detto et al., 2006; Detto, 2007). Small variations in cuticle topography may reflect fine-scale polarisation patterns that could be involved in individual identification (Zeil and Hofmann, 2001), a task for which a high e-vector acuity polarisation vision system would be ideally suited. Conspecifics tend to be viewed with a different part of the fiddler crab eye to that used for detecting potential predators, which opens up the possibility of regional specialisation of the polarisation vision system across the eye. Future experiments, in which polarisation stimuli are presented in different parts of the visual field, could determine whether differences in polarisation sensitivity occur in relation to the visual horizon.

Visually guided orientation and navigation behaviour could be greatly assisted by sensitivity to polarised light, and the relatively unobstructed mudflat environment affords fiddler crabs a full view of celestial polarised light cues (Zeil and Hofmann, 2001; Wehner and Labhart, 2006). For the majority of the time *U. vomeris* remain within 1–2 m of their home burrow. However, the location of the burrow is usually invisible beyond a distance of around 10–15 cm (Zeil and Layne, 2002; Ribeiro et al., 2006), and so individuals mainly rely on path integration to navigate around the home range (Zeil, 1998; Layne et al., 2003). Without external directional cues, such as the celestial polarisation field, path integration would quickly build up cumulative errors (Müller and Wehner, 1988; Cheung et al., 2007). On rare occasions, both males and females choose (or are forced) to wander across the mudflat in search of a mate and/or a new burrow. In such instances, celestial cues may prove essential for navigation. Other species of fiddler crab are known to navigate away from their home range on feeding excursions, and their movements have been linked to celestial cues, including polarisation (Herrnkind, 1968; Young and Ambrose, 1978). Many invertebrates employ specialised regions of the eye, such as a dorsal rim area, to detect the celestial polarisation field (reviewed by Wehner and Labhart, 2006). Fiddler crabs show some anatomical specialisations in the dorsal part of the eye that may be related to such a function (Alkaladi, 2008), but this does not seem to be associated with a discrete dorsal rim area. Such a lack of a low-resolution dorsal rim area is counter to the hypothesis that fiddler crabs use celestial polarisation cues, given that high spatial resolution is not a necessary requirement for such a function. Perhaps competing predator surveillance functions in the dorsal part of the eye maintain a higher spatial resolution than is needed for navigation alone.

Polarisation discrimination model

We have shown that the fiddler crab *U. vomeris* has a highly acute polarisation vision system. However, it is important to consider our results in the context of the known anatomy of the fiddler crab eye. Orthogonally oriented polarisation receptor systems (Alkaladi, 2008) are expected to have null-regions within which the determination of e-vector angle is ambiguous (Bernard and Wehner, 1977). For example, a horizontal/vertical receptor system fails to discriminate between polarised light sources with e-vectors at –45 and 45 deg, and neither can be distinguished from unpolarised light: All three of these conditions stimulate horizontal and vertical receptors equally, producing zero contrast in receptor activity. Such confounds can theoretically be eliminated by egocentric tilting of the receptor array, which has the effect of shifting the null point away from the confounding region, or by introducing a third polarisation detector with a different orientation (reviewed by Wehner and Labhart, 2006). Fiddler crabs maintain a strict alignment of the eye with the visual horizon (Nalbach et al., 1989; Zeil, 1990), and are not thought to possess polarisation detectors oriented in a third direction (Alkaladi, 2008), potentially leaving them exposed to these null point effects. A consequence of this is that stimuli with a fixed e-vector difference will produce different levels of photoreceptor contrast depending on their orientation relative to the microvillar detector array. This leads to changes in threshold e-vector discrimination values across the range of absolute orientations. A further confound is introduced by the percentage polarisation (or in this case ellipticity). As percentage polarisation decreases, so too does the apparent contrast in a polarisation cue (Bernard and Wehner, 1977). The co-variations in e-vector angle and ellipticity from the stimuli (as a result of the modified LCD) used in this experiment therefore have the potential to produce a range of confounds that need to be accounted for.

To gain a crab's-eye perspective on the discriminability of the polarised stimuli and to further understand the potential confounds associated with e-vector angle, partial polarisation and ellipticity, we modelled some of the physical features of the fiddler crab's orthogonally oriented photoreceptor array. Using a simulated fiddler crab photoreceptor constructed from a spectrophotometer coupled to a horizontal and vertical Polaroid filter (Fig. 5A and see Materials and methods for details) we measured the contrast in model receptors within ommatidia and between ommatidia viewing the stimulus and background across all stimulus settings. The within-ommatidia horizontal/vertical receptor contrast (C_{HV}; Fig. 5B) is determined by the function:

$$C_{HV} = \frac{h - v}{h + v}, \quad (1)$$

where h is horizontal intensity and v is vertical intensity. The C_{HV} measurement from the stimulus and background parts of the visual field are then compared by a hypothetical interneuron to produce a stimulus/background contrast value (C_{SB}; Fig. 5C) as follows:

$$C_{SB} = \left| \left\{ \frac{h_S - v_S}{h_S + v_S} \right\} - \left\{ \frac{h_B - v_B}{h_B + v_B} \right\} \right|, \quad (2)$$

where S is stimulus, B is background, h is horizontal intensity and v is vertical intensity. C_{SB} estimates the difference in polarisation contrast between ommatidia viewing the stimulus and those that view the background, a measure that is roughly analogous to spatial

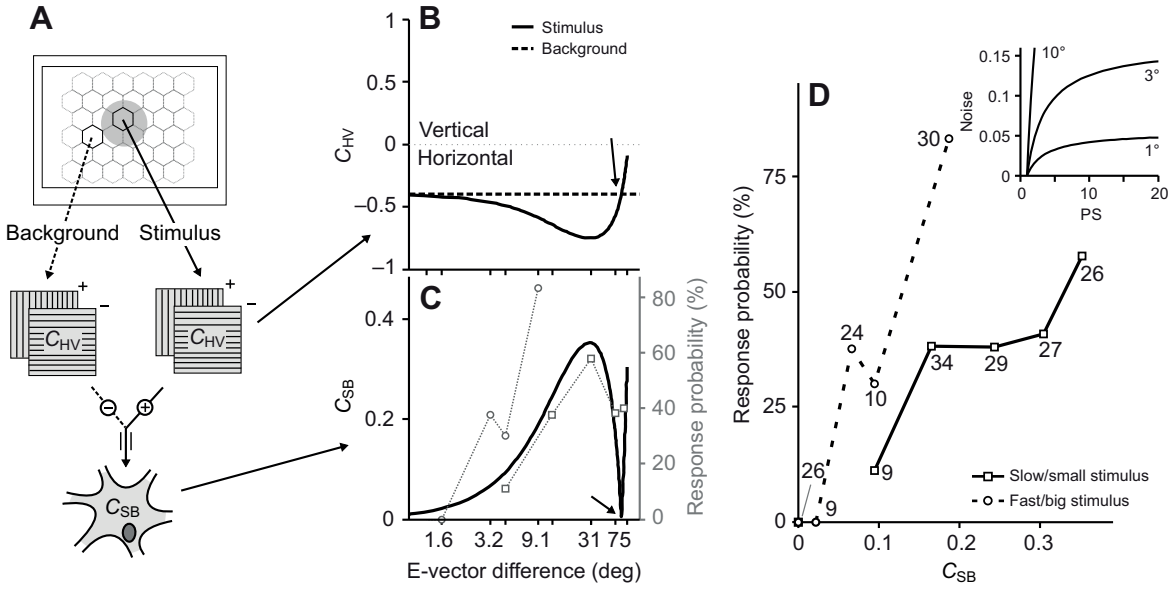

Fig. 5. Results from the perspective of a hypothetical fiddler crab visual interneuron. (A) Individual ommatidia viewing either the stimulus or the background produce measures of horizontal/vertical polarisation contrast (C_{HV}), which are then compared by a hypothetical interneuron to produce a value of stimulus/background contrast (C_{SB}). (B) C_{HV} for stimulus and background across the range of possible stimulus settings. (C) C_{SB} relative to e-vector difference with original response data from Fig. 4 overlayed in grey (right *y*-axis). A zero contrast null point occurs at an e-vector difference of 64 deg (B,C; black arrows). (D) Fiddler crab response probabilities plotted against stimulus/background contrast. Numbers indicate the number of trials contributing to each data point. Inset graph represents the minimum polarisation sensitivity (PS) and receptor noise required in this case to detect a 1, 3 and 10 deg e-vector difference.

representations of colour distance in a dichromatic system (e.g. Chittka, 1992). Given that fiddler crabs are known to possess a stable orthogonal receptor array, C_{SB} is arguably a more relevant measure of visual contrast for complex polarisation cues than simply the difference in e-vector orientation.

When the original response data are overlayed with the modelled C_{SB} values, the unexpected dip in response to the two highest e-vector difference stimuli (57 and 75 deg) closely matches a dip in C_{SB} (Fig. 5C). This local dip in C_{SB} is caused by a discrimination null point, at which the stimulus e-vector is –32 deg while the background e-vector is 32 deg, producing an e-vector difference of 64 deg but a C_{SB} value of zero. Replotting response probabilities against C_{SB} values removes the surprising drop in response probability at the high contrast end, and produces a roughly linear increase of response probability with increasing stimulus/background contrast (Fig. 5D).

Is the detection of a 3.2 deg e-vector difference possible given what we know about the physiology of fiddler crab photoreceptors? This capability is likely to be limited by two main factors, the polarisation sensitivity (PS) of the photoreceptor cells and the noise inherent in the phototransduction cascade. An accurate PS value for *U. vomeris* is unknown. However, other related species, such as grapsid crabs, have been shown to have high PS values of around 10 or 11 (Stowe, 1980). Direct measurements of receptor noise in *U. vomeris* are also lacking, but estimates from other animals suggest that noise should fall somewhere in the range of 1–10% of total receptor activity depending on ambient light levels (Vorobyev and Osorio, 1998; Vorobyev et al., 2001). If we assume that photoreceptor outputs must differ by noise levels of at least one standard deviation, we can calculate the maximum level of noise that can be tolerated for the detection of our 3 deg e-vector signal by a visual system with a given PS value. To do this, we used an adaptation of the Vorobyev–Osorio noise-limited receptor model (Vorobyev and Osorio, 1998). The relationship between the PS and noise values needed to detect three different e-vector differences, 1, 3 and 10 deg against a 32 deg background (as used in our experiment), are plotted in the inset in Fig. 5D (M. Vorobyev, personal communication). This predicts that for a visual system with a conservative PS value of 5, our 3 deg e-vector contrast can be detected against a 32 deg background as long as noise levels fall below 9.7%, an estimate that is well within physiological probability. Furthermore, this estimate is based on the properties of single photoreceptor units. Signal-to-noise ratio can be increased by pooling groups of photoreceptors, thereby increasing the behavioural sensitivity to small differences in e-vector angle.

We have shown that the fiddler crab *U. vomeris* has a highly sensitive polarisation vision system, able to detect differences in e-vector angle as small as 3.2 deg. This is the most acute polarisation vision yet described in any crustacean. Polarisation vision is therefore likely to play a vital role in the visual ecology of this species, and our results imply that it is the polarisation properties of objects, rather than just large field stimuli such as celestial cues or large water bodies, that are of use to these animals. These findings, coupled with existing knowledge of the behavioural ecology of this species and the ease with which the geometry of their natural visual environment can be reconstructed, make *U. vomeris* an ideal model species for future investigations into the ecology of polarisation vision.

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