

Burrow surveillance in fiddler crabs

II. The sensory cues

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Summary

Using crab-like dummies, we have shown previously that fiddler crabs [*Uca vomeris* (McNeill)] defend their burrows against intruders in a burrow-centred frame of reference. The crabs respond whenever an intruder approaches to within a certain distance of the burrow entrance, and this distance is independent of the approach direction. We show here that the crabs combine information from the path integration system on the location of their invisible burrow and visual information on the retinal position of an intruder to make this allocentric judgement. Excluding all alternative visual cues, we propose that the crabs employ a small set of matched visual filters to determine the relationship between a crab-like object and the invisible burrow. To account for the constantly varying distance between the crabs and their burrows, the state of the path integrator may select the appropriate one of these retinal ‘warning zones’. We have shown before that burrow-owning fiddler crabs are extremely responsive to potential burrow snatchers, which we simulated with crab-like dummies moving across the substratum towards the burrow of residents. The crab’s decision to respond to these dummies

depends mainly on the spatial arrangement between itself, its burrow and the approaching dummy. The most important factor predicting response probability is the dummy’s distance from the crab’s burrow: the crabs are more likely to respond the closer the dummy approaches the burrow. The dummy–burrow distance not only determines the overall response probability but also the timing of burrow defence responses (i.e. when the crabs decide to react). Most interestingly, this response distance is independent of the dummy’s direction of approach to the burrow. In addition, the crabs respond earlier to a dummy approaching their burrow if they themselves are further away from it, indicating that knowledge of their own distance from the burrow has an influence on their decision to respond. These results raise a number of interesting issues, which are the focus of this paper, regarding the cues and the information used by the crabs in burrow surveillance.

Key words: matched visual filter, path integration system, burrow defence response, burrow surveillance, sensory cue, fiddler crab, *Uca vomeris*.

Introduction

The observation that fiddler crabs are very sensitive to other crabs approaching their burrows is not trivial in terms of information processing. As a crab moves away from its burrow on a feeding excursion or to interact with other crabs, it needs to assess the movements of other crabs, not in relation to itself (i.e. in an egocentric frame of reference) but in relation to a location in space (i.e. in an external frame of reference). The situation is aggravated by the fact that, due to the perspective foreshortening and the visually cluttered substratum, crabs cannot see the burrow entrance when they have moved more than approximately 15 cm away from it (Zeil and Layne, 2002). The crabs therefore cannot rely exclusively on vision for burrow surveillance. The question then becomes, how do foraging crabs know whether another crab is approaching their invisible burrow? The question is intimately related to the problem of

how crabs find their way back to their burrows, especially when they need to return to them swiftly in times of danger. From homing experiments, it is clear that crabs employ path integration to stay ‘attached’ to their burrows, which means that a foraging crab knows the direction and the distance at which the burrow lies (Cannicci et al., 1999; von Hagen, 1967; Land and Layne, 1995b; Zeil, 1998; Zeil and Layne, 2002). How can this information be used to inform the visual system when to trigger a response to a crab moving through the visual field? Again, the results of our behavioural analysis show that this cannot be a trivial task: when burrow owners respond to a crab-like dummy, they time their responses based on the dummy’s distance to their burrow irrespective of whether the dummy approaches from far away beyond the burrow or whether it moves closely past the crab (Hemmi and Zeil, 2003a).

Here, we propose that burrow surveillance in fiddler crabs is based on a pragmatic matched filter that incorporates the invariant properties of the topography of vision in a flat world and information from the path integration system to provide a robust and simple solution to the crucial task of protecting an invisible resource. We use the same data set we presented in a preceding paper (Hemmi and Zeil, 2003a), but now ask what cues guide the crabs' response to crab-like dummies. Part of this work has been published in abbreviated form elsewhere (Hemmi and Zeil, 2003b).

Materials and methods

For details of the data set, the analysis of behaviour and the statistical methodology, see Hemmi and Zeil (2003a).

To reconstruct the visual cues involved in burrow surveillance, such as the position and the angular size of the dummy in the visual field of the crabs, we determined the relationship between the size of the crabs, as measured by carapace width, and their eye height above the surface. We randomly caught 24 animals and measured their carapace width with callipers. The crabs were then placed back onto the mudflat in front of a vertical wall opposite a horizontal video camera, the lens of which was approximately 2 cm above ground. The crabs were filmed while sitting at the base of or walking along the wall and were subsequently released. From the recordings, we measured the eye height above ground for the same crabs in both a sitting and a walking posture (see also Zeil and Layne, 2002).

Results

The task

In terms of information processing, the two most striking results of our behavioural analysis are: (1) that the probability of a crab responding to an approaching dummy and the timing of the crab's response depend mainly on the dummy's distance from the crab's burrow and (2) that this distance does not depend on the dummy's approach direction relative to the crab's home vector (Hemmi and Zeil, 2003a,b). This is despite the fact that the distance between the crab and the dummy varies significantly with the dummy's direction of approach. For instance, when a dummy approaches from the crab's side of the burrow it can come very close to the crab itself. By contrast, when it moves in from beyond the burrow, the distance between the crab and the dummy will always remain large. When responding to dummies moving along these different paths, the crabs thus assess them not in relation to themselves (i.e. in an egocentric frame of reference) but in a frame of reference centred on their burrow (Hemmi and Zeil, 2003a). This result rules out simple, egocentric response criteria such as an apparent size threshold or retinal position, which vary significantly with the dummy's direction of approach (Fig. 1). For instance, if the crabs used an apparent size threshold to determine when to respond to a dummy, we would expect the apparent size of the dummy at the time of

response to be constant, irrespective of the dummy's approach direction. This is clearly not the case (Fig. 1A). Dummies that approach the burrow from the side opposite to the crab (small track angles) are responded to at much larger crab–dummy distances, and therefore their apparent size is only half of the apparent size of dummies that approach from the crab side of the burrow (large track angles), which are allowed to approach the crab much closer (Fig. 1A). Equivalent arguments can be made for the dummy's elevation (Fig. 1B) and azimuth relative to the burrow (Fig. 1C) at the time of response. Crabs do not simply respond when the dummy is seen at a certain retinal position.

What cues would allow crabs to estimate the distance between a dummy and their burrows? The determination of the distance between two objects irrespective of viewing direction and viewing distance is a difficult geometrical task requiring knowledge of the length of two vectors and of the angle between them (Fig. 2). In burrow surveillance, crabs would thus need to know their own distance from the burrow (cb), their own distance to the dummy (cd) and the difference in angular position of the dummy and the burrow in the visual field (α). Given that they can acquire this information, crabs could then, in principle, exploit the relationship expressed by the equation shown in Fig. 2 to determine the distance (db) between the dummy and the burrow. Before we ask whether crabs really do need to solve quadratic equations in order to protect their burrows, we will first establish what information they have available to solve the task.

The sensory cues employed in burrow surveillance

We know from previous work that path integration provides fiddler crabs with information on their own distance to the burrow and on the direction in the visual field in which it lies (Zeil, 1998; Zeil and Layne, 2002). While the distance to the burrow is directly available from the path integration system, the angle between the dummy and the burrow requires some additional visual input. Visual information on its own is, in most cases, not sufficient to determine the location of the burrow because the crabs cannot see the burrow entrance once they are more than 15 cm away from it (Zeil and Layne, 2002). The angular separation between a dummy and the burrow can be measured directly from their retinal position only when both are visible at the same time but otherwise needs to be determined by combining information from the path integration system on burrow location with the retinal position at which the approaching dummy is seen. The computational task of implementing this sensor fusion is actually not as complicated as it first seems because foraging crabs also use information from their path integration system to keep their longitudinal body axis aligned with the home vector (Ens et al., 1993; Land and Layne, 1995b; Zeil, 1998). The direction in which the burrow lies is thus always viewed by the same part of the retina.

We are left with the question of how the crabs might determine the distance between themselves and the dummy. There are five ways in which animals with fixed-focus

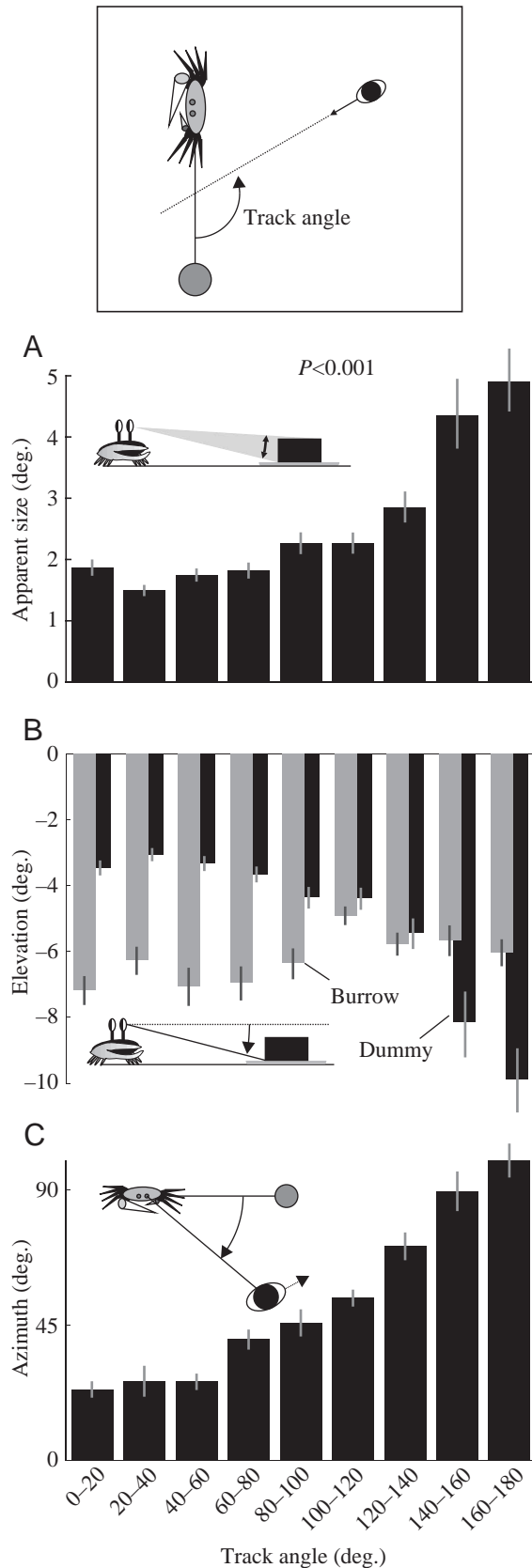


Fig. 1. The retinal size and position of the dummy on the crab's retina at the time of response. Each measure is plotted as a histogram against the dummy's approach direction (track angle; see inset at the top). Vertical lines mark 1 s.e.m. above and below the mean. (A) Vertical retinal size increases with track angle (REML; $N=419$, Wald/d.f.=31.86, d.f.=8, $P<0.001$). The results for the horizontal angular size of the dummy are equivalent. (B) Dummy elevation in the crabs' visual field at the time of response increases with track angle (black bars). The elevation of the burrow (grey bars), by contrast, varies little, indicating that the crab-burrow distance was relatively constant across different track angles. (C) The azimuth directions relative to the burrow at which the dummy is seen become larger with track angle. Due to the strong asymmetry of these distributions, means for A and B were determined on a logarithmic scale.

apparent size of an approaching object (looming; Collett and Harkness, 1982; Schwind, 1989; Zeil, 2000). In the following, we will analyse the behavioural evidence we have on burrow surveillance in fiddler crabs with the aim of identifying the mechanism of distance judgement involved.

Disparity

It is very unlikely that the crabs can rely on disparity cues to determine a dummy's distance for the following reasons. Like most fiddler crabs, *Uca vomeris* carry their eyes close together on long, vertical stalks. With an eye separation of approximately 5 mm and a horizontal inter-ommatidial angle of 2° (Land and Layne, 1995a; Zeil and Al-Mutairi, 1996; Zeil et al., 1986), binocular disparity cues do not allow the crabs to distinguish distances between 14 cm and infinity (Burkhardt et al., 1973). In addition, the accuracy and range of distance judgements based on binocular disparity decrease sharply in the lateral field of view, where the effective eye separation approaches zero. As foraging crabs are always oriented sideways towards their burrows (Ens et al., 1993; Land and Layne, 1995b; Zeil, 1998), disparity cues provide no useful distance information where it is needed most for burrow surveillance. Finally, the median distance between crab and dummy at the time of response in our experiments was 30 cm (Hemmi and Zeil, 2003a), which is well outside even the crabs' maximal range of stereopsis in the frontal visual field. We can therefore rule out disparity as a cue to distance in the context of burrow surveillance.

Image motion

Our behavioural evidence also speaks against image motion as providing possible cues to the distance of a dummy. The crabs generally do not move before they respond to an approaching dummy (Hemmi and Zeil, 2003a) and therefore do not generate motion parallax signals that would indicate its distance. We can also rule out other image motion cues to distance, such as the expansion rate of the dummy's apparent size, the rate at which the dummy's elevation changes, and time to contact. For these to be reliable indicators of distance, the dummy would have had to approach the crab more or less

compound eyes could measure the distance to an object: disparity (stereopsis), image size, elevation, motion parallax and other image motion information, such as the increase in

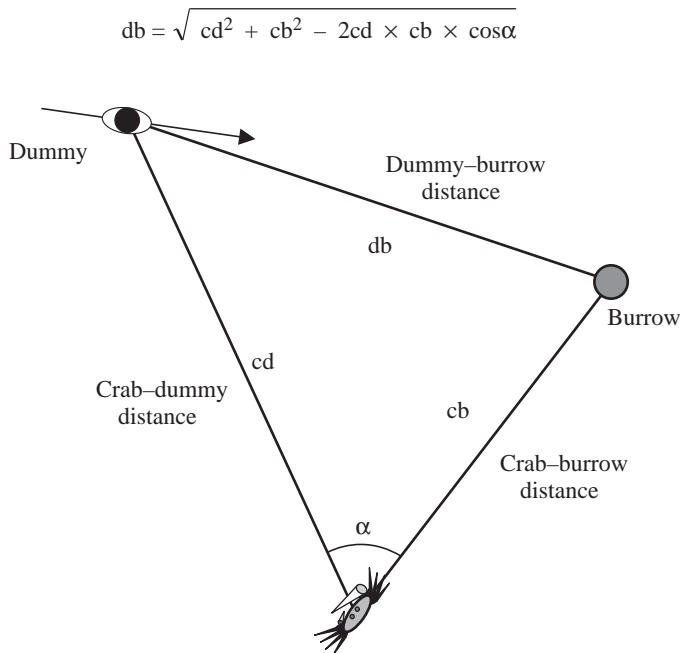


Fig. 2. The geometry of the burrow surveillance task. A crab needs to measure the dummy–burrow distance (db) independent of its own crab–burrow distance (cb) and the angle (α) between the direction in which it sees the dummy and the direction in which the burrow lies.

directly, which was rarely the case in our experiments. In fact, the movement direction of the dummies relative to the crabs differed greatly for the different approach directions. In addition, time to contact and other measurements that rely on the speed of retinal change should be proportional to the dummy's speed of motion. We found, however, no effect of the dummy's speed on the crab's probability of response or on the timing of the response (Hemmi and Zeil, 2003a).

Image size and elevation

We are thus left with image size and elevation as possible cues for the crabs to measure the dummy's distance. The apparent size of an object is one of the simplest distance measures available to animals, and crabs are known to use this cue in a variety of behavioural situations (Land and Layne, 1995a; Nalbach, 1990). The distance–size ambiguity that affects apparent size measurements may not matter in the context of burrow surveillance since, for a given burrow owner, only crabs from a narrow size class of conspecifics pose a threat to the burrow: much larger crabs would not be able to enter the burrow and much smaller animals are easily evicted.

Assuming that the crabs used the apparent size of the approaching dummy to determine when to respond, we would expect the distance between the crab and the dummy at the time of response to increase with increasing dummy size. However, as documented in Fig. 3A, the crab–dummy distance at this moment is independent of both the dummy's vertical (filled dots) and horizontal (open dots) size. On the other hand, assuming that the size of the dummy (real or apparent) does

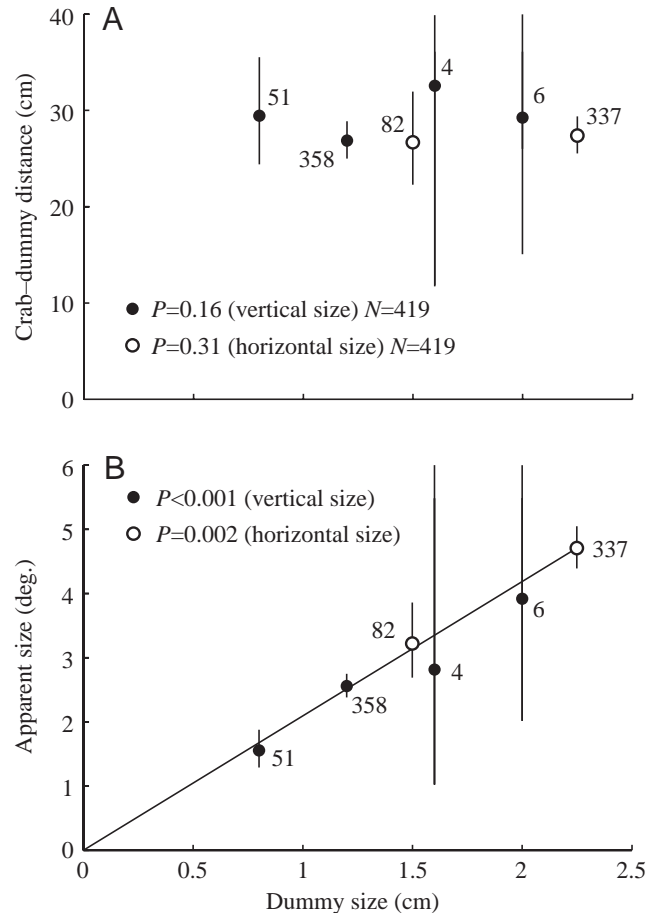


Fig. 3. The effect of dummy size on response distance. Due to the strong asymmetry of the apparent size distribution, means were taken on a logarithmic scale. The vertical lines represent the 95% confidence interval. (A) The crab–dummy distance at the moment of response is independent of the dummy's vertical (black dots; REML; $N=419$, Wald/d.f.=2.01, d.f.=1, $P=0.156$) and horizontal (open dots; REML; $N=419$, Wald/d.f.=1.03, d.f.=1, $P=0.309$) size. (B) The apparent size of the dummy at the moment of response is accurately predicted by both its vertical (black dots; REML; $N=419$, Wald/d.f.=13.75, d.f.=1, $P<0.001$) and its horizontal (open dots; REML; $N=419$, Wald/d.f.=7.18, d.f.=1, $P=0.007$) size. The line connects the right-most point with the origin.

not affect the crab's decision of when to respond, we would expect the mean angular size at the moment the response is triggered to increase with the absolute size of the dummy. This is true whatever the response criterion may be and regardless of whether the crabs assess the dummy relative to themselves or relative to the burrow. The dummy's mean apparent size at the time of the response is indeed strictly correlated with its real size (Fig. 3B; vertical size, filled dots; horizontal size, open dots). For small angles, the different angular sizes should all fall on a straight line through the origin, the slope of which is determined by the mean response distance between the crab and the dummy. The line in Fig. 3B connects the origin and the horizontal angular size value for the 2.25 cm-wide dummy, for which we have the largest number of measurements. The

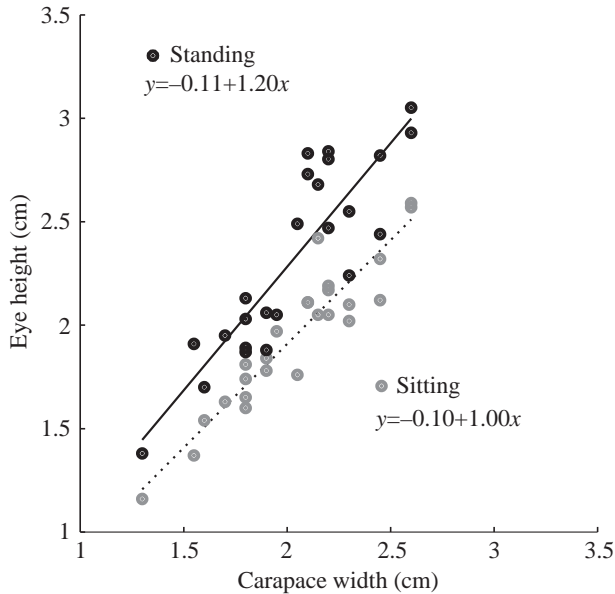


Fig. 4. The relationship between eye height and carapace width for sitting (grey dots) and standing (black dots) crabs. The straight lines are least squares fits to the two distributions (Zeil and Layne, 2002).

fact that all other angular size measurements are accurately predicted by this theoretical line demonstrates clearly that the apparent size of the dummy did not influence the crabs' decision when to respond. Note that the absence of a size–distance ambiguity (Fig. 3A) is strong evidence that the crabs know the distance to the dummy at the moment they respond.

Retinal elevation

We have thus ruled out all the possible cues to distance the crabs could exploit, with the exception of retinal elevation. In a flat environment, the retinal elevation of an object's point of contact with the ground is uniquely determined by the distance of the object from the observer (Schwind, 1989; Sedgwick, 1983; Zeil et al., 1986). To determine the elevation at which the crabs saw our dummies, we needed to estimate the height of their eyes above ground. In order to do this, we established the relationship between the height of the eyes and the carapace width of 24 *U. vomeris*, both when they were sitting and when they were standing or running (Fig. 4). There is a clear linear relationship between eye height and carapace width. To avoid having to capture the animals involved in the behavioural experiments, we determined their carapace width from 5–10 video frames per crab. The standard error within crab measurements was less than 15% in all cases. Assuming that the crabs were standing when making their decision to respond, we used the following equation to determine their eye height in our experiments (Fig. 4): eye height = $-0.11 + (1.2 \times \text{carapace width})$.

The median elevation of the dummy at the time of response is -4.4° , and 75% of the responses occur when the dummy is at an angular distance from the burrow of between -2.3° and

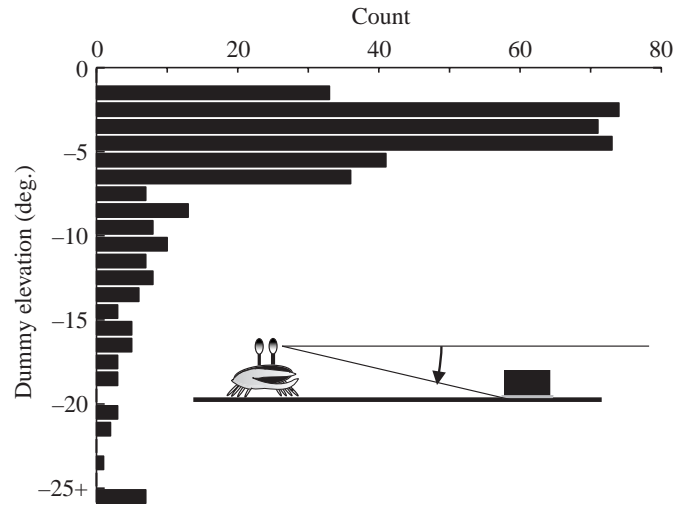


Fig. 5. The elevation at which the dummy appears in the crab's visual field at the moment of response. Elevation is measured relative to the horizon at the point of contact between the dummy and the ground.

-11° (upper and lower 12.5th percentile; Fig. 5). Less than 2% of the responses happen when the dummy has an elevation of less than -1.5° . An elevation of -1.5° translates into a distance of 76 cm for a crab with a 2 cm eye height. Note that for the same crab, the limit for depth perception based on elevation lies beyond 2 m, assuming a 2 cm eye height and a vertical inter-ommatidial angle of 0.5° close to the horizon (Land and Layne, 1995a; Zeil and Al-Mutairi, 1996). The elevation of the dummies at the time of response is thus clearly within the range of angles that can, in principle, be resolved by the crabs. A large part of the variation in the histogram of dummy elevations is due to the fact that a dummy's elevation at response time depends strongly on its approach direction (Fig. 1B).

It therefore appears that the crabs have all the information they need to determine a dummy's distance from their burrows. They know their own distance from the burrow, they can measure the angle between the dummy and the burrow and they can determine how far the dummy is away. To work out the dummy's distance from the burrow, however, the crabs would need to combine these measurements along the lines suggested by the equation in Fig. 2. How could this be achieved?

How crabs determine a dummy's distance from their burrows

The relevant visual parameters that allow a crab to determine a dummy's position relative to the burrow are the dummy's azimuth and its elevation in the visual field. Fig. 6 shows the paths of the dummies, as seen by a crab, in retinal coordinates. To generate these retinal paths, we assume that the crab's longitudinal body axis was always aligned with the home vector such that one side always pointed directly at the burrow (azimuth = 0° ; Ens et al., 1993; Land and Layne, 1995b; Zeil, 1998). Because the eyes of the crabs are roughly cylindrical in

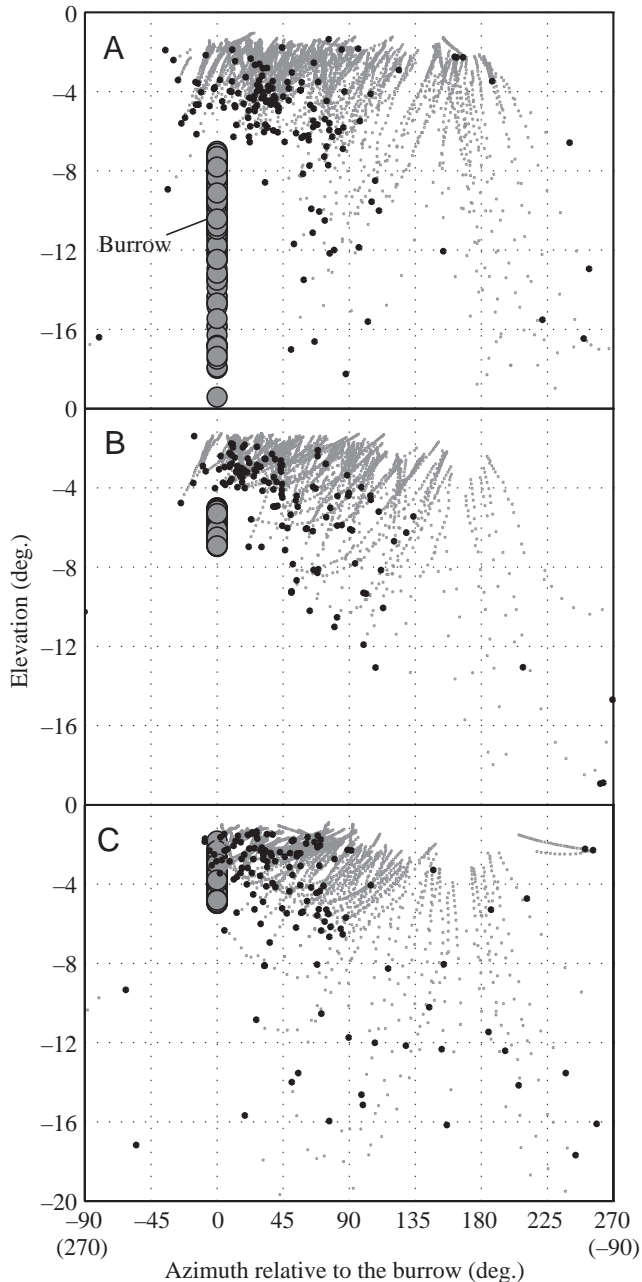


Fig. 6. Dummy paths in retinal coordinates as they would have been seen by the crabs. The paths (grey dots) are shown from the moment the dummies became visible in the recording area until the crabs reacted (black dots). Paths are selected in A–C according to the retinal elevation of the burrow entrance (large grey circles) at the start of each experiment, which is a function of crab–burrow distance and eye height above ground: (A) -20° to -7° , (B) -7° to -5° and (C) -5° to 0° . The lower the burrow is seen in the visual field, the closer a crab was to its burrow.

shape, such a Cartesian representation appears justified. The dummies approached from a distance and are therefore initially always seen at high elevations, moving down in the visual field as they come closer. As we already know from the previous analysis, the retinal positions of the dummies at the time a crab

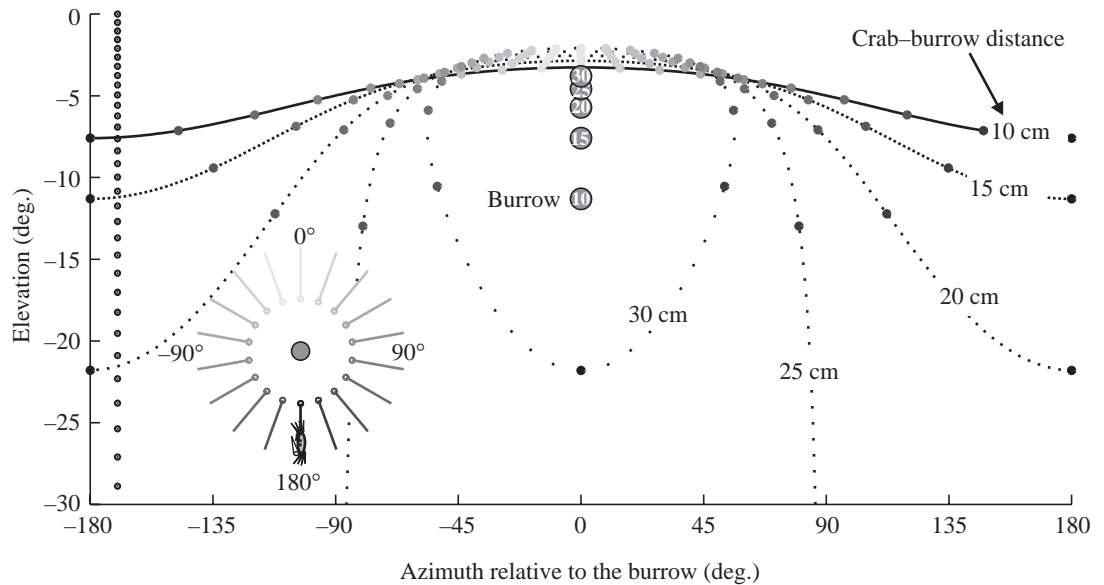
responds are widely scattered throughout the visual field (Fig. 6A–C, large black dots). However, the elevation of the dummy at the time of response tends to decrease with increasing azimuth distance between the dummy and the burrow. This is a direct consequence of the fact that the crabs respond at a roughly equal dummy–burrow distance irrespective of the direction from which the dummy approaches. For each azimuth, there is a critical elevation where the dummy is a given distance away from the burrow, and these combinations of elevation and azimuth angles define on the substrate a circle of a given radius around a crab's burrow.

For a given dummy–burrow distance, this set of critical elevations is only affected by the distance of the crab to its own burrow. The dotted lines in Fig. 7 show the fitted retinal projection of a circle with a 25 cm radius around the crab's burrow. The five lines show the projections of the same 25 cm circle for five different crab–burrow distances between 10 cm and 30 cm. When the crab is close to its burrow, say 10 cm away, the projection of the 25 cm circle around the burrow appears rather flat across the visual field (Fig. 7, solid black line). As the crab moves further away from the burrow, the projection becomes steeper until the whole 25 cm circle is seen in the frontal visual field, once the crab itself has moved further than 25 cm away from the burrow. The grey dots on each of these projections correspond to the position where dummies, approaching from different directions, would reach a dummy–burrow distance of 25 cm (see inset for the grey-level code of approach directions). To demonstrate that the resolution with which the crab can measure an object's elevation is adequate for the task at hand, we have schematically added the vertical component of the crab's sampling array as a vertical row of black dots along the y-axis (see Land and Layne, 1995a).

Fig. 8 shows the fitted values of the statistical model (see Hemmi and Zeil, 2003a) predicting the dummy's position (dots) for different approach directions (grey-level coded line segments) at the time of the response for a crab–burrow distance of 15 cm (Fig. 8A) or 25 cm (Fig. 8B). The same data are shown in retinal coordinates for a collapsed visual field ($0^\circ \leq \text{azimuth} \leq 180^\circ$) in the bottom panels (Fig. 8C,D). The solid and dotted curves in Fig. 8C,D show the projection of the mean response distance ± 2 S.E.M. (solid and dotted circles in Fig. 8A,B). For a given response distance, the relationship between the azimuth and the elevation at the time of response becomes steeper as the crabs move away from the burrow, as predicted by Fig. 7. However, the effect is not as strong as expected, because the crabs at the same time increase the mean response distance, which counteracts the effect that the increased crab–burrow distance has on the projection (compare Fig. 8A with Fig. 8B; see also fig. 11A in Hemmi and Zeil, 2003a).

We have marked the position of the burrow in the crabs' visual field (Fig. 8C,D), although in most situations the crabs cannot actually see their burrow (Zeil, 1998; Zeil and Layne, 2002). To appropriately adjust the elevation of the dummy at

Fig. 7. Retinal position of all points in the visual field of a crab that are 25 cm away from the crab's burrow. The positions are shown for different crab–burrow distances (solid and dotted lines), as labelled. On these lines of equal dummy–burrow distances we marked the positions of dummies approaching from different directions with grey dots. The approach directions are grey-level coded, with smaller track angles being represented by progressively lighter greys (see inset). Note how the position of the burrow



moves upwards in the visual field of a crab as it moves further away from its burrow (grey circles at 0° azimuth). The vertical line of small black dots along the y-axis indicates the elevation in which consecutive neighbouring vertical rows of ommatidia are facing, to show the pronounced increase in vertical resolution towards the horizon and the approximate level of resolution with which the dummies are seen by the fiddler crab eye (after Land and Layne, 1995a; Zeil and Al-Mutairi, 1996).

which they initiate their response the crabs thus have to rely on path integration to inform the visual system about the distance to the burrow.

Our statistical model predicts that for crab–burrow distances of more than 25 cm, the mean response distance would be less than the crab–burrow distance. In this situation, however, the crabs appear to treat dummies passing very close to them differently, in that they respond by retreating towards their burrows whenever the dummy threatens to pass them. Fig. 8C,D also shows that the direction in which the dummy moves across the retina prior to the response (straight line segments leading up to the response position marked by the dot) hardly influences the response timing, despite the fact that the directions of motion of the dummy's image are quite different depending on whether the dummy's path crossed the crabs home vector on the crab's side of the burrow or not.

Discussion

When we designed our experiments to investigate burrow surveillance in fiddler crabs, we hoped to discover a simple set of visual cues that trigger the crabs' responses. However, the analysis of the crabs' behaviour clearly showed that the decision to respond is not based on the dummy's position or motion relative to the crab itself but relative to the crab's burrow (Hemmi and Zeil, 2003a). This indicated that the crab's task is necessarily more complicated, requiring it to estimate the distance between the dummy and the burrow independently of the direction of approach of the dummy. The large variation in the distances between the dummy and the burrow at the time of response, as well as between the crab and its burrow

(fig. 11A in Hemmi and Zeil, 2003a), rather than supporting a threshold hypothesis, suggests that the crabs assess an intruder's distance from the burrow in a graded fashion. Their probability of response increases strongly as the intruder gets closer to the burrow (fig. 8 in Hemmi and Zeil, 2003a). For any given crab–burrow distance, there is a simple mapping of distances away from a crab's burrow across the retina (Figs 7, 8). This mapping changes quite strongly as the crab moves away from its burrow.

A matched filter for burrow surveillance

The most interesting aspect of the results shown in Fig. 8 is that they suggest a structure for a matched filter (*sensu* Wehner, 1987), which the crabs could use to relate a dummy's azimuth and elevation to its distance from the invisible burrow. Rather than solving difficult geometrical equations, they may be able to use the predictable geometry of their environment to employ a comparatively simple retinal filter to detect dummies or other crabs that have approached to within a certain distance of the burrow. Prerequisites for such a 'built-in' surveillance system are (1) that the crabs keep their body aligned with the home vector, which they do (Ens et al., 1993; Land and Layne, 1995b; Zeil, 1998; Zeil and Layne, 2002), and (2) that they are able to account for their own distance away from the burrow (von Hagen, 1962; Zeil, 1998; Zeil and Layne, 2002). What would such a neural filter look like?

For a given crab–burrow distance, a single neuron with a large receptive field could provide an accurate intruder–burrow–distance–related signal. Such a cell needs to be sensitive to small objects and it needs to respond more strongly the closer an object is seen near the burrow. Since the

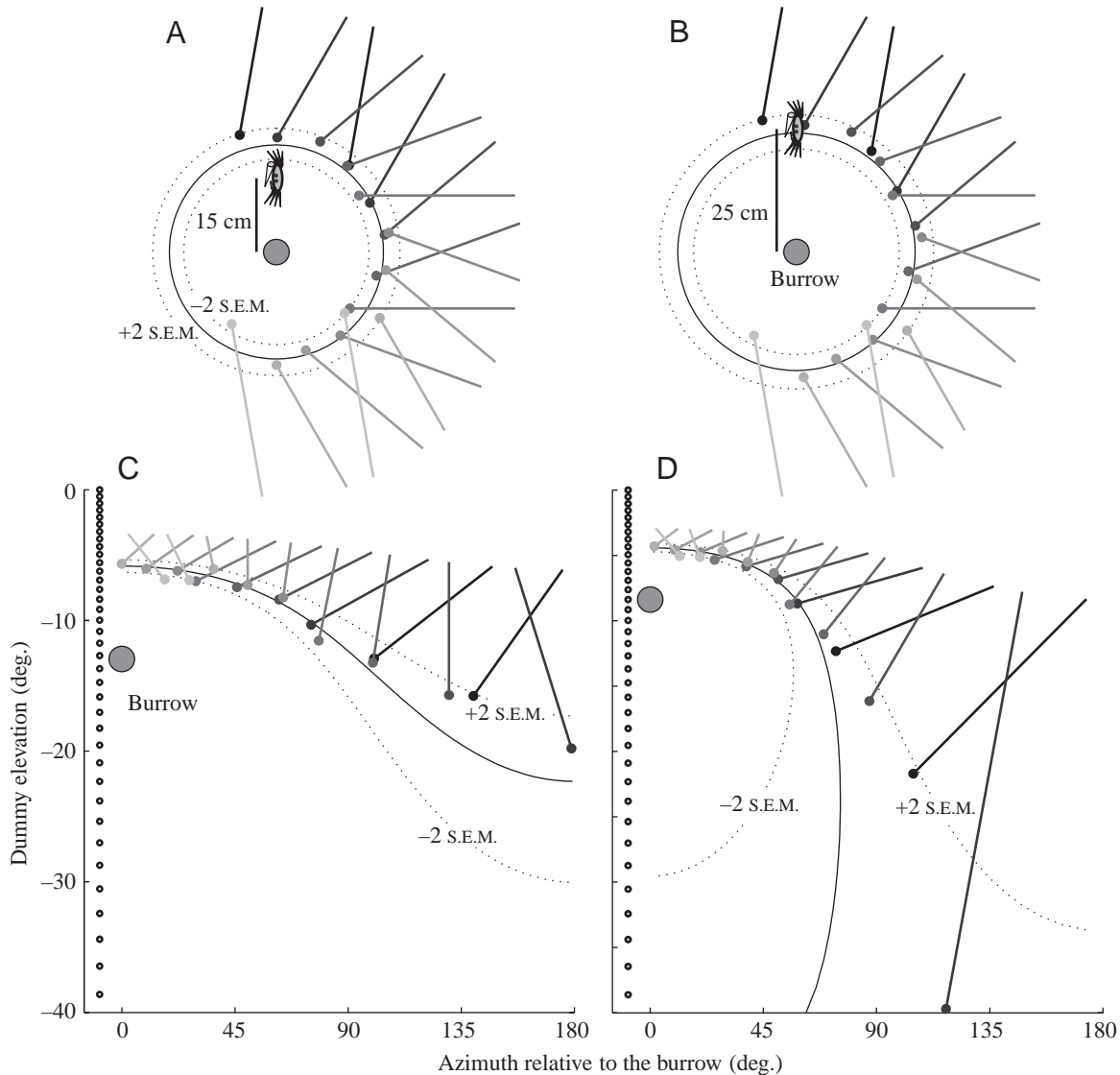


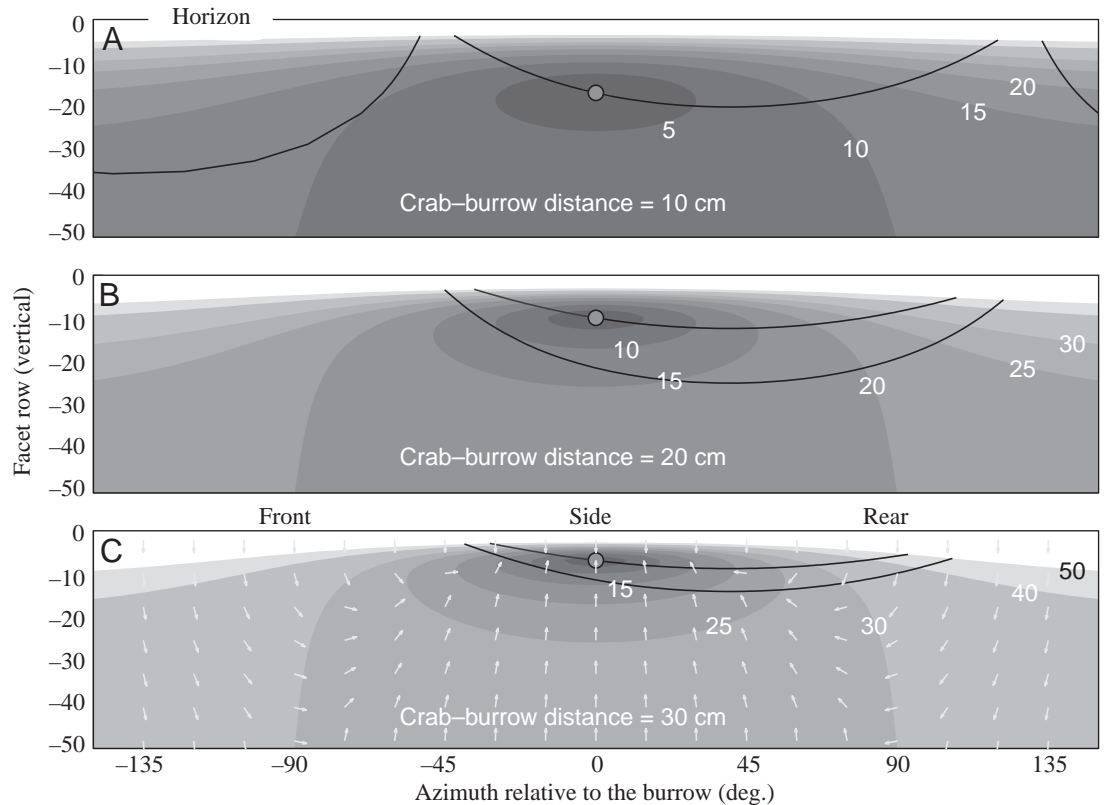
Fig. 8. Model fits for the position of the dummy relative to the burrow and the crab at the time of response for a crab–burrow distance of (A) 15 cm and (B) 25 cm. The fits are made for all dummy approach directions (track angles) and crab side values (see Fig. 1C) used in the model (Hemmi and Zeil, 2003a). For each track angle/crab side combination, we plotted the dummy's trajectory as a solid line from a distance of 50 cm to the burrow until the crab reacted (dot). For example, the black line at the top of A, just above and slightly to the left of the crab symbol, shows the approach path of a dummy for a track angle of 10° ($0\text{--}20^\circ$ track-angle bin) at the median track distance of 10 cm and a crab-side value of one. The crab initiates the reaction when the dummy reaches the black dot at the end of the line. The radius of the solid circle equals the fitted mean of all response distances ± 2 S.E.M. (dotted circles). (C) and (D) show the same data in retinal coordinates as seen by the crab. The continuous and dotted lines in C and D are the projection of the mean response distances ± 2 S.E.M. (circles in A and B).

longitudinal body axis of crabs is aligned with the home vector, such a burrow-distance-dependent output could be achieved by appropriately weighting the contributions of local input elements across the retina according to the map of distances to burrow, shown as a 'view from the cockpit' of a fiddler crab in Fig. 9A. The input elements are likely to be local motion or flicker detectors. A distance cell of this kind would provide no information on where an intruder actually is but would accurately monitor its distance from the burrow. The output of such a neuron would, however, only be correct for a small range of crab–burrow distances: 10 cm in the case of Fig. 9A.

This limitation could be overcome by having a small number of such cells each tuned to a range of crab–burrow distances (Fig. 9B,C). A signal from the crab's path integration system, which monitors the crab's own distance from the burrow, could then select the cell or the combination of cells with the appropriate distance mapping for the crab's current position. A very small number of large field cells would be sufficient to accurately measure an object's distance from the burrow, irrespective of the object's approach direction and the crab's own position relative to the burrow. Burrow surveillance thus requires an integration of information from the path integration

Fig. 9. The mapping of burrow distance onto the ommatidial array. Shown is the visual field of a crab that is (A) 10 cm, (B) 20 cm or (C) 30 cm away from its burrow. The burrow location is marked by a grey circle. The labelled contour lines within each plot correspond to positions in space that have a fixed distance from the crab's burrow. Contours have been drawn for 5, 10, 15, 20, 25, 30, 40 and 50 cm. The solid black lines show the retinal path of a set of two fictitious dummies that approach the burrow from a distance of 50 cm and move either directly over the crab's burrow or move 10 cm past the burrow. In contrast to the previous figures,

elevation has been transformed into facet rows. The x -axis (azimuth) scale has been adjusted such that individual ommatidia would take up equal space along the x - and the y -axes. These transformations reduce but do not eliminate the effect of perspective foreshortening. The white arrows in C show the local directions of the distance to burrow gradient on the eye.



system with visual information about the retinal position of other crabs.

However, we have also shown that the crabs respond only to dummies that actually approach the burrow and ignore dummies that move away from it, even if those dummies are close to the burrow (fig. 9B in Hemmi and Zeil, 2003a). The probability that the crabs respond to a dummy approaching the burrow is more than three times higher compared with when the dummy moves away. This observation suggests that the crabs are not only sensitive to the distance of an intruder from the burrow but also to its direction of movement relative to the burrow. There are two basic ways in which this sensitivity could be implemented at the neural level. The first possibility is to monitor the output of distance neurones exhibiting properties as we proposed above. An increase of these cells' output would indicate that an object is approaching the burrow; a decrease would signal that the object is moving away. If the underlying distance weighting is strong, this simple and robust method would make the crabs sensitive to changes in object position in the order of one inter-ommatidial angle. The second possibility is that the distance neurones are also sensitive to the direction of the local retinal image motion by integrating over a regularly spaced array of appropriately aligned motion detectors with the appropriate input weights. An object approaching the burrow must have a motion component

pointing along the gradient of a burrow-distance map (arrows, Fig. 9C) but it does not matter whether the object moves directly towards the burrow or not. All that is needed in order to measure this motion component is an alignment of the directional selectivity of local motion detectors with this burrow-centred distance gradient (the local direction on the eye in which the distance to the burrow changes fastest). Such directionally sensitive distance neurones would then only respond when there is a motion component towards the burrow.

It is interesting to note that, as a direct consequence of the perspective distortion, the retinal image of an object that moves over flat ground directly towards the burrow (solid line through the burrow in Fig. 9A–C) does not always move directly towards the retinal position of the burrow nor does it move along the distance gradient towards the burrow (arrows, Fig. 9C). The neurones we proposed above could therefore monitor whether an object approaches the burrow or not, but their activity would not allow the crab to decide how directly the object was aiming at the burrow. This can be verified by comparing the solid line passing through the burrow in Fig. 9C, which indicates the retinal path of an object that approaches the burrow directly, with the local distance gradient (arrows). This performance of the cells is in accordance with the behavioural results showing that crabs are able to distinguish

between dummies that move towards and those that move away from the burrow but cannot distinguish between trajectories that pointed more or less directly at the burrow (figs 8, 9 in Hemmi and Zeil, 2003a). However, as long as there is a motion component in the direction of the burrow, these neurones will signal it.

Our data do not allow us to decide at this stage whether or not burrow surveillance in fiddler crabs involves directionally sensitive neurones. The two alternatives, distance monitoring and directionally sensitive distance cells, would both allow the crabs to measure whether the object approaches the burrow or not (fig. 9 in Hemmi and Zeil, 2003a) but would not provide clear information on whether it does so on a direct path (fig. 8 in Hemmi and Zeil, 2003a). The only available information addressing this issue is the observation that the dummy's speed has no effect on the response probability or on the response distance. This result would favour the notion that the crabs monitor the direction of motion through the distance-monitoring cells rather than relying on direction-sensitive distance neurones. Further experiments should allow us to distinguish between the two alternative models. If the crabs relied on directionally selective motion sensitivity, the response probability for a given dummy–burrow distance should vary with a dummy's direction of motion, while there should be no such variability if the crabs only monitored dummy–burrow distance.

Neurones like the ones we suggest to be involved in burrow surveillance are not unknown in invertebrates. The large tangential neurones in the lobula plate of the fly, for instance, act as neural filters tuned to rotatory optic flow fields (e.g. Krapp et al., 1998). Barnes et al. (2002) have recently recorded from large-field interneurons in the crab lobula, the local directional motion sensitivities of which are arranged across the receptive field in such a way that they are likely to respond to translatory optic flow fields. However, in contrast to these examples, the neurones that we suggest to be involved in burrow surveillance in the fiddler crab should only respond to small objects and not to global image motion. The lobula giant motion detector (LGMD) of the locust does seem to have the appropriate blend of properties. It is a large neuron with a wide receptive field, it is sensitive to small objects, and the direction tuning of its local motion sensitivity varies systematically across the receptive field (e.g. Gabbiani et al., 2001; Rind and Simmons, 1999). However, the local directional sensitivities of the LGMD are arranged such that the neuron also responds to looming stimuli that are on a direct collision course with the locust, a property which we would not expect to see in burrow surveillance neurones.

Conclusion

What on first sight appeared to be a complex geometrical problem, namely to determine the distance between two objects independent of viewing direction and distance, can thus be reduced to a relatively simple task, the information for which is available directly from the retina. The decision rules exploit the predictability of the crab's visual world and rely on

the crab's path integration system for the information about the burrow position. The underlying neural machinery is thus yet another candidate for a matched neural filter, not only matched to the physical environment but also to the social environment in which the crabs live. It allows crabs to be very selective and respond to other crabs only when they are actually threatening burrow ownership. It allows them to ignore more distant crabs and neighbours that are close to the burrow but do not actually approach it. And it allows them to optimise the time they spend in burrow defence by recruiting information from the path integration system to adjust the distance at which they respond to an intruder depending on how far away from the resource they are themselves. We would finally like to point out that the structure of the matched filter we suggest is eminently testable in both behavioural and neurophysiological experiments.

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