

Mechanisms of homing in the fiddler crab *Uca rapax*

2. Information sources and frame of reference for a path integration system

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Summary

Fiddler crabs *Uca rapax* are central-place foragers, making feeding excursions of up to several meters from their burrows. This study investigates the sources of directional and distance information used by these crabs when returning to their burrows. We tested the spatial frame of reference (egocentric or exocentric), and the source of spatial information (idiothetic or allothetic) used during homing. We also tested which components of their locomotion they integrated (only voluntary, or voluntary plus reflexive).

Fiddler crabs in their natural mudflat habitat were passively rotated during normal foraging behavior using experimenter-controlled disks, before they returned home. Crabs resisted passive rotations on the disk by counter-rotating when the disk turned, which was a compensatory response to unintended movement. Crabs were usually situated eccentrically on the disk, and therefore were also subjected to a translation when the disk rotated. No crab actively compensated for this translation. Crabs that fully compensated for disk rotation made no directional homing error. Crabs that did not fully compensate homed in a direction that reflected their new body orientation. In other words, if we succeeded in reorienting a crab (i.e. it undercompensated for disk rotation), its homing error was equal to the angle by which it had been reoriented, regardless of the magnitude of the optomotor compensation.

Computer-modelled crabs, each equipped with a path integrator utilizing different combinations of external (allothetic) and path-related (idiothetic) input, traversed

the digitized paths of the real crabs. The home vector computed by the model crab was then compared to the homing direction observed in the real crab. The model home vector that most closely matched that of the real crab was taken to comprise the path integration mechanism employed by fiddler crabs. The model that best matched the real crab gained direction and distance idiothetically (from internal sources such as proprioceptors), and integrated only voluntary locomotory information.

Crabs were also made to run home across a patch of wet acetate, on which they slipped and were thus forced to take more steps on the homeward path than theoretically required by the home vector. Crabs whose running velocity across the patch was unusually low also stopped short of their burrow before finding it. Crabs whose running velocity was not impeded by the patch did not stop short, but ran straight to the burrow entrance, as did control crabs that ran home with no slippery patch. We interpret this to mean that the velocity of some crabs was impeded because of slipping, and these therefore stopped short of their burrow after having run out their homing vector. This is positive evidence in support of the hypothesis that path integration is mediated either by leg proprioceptors or by efferent commands, but our data do not allow us to distinguish between these two possibilities.

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

Introduction

In order to return to a place they have previously visited, many animals use a form of coding of their movements, called path integration by Mittelstaedt and Mittelstaedt (1980), wherein information arising from the animal's own movement is used to update the animal's memory of its position continuously in the form of a vector joining the animal's

current location with the goal (for example reviews, see Schöne, 1984; Gallistel, 1990; Papi, 1990, 1992; Wehner, 1992; Maurer and Seguinot, 1995; Etienne et al., 1996; Benhamou and Poucet, 1996; Wehner, 1996; Benhamou, 1997; Healy, 1998; Capaldi et al., 1999; Giurfa and Capaldi, 1999; Redish, 1999; Collett and Collett, 2000). Thus a desert ant,

having reached a feeding site over 100 m from home after following a sinuous path several hundred meters long, is able, using path integration, to return home in a straight line (Wehner and Wehner, 1990).

To understand how an animal homes – that is, returns to a place previously visited – there are two pre-eminent questions to be answered. First, what is the frame of reference – egocentric or exocentric – in which the goal location is encoded? There is ambiguity in the literature about what constitutes egocentric and exocentric reference systems (Etienne et al., 1999). Path integration was originally formulated in exocentric coordinates (Mittelstaedt and Mittelstaedt, 1973); it might conceivably be encoded that way, and this can be explicitly tested (Benhamou, 1997). A defining feature of an egocentric reference system is that the home vector is head-referred, that is, the goal direction is at all times specified by an angle relative to the animal's head or anterior/posterior body axis. This does not preclude the use of an external compass for estimating changes in direction during an excursion, which may then be integrated to update the head-referred direction of home without reference to the absolute compass direction. In contrast to this, in an exocentric frame of reference (also called geocentric, allocentric or earth-bound) the goal location is specified in terms of its relation to, for instance, the spatial layout of landmarks in the region of the goal, or by a home vector whose direction is specified by an angle relative to the sun's azimuth or to arbitrary earth-bound axes, regardless of the current orientation of the animal's head. An effective way to distinguish between ego- and exocentric systems, then, is to passively rotate animals in the presence of stationary external cues, or in the dark if the animals are also known to utilize exocentric landmarks. The home vector (generated under the particular experimental conditions) is truly egocentric if the animals make a directional homing error equal to the amount by which they were rotated. This approach can be confounded if the animals sense and integrate passive rotations, for instance *via* the vestibular system (Etienne, 1980; Etienne et al., 1986). The apparent 'internal compass' resulting from this integration does not indicate a true absolute reference or compass, however, but rather a sensitive integration apparatus, which can be overcome if the animals are rotated at low angular velocities (Mittelstaedt and Mittelstaedt, 1980, 1982).

The second question to be answered, irrespective of whether the frame of reference is egocentric or exocentric, is what is the source of spatial information used to compute the home vector? This may be idiothetic or allothetic, depending on whether the spatial information to be integrated is internal or external, respectively, to the animal. For example, an animal computing its home vector from idiothetic sources may be integrating leg proprioceptor input accumulated during its outward path, while an animal computing its home vector from allothetic sources may be measuring its turns with respect to the position of the sun. As noted above, it is feasible for the former to produce an exocentric home vector (e.g. Mittelstaedt and Mittelstaedt, 1973), and for the latter to produce an

egocentric home vector (see Benhamou et al., 1990). In any case, this categorization of the source of sensory information marks the starting point for the study of the sense organs involved, from which point work on the neurophysiology of path integration can proceed.

Homing in fiddler crabs is of particular interest for a number of reasons. They are central-place foragers with a uniquely strong attachment to their point of reference (von Hagen, 1967; Land and Layne, 1995; Zeil, 1998; Layne et al., 2003). Indeed, they maintain a fairly rigid orientation relative to it by pointing the transverse axis of their body more or less towards home throughout their foraging excursions. Thus, for the study of homing, fiddler crabs are exceptional in that they may not have to return home in order to give an observer a read-out of their notion of the direction of home. They also have an unusual mode of locomotion in that, like most other crabs, they can walk in virtually any direction relative to their body axis. Therefore, a change in direction of travel can be effected by a change in walking direction, with no body turn necessary (Barnes, 1990). This gives them an additional degree of freedom compared to forward-walking animals, but also additional sensory information that must be integrated.

Path integration appears to be the principal mode of homing in all fiddler crabs during their short-range foraging excursions. However, evidence for the cues relevant to this task is largely inconclusive or incomplete (Vannini and Cannicci, 1995), and we are still largely ignorant of the sensory systems involved. The fact that all fiddler crab species tested ignore landmarks near their burrows when displaced a short distance (von Hagen, 1967; Zeil, 1998; Cannicci et al., 1999; Layne et al., 2003) suggests that the relevant spatial information does not include local landmarks. However, it may still include global cues, such as the sun, and it has been suggested that fiddler crabs use an exocentric compass to maintain body orientation (Zeil, 1998). This indicates not only that they might utilize allothetic direction information, but it also raises the question of whether the home vector direction might be coded with respect to the same exocentric cue.

The present paper is devoted to identifying fiddler crabs' spatial frame of reference (exo- or egocentric), and their sources of spatial information (allo- or idiothetic) using two types of experiment: passive rotation, and running on a slippery patch where distance covered per step was often reduced. In the former, we passively reoriented the crabs relative to their natural surroundings, and observed their attempts to return home. Specific hypotheses about the information used in path integration were tested by digitally, recursively reconstructing the paths while altering or removing certain path-related variables. A home vector reconstructed this way should be identical with the observed homing path if our model is based on the same information used by the crab. In the slippery patch experiment, crabs ran home while their feet slipped on an acetate substrate. This uncoupled motor output and some types of sensory feedback from real-distance traveled. Our results show that fiddler crabs' home vector is derived from idiothetic information and stored in an egocentric

frame of reference. An important finding is that the crabs are selective about which path-related information they integrate. Some of these results, analyzed in a simpler way, are reviewed by Zeil and Layne (2002).

Materials and methods

These observations and experiments were carried out on the fiddler crab *Uca rapax* (Smith) in Caroni Swamp, Trinidad, during July and August 1999. We rotated the crabs on a turntable. These turntables consisted of Perspex disks, 8 cm in diameter, having a groove around their circumference in which fishing line was threaded. These could then be rotated around a central spindle, which was pushed into the mud near the burrow, by pulling the line. The disks were covered in a layer of soft, wet mud so that foraging crabs would not avoid them. Crabs were videotaped from above at 25 frames s^{-1} using a Canon Vision EX1 8 mm video camera on a tripod. Points on the right and left side of the crab were digitized 5 times s^{-1} , using a frame grabber and image analysis software (LG-3 and ScionImage, Scion Corp., Frederick, MA, USA). The disk was similarly digitized, using two points near its edge. The digitized data were analyzed using Matlab (The Mathworks Inc., Natick, MA, USA) to determine the disk and crab movement and orientation. To reduce the discrete sampling noise, the data were smoothed with a three-point moving average having weights 1:6:1. The disk movement was calculated from changes in the slope of the line connecting the two points. The crabs' orientation was calculated from the slope of the line connecting the two digitized points on the crab. The crabs' bearing relative to the burrow was calculated from the slope of the line connecting points at the crabs' center and the burrow. Experiments were predominantly, but not exclusively, carried out on male crabs.

Experimental rationale

Disk rotation experiment

Crabs actively opposed disk rotation by counter-rotating via a rotational compensatory response (e.g. the optomotor response). This compensation often continued after the disk ceased rotating, but was usually incomplete, meaning the crab maintained a new orientation after disk rotation ceased that was deflected from the original one in the direction of disk rotation. Thus we succeeded in reorienting the crabs. Crabs were then either frightened home or returned home on their

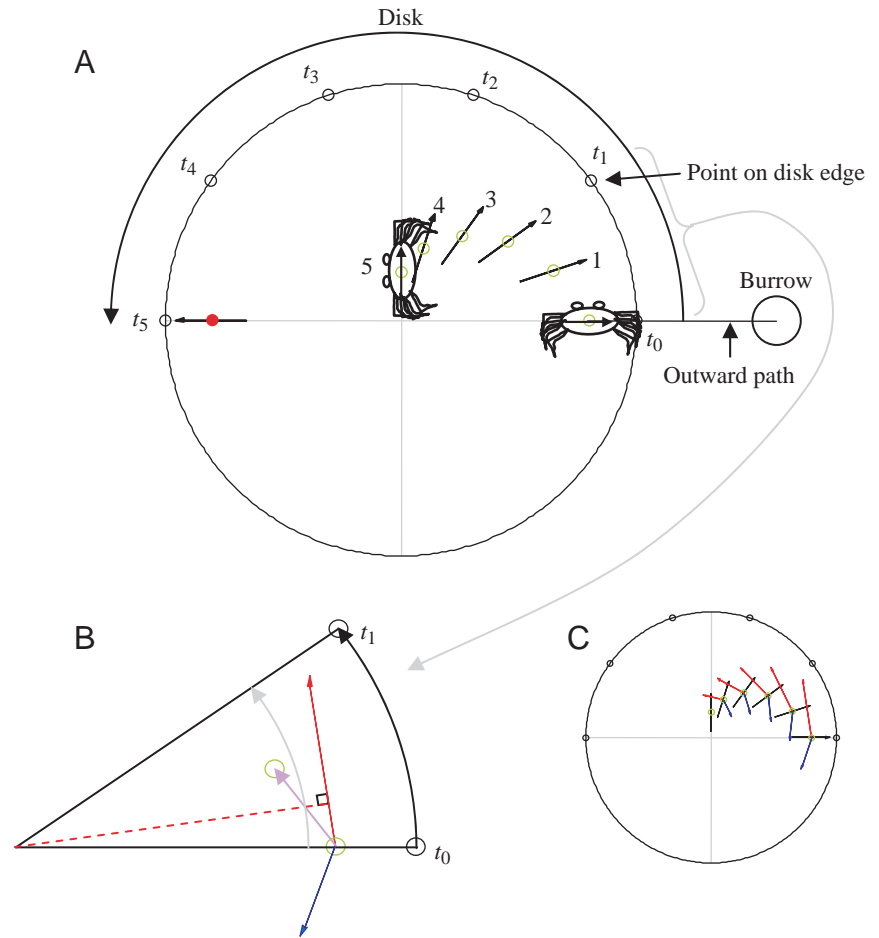


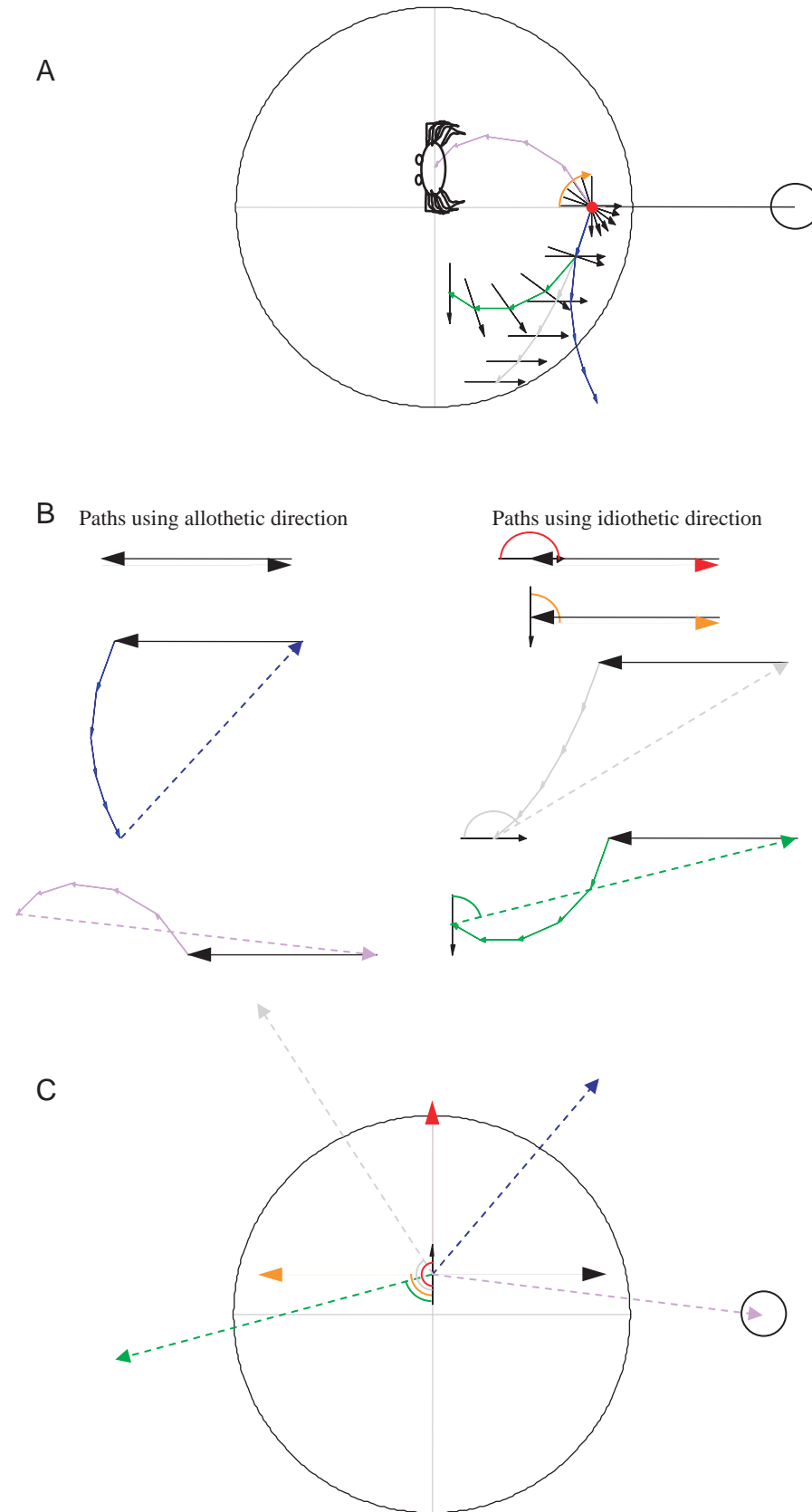
Fig. 1. Illustration of the method used for deriving imposed- and self-translation. (A) Hypothetical experiment in which a crab is rotated on a disk (see text). The crab's transverse axis is denoted by an arrow on its body pointing to the homeward side. Numbered green open circles indicate the crab's position at each time point. The red circle indicates the final position of the crab if it had not moved (see text for details). (B) The experiment between times t_0 and t_1 . The absolute translation vector (violet arrow) is digitized from video. The imposed translation vector (red arrow) is normal to the radius (red broken line) bisecting the crab's position at t_1 and t_2 (green open circles), and thus estimates the mean of all (unmeasured) imposed directions between the two discrete sampling times. It is the same length as the arc passing under the spot bisecting the crab's position at t_1 and t_2 (gray arc). The self-translation vector (blue arrow) is the vector subtraction of the imposed from the absolute translation vector; i.e. violet - red = blue. (C) Illustration of the imposed- and self-translation vectors (red and blue, respectively) for each step in the path shown in A. Green circles correspond to those in A.

own after foraging. Almost all of them missed home and began to search.

The digital reconstruction of the crabs' paths requires knowledge both of the movement imposed on the crab by the experimenter, and of the crab's self-movement. The method for deriving these from the disk rotation experiments is schematically illustrated in Fig. 1. In the hypothetical experiment shown, a crab walked from its burrow onto a disk, at which time its transverse body axis was still aligned with the direction of home (Fig. 1A). The disk was then rotated by $+180^\circ$, as indicated by the black arc. The experiment was

digitized at times t_0 – t_5 , with the disk rotating 36° per digitized step. The crab was not centered on the disk, so disk rotation

imposed translation as well as rotation. Thus, if the crab had made no effort to move it would have ended up at the position and orientation shown at the red dot on the left-hand side of the disk. However, the crab did not end up this way. The crab's actual position and orientation over time are indicated by green circles and black arrows, respectively, showing the crab had actually self-translated and self-rotated.



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Imposed- and self-translation are considered as vectors. The translation imposed by the disk is a vector whose direction and length depend on the crab's angular and radial position on the disk, respectively. The method of computation is described in the legend to Fig. 1, and the imposed translation vector is represented by the red arrow in Fig. 1B for the period t_0 – t_1 . The absolute translation vector is simply the movement seen on video by the observer and, for the period t_0 – t_1 , is represented by the violet arrow joining the positions of the crab at t_0 and t_1 . Finally, the crab's self-translation vector is computed from the relationship:

$$\text{Self} + \text{Imposed} = \text{Absolute}$$

and, for the period t_0 – t_1 , is represented by the blue arrow in Fig. 1B. The variation in imposed- and self-translation vectors during the course of the imposed disk rotation can be seen in Fig. 1C, where

Fig. 2. Possible paths recorded by the model path integrator. (A) Different versions of the hypothetical path shown in Fig. 1. Three of these paths (black, blue and violet) rely on an external compass for direction information (allothetic), while four of them (red, orange, green and gray) rely on an internal source of direction information (idiothetic). The latter include an arrow for the transverse body axis, signifying that all directions are measured against this. (B) Summary of possible paths from A. All integration mechanisms record the outward path (large black arrows); thereafter they diverge. Idiothetic paths show the final recorded orientation of the body axis (small black arrows) and the angle of the home vector measured against this (colored arcs). Home vectors are all in broken arrows. (C) Hypothetical home vectors for all seven model paths. See text and Table 1 for a description of the path-integration mechanism used to obtain each path.

they are shown for each step in the experiment. The lengths of the imposed translation vectors (red arrows) become smaller as disk rotation proceeds, because the crab gets closer to the center of the disk.

The imposed rotation is equal to the rotation of the disk, the absolute rotation is the rotation seen on video by the observer, and the self-rotation is computed from the same relation as for translation, i.e. Self + Imposed = Absolute.

Actual paths in which foraging crabs were successfully reoriented are compared to seven model (reconstructed) paths that have different path integration mechanisms. These model paths differ from each other in essentially three ways: (1) their source of direction information (idiothetic or allothetic); (2) whether or not they integrate the self-translation on the disk (it is possible that some of this self-translation may be an error in the compensatory control system); (3) whether or not they integrate self-rotation associated with the compensatory optomotor response.

The model paths resulting from different combinations of these variables are shown in Fig. 2 for the imaginary disk rotation experiment illustrated in Fig. 1. They are summarized in Table 1. Each one is reconstructed from the direction, distance and rotation known for each step, with appropriate alterations to the raw data. These paths represent possible versions of what was stored by the path integrator, and the resulting home vectors are shown as broken lines in Fig. 2B. These home vectors, if applied to the model crab, would result in homing runs as seen in Fig. 2C.

The black, blue and violet model paths all assume that the crabs gain their directional information from allothetic sources; i.e. sources external to the animal like the sun or distant landmarks. Because of this, the question of whether they integrate their compensatory turns is not applicable, because they record the correct bearing with each step whether or not they compensate for disk rotation. The three paths differ depending on whether or not they integrate none, some or all of their total translation during disk rotation.

Black path: cumulative addition of self-translation vectors during outward path, their directions measured allothetically (against e.g. the sky). Body rotation is also measured allothetically. In this model, neither the imposed nor the self-translation occurring during disk rotation is integrated.

Blue path: cumulative addition of *all* self-translation vectors,

measured allothetically. Body rotation is measured allothetically. In this model, imposed translation resulting from disk rotation is not integrated.

Violet path: cumulative addition of *all* self- and imposed-translation vectors, measured allothetically. Body rotation is measured allothetically. This is a special case in that it is the only model that leads precisely back to the burrow entrance (Fig. 2C).

The red, orange, green and gray model paths all assume that the crabs gain their directional information from idiothetic sources; i.e. sources internal to the animal like leg proprioceptors or statocysts. The red and orange paths assume that the crabs did not integrate their translation during disk rotation, while the green and gray paths assume that the self-translation component was integrated. Final distinctions (between red and orange on the one hand and green and gray on the other) are based on whether or not the crabs integrated their compensatory turns.

Red path: cumulative addition of self-translation vectors during outward path, their directions measured idiothetically (against body axis). Body rotation is cumulative self-turns (measured idiothetically), *except* compensatory response. As in the black path above, neither the imposed nor the self-translation occurring during disk rotation is integrated.

Orange path: cumulative addition of self-translation vectors during outward path, their directions measured against body axis. Body rotation is cumulative self-turns, *including* compensatory response. As in both black and red paths, neither the imposed nor the self-translation occurring during disk rotation is integrated.

Gray path: cumulative addition of *all* self-translation vectors, as measured against body axis. Body rotation is cumulative self turns, *except* compensatory response. As in the blue path, imposed translation resulting from disk rotation is not integrated.

Green path: cumulative addition of *all* self-translation vectors, as measured against body axis. Body rotation is cumulative self-turns, *including* compensatory response. As in the blue and gray paths, imposed translation resulting from disk rotation is not integrated.

As stated above, although almost none of the crabs in the experiments hit home, their path integrators should have compiled a record from the crabs' movements that under natural conditions would allow them to return home accurately.

Table 1. Assumptions underlying the path integration mechanism that would result in each of hypothetical foraging/homing paths illustrated in Fig. 2

Hypothetical path	Direction information	Integration of self-translation during disk rotation?	Integration of imposed translation resulting from disk rotation?	Integration of compensatory turns?
Black	Allothetic	No	No	No; direction from e.g. sky
Blue	Allothetic	Yes; measured against e.g. sky	No	No; direction from e.g. sky
Violet	Allothetic	Yes; measured against e.g. sky	Yes; measured against e.g. sky	No; direction from e.g. sky
Red	Idiothetic	No	No	No
Orange	Idiothetic	No	No	Yes
Green	Idiothetic	Yes; measured against body axis	No	Yes
Gray	Idiothetic	Yes; measured against body axis	No	No

Thus, in the Results section that follows, we use the crabs' own movements to determine what was recorded by the path integrator.

Slippery patch experiment

These experiments were performed to induce errors in distance measurement. A straightened metal coat hanger was used to maneuver a sheet of clean, wet acetate, 10.715 cm × 15 cm, between the crab and its burrow. Crabs were then frightened by a piece of cloth attached to the end of a thin stick waved directly over them. This prompted them to run home over the slippery patch. Running velocity *vs.* time curves were drawn for experimental crabs, and for controls that had been frightened home without a slippery patch. Experimental crabs sometimes slipped noticeably; i.e. they made slower than normal progress across the patch. The running velocity *vs.* time curves for slipping crabs were then compared to the controls. In this comparison, an averaged velocity *vs.* time curve for the controls was used. The control trials lasted different lengths of time, and thus had different numbers of data points, but we wanted the average curve to reflect the shape of the individual control curves, not necessarily the precise timing. Therefore, to calculate the average control velocity *vs.* time curve, individual curves were normalized to their maximum time (i.e. they all had a relative time axis going from 0 to 1.0). The data were then graphically redigitized at an arbitrarily high spatial frequency using Scion Image software, so that all curves had 216 data points. These new paths were then averaged, and the resulting mean curve was rescaled to the appropriate length of time for comparison with each experimental curve. Further details and justification are given in the Results.

Mean values are reported \pm S.D.

Results

Disk rotation experiment

We performed 15 successful disk rotation experiments. Disks were rotated an average of 305° (range: 71–641°), and crabs compensated for an average of 92±7.0%, of disk rotation. These results are summarized in Table 2. Crabs with good compensation tended to have their disk rotated more, since the goal was ultimately to reorient them, not to observe their response to a standardized disk rotation. Interestingly, crabs often continued to counter-rotate after the disk stopped, as seen in Figs 3 and 5. This was not because they had external compass information, however, because these crabs usually ended up under-compensating, which would not have happened if they had been orienting to an external cue. On average the crabs compensated by 21.4±20.6° after their disk stopped, which was equivalent to 7.7±9.6% of their total compensation.

We will closely examine three of the rotation experiments. These three are chosen for their ability to illustrate important points, not necessarily for their adherence to any particular outcome. Fig. 3 is the first such example. The crab's transverse body axis is indicated an arrow pointing to the burrow side (see Fig. 3A inset); it was digitized once per second, and is shown from the start of disk rotation until the crab reached home. The disk was rotated counter-clockwise by 482° over 11 s, but the crab actively compensated for this (compare body and disk orientation in Fig. 3B, or crab and disk angular velocity in Fig. 3C) and continued to do so for 5 s after disk rotation ceased. For this and other crabs who continued to compensate after the disk had stopped, it was common for them to do so in fairly abrupt turns, as seen at $t=15$ s in Fig. 3B,C. Note that after this turn, however, the crab's orientation reached a more or less steady state. It was therefore at this point, indicated by

Table 2. Summary of results from all 15 trials, including the crabs' orientation error when the disk started rotating, imposed disk rotation, optomotor compensation and homing error produced by seven potential path-integration mechanisms

Trial	Initial error	Disk	Compensation	Homing error						
				Black	Blue	Violet	Red	Orange	Green	Gray
1	-5.0	482	480	-3.7	-6.8	-9.5	-5.8	41.9	49.6	-6.2
2	-22.5	298	266	-36.7	-41.6	-27.0	2.0	-63.1	-58.3	5.4
3	5.6	497	434	-49.8	-90.8	-38.2	9.4	61.1	47.3	-37.4
4	-16.7	227	186	-52.5	-102.7	-33.7	16.9	-178.9	-166	27.6
5	-6.4	440	429	-9.8	-11.7	-13.6	-16.3	-32.0	-32.5	-16.2
6	8.1	641	617	-10.6	-7.6	-5.0	-15.0	-39.2	-38.9	-1.2
7	13.6	122	121	-3.5	-5.4	-3.6	27.4	99.2	105.7	31.5
8	0.4	283	254	-28.9	-35.4	-11.8	32.9	-103.4	-100.8	38.4
9	-5.9	139	123	-20.2	-25.6	-8.2	6.0	107.0	113.7	5.5
10	15.3	311	305	-7.1	-7.7	-7.8	-7.0	-44.8	-44.0	-8.1
11	4.8	101	89	-3.1	0.7	-0.9	1.4	66.0	60.0	0.2
12	0.7	595	574	-16.6	-12.4	-16.0	-6.9	-76.3	-84.9	-9.8
13	22.5	204	177	-27.9	-46.1	-29.3	7.9	164.5	165.9	-7.0
14	-24.5	166	141	-28.9	-47.5	-34.9	-17.1	139.2	163.4	-12.5
15	16.5	71	54	-8.3	-24.8	-41.1	-9.4	76.2	97.6	-4.5

Initial error, crabs' orientation error when the disk started rotating; Disk, imposed disk rotation; Compensation, optomotor compensation.

Trials shown in Figs 3–5 are in rows 1–3, respectively.

All values are in degrees.

a vertical arrow in Fig. 3B, that we determined the crab had finished compensating. The crab's under-compensation, then, is the initial orientation minus the orientation at $t=16$ s, and in this case is $\sim 1^\circ$, meaning that this crab compensated for nearly all disk rotation.

Despite its perfect compensation, this crab missed home by a small amount and only found it after a short search. Why did this crab miss home? The reconstructed home vectors in Fig. 3D give a clue. The way to assess these paths is to note which home vectors come close to matching the crab's own

homing path, indicated by the cyan (light blue) colored arrow. The assumptions underlying these paths should be provisionally accepted as being consistent with the true path integration mechanism, while those paths that diverge greatly from the observed one should be considered to have assumptions that are contrary to the true mechanism. For instance, green and orange are the only paths to integrate

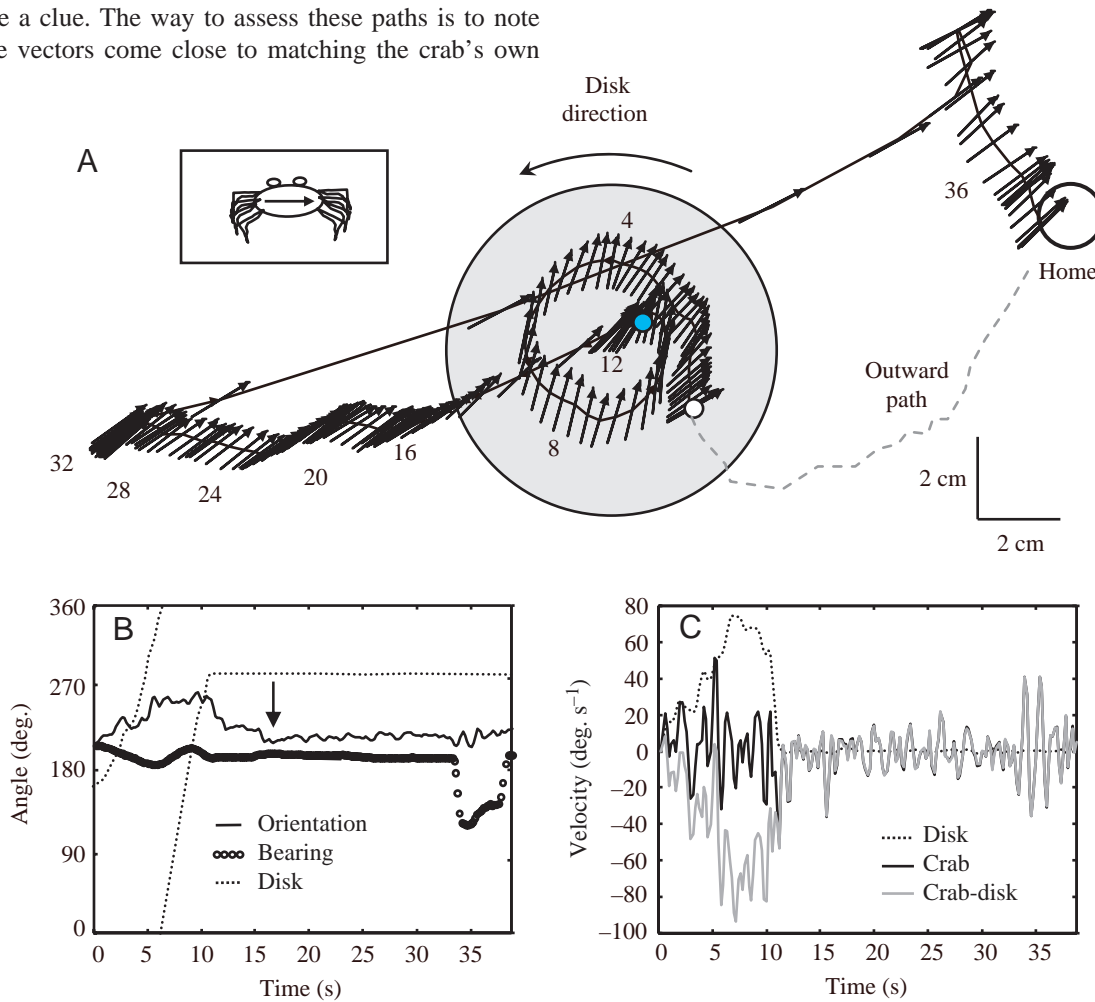
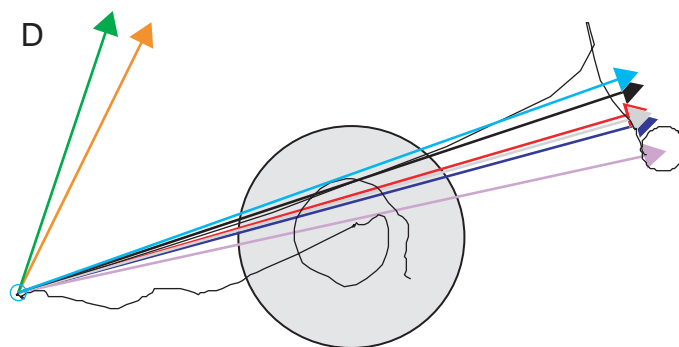


Fig. 3. Example of a trial in which a crab fully compensated for disk rotation. (A) Transverse axis of the crab's body (inset), digitized at 200 ms intervals, shown from the start of disk rotation until the crab reached home. Numbers are in seconds after rotation began. Large tinted circle, rotating disk; white circle, position of crab when disk rotation started; blue circle, position of crab when rotation disk ceased. (B) Orientation and bearing of crab and disk over time. Compensatory body rotation by the crab was assumed to have ceased at the time indicated by the black arrow. Note the similarity of this body orientation with that at the beginning of the experiment. (C) Crab and disk angular velocity, and crab angular velocity relative to the disk over time. (D) Reconstruction of seven possible home vectors computed by the path integrator, superimposed on the crab's actual path as in A. See text for details.



compensatory turns, and the fact that they both differ from the observed path by a large angle casts doubt on the notion that the true mechanism integrates these turns. The violet path assumes the crab can integrate its absolute movement, which might conceivably be achieved by integrating its angular and linear momentum. However, fiddler crabs apparently lack the ability to integrate imposed translation using momentum or

any other cue (Zeil, 1998; Cannicci et al., 1999; Layne et al., 2003). Thus, the violet home vector deviates from the observed homing path by an angle that depends on the amount the crab was reoriented and displaced.

The remaining four paths are not very different in their accuracy, for two reasons. First, the crab did not self-translate very much while the disk rotated, making it difficult to distinguish between the red and gray options, and between the black and blue. Second, because of this individual's excellent rotational compensation, we failed to reorient it, making it difficult to distinguish between the non-optomotor-integrating idiothetic and allothetic options. In fact, this result does not even address the issue of directional compass cues. It does, however, show that a great deal of self-locomotion, in the form of $\sim 480^\circ$ of compensatory rotation, did not contribute to the true home vector. Because of this crab's perfect compensation and lack of self-translation, our experiment boiled down to a passive translation. This crab missed home in the direction and by the distance that it was passively translated by the disk.

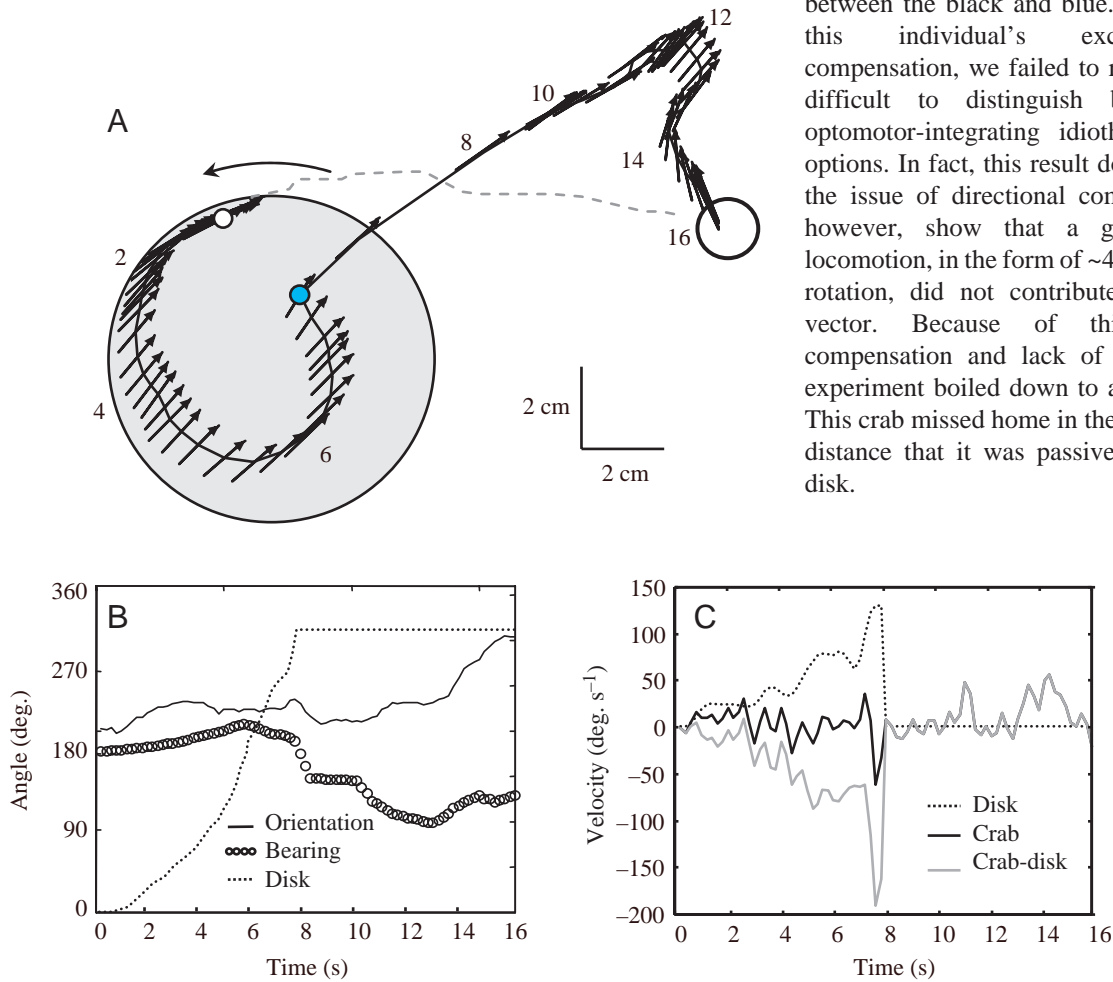


Fig. 4. Example of a trial in which a crab under-compensated for disk rotation, and had little self-translation during disk rotation. (A) Crab's transverse body axis digitized at 200 ms intervals; conventions as in Fig. 3. (B) Orientation and bearing of crab and disk over time. Compensatory body rotation ceased when disk stopped, and the crab homed immediately thereafter. (C) Crab and disk angular velocity, and crab angular velocity relative to the disk over time. (D) Reconstruction of seven possible home vectors computed by the path integrator, superimposed on the crab's actual path as in A. See text for details.

What happens when crabs do not fully compensate for disk rotation? Our second example, illustrated in Fig. 4, shows a crab that experienced counter-clockwise disk rotation of 298° over 7.8 s. Unlike the previous example, it attempted to return home immediately after the disk stopped, at which time it remained under-compensated for disk rotation by 32° . It missed home by approximately this amount. The only variable that the black, blue and violet vectors share – and do not share with the red and gray vectors, which both closely match the

true homing path – is that their direction component is measured relative to some allothetic cue. This suggests that the crab did not use allothetic direction cues. The poor accuracy of the orange and green vectors again suggests the crab did not integrate its compensatory rotation. The similarity of the red and gray vectors (and the blue and black vectors) is due to the fact that, once again, this crab did little self-translating during disk rotation. Overall Fig. 4 was the most common type of outcome from our experiments, despite the fact that several

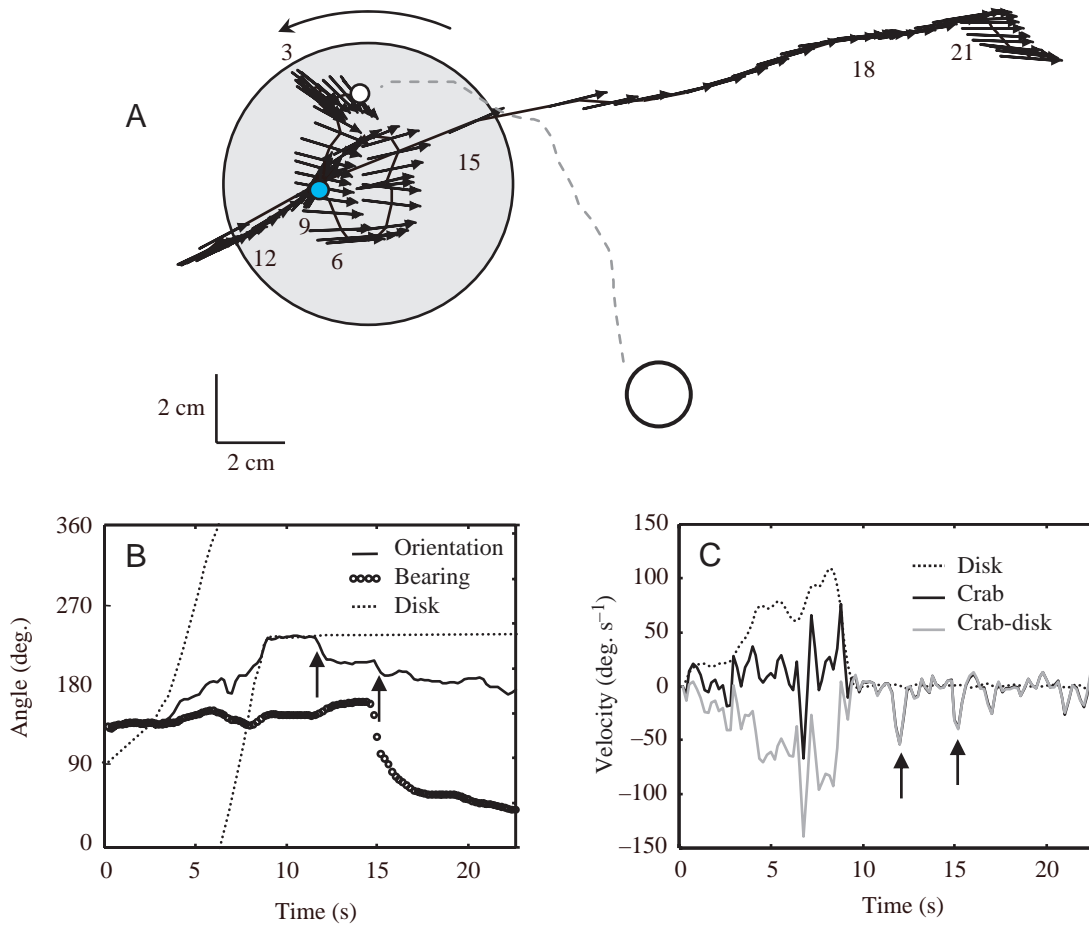


Fig. 5. Example of a trial in which a crab under-compensated for disk rotation, and had significant self-translation during disk rotation. (A) Crab's transverse body axis digitized at 200 ms intervals; conventions as in Fig. 3. (B) Orientation and bearing of crab and disk over time. Black arrows, two abrupt compensatory turns occurring after disk rotation ceased, the second of which is in mid-return; note the coincident large change in bearing, caused by the run home.

(C) Crab and disk angular velocity, and crab angular velocity relative to the disk over time. (D) Reconstruction of seven possible home vectors computed by the path integrator, superimposed on the crab's actual path as in A. See text for details.

crabs were very near prominent landmarks that might have guided them. In one case a small mangrove sapling situated ~1cm from the burrow entrance apparently provided no directional cue for a crab rotated just 9 cm away, and it missed home by 26°, almost exactly the amount by which it under-compensated (27°). The crab in Fig. 4 did eventually re-enter its own burrow, but did so leading with the opposite side of its body from normal. Crabs normally enter their burrows leading with the side of the body that faced the burrow during their foraging excursion. Leading with the opposite side occurred very rarely, generally after an experimental manipulation caused a crab to lose its burrow.

Our third example, illustrated in Fig. 5, shows a crab whose disk was rotated by 497° over $t=8$ s, but compensated for all but 63° of disk rotation. As in Fig. 3, this individual made two abrupt compensatory turns after the disk stopped to reorient itself, including one in mid-return near $t=16$ s (see vertical arrows in Fig. 5B,C). For the point of final compensation, we used the start of the return home near $t=12$ s. This example is included because significant self-translation by the crab during disk rotation allows us to assess whether this was likely to have been integrated. Note that the red vector is close to the true

homing path, but the gray vector deviates from it considerably. Clearly, in this case at least, self-translation was not integrated, but was probably an unintended part of the compensatory response.

To get a picture of the responses in general, we have compared the directions of the model home vectors with the observed homing directions (Fig. 6), the latter being derived from the slope of the linear regression line that fits the crabs' return path. All data were normalized to counter-clockwise disk rotation, and plotted in unit polar coordinates relative to the observed homing direction, which was set to 0° (see Fig. 6A). Only the direction of the return path, rather than the exact location to which the crabs attempt to home, is treated here because determining the location of the end of the home vector is much less precise than determining its direction. The return directions of all allothetically measured home vectors (Fig. 6B–D) are shown to be significantly clockwise of the observed homing path. This is to be expected if most crabs under-compensated for disk rotation to some degree, and made a homing error of the same or similar angle.

The return directions of idiothetically measured vectors that include compensatory turns (Fig. 6F,G) are nearly randomly

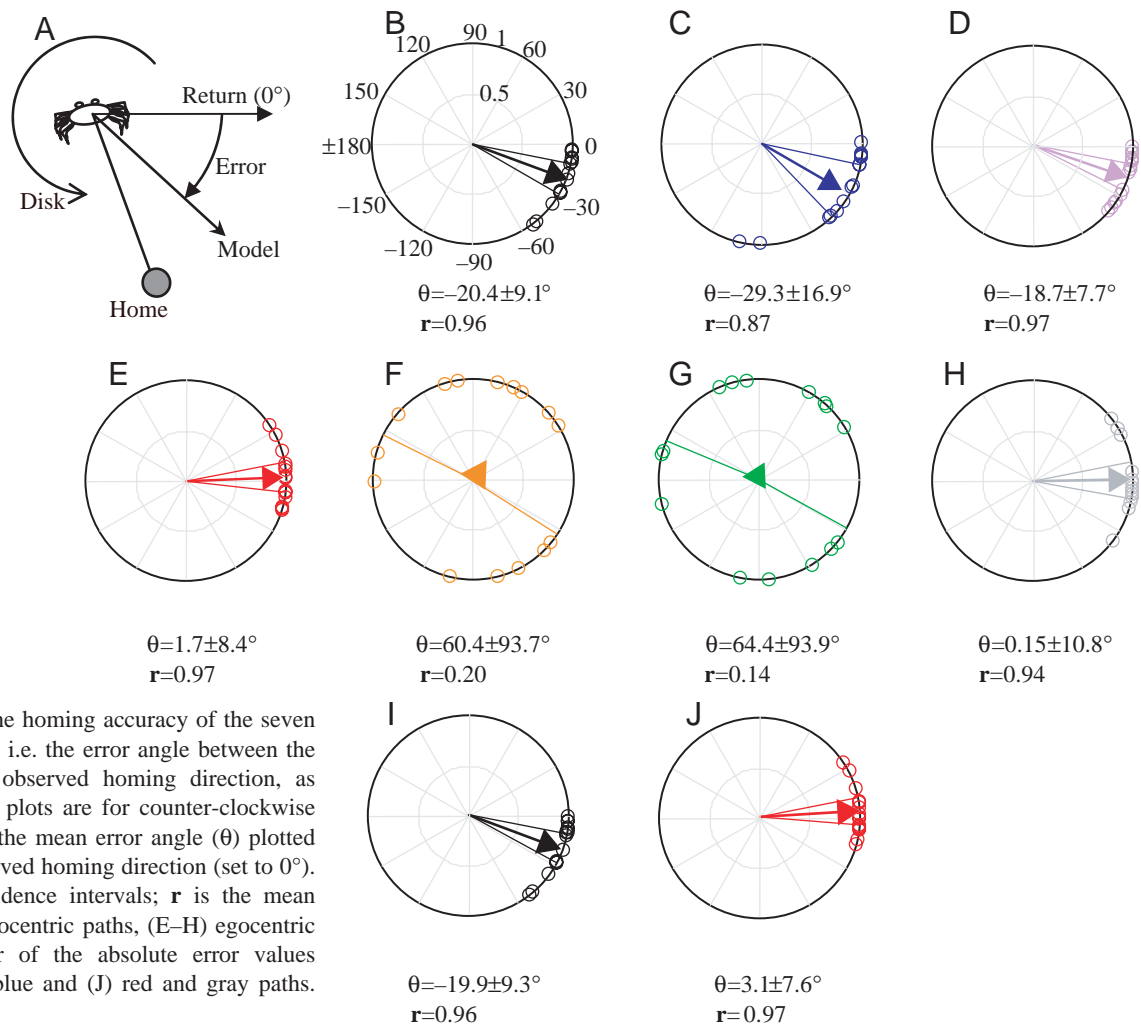


Fig. 6. Comparison of the homing accuracy of the seven path-integration models, i.e. the error angle between the model vector and the observed homing direction, as illustrated in (A). Polar plots are for counter-clockwise disk rotation and show the mean error angle (θ) plotted with respect to the observed homing direction (set to 0°). Values are $\pm 95\%$ confidence intervals; r is the mean vector length. (B–D) exocentric paths, (E–H) egocentric paths, (I, J) the smaller of the absolute error values between (I) black and blue and (J) red and gray paths. See text for details.

dispersed, strongly indicating that fiddler crabs distinguish between compensatory turns and those that are non-compensatory. The red and gray vectors (Fig. 6E,H) are centered very closely around the homing direction, with the red having slightly tighter clustering. This result, along with the clockwise bias of the black, blue and violet paths, explicitly addresses whether the spatial frame of reference used for computing the home vector is exocentric or egocentric, regardless of whether it was compiled from path integration or not: an exocentric vector should not change when an animal is turned on the spot (Benhamou, 1997). However, the home vector of these crabs rotated by almost exactly the amount that we reoriented them. The average under-compensation by all crabs was $21.8 \pm 16.1^\circ$ (calculated from data shown in Table 2), which is very close to the direction of the mean vector in Fig. 6I, i.e. $19.9 \pm 9.3^\circ$. This confirms that fiddler crabs have an egocentric frame of reference, and that they utilize idiothetic direction information, but it leaves open the question of whether or not self-translation observed during disk rotation was intentional (and integrated). This question is not central to our main conclusions, but we did notice that in all but one experiment, when the red vector did not closely match the observed homing path, the gray vector did, and *vice versa*. We have therefore plotted the smaller of the absolute error angles between red and gray, and between black and blue, the allothetic pairs which differ only in their integration of self-translation (Fig. 6I,J). The allothetic mean angle remained significantly different from the observed homing direction, while the idiothetic remained statistically indistinguishable

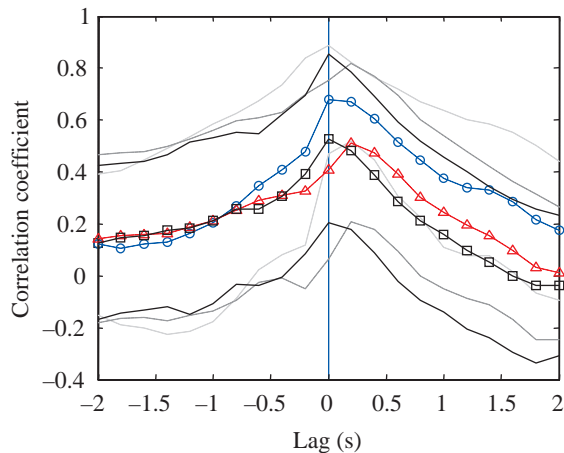


Fig. 7. Examination of the input–output relationships of the crab's compensatory rotation on the disk. Means (solid lines) and s.d. (broken lines) of time-lagged cross-correlations for all 15 trials, between: crab egocentric and disk angular velocities (sign reversed, blue line with circles); crab egocentric angular velocity and crab orientation (sign reversed, red line with triangles); crab egocentric angular velocity and orientation error (this is affected by both rotation and translation; black line with squares). Positive lags indicate disk angular velocity, crab orientation or orientation error leading in time, negative lags indicate crab egocentric angular velocity leading.

from the observed homing direction. Fig. 6J did produce a plot with tighter clustering, but the mean angle was slightly larger than in Fig. 6E,H. Therefore the question of whether self-translation on the disk was intentional and integrated or not remains unanswered. But the comparison with Fig. 6I does lend further support to the notion that the crabs utilized idiothetic rather than allothetic direction information.

The control of body turning was investigated by computing the cross-correlation coefficient between potential inputs and outputs of the control system, at different time lags. We used only the time periods during which compensation was active. We found that the correlation was highest ($r=0.68$) between egocentric crab angular velocity (i.e. relative to the disk) and disk angular velocity, but this was at zero lag, which is not indicative of a causal relationship (Fig. 7). However, this correlation with disk angular velocity was higher over all lags than that with body orientation (which peaks at $r=0.51$), or with orientation error ($r=0.53$; orientation error = bearing minus orientation; see Zeil, 1998). When combined with other data presented here, this result suggests that compensatory rotation is induced by the disk angular velocity, as sensed either visually or vestibularly. This is in contrast to what Zeil (1998) found for *U. l. annulipes*, where the highest correlation was between crab angular velocity and body orientation, at a lag of 40 ms. We address this difference between our results and Zeil's in the Discussion.

Slippery patch experiment

The results described so far in this paper make clear that a fiddler crabs' home vector is coded egocentrically using idiothetic spatial information. However, there are few clues as to the sensory modes involved. Here, we attempt to determine how fiddler crabs measure distance, using an experiment that distinguishes two categories of sensory cue. The first category consists of cues that could only be derived from real movement over the ground, such as optic flow and vestibular signals. The second category consists of cues that we could experimentally dissociate from real body movement by use of a substrate on which the crabs slipped (the slippery patch), such as proprioceptors and central motor commands.

The experiment consisted of maneuvering a slippery patch of wet acetate between a foraging crab and its burrow. When crabs were scared from above, they ran across the patch, and, as it turned out, individuals either slipped and stopped briefly short of home, or did not slip and ran directly to their burrow. Slipping was characterized qualitatively by cartoon-like running-without-moving behavior, and quantitatively by a depression of running velocity while on the patch. The rationale behind this experiment was that, if crabs measured the distance of their return home by means of cues that are derived from movement with respect to the ground such as, for instance, optic flow, then they should return directly home whether they slipped or not. If they slipped they might take longer, but, like crabs that did not run over a patch, they would not stop short of home. Since bees (and, possibly, desert ants) can measure distance using optic flow (Wehner, 1992; Esch

and Burns, 1995, 1996; Ronacher and Wehner, 1995; Srinivasan et al., 1996; Esch et al., 2001; but see Ronacher et al., 2000), this was obviously a reasonable possibility. On the other hand, if crabs measured the distance of their return home by means of proprioceptive cues, then those crabs that slipped should 'play out' their home vector, and stop sooner than control crabs who did not slip or who did not run over the patch. Proprioceptive input from the legs might be a measure of 'effort over time' or some measure of motor output that, at its crudest, might be 'number of steps'. Thus, in this second category of cues, but not in the first, slipping crabs should stop before reaching home.

One example of such an experiment is shown in Fig. 8, in which the crab was scared when it was 30 cm from home. After a few initial steps, the crab stopped running when it reached the front edge of the patch (this was the only individual to do so), but then proceeded to run across the patch, and stopped 7 cm before reaching home (at large gray arrow, Fig. 8A). The qualitative observation of slipping by this crab was confirmed by the fact that its average running velocity on the patch was 16.8 cm s^{-1} (Fig. 8B), which is much lower than normal escape velocity, around 70 cm s^{-1} among controls (see Fig. 9B).

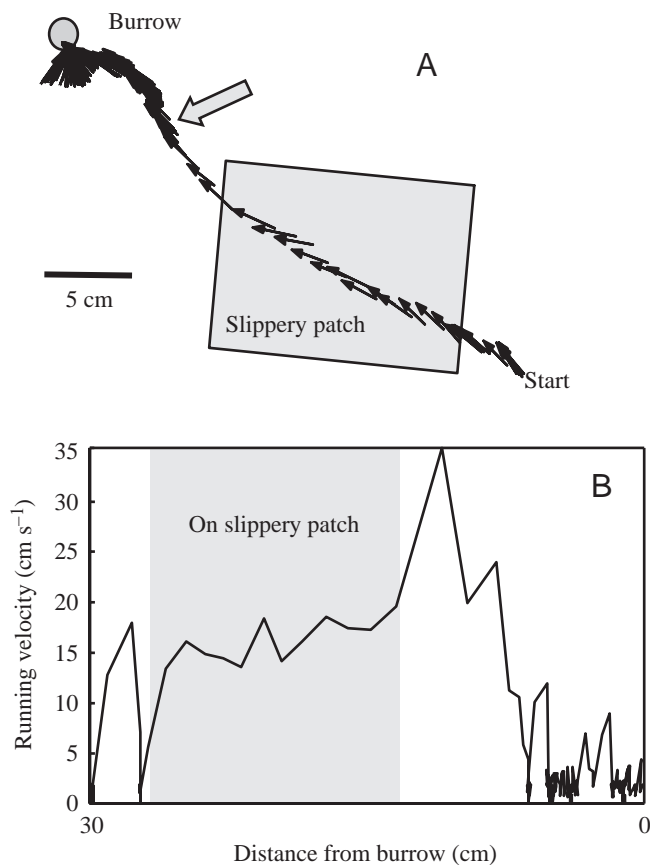


Fig. 8. Example of a slippery patch experiment. (A) The crab was frightened when situated at 'start', ran over the slippery patch (gray rectangle), and stopped at the filled arrow, before finding its way home. (B) Plot of crab running velocity against distance run. The shaded area indicates when the crab was on the slippery patch.

We performed such trials on 14 crabs, of which ten were 'slippers' and four 'non-slippers'. We also performed four controls in which foraging crabs were scared home with no patch. The mean starting distance from home was $26.4 \pm 4.3 \text{ cm}$ for the slippers, $25.7 \pm 1.5 \text{ cm}$ for the non-slippers, and $16.9 \pm 5.4 \text{ cm}$ for the controls. Data are plotted as running velocity relative to home (i.e. closing speed) against proportion of distance home (d/D , where d is the distance home from any point in the digitized path, and D is the starting distance from home, Fig. 9A). This plot, which emphasizes the position where the crabs stopped in relation to home, illustrates two features of their behavior on the slippery patch. First, crabs that were qualitatively observed to slip (red lines) stopped briefly before they reached home; i.e. their running velocity dropped to zero before reaching home. On the other hand, crabs that ran over a patch but were not observed to slip (blue lines) and crabs that were frightened home with no patch (black lines) ran straight home without stopping. Second, crabs that slipped generally had lower running velocities while they were on the patch (on-patch intervals are indicated by solid line segments) than either non-slippers or controls at a similar stage of the run home. Thus, those crabs with depressed running velocities while on the patch stopped short of home. These results are consistent with the hypothesis that, on returning home, fiddler crabs 'play out' a home vector, and stop when that vector is exhausted. Indeed, some crabs even stopped within 2 cm of home, a distance from which they probably could see the burrow entrance. Such crabs ran the short distance home immediately after stopping (within 500 ms), presumably because they located home visually. Thus, while undisturbed short-range (within about 5–6 cm) homing, as in foraging, is aided by visual contact with the goal (Zeil, 1998), rapid homing, as during escape, can result in a short delay between using the home vector system and the visual system to find home. This implies that the visual mechanism does not function during rapid escape until the home vector is exhausted, as in bees (Wehner et al., 1990) and ants (Wehner et al., 1996; but see Zeil, 1998). These results also suggest that the distance home is not measured using optic flow or vestibular information. If it had been, crabs that slipped should have continued running until they had measured out the correct distance home, regardless of the time or number of steps taken, time spent running at any particular velocity, etc.

Fig. 9B shows the mean running velocity for slippers (red line) and controls (black line), the latter being the combined non-slippers and controls. We combine these because they are not significantly different (see Fig. 9C) and so can both be used as controls, and we will refer to the combined non-slipper and control paths as controls from this point forward. An obvious question to ask is whether the distance by which the crabs fell short of home was related to the amount of slippage.

The first step in answering this question involves plotting running velocity against proportion of total running time (t/T , where t is elapsed time to any point in the digitized path, and

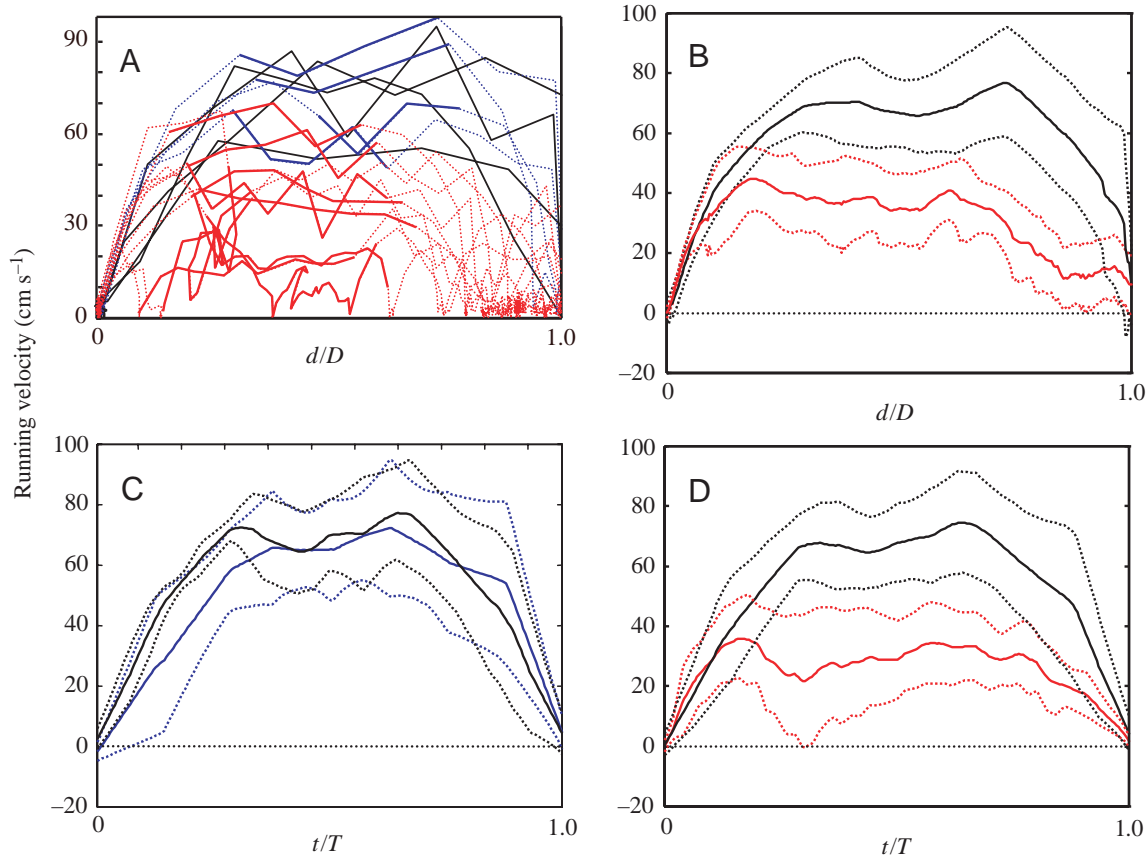


Fig. 9. Running velocity of escaping crabs. (A) Running velocity plotted against relative distance home (d/D). Red lines, crabs that ran over the patch and stopped before reaching home; blue lines, crabs that ran over the patch but did not stop before reaching home; black lines, control crabs that did not run over a patch. Red and blue lines are solid where the crabs were on the patch. (B) Mean of running velocity profiles plotted against relative distance home (d/D). Controls (including both no-patch and non-slippers), black line; slippers, red line; lines are mean running velocity \pm s.d. (dotted lines). (C) Mean of running velocity profiles of controls (no patch, black line) and non-slippers (blue line) plotted against relative time until first stop (t/T); lines are mean running velocity \pm s.d. (dotted lines). (D) Same data as in B but plotted against relative time until first stop (t/T).

T is the time of the first stop). In the case of controls and non-slippers this first stop is at home, while in the case of slippers it is before reaching home, but is presumably the end of the home vector (see Fig. 9D). Assuming all crabs ran out an internal representation of the home vector, the discrepancy in slipper running velocity relative to controls, when integrated over the running time for a particular trial, should be equal to the observed shortfall in that trial. An equivalent, but simpler, approach is to say that the control velocity profile integrated over the running time (T) should be equal to the length of the home vector for a crab that ran for time T , i.e. the crab's starting distance. Stated more formally, the area (A) under a velocity (v) curve plotted against time equals distance (D); i.e.

$$A = \int_0^T v \cdot dt = D. \quad (1)$$

This estimated home vector length can then be compared to the actual distance home.

This hypothesis rests on the assumption that crabs ran with the same effort on the patch as they did off it; i.e. the controls represent what the slippers would have done with no patch, and therefore the home vector will be realized among slippers in terms of time spent running. Alternatively, if crabs measured the home vector by counting the number of steps, the hypothesis assumes the same step frequency in slippers and controls, and so time spent running is still the relevant integration parameter.

To support this assumption we can report subjectively that the slippers were never observed to stop running while on the patch, and so there is no reason to believe their effort was less than that of the controls, which also did not stop until reaching home. A quantitative comparison of the controls to the non-slippers (Fig. 9C) also supports this assumption. As mentioned above, the controls (black line) and non-slippers (blue line) were similar to each other over their entire length, which shows that the patch itself does not cause crabs to reduce running effort. This similarity in velocities is also interesting because the mean path lengths of the controls and non-slippers were

quite different (16.8 and 25.7 cm, respectively). Thus, within the range of path lengths we recorded, the shape of the escape velocity profile over relative distance is quite consistent. This means that it may reasonably be used as an estimate – when scaled to the correct length of time – of what slipper paths of various lengths would have been without the slipping.

Using this reasoning, how well were we able to estimate the length of the home vector from the crabs' own behavior? First, in Fig. 10A we compare the observed running distance of the slippers, D_{obs} , to their starting distance, which we assume to be the length of the home vector \mathbf{D} (open circles). The regression line relating the two is given by:

$$D_{\text{obs}} = 0.849\mathbf{D} - 2.92 \quad (r^2=0.751; F=24.1, P=0.001). \quad (2)$$

This shows that slippers ran about 85% of the correct distance. We then compare our estimate of the home vector length (the control velocity curve integrated over the time of observed running by slippers) to the real distance home (filled circles). The regression line relating these is:

$$\mathbf{D}_{\text{est}} = 1.45\mathbf{D} + 7.01 \quad (r^2=0.0649; F=0.556, P=0.477). \quad (2)$$

It is clear that our estimate is inaccurate, and overestimates the length of the home vector by as much as 400%. The estimate error, defined as the ratio of the estimated home vector length to starting distance ($\mathbf{D}_{\text{est}}/\mathbf{D}$), does not depend on D_{obs} ($F=0.21, P=0.66$) or on \mathbf{D} , as indicated by the lack of significance in the regression above.

What is the source of our estimate error? Fig. 10B shows a comparison between estimate error and time spent running. The regression line is:

$$\mathbf{D}_{\text{est}}/\mathbf{D} = 1.91T + 0.115 \quad (r^2=0.935; F=114.4, P<<0.001), \quad (3)$$

showing that our estimate error grows quite closely with running time. This means that the control velocity curve was consistently integrated over a longer time than necessary to achieve \mathbf{D} , which implies that crabs ran for longer than they would have if they were not slipping.

Why would the slipping crabs run for longer than they needed to? A possible explanation is that they continued running because they failed to sense some cue indicating arrival at home. However, they eventually stopped, presumably despite not sensing this cue since they did not reach home. One could similarly argue that fiddler crabs have the flexibility to run the length of their home vector plus or minus a fudge-factor in the event that they reached home sooner or later than expected, to account for possible navigation errors. However, our slipping crabs ran for as little as 96% or as much as 400% of the correct running time (the mean was 172%), which is hardly a reasonable fudge-factor, and all of them stopped without having sensed their arrival at home.

We believe the best explanations for our estimation error are as follows. Either slipping crabs have feedback about their slippage but still, for some reason, stop short of home; or slipping steps provide less input to their putative proprioceptive measurement mechanism, thus requiring more

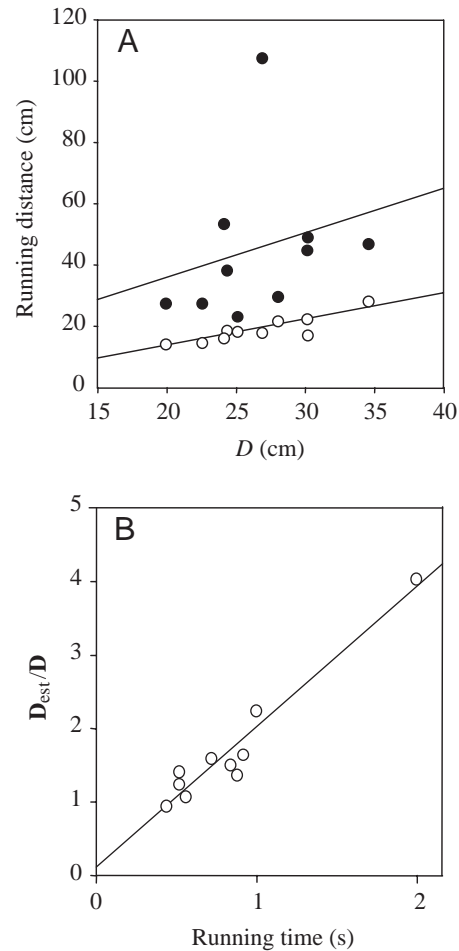


Fig. 10. Estimation of length of home vector from time spent running by slipping crabs. (A) Observed running distance D_{obs} (open circles) and estimate of home vector length \mathbf{D}_{est} (filled circles) plotted against starting distance D , which is assumed to be equal to true home vector length. (B) Relative error in estimate of home vector length ($\mathbf{D}_{\text{est}}/\mathbf{D}$) plotted against observed running time. Lines of best fit, calculated by the method of least squares. See text for details.

steps to cancel the neural correlate of the home vector. Support for both of these possible explanations comes from work on other crustaceans. Crayfish walking over a slippery patch showed altered motor output patterns during steps when the legs slipped, a clear indication that slips are detected by proprioceptors and lead to compensatory reflexes (Barnes, 1977). Equally, force-sensitive mechanoreceptors such as the cuticular stress detectors and funnel canal organs measure ground reaction forces generated during stepping, forces that would undoubtedly be lower during steps when the leg slipped (Klärner and Barnes, 1986; Libersat et al., 1987). Clearly, more data are needed to understand this result, but a mechanism involving force-sensitive mechanoreceptors is particularly attractive because it could provide a good measure of 'effort over time'. Certainly, the use of visual and/or vestibular information seems to be the sensory mechanism that is least consistent with these results.

Discussion

The home vector

Fiddler crabs were rotated through various angles relative to their natural environment under sunny skies. Although they had a very strong tendency to oppose rotation, compensation was usually not perfect. Their subsequent homing directions indicated that the angular error of the crabs' home run was approximately equal to their compensation error, i.e. the amount of imposed rotation they had previously failed to compensate. In addition, their homing directions reflected the passive translational displacement resulting from disk rotation. Paths reconstructed under the assumption that all directional information is gained idiotically and that compensatory activity is omitted are by far the most accurate in terms of homing. These results suggest that *U. rapax* have no absolute information about their orientation in space, and do not measure or store their own direction relative to a fixed external cue. While they have reflexes based on vestibular, leg proprioceptor, and visual information for keeping their orientation constant, all such compensatory movements are ignored by the path integrator.

The source of spatial information

Crabs have many sources of sensory spatial information at their disposal, which could potentially contribute to homing. Fiddler crabs have good vision, for motion (Nalbach and Nalbach, 1987; Nalbach, 1989), object discrimination (Langdon and Herrnkind, 1985) and the pattern of polarized skylight (Herrnkind, 1983). Also, crabs have the most sophisticated vestibular apparatus among arthropods, a statocyst organ capable of providing both rotational and linear acceleration information (Sandeman, 1975, 1983). Finally, they have leg proprioceptors that mediate both eye movements and leg reflexes, and aid in limb coordination (Varju and Sandeman, 1982; Clarac and Barnes, 1985; Paul et al., 1998).

However, the disk experiments described here argue against gaining direction information visually, and distance information gained through visual integration of optic flow is discounted by the slippery patch experiment. Thus, except by helping to maintain the desired body orientation, vision has very little to do with homing in *U. rapax*, except during search behavior when the home is not immediately found. Vestibular, magnetic and chemical signals are excluded by these same experiments.

For potential sensory information, we are left with leg proprioceptors. This possibility raises the question of how crabs standardize the measure of distance for different locomotory patterns they may use at different velocities. In ghost crabs *Ocypode quadrata*, whose accurate homing during daylight hours seems to be based on visual landmark memory (Hughes, 1966; Linsenmair, 1967), step frequency increases with velocity during running at speeds of up to about 1 m s^{-1} . However, at the highest running speeds, step frequency is unrelated to velocity, which is modified by altering step length (Blickhan and Full, 1987). Also, fast-running ghost crabs have an aerial phase during which there is no contact with the ground, and use

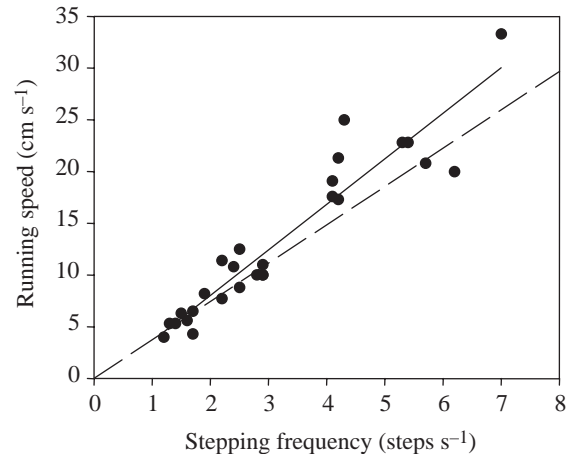


Fig. 11. Relationship of frequency of stepping to overall running velocity in fiddler crabs. Data for *Uca pugnax* reanalyzed from Barnes (1975). Because of the limitations imposed by the 64 frames s^{-1} filming rate, sequences of running with velocities above 35 cm s^{-1} were not analyzed in the original report. The continuous line is the line of best fit for the data calculated by the method of least squares, while the broken line is a theoretical line which assumes that increases in velocity are produced entirely by increases in stepping frequency. The fact that the actual line is steeper than this indicates a small additional role for increases in step length (ca. 12% of total). Values ($N=27$) are means for sequences of locomotion varying in duration from 0.4 to 14 s.

fewer legs – only the second and third walking legs on the trailing side of the body – at highest velocities (Burrows and Hoyle, 1973). Fiddler crabs *Uca pugnax* have not been observed to exhibit any aerial phase and use all legs when running (Barnes, 1975), but Barnes's filming speed of 64 frames s^{-1} did not permit a quantitative analysis of the highest running speeds. Further analysis of these data shows that, for velocities of up to 35 cm s^{-1} (the highest speeds analyzed), increases in speed are largely achieved by increasing stepping frequency. Increases in step length contribute only about 12% to the total increase in velocity (Fig. 11).

Voluntary versus intended locomotion

We prefer the term 'idiotetic' rather than 'kinesthetic' to describe the type of spatial information integrated by fiddler crabs, because it is still unclear whether or not crabs specifically use proprioceptive information, which narrowly defines a kinesthetic mechanism. Alternatively or additionally, they may use some other sort of internal information (e.g. central command information, i.e. efference copy) which, along with proprioception, falls into the broader definition of an idiotetic mechanism (Mittelstaedt and Mittelstaedt, 1973). It is difficult to see how an efference copy mechanism could lead the crabs in the slippery patch experiment to run for an unnecessarily (compared to normal conditions) long time. And in its simplest form (number of steps), it would produce greater errors than are observed, because of the contribution of step length to changes in velocity.

To distinguish between the efference copy and proprioception alternatives, it is probably necessary to ablate the sense organs putatively involved. This was done in spiders by Seyfarth et al. (1982), who showed that idiothetic memory depends at least partially on information from lyriform organs in the femora. The proprioceptors in the legs of crabs, however, have not been studied in the context of path integration. Since our results indicate that locomotion associated with the rotational compensatory response is not integrated, nor are passive rotations or translations, then there are two possibilities for what is fed into fiddler crabs' path integrator. Either (1) proprioceptive and/or vestibular information gated by central commands for 'voluntary' (i.e. not reflexive) locomotion, or (2) the central commands themselves. We are mildly in favor of central commands (efference copy) as the source of information, because the clear selectivity in which type of locomotion crabs integrate makes the central command theory slightly simpler. Fig. 12 depicts this mechanism (simpler in the sense of a circuit because it lacks a gate or switch), added to the well-known optomotor circuit (see e.g. Horridge, 1966), with disk rotation as its input. When the disk rotates, angular velocity information is sensed (e.g. visually or vestibularly), and stimulates the motor system *via* a route that bypasses the path integrator. When the crab walks voluntarily, the efferent commands for this are copied to the path integrator, which updates the continuously computed home vector for immediate retrieval.

It makes sense for a path integrator to integrate sensory feedback arising from 'voluntary/intended' efforts, and to ignore that from 'involuntary/unintended' efforts. Our reasoning comes from the fundamental purpose of compensatory reflexes such as the optomotor response (for a delightful discussion of the application/relevance of the term 'reflex', see Prochazka et al., 2000). It is widely accepted that this response functions to maintain (though not acquire) a desired body orientation in the face of external disturbances, or a biased or imprecise motor system. If the response is robust, then for a foraging crab it will result in the crab taking the desired path. If for some reason its action is required to produce the desired path, it follows that the activity of this system does not constitute a true record of the path actually taken. Indeed,

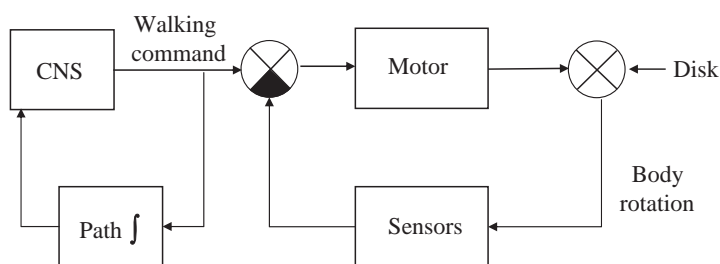


Fig. 12. Proposed system for selective integration of voluntary locomotion (in the form of commands from the CNS), and for avoiding integration of involuntary locomotion (originating from the optomotor response). This is a simplified version of this system. In reality, the efference copy would require a gain that matched that of the optomotor portion of the circuit.

if integrated it would give an incorrect home vector, as shown by the orange and green model paths in this study. To make an analogy, integrating this information would be similar to a flying bee deriving the direction and distance of its path by measuring flying effort and direction. If there was a cross wind, and the bee adjusted its flight to compensate, the relationship between the bee's effort and its real path would break down. Although the desired path was maintained, the bee would have integrated the desired path plus the wind. There are two ways to get around this problem. Either use an external cue such as optic flow, landmarks and sky light (as bees do), or else 'know' what portion of your motor output is compensatory, and ignore that while integrating the rest, which is the strategy that crabs seem to have adopted.

A point that needs to be reconciled with the results of Zeil (1998) concerns the control of turning by crabs, and the subsequent conclusions regarding the use of exocentric compass information. Zeil, studying *U. lactea annulipes* and *U. vomeris*, found a relatively high cross-correlation coefficient between crab egocentric angular velocity and body orientation, and noted that crabs fully compensated for imposed rotation. The clear conclusion was that their turning velocity on the disk must be driven by an orientation error, and not by disk angular velocity, i.e. they employed a position servo rather than a velocity servo. In order for this to occur, crabs must have absolute orientation (i.e. position) information, and could therefore be concluded to have access to an external compass, such as sky cues or distant landmarks.

In the 15 trials that comprised our study of *U. rapax*, egocentric angular velocity was reasonably well correlated with orientation error, although several trials resulted in a large lead of body rotation relative to orientation. The best correlation we found was between crab egocentric angular velocity and disk angular velocity. This correlation is reflected in the similarity of their time courses in Figs 3C, 4C and 5C. This implies that disk rotation, not orientation error, drives *U. rapax*'s turning efforts. It is difficult to separate orientation error and disk rotation as driving stimuli, because they are highly interrelated. When a crab counter-rotates on a disk, it may be responding to the rotation – with a time lag – or to the accumulating orientation error. Even when the time course of crab angular velocity more strongly resembles that of the orientation error, this may be because of a discontinuous and/or variable compensatory response (driven by rotation). One of us (Layne, 1998) has observed a highly temporally variable body rotation by *U. pugilator* in response to rotation of a visual surround. This response was often much smaller than the stimulus (i.e. it under-compensated for the rotation), meaning the crabs' responses were not driven by their orientation relative to external coordinates.

This conclusion – that the crabs compensate for imposed rotation (and perhaps also differences between intended and actual movements) by means of their velocity-driven optomotor response – is of interest in terms of the uses that crabs make of optic flow

information. There is a wealth of data from insects showing how optic flow is used in a variety of tasks including estimating distance traveled (Esch et al., 2001), controlling flying speed (Srinivasan et al., 1999), initiating landing responses (Srinivasan et al., 1996) and gaining a three-dimensional view of the world (Lehrer, 1996), but equivalent evidence for crustaceans is lacking. Yet free-walking crabs use eye movements to separate the rotational and translational components of optic flow, a necessary step in making its information content more available (Barnes, 1990; Paul et al., 1998). There are also visual interneurons within the crab optic tract specifically tuned to components of optic flow (Barnes et al., 2002). The evidence provided by this study that the rotational component of optic flow is involved in the maintenance of a straight course despite external influences is thus especially welcome.

One resolution of the disparity between our results and Zeil's might be that the apparent differences between species in the measurement of direction are real, rather than due to methodological differences. This leads to the intriguing possibility that there are navigational differences between species that are related to social behavior and burrow usage (see Zeil and Layne, 2002). Zeil (1998) reports that *U. lactea annulipes* males may 'keep' several of the females in their local vicinity, repeatedly visiting their various burrows. It has not yet been documented whether males visit more than one female burrow without returning home, but when scared they do escape to their own burrow even when they are very near that of one of their harem. Keeping several burrows active in this way, and remembering which one is home, is clearly a more formidable memory and navigation task than keeping track only of one's own burrow, and *U. rapax* and *U. pugilator* have not been observed to do it. Perhaps additional cues are used by species that have adopted a social behavior that makes the task of path integration more difficult. There is also the possibility that different cues are used for different tasks. The sand fiddler crab *U. pugilator* bases its large-scale movements (up or down the beach) at least partially on time-compensated menotaxis to the sun or polarized sky light (Herrnkind, 1968, 1972), but when reoriented on a disk during near-burrow foraging, they act very much like the *U. rapax* in the present study (J. E. Layne, unpublished observations). Comparative studies within fiddler crabs may provide insights into the co-adaptation of fiddler crab navigational mechanisms and the behavioral requirements of their owners.

In conclusion, although the path reconstruction method simulated the crabs' path integrator well enough to produce a mean vector of length 0.97 or 0.94 (Fig. 6E,H) with an average homing error of $<2^\circ$, the variation (s.d. $\leq 10.8^\circ$) of these models shows that they do not duplicate crabs' natural accuracy. We believe that our inability to match this accuracy is due to the likelihood that some fraction of the rotations and translations the crab performs during disk rotation are integrated (very small in the case of rotations), while some are not, and it is impossible for us to distinguish the two. The differential integration of sensory or central information by the path

integrator is probably related to the 'voluntary/intended' versus 'involuntary/error' nature of the locomotion in question. This question of the source of our computational inaccuracy is a minor caveat, however, to the major argument that *U. rapax* do not use an external source of compass information; they integrate idiothetic information, to form an egocentric home vector, but they are selective in which idiothetic information they integrate, and rightfully so.

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