

Mechanisms of homing in the fiddler crab *Uca rapax*

1. Spatial and temporal characteristics of a system of small-scale navigation

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Summary

Fiddler crabs *Uca rapax* are central-place foragers, making feeding excursions of up to 2 m from their burrows. We describe the natural feeding excursions of path-integrating fiddler crabs and analyze their paths for signs of significant systematic or random navigation errors. No signs of any systematic errors are evident. Random errors are small, probably due to a combination of the short length and low sinuosity of the foraging paths, as well as the fiddler crabs' unique method of locomotion that allows them to remain oriented to their burrows throughout the foraging path and to minimize large body turns. We further examined the extent to which their body orientation during foraging (transverse body axis pointing more or less towards home) accurately represented their stored home vector. By examining sequences of fast escape, we have shown that crabs can correct for deviations of their transverse body axis from home during

their escape path. Thus their stored home vector is independent of their moment-to-moment body orientation.

Crabs were subjected to passive translational displacements and barrier obstructions. Responses to translational displacements were identical to those observed by previous authors, namely that crabs returned in the correct egocentric direction and distance as though no displacement had occurred. Covering the burrow entrance resulted in crabs returning to the correct position of the burrow, and then beginning to search. When a barrier was placed between foraging crabs and their burrow, crabs oriented their bodies toward the burrow as accurately as with no barrier.

Key words: fiddler crab, *Uca rapax*, path integration, homing, spatial orientation, central-place forager, systematic error.

Introduction

Fiddler crabs have the remarkable habit of aligning the transverse axis of their body with the direction of their burrow as they forage in their mudflat or sand flat habitats (Land and Layne, 1995; Zeil, 1998). Many species have two modes of foraging: one in which they leave their burrows and walk tens of meters to the water's edge at low tide, during which no burrow alignment is maintained, and one in which they remain close to home and feed on the local substrate. This latter behavior may take them more than one meter from home, but they remain fairly well aligned with home throughout. Thus, for the study of navigation, fiddler crabs are exceptional in that they do not have to return home to give an observer a read-out of their notion of where home is.

Many semi-terrestrial decapods, including fiddler crabs, use visual cues such as landmarks or sky light to control their large-scale movements between their supralittoral burrows and foraging sites near the water's edge (Altevogt and von Hagen, 1964; for reviews, see Herrnkind, 1968, 1972; Altevogt, 1965; Wehner, 1992; Vannini and Cannicci, 1995), or to regain the

previous foraging direction after visiting the burrow (Luschi et al., 1997). They also use wave direction and beach slope (Cameron and Forward, 1993). However, for their small-scale orientation to the burrow, fiddler crabs do not utilize the same information as for the large-scale movements. All fiddler crab species tested ignore landmarks near their burrows when displaced a short distance (von Hagen, 1967; Zeil, 1998; Cannicci et al., 1999), and we have shown conclusively that *Uca rapax* compute a purely egocentric home vector, indicating they use only path integration for homing (Layne et al., 2003). Though we are still largely ignorant of the physiology underlying path integration in all animals, the evidence from fiddler crabs indicates that they utilize idiothetic information (probably proprioceptive or efferent signals; Layne et al., 2003; but see Zeil, 1998).

Path integration is a computational process that by nature is prone to the accumulation of errors. Analysis of both experimentally manipulated and natural outbound paths has demonstrated that the algorithm often does not compute the

correct direction and distance of home, but rather an approximation (Bisetzky, 1957; Görner, 1958; Müller and Wehner, 1988; Wehner and Wehner, 1990; Seguinot et al., 1993). Such coding thus contains a systematic error, which may provide hints about the computational algorithm at work. Furthermore, due to the imprecise nature of biology, path integration is also subject to random errors in measurement and/or computation (Benhamou et al., 1990; Maurer and Seguinot, 1995). Random errors have a greater impact on homing accuracy when the spatial information being integrated is purely idiothetic (Benhamou et al., 1990). Because the fiddler crab *U. rapax* homes by path integration using only idiothetic information (the continuous calculation of a home vector using internal measurements of their locomotion), it may be especially susceptible to random errors.

In this paper we analyze natural foraging paths of *U. rapax* with the aim of understanding the relationship between the crabs' tendency to orient their bodies with respect to their burrows and the stored home vector. In particular, we look for evidence of systematic and random errors. We also discuss the unique foraging behavior of this animal in light of the way errors are accumulated by path integration algorithms.

Materials and methods

Observations and manipulations

These observations and experiments were carried out on the fiddler crab *Uca rapax* (Smith) in Caroni Swamp, Trinidad, during July and August 1999. This paper deals with observations of the natural behavior of crabs foraging in the vicinity of their burrows, and with experiments in which crabs were manipulated in a number of different ways. First, their burrow entrance was obscured by a vertical barrier whilst they foraged nearby; second, their burrow entrance was covered while they were foraging; third, they were displaced by translation. Two further forms of manipulation, passive rotation of foraging crabs, and an experiment in which crabs were made to run over a patch of slippery substrate, are the subject of the accompanying paper (Layne et al., 2003).

To obscure the burrow visually, an L-shaped cardboard barrier was lowered slowly from above on a wire coat hanger, until it rested between a foraging crab and its burrow entrance. In the burrow-covering experiments, a sheet of mud-covered acetate attached to a length of fishing line was dragged over the burrow entrance. To translate foraging crabs, a similar sheet of mud-covered acetate (10.3 cm wide and of variable length) was attached to fishing line, which was threaded through a tent peg situated to the side of the burrow. This allowed us to move the acetate without lifting it, and thereby translate the crabs without disturbing them.

Sampling and digitization

The fiddler crabs were videotaped from above at 25 frames s^{-1} using a CanonVision EX1 8 mm video camera on a tripod. Two lateral points on the carapace (left and right side) were digitized 1, 5 or 25 times s^{-1} , depending on the

speed of the crab's movement, using a frame grabber and image analysis software (LG-3 and Scion Image, Scion Corp., Frederick, MD, USA). The digitized data were then analyzed using Matlab (The Mathworks Inc., Natick, MA, USA) to determine the crab's position and orientation. To reduce small sampling errors, the data were smoothed with a three-point moving average having weights 1:6:1. The crab's orientation relative to an arbitrary coordinate system (the video screen) was calculated from the slope of the line connecting the two points on the crab. The crab's bearing (direction from its burrow) was calculated from the slope of the line connecting points at the crab's center and the burrow (see lower inset in Fig. 1Ai for definitions, which follow those of Zeil, 1998). The crab's distance from home is defined as the distance between the center of the carapace (the point midway between the two digitized lateral points) and the center of the burrow; both carapace and burrow were approximately 2 cm wide.

Analysis

In analyzing burrow orientation with and without a barrier, we examined the spatial and temporal characteristics of 13 foraging paths, and present six of these graphically in order to illustrate the variability in burrow orientation within and between foraging excursions. We excluded from the statistical analyses of foraging behavior, though not from the figures, portions of the digitized path that were within 5 cm of home. This is because these are so close to home that a small change in bearing can create a disproportionately large orientation error. Furthermore, because home is certainly within the crabs' visual range (Zeil, 1998), this may allow the crab to tolerate very large errors in its burrow orientation that obviously do not correspond to the home vector, and might have affected our interpretations of orientation error in relation to path integration. Values are reported as means \pm s.d.

Results

Orienting to the burrow while foraging

Feeding in fiddler crabs is dependent on the organic content and percentage water saturation of the substrate (Reinsel and Rittschof, 1995). But, while these factors may influence the crabs' radial distance from the burrow, their foraging paths are characterized by a basic structure upon which this variation in radial distance is superimposed. As has been documented by a few previous workers, most recently by Zeil (1998), crabs orient the transverse axis of their body towards home, and they progress around home in one direction. The direction – clockwise or counterclockwise – can change between foraging bouts. Fig. 1Ai shows the path of a typical foraging excursion, digitized at a rate of 1 frame s^{-1} . An arrow pointing to the burrow side, as shown in the boxed inset, indicates the crab's transverse body axis. Many species of fiddler crab usually forage in straight paths that radiate out from the burrow entrance and return home along nearly the same line (e.g. Zeil, 1998). However, they are also capable of 'circumferential' paths like those shown in Figs 1 and 2, and in *U. rapax*

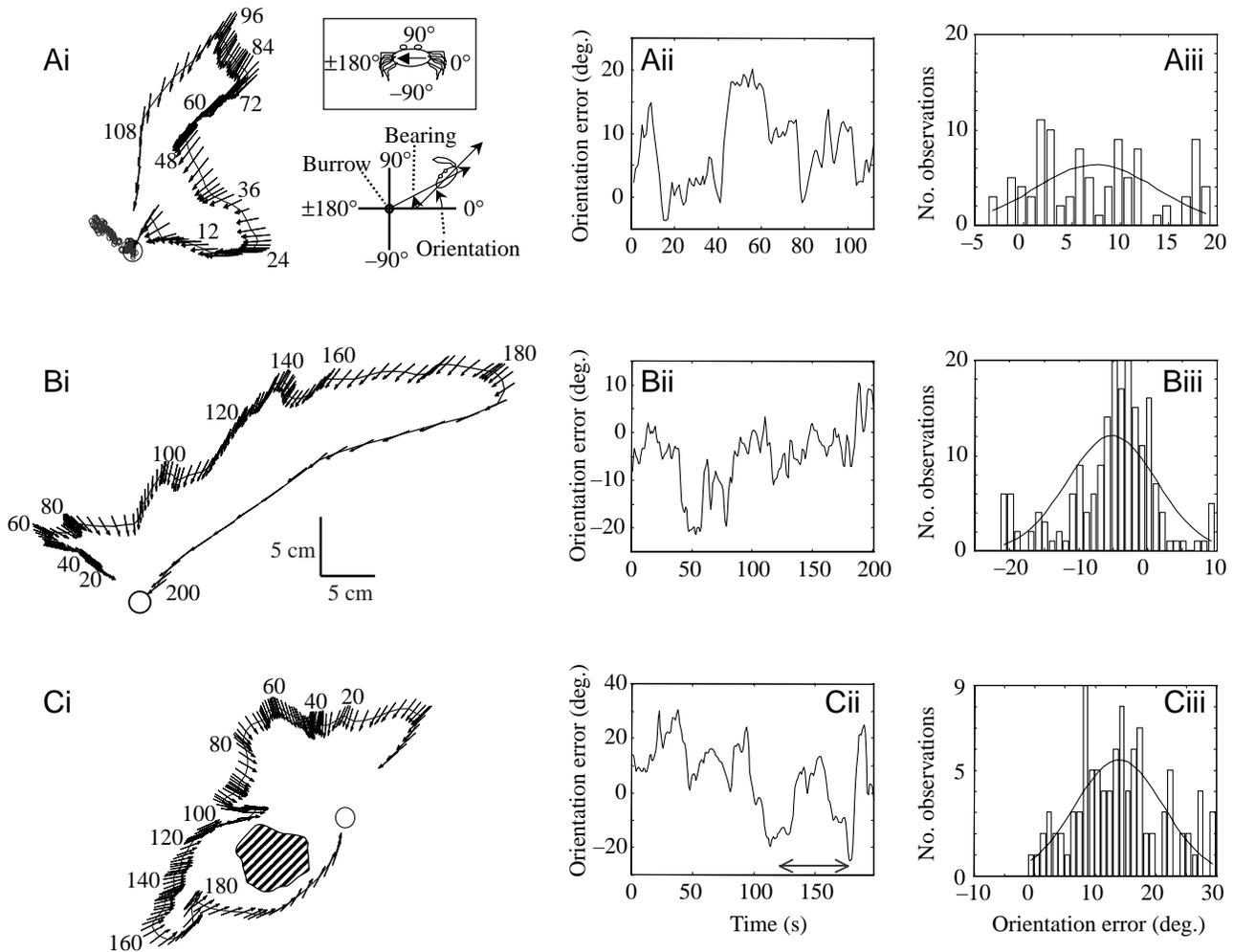


Fig. 1. (A–C) Three examples of natural foraging paths, digitized at 1 frame s^{-1} . (Ai–Ci) Positions of transverse body axis of fiddler crab, with the arrow pointing toward the ‘homeward’ side, as seen in the boxed inset in Ai, for each digitized frame. The boxed inset also shows the convention for egocentric directions used throughout this paper. Numbers correspond to elapsed time (s). The center of the carapace is connected between frames. The burrow is the large open circle. Scale bars in Bi apply to Ai–Ci. The small gray circles in Ai adjacent to the burrow represent calculated burrow positions for each digitized step, assuming the burrow entrance were to lie directly in line with the crab’s transverse axis on its the homeward side (see Results for details). Open inset in Ai is a diagrammatic representation of the orientation error (see below). The hatched solid area in Ci is the base of a mangrove sapling. (Aii–Cii) Orientation error (degrees), defined as bearing minus orientation (inset in Ai), over time (s). The double-headed arrow in Cii indicates the time when the burrow was blocked from view by a mangrove sapling. (Aiii–Ciii) Frequency histogram showing the distribution of orientation errors in 1° bins, with an ideal normal probability density function overlaid (solid line).

circumferential paths are typical. The mean sector covered by the 13 crabs we analyzed was $99 \pm 46^\circ$, although it should be noted that these paths were selected for analysis because of their complexity and because the crab remained within the field of view of the camera. The figure thus represents parameters of relatively complex paths; the mean sector covered by a random set of natural paths would certainly be less than this. Since the crabs mainly move forwards and sideways, crabs always progress around the burrow entrance in a forward direction during their circumferential paths. Thus, in Fig. 1Ai, the crab’s left side is closest to the burrow entrance.

As has been pointed out by previous workers (Land and Layne, 1995; Zeil, 1998), this circumferential path is

interesting because it implies that the crab must know its distance from the burrow entrance at all times. In order to remain pointed homeward during such loops, the crab must change its orientation as it changes its bearing by an amount dictated by its distance from home.

In keeping with *U. lactea annulipes* and *U. vomeris* (Zeil, 1998) and also *U. pugilator* (Land and Layne, 1995), *U. rapax* do not always point its long body axis directly at home, but allows some drift and recovers the ‘correct’ orientation periodically. Fig. 1Aii shows what we will call the ‘orientation error’ – bearing minus orientation – over time for the path shown in Fig. 1Ai. For this individual, which traveled in a counter-clockwise direction, bearing was consistently greater than

orientation; i.e. the crab did not point its transverse body axis at home, but kept home slightly behind it. This means the error was biased towards the positive, but was periodically reset to zero.

To examine the crab's precise strategy of burrow orientation and perhaps gain some insight into the path integration algorithm, it is instructive to ascertain the nature of this bias in orientation error. For instance, is the error normally distributed around a biased mean? Or is the distribution of orientation error skewed or, if the error were periodically reset to zero as described above, bimodal? How do individual paths differ in this respect? Fig. 1Aiii shows a frequency histogram of the errors for those parts of the path >5 cm from home. The crab had a mean of error of $7.5 \pm 6.3^\circ$ and, in spite of the fact that there are subsidiary peaks near 2° and 18° , the error distribution was not significantly different from normal at the 95% confidence level (D'Agostino–Pearson K2 test, $P=0.07$; Zar, 1996). Thus, the orientation error tended to vary roughly equally to either side of a biased mean. Whether or not this bias in orientation error indicates an error in the direction of the home vector is a question we will take up below.

This is a fairly representative path. Out of 13 foraging paths overall – seven without and six with barriers – all were found to have a positive mean error if the crab went clockwise and a negative mean error if the crab moved counter-clockwise. This means that all crabs kept the burrow slightly behind them (in their rear hemifield). Six were found to have significantly normally distributed orientation errors at the 95% confidence level, and all of these had means that were significantly different from zero (Student's t -tests, all P values <0.05). Likewise, the grand mean (mean of the means) of the seven paths without barriers was also significantly different from zero ($-6.49 \pm 5.87^\circ$, Student's t -test, $P=0.026$), as was the grand mean of the six paths with barriers ($-8.84 \pm 2.10^\circ$, Student's t -test, $P<0.001$). To find this grand mean, all of the paths were normalized to the clockwise direction (the direction that results in negative orientation errors) by multiplying the counter-clockwise means (which are negative) by -1 .

Fig. 1B shows the path that took the crab farthest from home, out of the 12 that we recorded. Its maximum distance (40.3 cm) was exceeded by other crabs that were not recorded, because they foraged outside the field of view of the camera. Indeed, some foraged over 1 m from home and were (subjectively) seen to remain oriented to it. Since this crab traveled clockwise around its burrow entrance, its orientation error was generally negative (Fig. 1Bii). While most of the error appears to be fairly normally distributed around a mean of $-5.2 \pm 6.4^\circ$, this crab's error distribution is significantly different from normal (Fig. 1Biii; D'Agostino–Pearson K2 test, $P<0.001$). Thus the orientation errors for different paths may or may not be normally distributed around their mean.

The example shown in Fig. 1Ci is interesting in that, during the second part of its journey, the crab walked around a mangrove sapling that blocked its view of home. Moving counter-clockwise around its burrow entrance, this crab generally maintained a positive orientation error, as expected.

The interaction with the sapling introduced exceptional error values – it appeared, for a short time at least, to fixate the intruding edge of the sapling, before fixating the far edge which it intended to circumvent, causing this distribution to be different from normal. Data after 100 s from this crab were therefore excluded from all statistical tests because of the influence of the sapling on its orientation, and thus on our subsequent interpretations of orientation errors in the context of path integration. The errors before $t=100$ s, shown in Fig. 1Ciii, were normally distributed around a mean of $-13.9 \pm 7.3^\circ$ (D'Agostino–Pearson K2 test, $P=0.32$). It is notable, however, that although the interaction with an object near its burrow entrance caused the crab to assume a large orientation error, the burrow direction was recovered, abandoned, and finally recovered again when the crab returned directly home. Temporary losses of burrow orientation were also observed to occur when crabs interacted with conspecifics while foraging.

Orienting to the burrow from behind a barrier

The behavior illustrated in Fig. 1C raises the question of whether *U. rapax* needs to be in visual contact with its burrow entrance to align its body with it. Other species qualitatively appear to be able to maintain normal burrow orientation from behind a barrier that obstructs their view of the burrow entrance (Zeil, 1998), or at least are able to perform successful detours around opaque barriers (von Hagen, 1967; Herrnkind, 1972; Zeil and Layne, 2002, but body orientation not measured). Fig. 2Ai shows the path of a crab whose homeward line of sight was blocked by a cardboard barrier, introduced at $t=32$ s, just as this crab began its circumferential path. This experiment is similar to that performed by Zeil (1998) on *U. vomeris*. As in Zeil's study, *U. rapax* appear to orient similarly with and without such a barrier. Unlike the previous example with the mangrove sapling, this crab did not interact with the barrier in a way that obviously influenced its burrow alignment. Moving clockwise around its burrow entrance, this individual showed the same error bias (bearing > orientation) as the crabs with no barrier. While it did reduce its bias during part of the time behind the barrier, the mean error during this time was still positive, with a mean significantly different from zero ($5.9 \pm 6.2^\circ$, 95% CI = ± 1.03 , Student's t -test, $P<0.001$). Also, the error distribution was not significantly different from normal (D'Agostino–Pearson K2 test, $P=0.21$).

The example shown in Fig. 2B is somewhat unusual in that the error bias, while in the direction predicted from its movement around the burrow entrance, clearly increases in magnitude throughout the foraging excursion (Fig. 2Bii). Thus, more than in our other records, we had the impression that the crab may have accumulated a substantial integration error. The integration error does not, however, change linearly over time. The errors are also clearly not normally distributed ($-9.0 \pm 8.9^\circ$, D'Agostino–Pearson K2 test, $P<0.001$). Despite the impression that this crab had progressively 'lost' its correct home direction, it proceeded immediately home after making a detour around the edge of the barrier – a detour which induced an orientation error that exceeded 80° in magnitude.

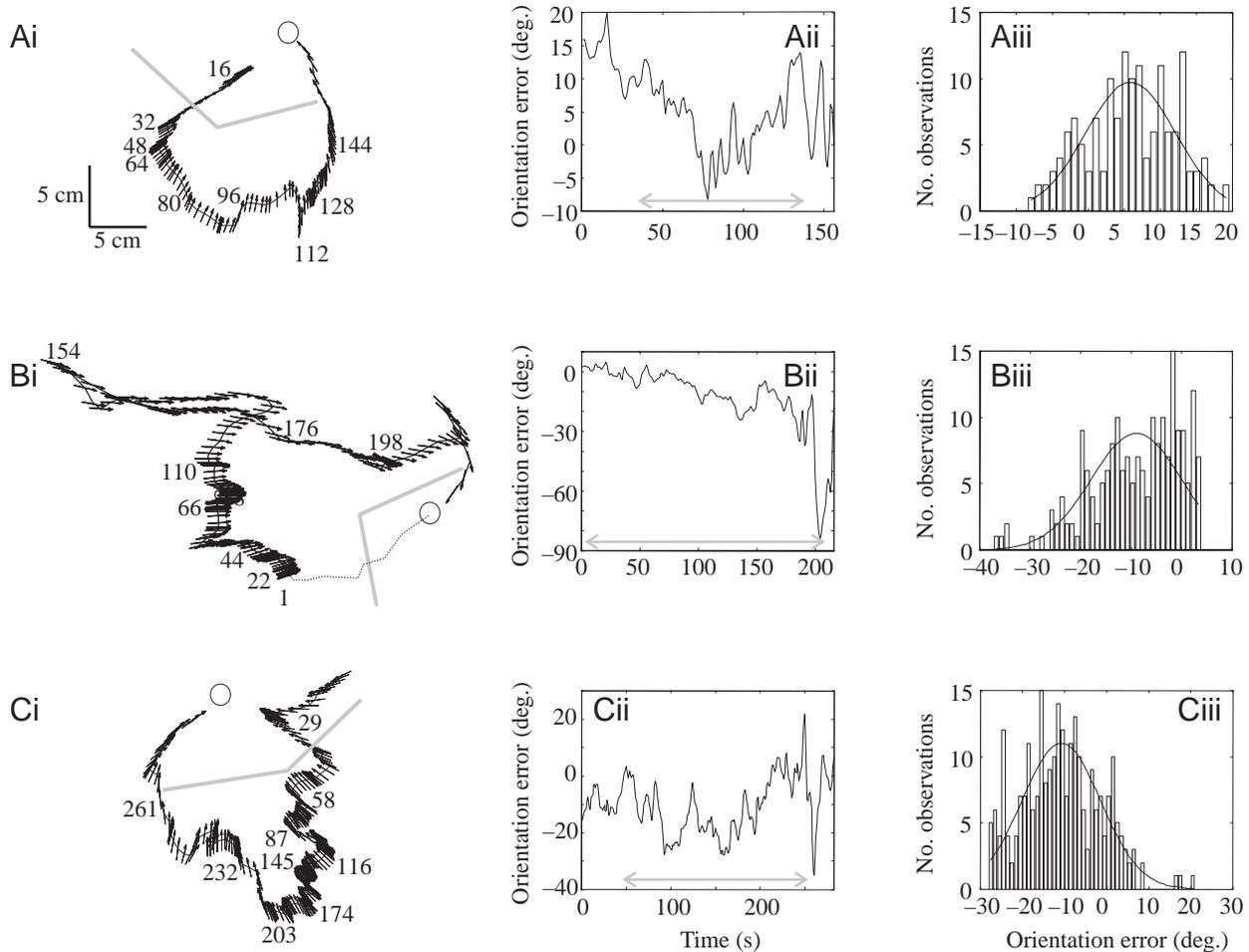


Fig. 2. (A–C) Three examples of foraging paths performed with a barrier (solid lines in Ai–Ci) between crab and burrow, digitized at 1 frame s^{-1} . Horizontal arrows (Aii–Cii) indicate when the barrier was between the crab and burrow. Conventions as in Fig. 1.

This apparent loss of home direction may have been due to an interaction with the edge of the barrier that the crab intended to circumvent. Fiddler crabs, when confronted with obstructions to their straight path home, make detours that seem to indicate they plan their route home – they visually assess the angle of the barrier relative to the home vector, and go around the barrier in a way that minimizes the detour distance (Zeil and Layne, 2002).

Our final example shows a fairly lengthy foraging path (Fig. 2C). This path has the predicted bias direction, and is normally distributed around a mean of $-10.7 \pm 9.3^\circ$ (D'Agostino–Pearson K2 test, $P=0.11$).

Comparing orientation error with and without a barrier

We have seen that a barrier can influence orientation by forcing a detour, and that this detour usually occurs without the crab making contact with the barrier. But we may ask whether such a barrier diminishes the crabs' ability to point towards home, or to maintain a typical orientation bias when the crab is not attempting to circumvent the barrier. In the following statistical comparisons between crabs with and without barriers, we used only those portions of the paths in

which the barrier lay between the crab and its burrow; these are indicated by the double-headed arrows in Fig. 2Aii–Cii. Portions of the path where the crab had a line of sight to the burrow entrance, and also detours around barriers, were excluded. Also, all data were normalized to the clockwise path direction as described above, so that mean orientation errors have a negative bias.

Two aspects of orientation error are considered – the error bias, which is the mean of the measured error values (as above), and the error magnitude, which is the mean of the absolute error values. The error bias indicates *in what direction* crabs point their body axes relative to the burrow direction, while the error magnitude simply indicates *how much* error there is regardless of what direction it is in, and might be thought of as one measure of the spread of error values.

In comparing orientation errors with and without barriers, we find that the mean error bias for the seven paths without a barrier is not significantly different from the six paths with a barrier (Student's *t*-test, $P=0.71$). Likewise, their error magnitudes are also not significantly different (Student's *t*-test, $P=0.91$). This quantitative analysis has therefore failed to provide any evidence that fiddler crabs need visual contact with

the burrow entrance or its immediate vicinity in order to align their bodies with it.

Temporal aspects of maintaining burrow orientation

Fiddler crabs have an error bias in the spatial sense, but does it occur temporally as well? For instance, does the burrow-alignment mechanism require an initial movement tangential to the burrow direction in order to calculate an appropriate body turn? In Fig. 3 a time-lagged cross-correlation of changes in bearing and orientation for the path in Fig. 1A (open circles) shows a fairly good correlation (coefficient = 0.59) at a 1 s lead of orientation change before bearing change. A similar cross-correlation for the path in Fig. 1B (filled circles) shows a relatively poor correlation, but one with a bimodal appearance – orientation change both leads and lags behind the bearing change by about 2 s. We interpret this to mean that, while the crab did not move tangentially to the burrow and turn simultaneously, it did one or the other first at different times.

It is possible that the temporal correlation between changes in orientation and bearing exists on a smaller time scale than our digitization frequency of 1 frame s^{-1} . We therefore redigitized the path in Fig. 1A at 5 frames s^{-1} , and found that the cross-correlation coefficient was much lower (0.26), and reached a maximum at a lag of -0.6 s (i.e. a 0.6 s lead of orientation change before bearing change). The lower correlation coefficient is probably due to increased digitization noise, as subjectively there did not appear to be oscillations of body orientation or position on this fine time scale. Thus, the resolution of 1 frame s^{-1} time scale gives a reasonable indication of which component of the movement occurs first.

Similar tests for all 13 paths produced both leads and lags

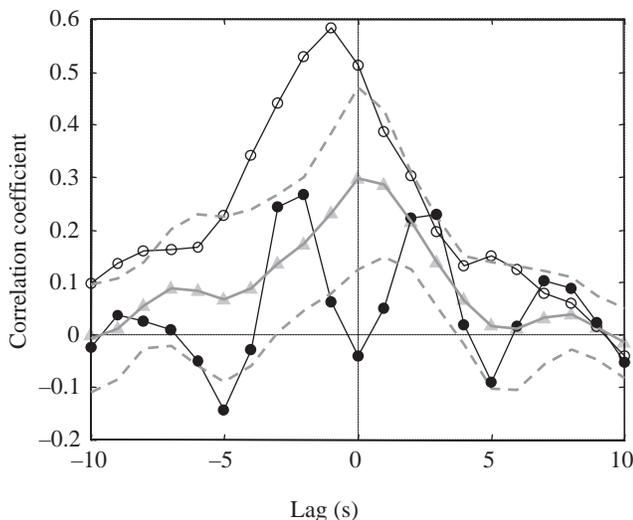


Fig. 3. Time-lagged cross correlation between change in orientation and change in bearing. Data shown are from paths in Fig. 2A (open circles), Fig. 2B (filled circles), the Fisher z -transformed mean of seven paths (filled triangles) and the 95% confidence interval (broken lines). Correlation coefficient is plotted on the y -axis, lag on the x -axis; a negative lag means change in bearing preceded a change in orientation.

by orientation against bearing, and a few with zero lag. The mean of the 13 cross-correlations (using the Fisher z transform; gray triangles in Fig. 3) shows zero lag. The presence of both leads and lags of change in orientation relative to change in bearing suggests that fiddler crabs can change either one of these parameters first, then adjust the other by the appropriate amount to remain more or less aligned with an unseen home.

Homing to a covered burrow

Covered burrow experiments have demonstrated that foraging fiddler crabs do not use the burrow itself as a landmark (von Hagen, 1967; Zeil, 1998). In Fig. 4A we show that our results from *Uca rapax* conform to previous results from other species. The figure shows three superimposed paths of frightened crabs returning to their burrow (gray circle), which has been covered by a muddy Perspex plate. The lines represent the paths taken by the center of each crab's carapace.

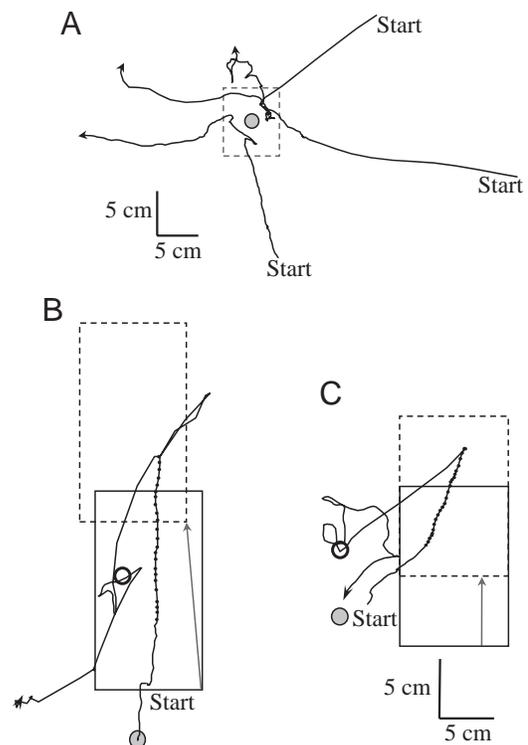


Fig. 4. Results from experiments involving (A) covering the burrow, (B) radial translational displacement and (C) tangential translational displacement. (A) Data from three different crabs were overlaid and aligned with one burrow entrance (filled gray circle); lines represent the center of each crab's carapace. (B,C) Position of muddy, mobile acetate sheet before (solid rectangles) and after (broken rectangles) displacement, with the sheets' motion vectors indicated by gray arrows. Fictive burrow entrances (large open circles) are found by adding this motion vector to the true burrow entrance (gray filled circles). Lines represent the center of each crab's carapace, the period during which the crabs were on a moving substrate being indicated by connected black dots. In these figures, 'start' indicates the beginning of the digitized track; in A, only the homeward part of the crabs' tracks were digitized, while in B and C both outward and homeward journeys were digitized. Scale bar in C also applies to B.

In each case they stopped on the plate within about half a body length of home position, before searching or running again. This is in contrast to Zeil's finding (Zeil, 1998) that *U. vomeris* sometimes stopped several centimeters short of home before commencing to search, and in fact seemed to center their search on that point.

Homing after passive translational displacement

Passive displacement experiments have previously been carried out by Zeil (1998) and Cannicci et al., (1999). In Fig. 4B,C, fiddler crabs were passively displaced on a sheet of muddy acetate, either more or less radially (Fig. 4B) or tangentially (Fig. 4C) away from their burrow entrances (large gray circles). The crab's path during the displacement of the acetate sheet is indicated by black dots, the acetate sheets before and after movement by solid and broken rectangles, respectively, and the motion vectors of the acetate sheets by arrows. The positions of fictive burrow entrances (large open circles) were calculated by adding the motion vector of the acetate sheet to the position of the burrow entrance. As in the previous studies cited above, *U. rapax* invariably returned to the fictive burrow when homing, and then commenced to search. As noted by Zeil (1998), this persistent homing to the fictive burrow, despite walking during and after the passive displacement (Fig. 4B), indicates a well-defined home vector derived from active, but not passive, movements, even when these occur simultaneously. Some of these experiments were done in the presence of clear local landmarks (as were some by Zeil, 1998), and all were on a sunny day. Thus, crabs must have used route-based information only, not in combination with local visual landmark cues as in, for example, the spider *Agelena labyrinthica* (Moller, 1970; Moller and Görner, 1994).

Path integration errors

Here we ask whether the path integration system of fiddler crabs accumulates errors over the course of a foraging trip. Two types of errors are possible in a path integration system, systematic errors and random errors. Systematic errors should be small, having been minimized by natural selection (Benhamou and Poucet, 1996), and they are usually only discovered by experimentally restricting the outward path. However, on rare occasion, naturally foraging desert ants reveal a systematic error when the path is heavily biased in its turning directions (Wehner and Wehner, 1990). Indeed, a

systematic error in fiddler crabs should by definition create a change in the orientation error that is consistently related to some temporal or geometric aspect of the foraging path. If, for instance, many crabs performed clockwise circumferential foraging paths, and their orientation error became progressively more negative as their path lengthened, this might be analogous to the desert ants' homing error, or the well-documented tendency for vertebrates and invertebrates alike to bias their returns after following an L-shaped path (e.g. Etienne et al., 1998). To test whether a systematic change in orientation error exists, we again normalized the 13 foraging paths to the clockwise direction. By so doing, we compared errors that had putatively been induced by similar biases in locomotion. After combining the data, we calculated regression lines relating orientation error to each of three path parameters that might be associated with a source of systematic error, namely time, cumulative path length and cumulative turns (i.e. the cumulative sum of all changes in body orientation). The relationships determined in this way should indicate whether orientation error changed with an increase in any of these three independent variables.

We found that ten out of thirteen paths showed a significant correlation between orientation error bias and time (Table 1, row 'bias'). Of these ten, six showed a decrease in error bias, the other four showing an increase. Similarly, while eight of the thirteen paths showed a significant correlation with increasing path length, four of these eight showed a decrease in error bias while four showed an increase. A similar pattern was seen in the relationship with cumulative turns. Thus crabs may show an increase, decrease or no change in orientation error, and which of these they show does not relate to any parameter we have found. For instance, we found no significant correlation between the slopes of these regressions and total foraging time, total path length, total turns or total arc sector (which is derived largely from turns and increasing path length; least mean squared regressions, all $P > 0.229$). We see no compelling evidence of a systematic error in these results.

The path integration system might, nevertheless, commit random errors. If error magnitude (the absolute value of orientation error) tended to grow as the path lengthened, then this might indicate growing inaccuracy in the home vector that does not favor a particular direction. Using the same regression technique as described above for systematic errors, we found

Table 1. Summary of regression analyses for 13 individual foraging paths

Error	Time		Path length		Turns	
	$P < 0.05^*$	Decrease [†]	$P < 0.05^*$	Decrease [†]	$P < 0.05^*$	Decrease [†]
Bias	10/13	6/10	8/13	4/8	9/13	5/9
Magnitude	6/13	3/6	5/13	3/5	6/13	3/6

The orientation errors (bias) or their absolute values (magnitude) were plotted against the independent variables of time, cumulative path length and cumulative turns. The linear regression was calculated using the method of least squares.

*The ratio of paths for which $P < 0.05$ (analysis of variance), indicating a significant correlation.

†The ratio of the significant correlations for which error tended to decrease over the independent variable.

that the results again show a balanced outcome for each comparison (error vs. time, path length and turns). In all three comparisons, just under half of the paths showed a significant correlation, and half (or just over half) of the significant ones showed a decreased error with the remainder showing an increased error (Table 1, row 'magnitude'). Given this balance, it is not surprising that, once again, there was no correlation between the slopes of these regressions and total foraging time, total path length, total cumulative turns and total arc sector (least mean-squared regressions, all $P > 0.349$). We therefore see no compelling evidence for substantial random errors. This is also not surprising, in light of the fact that, at the end of each foraging excursion, each crab successfully returned home without searching.

However, if fiddler crabs do use path integration, it is not reasonable to assert that there are no errors at all. We therefore prefer to conclude that any random errors accrued were not large enough to preclude homing, and that accumulated random error in the home vector was not responsible for a significant proportion of the observed orientation error. The same argument may be applied to the question of systematic error, and will be taken up again in the Discussion. For the moment, the invocation of a systematic error is not necessary. Instead, we assume the pattern of orientation error arises from the fact that there is significant alignment flexibility afforded by the path integration system, but that deviations from perfect alignment are fully integrated.

The home vector and fast escape

The possible relationship between the orientation error and home vector warrants further scrutiny. Since fiddler crabs only point roughly towards home, the question arises as to whether they have access to the correct home vector even while they are not aligned with home, or whether the observed variation in orientation is a reflection of variation in the home vector itself. If orientation errors were kept very small, the easiest mechanism for returning home would be to walk laterally to the side opposite the one used during the outward journey. This would be a version of the simple 'route-reversal' mechanism (Lorenz, 1943), made even simpler by the fact that crabs need not turn 180° to make the return trip. The small gray circles in Fig. 1Ai are 'false burrows', calculated by assuming the memory-stored burrow entrance position had the correct, integrated distance, but that its direction is determined by the crab's orientation (the arrow direction). The spread of these false burrows is considerably greater than the spread of home vectors we infer from observing homing crabs and, given that this crab homed perfectly, we doubt that its home vector ever pointed at these false burrows.

Any time a crab is frightened by an experimenter, it is likely to be misaligned to some degree (e.g. Fig. 1). The fact that it invariably returns directly home appears to support the idea that the crab has a continual memory of its own misalignment; i.e. that it has constant access to the correct home vector. However, since it is likely that fiddler crabs use visual contact with their burrow to help guide the *final* stage of the return

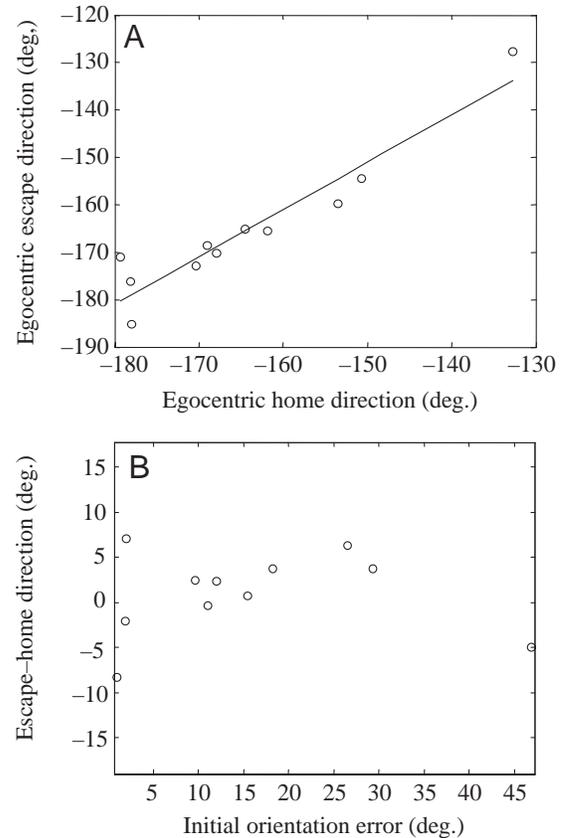


Fig. 5. (A) Escape directions of foraging crabs in relation to the true home direction and (B) the difference between escape and home direction in relation to the crabs' orientation error at the start of the escape run. All directions are in egocentric terms, and follow the convention in Fig. 1A inset. The line of best fit, calculated by the method of least squares, is shown in A.

home (Zeil, 1998), a slightly inaccurate home vector (possibly indicated by an orientation error) may not result in missing home. It would thus not be visible to the experimenter as a homing error. Comparing the direction of fast escape to home direction in foraging crabs with different initial orientation errors reveals that escape direction matches home direction very closely (Fig. 5A; 1 ms regression, $y = 0.9989x - 1.1734$, $r^2 = 0.9006$, $F = 81.53$, $P < 0.001$), and that the difference between escape direction and home direction is not related to the crabs' initial orientation error (Fig. 5B; $F = 9.6 \times 10^{-5}$, $P = 0.9924$).

We also try to address the issue of a crab's access to an up-to-date home vector by analyzing the temporal characteristics of the return path of a crab that had a large orientation error at the time it was frightened.

Fig. 6 shows a male fiddler crab 'out of alignment' by 29.3° at the time it was frightened (Fig. 6A, second 65). The foraging path (0–65 s) was digitized once per second, and the escape path (65 to 65.4 s) was digitized 25 times per second. The crab responded to the threat by engaging three components of its escape behavior simultaneously:

(1) It *ran in the home direction* – the first steps were towards home (egocentric running direction and direction of home with

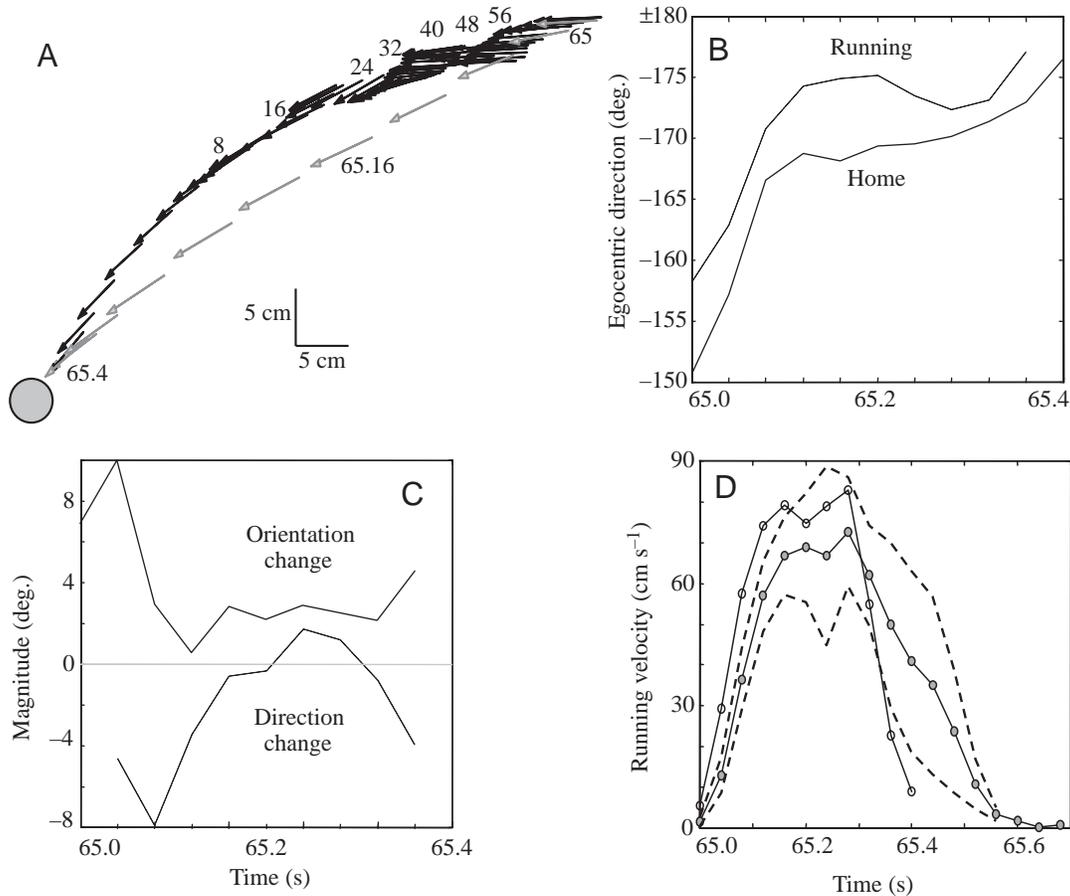


Fig. 6. Escape path of a crab having a large orientation error when it was frightened. (A) Crab's transverse body axis during foraging (black arrows) and escape (gray arrows); it was frightened at $t=65$. Foraging behavior was digitized at 1 frame s^{-1} , while escape was digitized at 25 frames s^{-1} . (B) Plot of egocentric running direction (dotted line) and egocentric home direction (solid line) plotted against time during escape (i.e. from 65 to 65.4 s); (C) Changes in orientation (body turns; solid line) and changes in egocentric running direction (dotted line) during fast escape. (D) Time course of running velocity of escaping crab (open circles) compared to the similar time course for eight other escaping crabs (gray circle, broken gray line shows $\pm \text{S.D.}$). For correlating two behaviors in time, it must be remembered that turns and running direction are first derivatives of orientation (a position measurement), and change in running direction is a second derivative of orientation. It then follows that, if orientation has n observations, then turns and running direction have $n-1$ observations, and change in running direction has $n-2$ observations. We therefore associate the ' n th' turn or running direction with the n th orientation (see running direction vs. home direction in B), and the n th change in running direction with the n th+1 turn (see running direction change vs. orientation change in C).

respect to body transverse axis are similar – as close as 4.2° from each other at 65.08 s: Fig. 6B).

(2) It *turned its body* to point towards home with its transverse axis – the crab rotated 18.1° to reduce its orientation error within the first 120 ms (egocentric home direction reduced from -150.7° to -168.8° between 65 s and 65.12 s: Fig. 6B).

(3) It *changed its running direction* relative to its own body axis – the crab changed egocentric running direction by -16° within the first 120 ms (change from -158.3° to -174.3° between 65 s and 65.12 s: Fig. 6B).

These are the closed-loop versions of the behaviors recorded open-loop by Land and Layne (1995). Combined with the change in bearing, these activities caused the crab to reduce its orientation error by 62% while reducing its distance to home by 26% within 120 ms of beginning its escape. This fast

correction of body alignment, especially when compared to running distance, indicates that the crab had instant access to the correct homing vector, which was different from its initial orientation error. It also appears that this access is continuous.

In order to continue running towards home, it is not enough to execute the direction and distance components of the home vector in an arbitrary manner. It would be correct, for instance, to execute the direction component by turning, then the distance component by running, but it would not be correct to do these in reverse order. The fastest way to return home may be to begin running immediately, and to run in a straight line. However, unless the crab is perfectly aligned with home, this requires something considerably more complex than the method just described: any change in orientation (i.e. body turn) must be equal but opposite to a change in egocentric running direction for each step of the way. If the crab's motor system is capable

of producing such an agreement between these two components of escape, then in theory fast escape would not require the continued involvement of the path integration system. It would only need the initial direction and distance, and escape could proceed in a ballistic manner; i.e. without feedback. In the case shown here, changes in orientation occurred with a slight lead compared to changes in running direction (Fig. 6C), leading to an error of about 7° in egocentric running direction during mid-escape (Fig. 6B). A cross-correlation analysis of changes in orientation and egocentric running direction showed that changes in running direction lag behind changes in orientation by 0.04 s (max. correlation coefficient = -0.7166). This discrepancy was corrected at the end of the run, but made for a very slightly curved path. More analyses of fast escape are needed, but it seems likely that the motor system does not produce turns identical to its changes in running direction, and so even crabs in fast escape must continue to update the home vector as they run, and adjust their locomotion to correspond to it. This behavior is a good example of separate control systems (for turning and egocentric running direction) that must operate in a highly cooperative manner to produce an adaptive behavior (escaping predators as quickly as possible). They apparently operate without information about the absolute position or direction of their burrow entrance that would provide feedback about their errors (Layne et al., 2003), but they may be able to make a continuous comparison with the stored memory of the home vector. The home vector, as an integrator of the crab's motor output (whether this is measured as efference copy or proprioceptive input), may provide error signals which mediate the relative outputs of the turning and direction systems during escape. Land and Layne (1995) showed that the turning and direction systems can, in fact, be dissociated, and it is an interesting question how the timing and magnitude of each are tuned to make the running crab hit its mark, and avoid being eaten.

It has been suggested that the reason fiddler crabs align themselves side-on to their burrow entrances is to facilitate escape. Since they run fastest sideways, maintaining this orientation may reduce the time needed to reorient their bodies before or during escape. This leads to the hypothesis that speed of escape may be inversely related to initial orientation error. However, the crab in Fig. 6 had one of the fastest escapes, despite starting with one of the largest orientation errors of any we observed. Fig. 6D (open circles) shows the escape velocity of the crab shown in Fig. 6A plotted along with the mean escape velocities of ten other crabs similarly frightened (solid gray line) and their 95% confidence intervals (dotted gray circles). The path is relatively short compared with the other eight, but the shape of the velocity profile for the escape is very similar. Linear regression analysis of eleven escape trajectories shows that both the mean and maximum escape velocity are not related to initial orientation error (mean initial orientation error = $13.9 \pm 9.8^\circ$; vs. mean velocity: $F=2.35$, $P=0.164$; vs. maximum velocity: $F=1.034$, $P=0.339$). This suggests that, within the limits of the orientation error normally seen in fiddler crabs (maximum around $\pm 30^\circ$ for *U. rapax*, unless faced with an obstacle), the

velocity of their home runs is not impeded by misalignment. Nevertheless, the speed-of-escape hypothesis may still explain why orientation error is usually kept within $\pm 30^\circ$.

A large initial orientation error would seem to necessitate greater coordination between changes in orientation and running direction. This coordination may be imprecise, which leads to the hypothesis that the curvature of the escape path will be inversely related to the strength of correlation between changes in orientation and running direction. Linear regression reveals that this relationship between path curvature, defined as straight-line distance divided by the distance traveled by the crab, and the maximum (z -transformed) correlation coefficient is significant ($F=5.65$, $P=0.0490$). This means that the coordination of turning and changing running direction does affect how straight the crab runs, but it does not affect how quickly the crab escapes. Escape velocity does not depend on path curvature ($F=1.02$, $P=0.341$), probably because crabs simply do not escape along very curved paths (maximum recorded escape path curvature was 0.9720), regardless of their orientation error or level of coordination.

Discussion

In the context of homing, two main conclusions may be drawn from studies of central-place foraging in fiddler crabs, including the present one. First, fiddler crabs have accurate and continuous knowledge of the location of home, which is gained by idiothetic path integration – that is, by the continuous calculation of a home vector using internal measurements of their locomotion. Second, the locomotory behavior of foraging fiddler crabs is exceedingly restricted compared to other path-integrating arthropods such as desert ants; they never stray very far from home and they do not vary their body orientation relative to the home direction by more than about 35° . This orientation is maintained by body turns whose magnitude depends on the crab's change in bearing and its distance from the burrow, and is periodically brought to zero. The crab does not measure its changes in bearing in the angular sense shown in Fig. 1Ai inset (i.e. against an exocentric frame of reference). More likely, it measures the component of its movements that are perpendicular to the direction of the burrow entrance. By so doing, the crab can remain oriented toward home so long as it keeps the ratio of tangential movements to body turns equal to its distance from home.

Effect of locomotory style and foraging path shape

The first conclusion above raises questions about the sensory modes that might be used, and the neural mechanisms that might underlie the measurement and integration of locomotory information; these are addressed in the accompanying paper (Layne et al., 2003). The second general observation, that fiddler crab foraging paths are characterized by extremely restricted locomotory patterns, raises questions about the computation of the home vector, and the effect of this type of locomotion on the computational accuracy. Analysis of natural foraging paths indicates that the integration algorithm does not

contain a systematic error, but it also fails to detect any substantial random measurement errors. Thus, we must also question the potential for fiddler crab foraging paths to reveal the nature of the computational algorithm. Two hypotheses must be considered: (1) that the unique foraging behavior minimizes the types of movements that are sensitive to random measurement errors, or (2) that it minimizes the types of movements that exacerbate a systematic error. Either way, the behavior may obscure the truth about whether fiddler crabs employ a geometrically correct or incorrect solution. Since we have not observed fiddler crabs to make homing errors (but see below), we cannot use observed errors to formulate a candidate algorithm containing the putative systematic error, as Müller and Wehner (1988) did for desert ants.

Burrow orientation may exist to ensure that the crab can race back towards home in the event of a threat to its burrow or itself. However, we have shown above that the homing speed is not diminished when the orientation error is near its natural maximum. Thus, alternatively, we can speculate that burrow orientation might arise from a physiological problem in the integration process, such as progressive failure with time of the memory-stored orientation error. Such a problem might be somewhat alleviated if the orientation error were frequently 'zeroed', as we have observed in fiddler crabs, if memory failure increased nonlinearly with time. However, we have observed one foraging crab to seemingly switch its orientation to a neighboring burrow for nearly 2 min (requiring a mean orientation error relative to the original burrow of about 30°), and then return home to the original burrow. The memory of navigational vectors is an interesting issue in fiddler crabs, since there are observations that some species may retain the relative positions of several burrows for long periods of time (Zeil and Layne, 2002). Returning to these burrows does not necessitate landmark memory or an external compass (Benhamou et al., 1990; Maurer and Seguinot, 1995), but if not it would indicate a fairly elaborate system of vector memories. The only crab we have seen to miss home without experimental manipulation was one that, while investigating a neighboring burrow, made a voluntary turn of about 170°. This crab seemingly overestimated its turn by about 10°, and performed a short search before finding home again. More observations of these infrequent naturally occurring errors are clearly required, since they might indicate whether errors are random or systematic. Our current data do not provide any compelling evidence for a systematic error.

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