

## RETINAL LOCATION IS THE KEY TO IDENTIFYING PREDATORS IN FIDDLER CRABS (*UCA PUGILATOR*)

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### Summary

**Fiddler crabs (*Uca pugilator* Bosc; Crustacea, Decapoda) feed and court in open, flat spaces. Their visual system has several putative adaptations to their flat habitat, including the tendency to keep the vertical axis of their eyes perpendicular to the plane of the substratum. It is hypothesized that one of the functions of this behavior is to distinguish accurately predators from conspecifics by aligning the region of the eye sensitive to predators with the region in space in which predators occur. To test this hypothesis, a crab was placed in a glass dish, and a moving stimulus was presented between 20° above and below eye level (horizontal). Stimuli below the crab's horizon hardly ever evoked escape responses, while identical stimuli above**

**the horizon produced escape responses whose frequency varied with the angular size, not the absolute size, of the stimulus. Experiments with artificial horizons showed that it is the position of the stimulus relative to the eye that is important, rather than its position relative to external cues such as the visible horizon, the vertical light gradient or the gravitational horizon. It is concluded that a crab responds to stimuli according to their position relative to its retinal equator. This conclusion is discussed in light of the crabs' natural behavior with respect to supra-horizontal stimuli.**

Key words: Crustacea, *Uca pugilator*, fiddler crab, vision, predator avoidance, spatial orientation.

### Introduction

Crabs, such as fiddler crabs, that live on sandflats and beaches have been dubbed 'flat-world' crabs because many aspects of their visual systems are adapted to their flat surroundings. One of these adaptations is the tendency to orient the vertical axis of their eyes perpendicular to the substratum (Zeil, 1990; Zeil and Al-Mutairi, 1996). The apposition compound eyes of these crabs have a narrow band of high vertical angular resolution that extends all the way around the eye at its equator, resulting from decreased inter-ommatidial angles between vertically adjacent rows in this area. The perpendicular eye orientation is achieved by visually fixating the horizon with this band, along with orientation information from the dorso-ventral light distribution and from gravity (Nalbach *et al.* 1989a). The eyes are then maintained in this position against disturbance in the pitch and roll planes by vertical optokinesis (Nalbach *et al.* 1989a,b).

There have been numerous hypotheses for the function of this eye orientation. First, it may serve to align the visual acute zone with the most information-rich region in space (Hughes, 1977; Zeil and Al-Mutairi, 1996). Second, it may allow the crab to gain depth information monocularly from the retinal elevation (or declination below the horizon) of the image of objects on the ground (Zeil *et al.* 1986). The particular gradient of vertical visual resolution in the eyes of these crabs is in agreement with this hypothesis and also suggests a third related hypothesis, size constancy. The gradient of vertical resolution decreases

dorsally and ventrally from a peak at the eye equator in such a way that the image of an object will always subtend the same number of ommatidia, regardless of its distance (but see Zeil and Al-Mutairi, 1996). Therefore, absolute size may be obtained simply by counting the number of ommatidia stimulated (Zeil *et al.* 1986). Fourth, the orientation of the eyes is thought to aid the optokinetic response by aligning the region of the eye containing the greatest horizontal optokinetic sensitivity with the direction in space in which rotational motion, but not translational motion, tends to occur (Nalbach and Nalbach, 1987; see also Barnes, 1990; Barnes and Nalbach, 1993). Finally, it may be a simple means of distinguishing predators from conspecifics. Male fiddler crabs respond to predators by freezing or escaping, and to conspecifics by performing a number of different behaviors, the most well-known of which is claw-waving. Field observations have shown that fiddler crabs escape from virtually any object moving above the horizon, regardless of its angular size, speed or shape, while objects below the horizon never cause escape responses and instead are often treated as conspecifics (Land and Layne, 1995a). Thus, it appears that the only factor influencing the reaction of the crab is an object's relationship to the horizon. This last hypothesis is the subject of this study.

The hypotheses listed above are not mutually exclusive, and it is notable that they all require sampling a particular direction in external space. This requirement raises a problem: because

flat-world crabs consistently orient their eyes perpendicular to the ground, there is constant correspondence between retinal location and direction in external space (at least along the vertical axis). Are the functions listed above specific to a retinal location or to a position in space? If the former is true, the function is 'location-constant', for it is specific to a location on the retina, and the eyes must be held perpendicular to the substratum to function properly. If the latter is true, the function is 'space-constant', and the retinal location mediating that function must be varied according some external reference as the eyes move (see Wehner, 1975; Wiersma, 1975). Stated in terms of the behavior being investigated in this study, the use of the horizon to identify predators, this question of constancy becomes, what aspect of the horizon really matters in distinguishing between predators and conspecifics, since in nature there is almost always a correspondence between horizons defined by gravity and the visible horizon, which are external references, and by the equator of the crab's eye. This study utilizes the escape response of fiddler crabs to artificial stimuli to test the hypothesis that they use the horizon to distinguish predators from non-predators. By determining whether the eye equator, or the visible or gravitational horizon, is the key in making this discrimination, this study also tests whether this discrimination is space- or location-constant. The results are then discussed in the light of observed natural behavior. A preliminary account of some of these results was given in Layne *et al.* (1997).

### Materials and methods

The fiddler crab *Uca pugnator* Bosc is a semi-terrestrial crab which is extremely abundant on the sandflats of southeastern North America. For this study, both male and female crabs, with carapace widths between 0.8 and 2.2cm, were caught during the summer of 1995 on a large sandflat in Beaufort, NC, USA, and kept unfed in an empty seawater table with a natural L:D cycle (12h:12h) for no more than 1 week prior to testing. Natural daylight was supplemented in the holding tank by indirect illumination from ceiling lights. Just before testing, crabs were moved to a white plastic container under a 40 W incandescent lamp. Behavioral tests were performed in a glass bowl which rested upon a rod projecting up into the center of a white vinyl drum (45cm wide, 76cm tall). A square stimulus (black cardboard, unless otherwise stated) was moved horizontally around the crab at a speed of  $8^\circ \text{ s}^{-1}$  using a motor, at a radial distance ( $r$ ) of either 11 or 22cm (Fig. 1). The stimulus size was 1, 2, 4 or  $8^\circ$  square, as seen by the crab, and was positioned at various elevations between  $20^\circ$  below the crab's eye level (assumed to be 1.5cm above the ground plane) and  $20^\circ$  above it. The stimuli were supported by a transparent plastic rod attached to the motor axle. The rod was 4mm square in cross section and created no visible refraction pattern: in preliminary trials, no crab ever responded to the plastic rod alone. Crab behavior/escape response was observed on a video monitor using a CCD camera positioned 30cm above the drum. The inside of the drum was lit from above by two 40W lamps

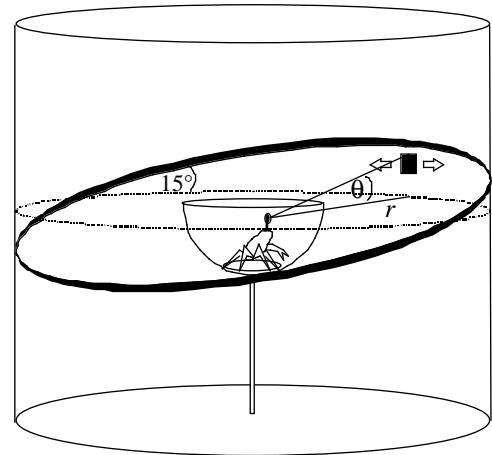


Fig. 1. Apparatus used to test the responses of crabs to the same stimulus above and below the horizon. The radial distance  $r$  between the crab and the stimulus is 22cm or 11cm, and the angle  $\theta$  is measured from eye height to the top edge of the stimulus. An artificial horizon of the type used in Fig. 3C, a stripe  $3^\circ$  wide and tilted by  $15^\circ$  to the horizontal (dotted line), is shown.

positioned 30cm above the drum on either side of the camera. No other lights in the laboratory were on.

Five experiments were performed: two were in an all-white drum with  $r=22\text{cm}$  and  $r=11\text{cm}$ , and one was in an all-black drum with  $r=22\text{cm}$ . For the remaining two experiments, a 'horizon' was introduced into the drum, whose plane was tilted  $15^\circ$  relative to the horizontal, so that it was  $15^\circ$  below the true (gravitational) horizon on one side of the drum, and  $15^\circ$  above it on the other side. On the basis of findings by Nalbach *et al.* (1989a) for another flat-world crab, *Mictyris longicarpus*, this is well within the angular range in which crabs will tilt their eyestalks to fixate a horizontal line with their acute zone. The plane of the artificial horizon intersected the glass bowl 1.5cm above the bottom of the bowl, at approximately crab eye level. In one experiment, the horizon divided the drum into white (upper) and black (lower) halves, offering both a visible horizon and a steep vertical light gradient, similar to the 'top white edge' shown to be the preferred contour for fixation by Nalbach *et al.* (1989a). In the final experiment, the horizon was a black stripe  $3^\circ$  wide (as depicted in Fig. 1). In the artificial horizon experiments, a small mirror was positioned so that a side-view of the crab's eyestalks could be seen by an observer looking down from above. The observer was positioned behind the illuminating light, and was thus not highly visible to the crab looking at the mirror, and the crab was not frightened by motion of the observer.

For each trial, a crab was placed by hand into the glass bowl and was observed for its response to the stimulus, namely, whether it attempted to escape. The bowl contained a few drops of  $2\text{mol l}^{-1}$  dextrose, and only crabs that began feeding when they were placed into the bowl were used. Crabs were tested within  $\pm 2\text{h}$  of low tide (low tides occur every 12.25h). Testing at low tide had the effect of normalizing the activity level of

the crabs over time, because they have strong, persistent tidal rhythms in activity, which exhibit a peak at low tide (Palmer, 1988). Testing only those animals that fed on the dextrose had the effect of normalizing the stress from handling between individuals, because *U. pugilator* do not feed and may not attempt to escape when they are highly stressed. An escape response was recorded if the crab did the following: (1) ran rapidly in the direction opposite to the stimulus, (2) tracked the stimulus as it ran, i.e. changed its running direction as the stimulus changed in azimuth, and (3) began running when or shortly after the stimulus began to move. The abundance of this species and its ease of capture allowed for the use of large numbers of animals. For each treatment (stimulus size at a given elevation), the number of trials (individual crabs) was usually 25 and ranged from 24 to 40. Each animal was tested once before it was released. Escape frequency was calculated as the proportion of trials in a treatment in which crabs showed the escape response.

The escape response of fiddler crabs in nature consists of three stages: (1) the animal freezes; (2) it runs to the entrance of its burrow; and (3) it enters the burrow (von Hagen, 1962; Land and Layne, 1995a). This order is not rigidly followed in every case. The inclusion of stage 1 is possibly dependent on the intensity of the stimulus, i.e. this stage is eliminated by large, conspicuous stimuli (J. E. Layne, personal observation). The experiments described here produced no prolonged freeze response (stage one) among those animals that escaped; these animals always either began running immediately at the onset of stimulus movement or showed a 'startled-freeze' response lasting less than 1 s, in which the crab made a quick, almost jumping, movement to a maximally erect posture, followed immediately by running. Each trial, from setting the crab in the bowl, commencement of feeding, to movement of the stimulus and escape, lasted less than 20 s. Animals that failed to commence feeding within approximately 15 s were not used.

## Results

### *Homogeneous white background, stimulus at 22 cm*

The importance of the horizon for identifying predators was tested by presenting identical black objects to the crab at various elevations relative to the horizon, against a homogeneous white background. The hypothesis is that, if the horizon is of primary importance in identifying predators, then a crab should react to an object above, but not to an identical object below, the horizon. Fig. 2 shows that this is the case: a stimulus very rarely produced an escape response when it was exclusively in the half of the visual field below the level of the crab's eyes, but when part or all of the stimulus was above this level, it evoked escape. The time from stimulus movement to response was always less than 1 s for 4° and 8° objects, and sometimes longer (1–2 s) for 2° objects. In response to a stimulus below the horizon, some crabs (approximately 10%) stopped eating and walked towards it, while the others stopped feeding only momentarily or not at all. This demonstrates that the crucial feature of the stimulus for eliciting escape is its

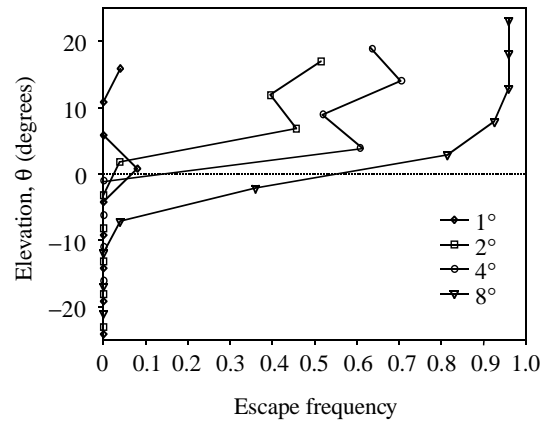


Fig. 2. Escape response frequency (the proportion of trials in which an escape response was invoked) for four different sizes of square, black-on-white stimulus, when moved a few degrees at  $8^\circ \text{ s}^{-1}$ . The  $1^\circ$  stimulus was ineffective, but the others were effective when the top of the square was above the horizon but not when it was below it. Larger stimuli resulted in a higher escape frequency. The 36 trials (four sizes, nine elevations) involved a total of 973 crabs. Elevation,  $\theta$ , is the angle from eye height to the top edge of the stimulus.

position relative to the horizon. Note also that, although there was no horizon visible to the crabs, they were able to discriminate between objects above and below eye level.

The differences between the four curves in Fig. 2 were much as would be expected if escape frequency depended on differences in the angular size of the stimuli on the crabs' retina (or possibly on its absolute size, see below). The largest ( $8^\circ$ ) stimulus evoked responses as soon as it intersected the horizon, whereas the  $2^\circ$  stimulus had to be wholly above the horizon before it became effective. Similarly, the  $8^\circ$  stimulus was almost twice as effective as the  $4^\circ$  or  $2^\circ$  stimuli, when it was above the horizon. In agreement with field observations (Land and Layne, 1995a), the  $1^\circ$  object produced almost no response.

The increase in escape frequency with increase in stimulus size could be explained in two ways: (1) the crab calculates the absolute size of objects above the horizon, or (2) absolute size is not important, rather there is a simple relationship between angular size and response frequency. The former hypothesis is tested in the next experiment.

### *Homogeneous white background, stimulus at 11 cm*

To measure absolute size, the crab must have some measure of distance, because absolute size is the product of angular size and distance. In principle, a crab might judge distance either by using binocular cues for stereopsis or by using the declination method proposed by Zeil *et al.* (1986). However, while stereopsis depends directly on real distance, the declination method does not. Instead, it uses the elevation of the image on the retina as a proxy for distance; the crab measures the angle between an object on the ground and the horizon (the object's 'base angle') and, assuming a flat substratum, uses this angle to calculate the object's distance.

Table 1. *Significance of differences between responses to stimuli at 22 and 11 cm, varying in either absolute or angular size*

Angular size (degrees)		Escape frequency at		P
at		11 cm	22 cm	
11 cm	22 cm	11 cm	22 cm	
Equal absolute size				
2	1	0.42±0.12	0.03±0.04	0.0005
4	2	0.63±0.05	0.46±0.06	0.0036
8	4	0.95±0.05	0.62±0.08	0.0005
Equal angular size				
2	2	0.42±0.12	0.46±0.06	0.52 (NS)
4	4	0.63±0.05	0.62±0.08	0.36 (NS)
8	8	0.95±0.05	0.95±0.02	0.33 (NS)

Stimulus distances were 11 cm and 22 cm.

Results of Student's *t*-tests (data were arcsine-transformed, and *t*-tests were performed with the Bonferroni correction for multiple use of data sets) on the differences in mean escape frequency at four elevations above the horizon.

The number of crabs tested per trial was 24–40; the total number represented in this table is 781 from 28 separate trials.

Values are means ± s.d. NS, not significant.

Using this distance and the object's angular size, the crab can calculate absolute size. Actual distance, and by extension absolute size, is not important for this mechanism. To determine whether there was any detectable effect of distance, the same stimuli were presented again at the same elevations as before but at a distance of 11 cm. If absolute size were important, and thus binocular cues are used, distance should not matter, and the response should be the same. However, if the crab uses only angular size, the nearer stimulus should be more effective.

The results are shown in Table 1. It is clear from the results that objects above the horizon that are of the same absolute size are treated quite differently at different distances (all had  $P \leq 0.05$ , Student's *t*-test), whereas objects of different absolute sizes but the same angular dimensions on the retina are not distinguished (all had  $P > 0.05$ ). This provides further evidence that absolute size is not important and that binocular cues are not used for estimating distance. This does not preclude the possibility, however, that the tendency to escape may be a function not only of perceived predator size but also of perceived distance.

The remaining alternatives are that distance is estimated by the declination of objects below the horizon or that it is not used at all; either way, the horizon is the key. The distinction between these alternatives will be examined in the Discussion.

#### *'Top white' horizon, tilted by 15°, stimulus at 22 cm*

Having established the primacy of the horizon in classifying animate objects, how is the horizon defined by the crab? One possibility is that the vertical light gradient contributes to this definition; since this gradient plays a role in orienting the

eyestalk correctly (Nalbach and Nalbach, 1987), it is reasonable to suppose that it might then play a role in the interpretation of what is subsequently seen, although it is clear from Fig. 2, in which there is no steep vertical light gradient, that it is not necessary. To determine whether the vertical light gradient is important in defining the horizon, a 'top white' horizon was added to the drum and tilted by 15° to the horizontal. Stimuli were presented at 5° elevation intervals, against either the high or low side of the horizon, or both, as indicated in the diagram in Fig. 3A. Stimuli appearing against the black and white backgrounds were white and black, respectively.

For this and the other horizon experiment, the most informative trials are those in which the stimulus is between the visible and true (gravitational) horizons, because these stimuli directly compare the respective effects of these horizons on the escape response. The combined results from 4° and 8° stimuli (Fig. 3A) show that the region between  $\theta = 0^\circ$  and  $\theta = +15^\circ$ , where  $\theta$  is the angle from eye height to the top edge of the stimulus (see Fig. 1), against the high-side stimuli were half as effective at evoking escape than at the same elevations in the previous experiment with an all-white background (Fig. 2). At other elevations, however, or when black stimuli were presented between 0° and +10° against the low side, escape frequency was approximately the same as in the previous experiment. This reduction in response for some stimuli could be due to their relationship to the vertical light gradient or the visible horizon, or to the reversal of stimulus/background shading. The latter two possibilities are tested in the next two experiments.

#### *Homogeneous black background, stimulus at 22 cm*

To test whether reversing the stimulus/background shading could produce the results in Fig. 3A, the experiment was repeated in a black drum using white 4° and 8° stimuli. While the results show that the strong response threshold remains at eye level, this arrangement is approximately half as effective in evoking escape as black-on-white for both stimulus sizes tested (Fig. 3B; compare Fig. 2). When crabs did escape, the response was usually delayed by several seconds relative to black-on-white trials. These observations indicate that the reduced escape frequencies between 0° and +15° in Fig. 3A can easily be explained by a lower sensitivity to white objects against a black background. It is not necessary to invoke the visible or anatomical horizon or the vertical light distribution for an explanation.

#### *Stripe 3° wide, tilted by 15°, stimulus at 22 cm*

It is clear that the horizon alone may influence escape, but which horizon? There are three possibilities: the true gravitational horizon; the visible horizon, which may be different from the gravitational horizon on a sloping beach; or the crab's anatomical horizon defined by the equator of the eye. To distinguish between these possibilities, a visible horizon was added to the drum and tilted by 15° to the gravitational horizon.

Approximately 15% of the crabs tilted their eyestalks to

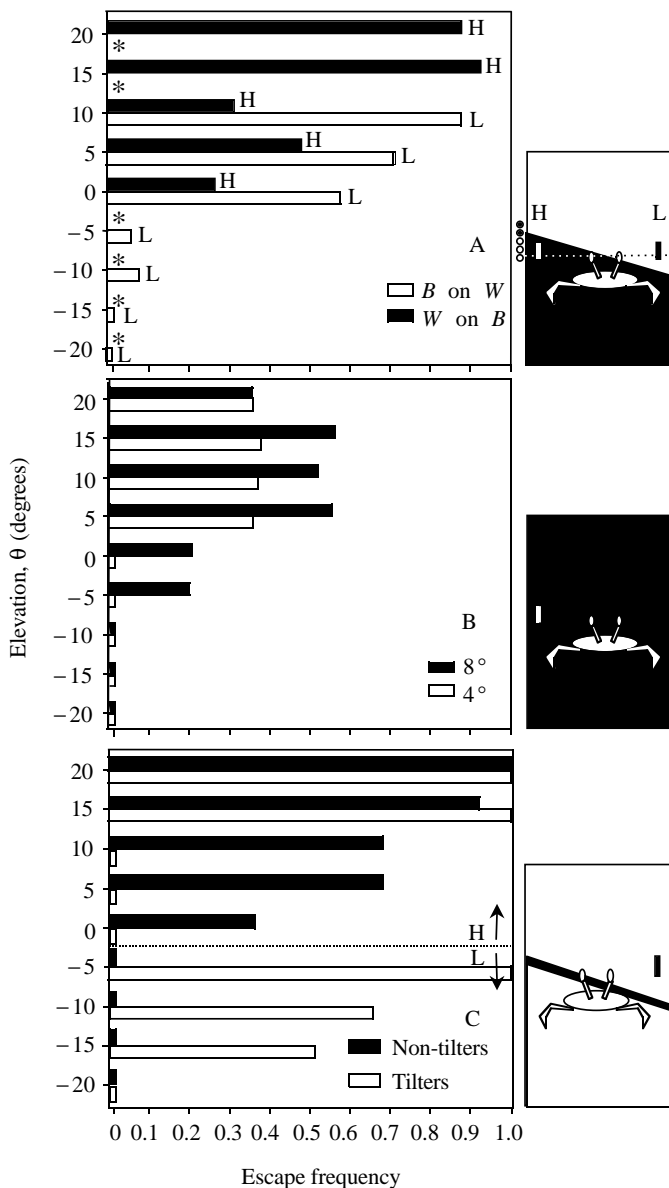


Fig. 3. Effect of background contrast pattern (indicated by the diagram) on escape behavior. (A) Effect of a 'top white' horizon (4° and 8° stimuli combined). Stimuli were presented against the high (H) or low (L) side of the horizon. Stimuli presented at elevations having a black (B) background were white, those against a white (W) background were black (filled and open bars, respectively). Stimuli were not presented below 0° against the high side or above +10° against the low side (circles in the diagram, with 0° indicated by a dotted line; an asterisk indicates no experiment). (B) Effect of white stimuli against a black background. (C) Effect of a visible horizon (a stripe 3° wide). Stimuli at elevations  $\theta \geq 0^\circ$  were presented against the high side of the horizon, while those at elevations  $\theta \leq 0^\circ$  were presented against the low side, where  $\theta$  is the angle from eye height to the top edge of the stimulus. Approximately 15% ( $N=81$ ) of the crabs tilted their eyes to conform with the 3° wide black horizon stripe (open bars), the remainder ( $N=457$ ) kept to the true gravitational horizon (filled bars). Note that for crabs with tilted eyestalks escape responses were only made above the visible horizon (the stripe), but for crabs with non-tilted eyestalks responses only occurred above the gravitational horizon, apparently ignoring the stripe. In both cases, these correspond with the anatomical horizon of the eye.

Among eyestalk tilters, visual fixation of the horizon was quite firm, continuing even as the crab frantically scabbled at the side of the bowl during its attempted escape, which caused considerable disturbance in body position. This strong apparent fixation of the stripe is probably mediated by the optokinetic system (which governs eyestalk stability) and not by the fixation response (which governs eyestalk position), because the fixation response tends to be rather slow (Nalbach *et al.* 1989a) and is probably unable to counteract the rapid disturbances imposed by the crab's escape. However, the initial fixation of the stripe upon entering the drum must have occurred quickly, for in several trials the escape response was evoked in tilt-eyed crabs only a few seconds after they had been placed into the drum.

Is there any object that can elicit escape below the horizon? When objects were moved below crabs held in a clear glass container in their natural habitat, no escape response was evoked by any of the objects tested, including the author's hand, a bucket, a shovel and even the predacious blue crab *Callinectes sapidus*. In contrast, if another fiddler crab was fixed to a transparent rod and held at high elevation, even at close range where shape discrimination should be possible, alarm was almost always the result.

### Discussion

Sand fiddler crabs feed and court in open, flat spaces and thus are at considerable risk from predation from a variety of predators (e.g. Bildstein *et al.* 1989). They have evolved a simple yet robust strategy for deciding whether an intruding object is a potential threat. This consists of determining whether the object exceeds a threshold angular size and whether it protrudes above the horizon. The object's speed and shape are not utilized (Land and Layne, 1995a) nor is its absolute size (Table 1): objects of the same size at the same

fixate the stripe with the equator of their eyes. The escape frequencies from stimuli at different elevations were strikingly different for crabs that did and did not tilt their eyes to fixate the stripe. For the non-tilters (Fig. 3C), the artificial horizon was essentially irrelevant: the crabs fled from stimuli above the gravitational horizon, but not those below it. The crabs with tilted eyes, however, fled when the stimuli were above the artificial visual horizon but not when they were below it. There were no exceptions. In this case, the gravitational horizon was irrelevant.

For the non-tilters, the eye equator corresponded with the gravitational horizon, and for the tilters it corresponded with the artificial horizon. The most parsimonious explanation of these observations is that in both cases it is the crab's anatomical horizon (the equator of the eye) that is used to determine whether a stimulus should evoke an escape response.

distance evoke escape when they are above the crab's eye level, but not when they are below it (Fig. 2). This means that position relative to the horizon is a sufficient cue for the stimulus to be classified as a predator.

#### *Space constancy*

How does the crab determine whether an object has penetrated the horizon? For a fiddler crab, this problem is essentially one of making an accurate match between the perceived position of the object on its eye and a specific direction in space (i.e. above or below the horizon), which suggests that it may be related to a space-constancy mechanism. Space constancy, the ability correctly to perceive the direction of objects despite their or one's own movement or position, can be achieved either by maintaining a fixed and space-constant position of the eyes or by continuously computing the actual deviations of the eyes with regard to a space-constant reference system (Wehner, 1975). It is tempting to think that predator detection in *U. pugilator* is an example of the second mechanism, mediated by a class of visual interneurons known as 'space-constancy fibers', because of their similarity in receptive fields. These fibers, found in crayfish (Wiersma and Yamaguchi, 1966), rock lobsters (Wiersma and Yaganisawa, 1971; Wiersma and Yamaguchi, 1967) and crabs (Wiersma, 1970; Wiersma *et al.* 1977), have as their potential receptive field the entire retina, but the actual receptive field is restricted to the area above the horizon, by afferent information from the statocyst, regardless of the orientation of the eye. In crayfish, the escape response is limited to the region above the horizon and does appear to be mediated by these fibers (Wiersma, 1975). However, all the evidence suggests that the first mechanism is the correct one for predator detection by fiddler crabs. As evidence for this, the eyes do align with the horizon, and whether the eyes are aligned with the gravitational horizon or with the visual horizon, the response depends upon the position of the stimulus relative to the eye itself (Fig. 3C). In other words, retinal location remains the key to evoking escape even though eye position changes relative to space-constant reference systems. One objection to this conclusion might be that the crabs' bodies were always horizontal in these experiments, and thus no deviation with respect to gravity was calculated, and the receptive fields of the space-constant fibers were never adjusted despite the tilt of the eyestalks. However, this implies a space-constancy mechanism that makes use of body orientation but not the angle between the eyestalk and the body. This seems both unlikely for an animal with such highly mobile eyestalks and impractical for an animal whose interest is served by a spatial reference system based on its physical surroundings, not on gravity. However, this evidence forms an admittedly weak link between the decision to escape from an object and the crab's general perception of spatial direction, and it is possible that these are independent of one another.

#### *A look at the alternatives to a location-constant system*

Because it is apparently designed optically and neurally for

the purpose of extracting a specific subset of all the information in its environment (see Introduction; also Zeil *et al.* 1989), the visual system of flat-world crabs can be described as a 'matched filter' in the sense of Wehner (1987). This term refers to the fact that, under some conditions, a sensory system may evolve to extract relevant information from the environment with great economy of resources and neural computation. However, this economy is often made possible by making assumptions about the environment that narrow the conditions under which the sensory system is accurate and reduce the flexibility of behavior. It is against the cost of making these assumptions that the benefits of economy (or the cost of the alternatives) must be weighed. It has been argued to this point that *U. pugilator* has a visual predator-detection system that is specific to a retinal location and that it relies on keeping its eyes positioned properly in space in order to ensure that its behavioral responses are appropriate. If the system is really this rigid, its success depends upon two assumptions: (1) that the substratum is flat, and (2) that the eyestalks have the proper orientation. It follows that the crab risks making errors of misidentification if these assumptions are violated. For instance, if the substratum is not flat, one crab may appear above another and be interpreted as a predator, and the ensuing escape response may result in the loss of feeding time or mating opportunities. If the eyestalks are not aligned correctly, then predators may approach more closely before they penetrate the horizon, increasing the chance of capture. It is easy to imagine that these assumptions are violated regularly, given the shifting topography of the sand and the fact that many fiddler crabs live where there is no clear view of the horizon for fixation.

To understand why such a potentially error-prone system is in place, consider the possible alternatives. One possibility would be to use the other space-constancy mechanism, i.e. to compute the deviation of the eyes from a fixed reference system. This requires information on body tilt and eyestalk position. While the former is available from the statocysts, the latter is apparently not available. In all attempts so far, no evidence of proprioceptors has been found in crabs (Horridge and Burrows, 1968; Horridge and Sandeman, 1964). Fiddler crabs are flat-world animals which, as argued below, may be unique in that the positions of their eyes need not be measured to make certain spatial judgments. It would be interesting to compare the escape habits of crabs that live on a rocky shore not on a flat surface.

Another system that could accurately identify predators, without relying on the local topography or a potentially flawed eyestalk orientation mechanism, would be identification by shape. This would require that the crab have adequate pattern-recognition abilities, which may be true. Visual patterns are important signals among fiddler crabs (Salmon and Hyatt, 1983): the males of several species build hoods or pillars in the mud near their burrows, which act as a visual beacon to females (Christy, 1988, 1995), and *Uca pugilator* has been shown to see and respond to some shapes by moving towards them and to avoid others, including stationary, bird-shaped objects (Langdon and Herrnkind, 1985; Langdon, 1971, as quoted in Herrnkind, 1983). They also recognize the species-

specific pattern of the males' claw-wave (Crane, 1957; Salmon *et al.* 1978). However, using shape to identify predators would also require visual acuity capable of resolving the shapes of moving objects as far away as possible. This may be where the method fails, for the fiddler crab's visual resolution, while quite good around the eye equator, is such that an approaching predator subtends only a few ommatidia unless it is quite close (e.g. a 30 cm tall bird at a distance of 4 m is only approximately three ommatidia tall) (see Land and Layne, 1995a). This becomes a problem if the predator is fast-moving and especially if the predator approaches from above, where visual resolution is greatly reduced. There is some evidence that shape need not be determined explicitly. In choice experiments, *U. pugilator* avoided round shapes and were attracted to vertical contours (Langdon and Herrnkind, 1985; Langdon, 1971). To a crab, these shapes might correspond to dangerous shore birds and protective marsh grass respectively.

An alternative method would be to identify predators by their size. As mentioned earlier, this requires that the crab first determine distance. The results of the present study show that absolute size and distance are not important for identifying predators. This conforms to existing theory, because the test distances in this study (22 and 11 cm) are greater than the theoretical maximum distance for binocular depth perception for these crabs (Burkhardt *et al.* 1973; Land and Layne, 1995a). This theoretical maximum distance depends on the horizontal inter-ommatidial angle and the inter-ocular distance and, in *U. pugilator*, is calculated to be only approximately 10–12 cm. Thus, while there is nothing in the present results suggesting that binocular vision is not important at close distances, possibly for social interaction (see Land and Layne, 1995a,b), it is useless as a component of a predator-detection mechanism because of its limited range.

There remains the problem of the declination method for measuring absolute distance and size and of distinguishing this as a possibility from the simpler retinal horizon method for telling friends from foes. According to the declination hypothesis, an object's distance is calculated from the angle below the horizon of its lower edge, which is multiplied by angular size to give absolute size. The conditions this system requires (a flat substratum, proper eyestalk orientation) mean that all objects larger than the crab, regardless of their base angle or angular size, will protrude above the horizon. Because it may be assumed that crabs run from objects that they perceive, by any method, to be larger than themselves, it is impossible to separate this mechanism behaviorally from the retinal location hypothesis. However, there are three reasons why the latter hypothesis is to be preferred. First, whether it operates *via* the declination method or the retinal location method, the predator-detection system appears to be location-constant rather than space-constant. Therefore, the declination method must rely on the same assumptions about topography and eyestalk orientation as does the horizon method, and it therefore has no technical advantages for verifying that an object is larger than the crab. With no advantage for the more complex alternative, it is parsimonious to favor the simpler, but

equally good, hypothesis. Second, the declination method depends on the ability visually to measure a vertical angle, the base angle, and it is therefore limited by the crab's vertical visual resolution. Despite the increased visual acuity of *U. pugilator* near the horizon, the declination method is limited by the crab's optics to a radius of approximately 2.5 m, but crabs readily respond at greater distances. Finally, probably the most powerful argument against the declination method is that crabs respond perfectly well to birds on the wing and other objects that appear wholly above the horizon. The declination method cannot account for this because, when no part of the object appears below the horizon, no declination angle exists and distance cannot be determined. Therefore, as with stereopsis and shape perception, the declination method of distance perception might be used for other purposes at close range, but it does not appear to mediate the escape response.

Given these arguments, the fiddler crab predator-detection system might be understood by turning to a theory of predator-prey interactions, which states that, in order to respond appropriately to potential predators, an animal needs information about its own immediate risk. If this information is costly to obtain, then evolution will favor fixed behaviors in response to a small amount of information (Sih, 1987). In the present context, it appears that the fiddler crab's habitat is consistently flat enough, and its eyestalk orientation mechanism precise enough, for a fixed response to stimuli at certain retinal locations to work as a means of detecting and avoiding predators. This removes the need to gain a lot of information about the threat, such as its shape and size, which is costly because it can only be gained at close distances. Thus, it may be concluded that the costs of errors which lead to loss of feeding time, mating opportunities, etc., are small relative to the benefits of the increased vigilance, larger detection radius and decreased reaction times inherent in the predator-detection system as it is presented here. A study of the risks posed by predators (e.g. Ens *et al.* 1993) and the costs (feeding, mating, energetic) of escape from moving objects would be useful for filling out this argument. The idea that the requirements for a flat substratum and precise eyestalk orientation are consistently met is supported by other visual/optical phenomena (see Introduction); namely, that the horizontal optokinetic sensitivity is restricted to the upper hemisphere and that the eyes' spatial resolution is strongly biased towards the horizontal band that usually looks at the horizon (see Zeil *et al.* 1986; Zeil and Al-Mutairi, 1996). While the former, neural phenomenon may be adjusted according to the orientations of eye and body (it is not known whether it is) and thus avoid these requirements, the latter anatomical phenomenon obviously cannot be adjusted, and its existence suggests that the requirements are met.

In contrast to these laboratory results, several important exceptions to the horizon rule can be observed in the field, in which the rule's underlying assumptions seem to be violated, but no error in identification is made. These exceptions indicate that the behavior is not as rigid as laboratory experiments suggest and that, in nature, more is required for activation of

the escape response than mere penetration of the horizon. For instance, juvenile crabs are much smaller than adults, which would routinely appear above the horizon, but this does not evoke escape in the juveniles. Also, owing to variations in the substratum, situations occur in which one adult is higher than another, and again there is no escape response. Finally, there is the claw-waving display by the males, in which their large chela is raised above the plane of the horizon; the claw is raised especially high when females are close, yet there is no escape response (but see below).

What, then, are the additional criteria for classifying predators? One is the brightness contrast between the object and background. As has been shown (Figs 2, 3B), dark objects against a white background are much more effective at evoking escape than white objects against a dark background (c.f. Herrnkind, 1968, 1972). This is also readily apparent to the observer in the field, who if backed by trees or a building will be allowed to approach much closer to the crabs and enjoy much more freedom of movement than if backed by blue sky. It makes good sense for the nervous system of these animals to emphasize dark objects against a light background for detecting predators because, in their sandflat/beach habitat, the upper hemisphere of their visual world is nearly all bright sky, and since the majority of their predators approach from above, because they are larger or flying, they would appear dark against a light background. The lone exception is the blue crab *Callinectes sapidus*, which is an efficient predator of *Uca pugilator*, probably because this aquatic crab approaches fiddler crabs near the water's edge with only its eyes protruding above the water surface, thereby avoiding activation of the fiddler crab escape response (e.g. Hughes and Seed, 1995).

Another criterion for classifying a moving object may be its spatio-temporal pattern of movement. This study was not designed to test the response properties of fiddler crabs' motion sensitivity, but it should be noted that motion may play a role in the failure of fiddler crabs to run away from one another and from the tall, windblown grass near their burrows. The visual interneurons mediating escape may habituate rapidly, or be insensitive, to certain patterns of motion. For instance, neurons sensitive to small-field motion in brachyurans habituate rapidly to repeated stimulation and are often most sensitive to a particular pattern or direction of movement (see Wiersma, 1975, and references therein). It follows that cells will become and remain habituated if they match the prevailing movement of nearby vegetation. Additionally, it is possible that the crab is insensitive to the particular temporal motion pattern of grass. Wind tends to move plants sinusoidally, with most of the energy at low frequencies (MacMahon and Kronauer, 1976), and if animals can disregard this type of motion, they have gone a long way towards reducing the visual noise in their environment and can more easily detect other patterns of movement (Fleishman, 1985, 1992). Therefore, it may be that grass is discounted and predators are identified, at least partially, by their low-frequency sinusoidal or high-frequency non-sinusoidal movement, respectively.

While these factors and probably others may explain the lack

of escape from certain objects in the crabs' natural environment, their action is to alter the probability of escape from supra-horizontal stimuli and not to change the region of sensitivity on the eye. This is clear from the fact that the eyestalk orientation relative to the body or to external reference cues does not matter for identifying predators and from the fact that it is nearly impossible to elicit escape in fiddler crabs using objects held below them.

Experiments in which friendly stimuli are presented above the horizon have a correlate in nature, observed recently by Christy and Kreuter (1997). A male of the tropical species *Uca musica* may sometimes pursue a female that has just visited, and left, his burrow. After passing her, he performs an unusually high and sudden motion of the claw. Alternatively, if the male has constructed a hood at the entrance of his burrow, he may instead climb rapidly to the top of the hood. Both behaviors have the effect of frightening the female back into the male's burrow. He then follows and sometimes successfully mates with her. This may be a case of a 'sensory trap' (Christy, 1995), in which the male signal exploits the female's sensory system, which has evolved to identify predators and discount non-predators, by intentionally mimicking a predator, thereby increasing the male's fitness.

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