University of Cincinnati

Date: 11/13/2013

I, Luke Hong, hereby submit this original work as part of the requirements for the degree of Master of Science in Biological Sciences.

It is entitled:
Spatial navigation in fiddler crabs: Goal oriented path integration of Uca pugilator

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Spatial navigation in fiddler crabs:
Goal oriented path integration of *Uca pugilator*

A thesis submitted to the
Graduate School
of the University of Cincinnati
in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

in the Department of Biological Sciences of the College of Arts and Sciences

2013
by
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B.S. University of Cincinnati, 2010

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Abstract

The sand fiddler crab (Bosc 1802) *Uca pugilator*, returns to its burrow using spatial memory of its location created by path integration, a navigational strategy in which an animal measures and sums all locomotion in order to generate a vector leading from the current position to the starting point. It does this without using any directional information external to the body. However, when *U. pugilator* emerges from its burrow, it forages the surrounding substrate in a non-random fashion, and even does so in complete darkness. This means that, when the crabs emerge from the burrow, at some level they appear to ‘know’ the directions of previous excursions, and direct subsequent excursions with reference to these. Such a reference can only be obtained using stable and external directional cues. In order to find out what sensory cues *U. pugilator* uses to establish the required reference direction, I manipulated sensory cues from the burrow structure, from the surrounding substrate, and the ambient magnetic field, in a light-free environment while the crab was inside its burrow, and observed successive foraging excursions. Rotation of the burrow structure alone changes the crab’s excursion subsequent to that rotation, while rotation of the substrate surrounding the burrow, and rotation of the magnetic field produced no significant effect. This result supports the idea that *U. pugilator* measures and integrates movement information, i.e., that it continues path integration, even inside its burrow.

Path integration without external cues is more likely to accumulate navigation error than path integration with external cues, since any errors cannot be corrected by an external standard, and so errors are added to an existing vector that contains errors. Errors associated with path integration can be divided into two types: random errors,
which are generated by random noise in the measurement or neural calculation, and systematic errors, which are thought to be caused by faulty integration (summing) process. To determine whether *U. pugilator* commits one or both of these errors, I recorded foraging excursions of crabs in a light-free environment and observed any homing errors. One aspect of the paths, angular range, was significantly greater in excursions which missed the burrow than in those which did not. I also found significant correlations between the magnitude of homing error and all variables tested, with angular range having the highest predictive value.

In this paper, I present a complex and unique navigation system employed by *U. pugilator* and problems the animals face when they explore the environment; returning to a previously visited area and avoiding excessive accumulation of homing error. The results of studies presented here show unique and interesting solutions to the problems faced by navigation system without the use of stable external sensory information.
Acknowledgements

I would like to thank Dr. John Layne, who has been instrumental in my graduate study. I would also like to acknowledge Dr. George Uetz and Dr. Ed Griff for their helpful contributions. Thank you Parth Patel for assisting with data collection. I would also like to thank Dr. Dan Rittschof for collecting fiddler crabs in Beaufort, NC for this research.
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Chapter 1

Spatial navigation in fiddler crabs: Gaining absolute direction reference for goals away from home

Summary

The sand fiddler crab, *Uca pugilator* (Bosc 1802) emerges from its burrow when the tide falls and forages the surrounding substrate in a non-random fashion, even in complete darkness. This means that, when the crabs emerge from the burrow, the excursions are directed with reference to some knowledge of previous excursion directions. Such a reference can only be obtained using stable external cues. In order to find out what sensory cues *U. pugilator* uses to establish the required reference direction, we manipulated sensory cues which can be derived from the burrow structure, from the surrounding substrate, and magnetic field in a light-free environment while the crab was inside its burrow then observed successive foraging excursions. We found that the rotation of burrow structure changed the crab’s excursion subsequent to that rotation while the rotation of substrate surrounding the burrow, and rotation of the magnetic field produced no significant effect. These results suggest that *U. pugilator* continues path integration even inside its burrow.

Introduction

Accurate spatial navigation is essential for motile animals to reach specific locations suitable for foraging, reproduction, or shelter (Schöne, 1984; Papi, 1992). One of the more common navigational strategies is path integration, a navigational process
by which all locomotion is measured and vectorially summed to generate a single, memory-stored vector leading from the current position to the starting point (Mittelstaedt & Mittelstaedt, 1973). Path integration is a navigational strategy found in wide variety of animals including insects (von Frisch, 1967; Wehner & Wehner, 1986; Beugnon & Campan, 1989), arachnids (Mittelstaedt, 1985; Moller and Görner, 1994), crustaceans (Altevogt & von Hagen, 1964; Hoffman, 1984; Zeil, 1998), birds (von Saint Paul, 1982; Wiltschko & Wiltschko, 1982), mammals (Mittelstaedt & Mittelstaedt, 1980, 1982; reviewed in Etienne & Jeffery, 2004), and humans (Loomis et al., 1993).

The sensory cues used to measure movement of an animal for path integration are of two categories: idiothetic cues, which are produced by movement of the animal itself, and allothetic cues, which are external and independent of the animal, like a compass (Mittelstaedt & Mittelstaedt, 1973). Idiothetic cues, because they are derived from proprioception, vestibular acceleration, visual motion or internal motor commands, only provide rotational and translational information. On the other hand, allothetic cues are stable, external entities such as landmarks, celestial light patterns, gravity and magnetic fields, and thus provide constant and reliable reference direction. The difference between these is essential: using idiothetic cues is much more likely to result in less accurate navigation, because animals do not have any way of recalibrating their accumulated navigational error (Vickerstaff & Cheung, 2010).

_Uca pugilator_ (Bosc, 1802) inhabits intertidal mud/sand shores of North American Atlantic and Gulf Coast estuaries (Crane 1975). The crabs use burrows for shelter, predator avoidance, rehydration, and breeding (Christy, 1982; Zeil & Layne, 2002). Previous studies suggested that _U. pugilator_ returns to its burrow by purely idiothetic
path integration (Land & Layne, 1995; Walls & Layne, 2009). However, other *Uca* species routinely perform navigational feats seemingly impossible without allothetic cues. Namely, male *Uca vomeris* repeatedly visit neighboring females’ burrows, demonstrating a stable frame of reference in which they memorized the females’ burrow locations and recall them upon emerging from their own burrows (Zeil & Hemmi, 2006). During our preliminary study, even *U. pugilator*, which uses only idiothetic cues for homing by path integration and does not obviously revisit locations other than home, appeared to have a sort of allothetic compass, as indicated by the small angle (usually less than 20°) between sequential excursion directions. To do this they must know the direction of the previous excursion when they emerge from the burrow. The aim of this study is to identify the allothetic sensory cue(s), if any, *U. pugilator* uses to obtain absolute reference direction for foraging excursions.

To test potential sensory cues *U. pugilator* may use to find absolute reference direction, we independently rotated potential directional cues by 90° relative to each other between foraging excursions, while the crab was underground. If *U. pugilator* relies on the sensory cue being tested, we expected to find the subsequent excursions to be shifted by 90° from control excursions. If *U. pugilator* does not rely on the sensory cues under rotation, we expected to find no difference in excursion directions between the treatment groups. We manipulated three sources of directional information: The burrow, the substrate surrounding the burrow, and the magnetic field. Use of the geomagnetic field as a source of directional information has been demonstrated in many animals, including fruit flies (Gegear *et al.*, 2008), lobsters (Lohmann *et al.*, 1995), homing pigeons (Walcott, 1996), and mole rats (Marhold *et al.*, 1997). Despite nearly
half a century of study, magnetoreceptors in animals have yet to be physically identified, most likely due to the unique property of magnetic field which allows the magnetoreceptor to be miniscule in size - possibly even at the sub-cellular scale - and located anywhere in the body (Johnsen & Lohmann, 2008). Partially because of the lack of identified sensory organ, the physical bases of magnetoreception are still highly debated topic (for review of proposed mechanisms, see Johnsen & Lohmann, 2008). Another crustacean species, Atlantic spiny lobster *Panulirus argus*, distinguishes between magnetic north and south (Lohmann *et al.*, 1995), suggesting a possibility for *U. pugilator* to display a similar ability.
Materials and Methods

*Uca pugilator* were collected in Beaufort, North Carolina and were kept in the laboratory at the University of Cincinnati, Cincinnati, Ohio. Animals were housed in a 1.2 m diameter arena filled with substrate collected from the capture site, and were kept under a 12/12 hour light/dark cycle. A water pump on a six hour on-off cycle moved artificial sea water prepared with 19-29 ppt Instant Ocean to imitate a twice daily circadian tidal rhythm. High tide was scheduled 3 hours after light/dark cycle change.

**Experimental arena**

The experimental arena had dimensions of 22 x 25 x 4 inches (Fig. 1). A sand filled cylinder, 11 cm in diameter, in which the crab could dig its burrow, was embedded in the middle of the arena. The arena had an elevated false floor, level with the top of the cylinder. The arena floor was covered with ~0.5 cm of sand, which provided a foraging surface. The arena floor also prevented the crab from burrowing anywhere except in a small (3 cm diameter) hole at the center of the floor that corresponded to the center of the sand-filled cylinder. This allowed the cylinder containing the burrow to be rotated independently of any potential cues on the foraging surface around the burrow entrance (tactile, chemical), as well as any room- or earth-based cues. It also allowed the foraging surface, with its potential cues, to be rotated without rotating the burrow.

To manipulate magnetic polarity, we built a 1 meter cubical coil of 14 gauge copper wiring wound in a 2-axis double-wrapped coil arrangement (Kirschvink 1992). The winds were distanced 0cm, 37cm, 63cm, and 100cm from one end of a cube for each axis with 26, 11, 11, and 26 respective windings. The experimental arena was
placed inside the wooden cube so that the burrow entrance was at the 3D center of the coil system.

The animals were recorded from above in a light free environment with a HD camcorder under IR light from the camcorder. Each experimental animal was placed in the arena (see below) for 24 hours before trials to allow digging of the burrow and acclimation. Flaked fish food and water were added for food and moisture as needed.
**Fig. 1.** 3D rendering of the experimental arena. (A) Small hole in the foraging surface. (B) Cylinder containing the burrow. (C) False floor/foraging surface covered with sand. (D) A model fiddler crab.
Experimental procedure

There were a total of five treatments in this experiment, including a control treatment in which no sensory cues were manipulated. We only used the animal's foraging excursion when the animal left the burrow for more than one body length. Burrow tidying excursions (i.e. when the animal removed a ball of mud from the burrow and left it on the substrate) were not included, as animals would not have any incentive to return to previously visited area during such excursions (more in discussion). Time intervals between the excursions were not taken into account, but the crabs usually re-emerged from the burrow within couple minutes after manipulation.

In the burrow rotation treatment, we observed the initial excursion, and after each time the crab re-entered its burrow, the cylinder/burrow was rotated 90°, thereby manipulating any sensory cues derived from burrow structure relative to all other cues. We then observed the direction of the next excursion after manipulation.

In the burrow sham rotation treatment, the cylinder/burrow was rotated 360° to control for the effect of the rotation process such as vibration, and rotational acceleration from the burrow rotation treatment. After this cylinder/burrow rotation, any sensory cues derived from the burrow were aligned the same way as before, but the animal would have experienced any disturbances associated with the rotation process.

Foraging surface rotation treatment was the same as the burrow rotation treatment, except that we rotated the false floor 90° between excursions, to manipulate any sensory cues on the substrate surrounding the burrow.

For the magnetic field rotation treatment, we rotated magnetic polarity using the coil system described above. We first positioned the magnetic coil system so that each
axis would be 45° from ambient magnetic field polarity. As a control, at the start of the experiment, we set the electric current to be anti-parallel in each coil axis, which produced no artificial magnetic field (rest position), but did produce current, heat and vibration to match the experimental treatment. To manipulate magnetic polarity, we reversed the electric current on one of the coils so that the magnetic field strength would be equal and opposite of the other side, resulting in a 90° rotation of magnetic polarity (Fig. 2.). Electric current used in the coil system at rest was so that each axis would result in equal and opposite magnetic field strength when reversed. The ambient magnetic field had magnitudes of 17.42 μT for horizontal component and -41.30 μT for vertical component at the center of the coil.
Fig. 2. Illustrations to explain magnetic field rotation treatment. The angular change of magnetic field polarity between before (grey dashed and solid arrow) and after (black dashed and solid arrow) each configuration change was 90°. (A) Initially ambient field polarity is 45° from either coil axis. (B) To rotate the magnetic field 90 degree, we switched the electric current on y-axis coil from antiparallel to parallel, generating artificial magnetic field (grey dotted arrow) which was twice the magnitude and opposite the direction of y-component of ambient field. (C) To rotate the magnetic field 90 degree again from configuration B, we switched the electric current on x-axis coil, similar to what was done on y-axis coil in B. (D) To rotate yet another 90 degree from configuration C, we switched the electric current of y-axis coil to parallel, causing the
magnetic field on y-axis to return to ambient value. Switching the electric current from parallel to antiparallel on x-axis after configuration D, of course, returned the coils to configuration A while rotating the magnetic field 90 degree from configuration D.
**Data analysis**

Video was analyzed using custom script (MATLAB 7.5 R2007b, The Mathworks, Natick, MA, USA). We recorded the direction of the foraging excursions away from the burrow and calculated the angular difference between sequential excursions ($\Delta \theta_{\text{excursion}}$) by subtracting the homing direction of one excursion to the exit direction of the subsequent excursion. We defined excursions as when the crab moved farther than one transverse body length (~2 cm) from the burrow. Both homing and exit directions were found by using the location of the animal at one body length away from its burrow (Fig. 3).
Fig. 3. Example illustrating the angular difference between sequential excursions ($\Delta \theta_{\text{excursion}}$) away from its burrow (black filled circle). The unfilled circle has the radius of one body length of a crab, 2 cm, with the burrow as the center. The line from the burrow to the point marked with number 1 is the starting leg of the first excursion which is carried out following the direction denoted by black arrows. The crab completes the first excursion and returns to its burrow. The outward-bound portion of the second excursion is from the burrow to the point marked with number 2. $\Delta \theta_{\text{excursion}}$ is the angle along the unfilled circle on bolded portion, between inward-bound portion of the first excursion and outbound portion of the second excursion.
Statistical analysis

Statistical analyses were performed with MATLAB 7.5 R2007b using the Circular Statistics Toolbox by Philipp Berens. The Rayleigh test was performed to determine whether excursions were random or not. If sequential excursion direction were random, we would expect uniform distribution of $\Delta \theta_{\text{excursion}}$ values. The Watson-Williams test was used to determine whether $\Delta \theta_{\text{excursion}}$ values differ between treatments.

Results

We did not find any individual effect on $\Delta \theta_{\text{excursion}}$ in any of the treatments (Kruskal-Wallis Test, Control: $X^2_{4,20}=3.46$, $P=0.48$; Burrow Rotation: $X^2_{9,24}=12.41$, $P=0.19$; Sham Burrow Rotation: $X^2_{8,10}=10.05$, $P=0.26$; Magnetic Field Rotation: $X^2_{3,29}=1.48$, $P=0.69$; False Floor Rotation: $X^2_{8,23}=8.40$, $P=0.40$). Four magnetic coil configuration also did not have any significant effect (Kruskal-Wallis Test, $X^2_{3,29}=1.02$, $P=0.80$).

Frequency distributions of $\Delta \theta_{\text{excursion}}$ and mean $\Delta \theta_{\text{excursion}}$ for each treatment group is shown in Figure 4. We found non-uniform distributions for all experiments according to the Rayleigh test for circular uniformity (Table 1). It should be noted that our sham burrow rotation treatment was borderline significant for Rayleigh uniformity test ($z_{18}=3.01$, $P=0.047$).

The angles between sequential foraging excursions ($\Delta \theta_{\text{excursion}}$) were generally small without any manipulation, with an angular mean of 2.11° and 95% confidence interval (CI) of $\bar{\alpha} \pm 14.25^\circ$ (N=205; Fig. 4A).
The burrow rotation treatment had an angular mean of 41.89˚ which was significantly different from both 0˚ and 90˚ (95% CI = 79.88˚, 3.90˚, N=34; Fig. 4B). There was a significant difference between the burrow rotation treatment and both the control and sham control (burrow rotation vs. control: F$_{1,238}$=6.03, P=0.015; burrow rotation vs. sham burrow rotation: F$_{1,52}$=5.47, P=0.023). The sham burrow rotation treatment (\(\bar{\theta}=-16.59˚\), 95% CI = 35.34˚, -68.51˚, N=19) was not significantly different from the control (F$_{1,223}$=0.85, P=0.36).

We did not find any significant difference between the control and the foraging surface rotation (\(\bar{\theta}=13.86˚\), 95% CI = 45.73˚, -18.01˚, N=34; F$_{1,237}$=0.61, P=0.44) or between the control and the magnetic field rotation (\(\bar{\theta}=-8.50˚\), 95% CI = 12.94˚, -29.93˚, N=33; F$_{1,236}$=0.75, P=0.39). Details of all Watson-Williams Test results are shown in Table 2.

There was no significant difference in variance between treatments overall (Kruskal-Wallis Test, $X^2_{4,320}=6.80$, P=0.15).
Table 1. Rayleigh test of circular uniformity for data gathered. *P*<0.05 signifies non-uniform distribution.

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>Z</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>&lt;&lt;0.001</td>
<td>29.53</td>
<td>204</td>
</tr>
<tr>
<td>Bburrow rotation</td>
<td>0.007</td>
<td>4.85</td>
<td>33</td>
</tr>
<tr>
<td>Sham burrow rotation</td>
<td>0.047</td>
<td>3.01</td>
<td>18</td>
</tr>
<tr>
<td>Foraging surface rotation</td>
<td>0.001</td>
<td>6.42</td>
<td>33</td>
</tr>
<tr>
<td>Magnetic field rotation</td>
<td>&lt;&lt;0.001</td>
<td>12.38</td>
<td>32</td>
</tr>
</tbody>
</table>
**Table 2.** Analysis of variance table for the Watson-Williams Test. (A) Control vs. burrow rotation, (B) Control vs. sham burrow rotation, (C) burrow rotation vs. sham burrow rotation, (D) Control vs. foraging surface rotation, and (E) Control vs. magnetic field rotation.

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A)</td>
<td>Between groups</td>
<td>1</td>
<td>2.59</td>
<td>2.59</td>
<td>6.03</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>237</td>
<td>148.35</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>238</td>
<td>150.94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B)</td>
<td>Between groups</td>
<td>1</td>
<td>0.36</td>
<td>0.36</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>222</td>
<td>138.63</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>223</td>
<td>139</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(C)</td>
<td>Between groups</td>
<td>1</td>
<td>2.41</td>
<td>2.41</td>
<td>5.47</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>51</td>
<td>32.61</td>
<td>0.64</td>
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<tr>
<td></td>
<td>Total</td>
<td>52</td>
<td>35.02</td>
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<tr>
<td>(D)</td>
<td>Between groups</td>
<td>1</td>
<td>0.26</td>
<td>0.26</td>
<td>0.610</td>
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<tr>
<td></td>
<td>Within groups</td>
<td>237</td>
<td>146.42</td>
<td>0.62</td>
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<tr>
<td></td>
<td>Total</td>
<td>238</td>
<td>146.68</td>
<td></td>
<td></td>
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<tr>
<td>(E)</td>
<td>Between groups</td>
<td>1</td>
<td>0.31</td>
<td>0.31</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Within groups</td>
<td>236</td>
<td>138.81</td>
<td>0.59</td>
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<td></td>
<td>Total</td>
<td>237</td>
<td>139.13</td>
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Fig. 4. Frequency distribution of change of excursion direction ($\Delta \theta_{\text{excursion}}$) for (A) Control ($\bar{\alpha} = 2.11^\circ$, 95% CI [16.36°-12.15°], N=205), (B) burrow rotation ($\bar{\alpha} = 41.89^\circ$, 95% CI = 79.88°-3.90°, N=34), (C) sham burrow rotation ($\bar{\alpha} = -16.59^\circ$, 95% CI = 35.34°-68.51°, N=19), (D) foraging surface rotation ($\bar{\alpha} = 13.86^\circ$, 95% CI = 45.73°-18.01°, N=34), and (E) magnetic field rotation ($\bar{\alpha} = -21.42^\circ$, 95% CI = -0.30°-42.54°, N=33). The rings represent counts of frequency and bolded numbers outside the circle represent the angular difference. White (or black for foraging surface rotation) line is the mean angle.
Discussion

The result of our experiment shows that *U. pugilator* is capable of updating the directional component toward the previously visited location by sensing and integrating passive rotation imposed upon the animal while it is underground. As stated in the introduction, one of our main goals was to test whether crabs actually use absolute direction information. If *U. pugilator* merely conformed to the physical constraints imposed by the burrow without any real directional sensation, we would expect to see a change in excursion angle of 90˚ after the burrow rotation treatment. In our experiments, the 90˚ cylinder/burrow rotation was the only manipulation to produce a significant difference from control ($F_{1,238}=6.03$, $P=0.015$), but the mean was only 41.89°. There are two possible explanations for the 41.89° mean angle, both of which suggest that the animal is integrating passive rotation while it is inside the burrow.

The first explanation for the observed mean $\Delta \theta_{\text{excursion}}$ for 90˚ cylinder/burrow rotation is that the crab performed incomplete integration of the passive rotation. If the animal perceived, but only partially compensated for the passive rotation of the sand filled cylinder, we would expect a mean $\Delta \theta_{\text{excursion}}$ to be between 0˚ and 90˚. In our case the crabs apparently compensated for about half the imposed 90˚ rotation ($\bar{a} = 41.89^\circ$). This is much lower compensatory gain than measured in a previous experiment with *U. rapax*, where crabs were found to compensate for an average of 92% of passive rotation (Layne *et al.*, 2003). However, these experiments were performed above-ground in the daylight. Under this explanation, the mean $\Delta \theta_{\text{excursion}}$ of -16.59˚ after a 360˚ cylinder/burrow rotation is perplexing, since we would expect to see mean $\Delta \theta_{\text{excursion}}$ of around 180˚ if the animal compensated for about half of the 360˚ passive rotation, as
observed in 90° cylinder/burrow rotation. These seemingly contradicting results could indicate that the animal disregarded the 360° passive rotation due to excessive disturbance, i.e., its integration of angular acceleration failed.

The other, and perhaps more satisfying, explanation is that the crabs performed multisensory integration, combining information from more than one sensory modality in order to reduce error or find a compromise between conflicting cues, in this case for azimuthal direction (for review, see Cheng et al. 2007). The implementation of this process is modified here, since while the burrow certainly provides some sort of azimuthal information, this information cannot be of the familiar compass type; the only type of azimuthal information that can be derived from the burrow is the burrow’s plane of inclination relative to the ground’s surface. Furthermore, this plane provides an azimuthal reference only by means of a crab’s gravitational sense, i.e., if the crab senses that it is standing upright as it emerges from the inclined burrow, it will have the same azimuthal body orientation each time. In this way the burrow’s structure would physically constrain the crab’s direction of emergence, and its body orientation in azimuth would then be a predetermined default rather than discovered by sensory means. Even if the crab did not emerge the same way each time, it may measure its 3D angle relative to the gravity-defined default, and thus still use the burrow-surface plane by using only the gravitational sense as an unintuitive but impressively versatile azimuthal reference. If the crab then conferred computational weight upon its body azimuth and combined or integrated that with azimuth information from one other source, the expected mean $\Delta \theta_{\text{excursion}}$ after the 90° cylinder/burrow rotation would be between 0° and 90°. However, the other cues we tested which could provide a second
reference direction in a light free environment, such as tactile or chemical cues on the substrate and magnetic field polarity, showed no significant effect on excursion direction. If not one of these, what is the other source of directional information?

One possible source of directional information to compare with the 'default' body azimuth is one discussed above: idiothetic integration of passive rotation. Above, we proposed that the observed mean $\Delta \theta_{\text{excursion}}$ may be due solely to under-compensation for passive rotation, likely by under-integrating vestibular acceleration. However, if the crab were in fact able to measure almost all of the passive rotation, after 360° of passive rotation this cue would indicate the direction for the next excursion to be near 0°, which is what we observe. The same is true with respect to the 90° passive rotation – successful integration of passive body rotation would provide a ‘vestibular vector’ of 0°. On the other hand, the excursion azimuth indicated by burrow inclination/body orientation would be offset from the previous excursion by an angle equal to the passive rotation, in this case 90°. When these two directional cues are added or otherwise combined, the resulting direction would be between 0° and 90°, which agrees with the results from both the 90° and 360° rotations.

The idea that *U. pugilator* integrates passive rotation while inside its burrow is the opposite of what was found in a mouse navigation experiment in which the animal ignored passive rotation while inside its nest (Alyan, 1996). The possibility that the crab continues path integration inside its burrow is interesting since continuous path integration does not seem to have any clear evolutionary benefit. It is possible that initial azimuthal information derived from the burrow structure – ultimately from gravity – is
sometimes unreliable and idiothetically derived rotational information acts as an additional reference.

Path integration, the primary navigational strategy used by *U. pugilator*, requires the animal to sum all locomotion to form a single ‘home vector’ which points toward its nest. In order to revisit a goal away from its nest using path integration, an animal needs to be able to store the home vector value when at the goal, and during a subsequent excursion, recall and execute the stored vector (Collett & Collett, 2000). It is unclear, from this experiment, whether *U. pugilator* can store both direction and magnitude of the vector or just the directional component, although males of the Australian fiddler crab, *U. vomeris*, seem to store both, since they are able to remember the location of, and revisit, nearby female burrows (Zeil & Hemmi, 2006).

The angles between sequential foraging excursions (Δθ_{excursion}) for the control treatment were generally small (α=2.11°, N=205; Fig. 4A). As mentioned above, *U. pugilator* needs to return to its burrow for predator avoidance and rehydration (Zeil & Layne, 2002). Another reason for *U. pugilator*'s frequent return to its burrow may be an attempt to reduce navigational error. If, as is thought, *U. pugilator* navigates away from and back to its burrow using purely idiothetic path integration (Layne et al. 2003; Walls & Layne, 2009), they are subject to an accumulation of angular error (Cheung et al., 2008). *U. pugilator* may avoid accumulating too much error by returning to its burrow frequently to reset the home vector. Whatever the reason, the crab makes many foraging excursions during each low tide, and would benefit from knowing the directions of previous excursions. For instance, it may benefit from being able to return to the area it occupied prior to its last homing run. If that area was rich in nutrients, returning to
the spot and resuming foraging has obvious benefit. On the other hand, if the previously visited area did not have particularly nutrient-rich soil the crab would benefit from avoiding it, and performing the next excursion toward an area near, but not the same as, the previous one. This sampling strategy is similar to the feeding strategy of *Dotilla wichmanni* as described by Luschi *et al.*, in which the animals, when disturbed, quickly run into the burrow, and recommence foraging in same direction as before the homing run. This is thought to optimize feeding activity by avoiding area which has already been sampled (Luschi *et al.*, 1997).

The non-random excursion pattern recorded in a room devoid of light indicates that visual cues (celestial cues and visual landmarks) are not necessary for gaining absolute direction. This, by no means, means that *U. pugilator* in nature does not use visual cues to obtain absolute reference direction. Fiddler crabs use visual information for predator recognition (Layne, 1998), conspecific tracking (Land & Layne, 1995), courtship displays (Crane, 1975), and burrow defense (Hemmi & Zeil, 2003) and it will not be surprising for *U. pugilator* to rely on visual information to gain absolute direction reference to some degree. Previous attempts to demonstrate this, however, have been unsuccessful in North American fiddler crabs (Layne *et al.* 2003; but see Zeil, 1998 on Australian fiddler crabs).
References


Chapter 2

Spatial navigation in fiddler crabs: *Uca pugilator* makes predictable homing error.

Summary

The sand fiddler crab *Uca pugilator* (Bosc 1802) returns to its burrow after foraging excursions by measuring and summing all self-imposed movement to generate a vector from current position to its burrow. During the locomotion measurement, summing and execution, errors inevitably arise, and these can be divided into two types: random errors, which are generated by error in the measurement or calculation process, and systematic errors, which are thought to be caused by a faulty integration (summing) process. To determine whether *U. pugilator* commits one or both of these errors, we recorded foraging excursions of crabs in a light-free environment and observed any homing errors. We found that one aspect of the paths, angular range, was significantly greater in excursions which missed the burrow than in those which did not. We also found significant correlations between the magnitude of homing error and all variables tested, with angular range having the highest predictive value.

Introduction

Path integration is a navigational strategy by which an animal measures and sums all locomotion in order to know the direction and distance from the current position to the starting point (Mittelstaedt & Mittelstaedt, 1973). Path integration can be conceptualized by discretizing the path of an animal into units of arbitrarily small length. For each new step of the path, the step direction and length forms a small movement
vector. Each new vector is added to the last, and this process occurs continuously as the animal moves about. The addition of these small vectors produces a single vector stored in memory, which, when reversed, points from the current location to the starting point (the home vector). Path integration thus has three essential components: measurement, computation, and memory. When this process takes place in an animal, the measurements and the computations are done with imperfect sensory systems and imperfect neural circuits, respectively. Therefore, each new small vector has an associated error which accumulates in the recursive path integration process. The accumulation of error possibly leads to the loss of the goal and an increase in the costs and risks associated with this loss (see below).

Crabs have many sources of sensory spatial information at their disposal, which could potentially be used for the measurement of the small movement vectors. These sources fall into one of two categories. Idiothetic cues only provide information about the rotation and translation of the animal itself, while allothetic cues provide constant and reliable directional information (Mittelstaedt & Mittelstaedt, 1973). While path integrating with either type of sensory cue is inherently error-prone, navigation by idiothetic cues tends to accumulate more error, because measurement errors cannot be calibrated by an external standard, and therefore compound upon previous errors (Vickerstaff & Cheung, 2010).

It is somewhat surprising, therefore, that the sand fiddler crab, *Uca pugilator* (Bosc 1802), uses idiothetic path integration (Layne *et al.*, 2003b; Walls & Layne, 2009). Successfully returning to its burrow is crucial to *U. pugilator* because the burrow serves as a central point for feeding, courtship, mating, rehydration, and predator escape (Zeil &
Layne, 2002). A quick and accurate return to its burrow is especially important for predator escape because airborne predators can strike quickly, making even small errors, requiring even a second of delay in locating the burrow, potentially fatal. The importance of reaching the burrow and the error-prone navigation system used by *U. pugilator* provides an excellent opportunity for the study the nature of errors accumulated during path integration.

Two types of error may be incurred by the measurement and computational components of path integration: *Random errors* are generated by error in measurement or in the calculation process. They are characterized by the equal probability of over-estimation and underestimation, and occur even if the neural algorithm for summing vectors is mathematically correct. *Systematic errors*, on the other hand, are thought to be caused by a faulty integration process, i.e., the algorithm provides an estimate, rather than a mathematically correct account, of the location of home (Maurer & Sequinot, 1995; but see also Merkle *et al.*, 2005). Evidence of random error should be observed as a symmetrical scattering of homing errors, while the hallmark of systematic error is an asymmetrical bias in homing error that is quantitatively predictable from some aspect of the animal's excursion path.

Systematic error accumulation is widespread in many path integrating animals (Bees: Bisetzky, 1957; Spiders: Gorner, 1958; Ants: Müller & Wehner, 1988; Hamsters: Sequinot *et al.*, 1993; Human: Loomis *et al.*, 1993). Systematic errors show striking consistency across many species; following an L-shaped outward path many animals make an "inward" error, indicating that they may underestimate the angular turn in the outward path (Fig. 1; Etienne & Jeffery, 2004).
To examine the nature of navigational errors in fiddler crabs, we recorded the position of freely moving *U. pugilator* in a light-free environment and investigated effect of various path characteristics on homing error.
**Fig. 1.** Illustration of the characteristic "inward" systematic error. An animal makes an L-shaped outward journey from its starting point (S) toward its destination (D) following the thin line. The dotted line indicates the home vector without systematic error. Bolded line with arrow indicates the observed inward error.
Materials and Methods

Fiddler crabs (*Uca pugilator* Bosc, 1802) were collected in Beaufort, North Carolina, and housed in the laboratory at the University of Cincinnati, Cincinnati, Ohio in a 1.2 m diameter arena filled with mud and sand collected from the animals’ home site. Crabs were kept under 12/12 hour light/dark cycle, and a water pump on a six hour on-off cycle moving artificial sea water prepared with 19-29 ppt Instant Ocean to provide circa-tidal rhythm. High tide was scheduled 3 hours after light/dark cycle change.

**Experimental arena**

The experimental arena had dimensions of 22 x 25 x 4 inches. A cylinder with 11 cm diameter, in which the crab could dig its burrow, was embedded in the middle of the arena. The arena had a false floor covered with ~0.5 cm of sand, which provided a foraging surface, and also prevented the crab from burrowing anywhere except in a small (3 cm diameter) hole in the center of the floor that exactly corresponded to the center of the sand-filled column.

**Experimental procedure**

Crabs were left unmanipulated and were free to exit and enter the burrow at will. An excursion was considered acceptable for analysis when a crab moved farther than 4 cm from its burrow. The start of an acceptable excursion was considered to have begun when the crab was 2 cm, approximately one transverse body length, from home. A custom MATLAB (The Mathworks, Natick, MA, USA) script was used to automatically detect the crabs’ digital center of mass once every second (every 30\textsuperscript{th} frame).
We collected the following variables from foraging excursions for analysis: 1) total path length of each excursion, 2) total time the animal spent on excursion, 3) angular range of excursion; 4) the angular difference between departure and return directions, measured at 2 cm from the burrow, and 5) homing error, measured as the closest distance between burrow and the extended homing path (Fig. 2).

A crab was considered to have missed home if (5) above was greater than approximately one-half the rostro-caudal body length of the crabs tested, 8 mm. The rationale is that a crab whose center of mass missed its burrow by less than 8 mm may know that it is on course to detect the burrow with its anterior or posterior legs, and thus not be in error. For those excursions that missed the burrow, we recorded whether the crab made an inward or outward error.

Statistical Analysis

We used a Student's t-test to compare between excursions which missed the burrow and those that did not. On the excursions which missed the burrow, we used a $\chi^2$ test to determine whether the crabs are more likely to make inward or outward error. We also used regression analysis between the variables mentioned in Experimental Procedure and homing error. We excluded a single data point from analysis which was outside of the 95% confidence interval for all four measured variables.
**Fig. 2.** Illustration of an excursion and variables measured. The filled black circle is the burrow. Unfilled circles are circles with radii of 2 cm and 4 cm with the burrow as the center. Blue line with arrow is the path of the animal, with direction of travel indicated by small blue arrows. Path length and excursion time were only measured while the animal is outside of the 2 cm radius circle. The angular range is the angle between minimum and maximum angular value of an individual’s position during an excursion (the angle between dashed black lines). Departure-return difference is angle between start and end of the blue path measured at the 2 cm diameter, which is 35° in this figure. The excursion path immediately before reaching 2 cm radius circle was extended (red dashed line) and the closest distance between this and burrow was measured as homing error (HE, solid red line). Since the extended homing vector lies on the same side of the burrow as the start of the excursion, this is considered an ‘inward error’.
Results

We recorded a total of 256 excursions from 8 crabs (Fig. 3). The distribution of all variables measured had positive skew (Path Length: \( \bar{x} = 21.11 \) cm, median = 17.72 cm, S.D. = 15.50 cm; excursion time: \( \bar{x} = 353.50 \) s, median = 117.17 s, S.D. = 775.38 s; angular range: \( \bar{x} = 40.46^\circ \), median = 30.45\(^\circ\), S.D. = 33.76\(^\circ\); departure-return difference: \( \bar{x} = 25.62^\circ \), median = 16.22\(^\circ\), S.D. = 26.77\(^\circ\); homing error: \( \bar{x} = 0.48 \) cm, median = 0.37 cm, S.D. = 0.40 cm; Fig. 4).

Excursion time was significantly correlated with path length (\( F_{1,255} = 3.98, P = 0.047, R^2 = 0.015 \), Y-intercept = 20.23 s, slope = 0.0025), but not with other variables (excursion time vs. angular range: \( F_{1,255} = 1.43, P = 0.23, R^2 = 0.0056 \); excursion time vs. departure-return difference: \( F_{1,255} = 1.53, P = 0.22, R^2 = 0.006 \); excursion time vs. homing error: \( F_{1,255} = 2.18, P = 0.14, R^2 = 0.008 \)). Correlations among path length, angular range, and departure-return difference were all significant (path length vs. angular range: \( F_{1,255} = 356.16, P << 0.001, R^2 = 0.58 \), Y-intercept = 5.37\(^\circ\), slope = 1.66; path length vs. departure-return difference: \( F_{1,255} = 133.24, P << 0.001, R^2 = 0.34 \), Y-intercept = 4.27\(^\circ\), slope = 1.01; angular range vs. departure-return difference: \( F_{1,255} = 652.38, P << 0.001, R^2 = 0.72 \), Y-intercept = -1.58\(^\circ\), slope = 0.67).

Homing error was correlated with angular range, although the correlation explained only 4.4% of the variation (\( F_{1,255} = 11.83, P < 0.001, R^2 = 0.044 \), Y-intercept = 0.38 cm, slope = 0.0025). Path length (\( F_{1,255} = 2.70, P < 0.10, R^2 = 0.01 \)), excursion time (\( F_{1,255} = 2.18, P = 0.14, R^2 = 0.008 \)), and departure-return difference (\( F_{1,255} = 2.14, P = 0.14, R^2 = 0.008 \)) did not have significant correlation with homing error. The results of above regression analyses are summarized in Table 1. Multiple regression test using all
variables showed significant correlation with homing error, explaining 8.9% of the variation ($F_{4,253} = 6.12$, $P < 0.001$, $R^2 = 0.089$).

Excursions with some of the most extreme values were shown in Figure 5.
Fig. 3. Histogram of all variables measured. We observed positive skew in all variables recorded.
Fig. 4. Correlation plots between the variables measured. Following variables were significantly correlated: Excursion time vs. path length ($F_{1,255}=3.98$, $P=0.047$, $R^2=0.015$), path length vs. angular range ($F_{1,255}=356.16$, $P<<0.001$, $R^2=0.58$), path length vs. departure-return difference ($F_{1,255}=133.24$, $P<<0.001$, $R^2=0.34$), angular range vs. departure-return difference ($F_{1,255}=652.38$, $P<<0.001$, $R^2=0.72$), and angular range vs. homing error ($F_{1,255}=11.83$, $P<0.001$, $R^2=0.044$).
Table 1. Summary of regression analyses of measured variables all recorded excursions.

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<tr>
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<td></td>
<td>F</td>
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<td>R²</td>
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<td>Time</td>
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<td>Error</td>
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*A.R.=Angular Range, D-R=Departure-Return Difference, Error=Homing error.
DF=1,255.
Fig. 5. Example excursions illustrating some extremes among the measured variables. Green circle and red diamond are the start and the end of excursion, respectively (A) Most "common" excursion which did not have any value in top or bottom hundred of any four variables: path length, excursion time, angular range, departure-return difference, (B) excursion with one of the largest angular range and departure-return difference, (C) excursion with one of the longest excursion time, (D) excursion with one of the longest path length (E) excursion with one of the smallest homing error, and (F) excursion with one of the largest homing error.
46 out of 256 recorded excursions missed the burrow by more than 8 mm. Only angular range was significantly larger for the group of excursions which missed the burrow when compared to the group of excursions which did not (\(T_{255}=2.25, P=0.03\)). Path length (\(T_{255}=1.26, P=0.21\)), excursion time (\(T_{255}=0.39, P=0.69\)), and departure-return angular difference (\(T_{255}=1.03, P=0.30\)) did not have any significant difference between the group of excursions which missed the burrow and those that did not.

Among the excursions that missed the burrow, all variables measured – path length (\(F_{1,44}=5.27, P=0.03\), Y-intercept=0.93 cm, slope=0.0099), angular range (\(F_{1,44}=28.78, P<<0.001\), Y-intercept=0.79 cm, slope=0.0077), departure-return difference (\(F_{1,44}=11.98, P=0.001\), Y-intercept=0.97 cm, slope=0.0062), and excursion time (\(F_{1,44}=5.27, P=0.04\), Y-intercept=1.10 cm, slope=0.0001) – were significantly correlated with homing error (Table 2; Fig. 6). Angular range, with an R-square value of 0.40, explained the most homing errors, followed by departure-return difference (\(R^2=0.21\)), path length (\(R^2=0.11\)), then excursion time (\(R^2=0.09\)).

In a post-hoc partial correlation analysis with the excursions which missed the burrow, we found that only angular range had significant correlation with homing error when all other variables were controlled for (Path length: \(r=-0.0850, T_{41}=0.55, P=0.59\); Time: \(r=0.25, T_{41}=1.63, P=0.11\); Angular Range: \(r=0.45, T_{41}=3.25, P=0.002\); Departure-Return Difference: \(r=-0.1551, T_{41}=1.01, P=0.32\)). Multiple regression test using all variables for excursion which missed the burrow showed significant correlation with homing error with only slightly better \(R^2\) value than angular range alone (\(F_{4,42}=8.04, P<0.001, R^2=0.44\)).
All measured variables had a positive correlation with homing error. 35 out of 46 excursions had inward error, showing a significant bias in this direction ($\chi^2_1 = 11.26$, P<0.001).

There was a significant difference overall among the individuals tested (Single Factor ANOVA: $F_{7.249}=3.16$, P=0.003; Fig. 7). There was no significant difference among the individual for inward-outward error bias ($\chi^2_3=3.43$, P>0.5).
### Table 2. ANOVA table of regression analysis for (A) path length, (B) excursion time, (C) angular range, and (D) departure-return difference.

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Fig. 6. Plot and regression line of various dependence vs. homing error. (A) Path length vs. homing error ($R^2=0.11$), (B) excursion time vs. homing error ($R^2=0.09$), (C) angular range vs. homing error ($R^2=0.40$), and (D) departure-return difference vs. homing error ($R^2=0.21$).
Fig 7. Mean homing error for eight individuals analyzed. Error bars represents standard deviation for excursions from each individual (1: $\bar{x}=0.38$, S.D.=0.36, N=83; 2: $\bar{x}=0.64$, S.D.=0.44 , N=67; 3: $\bar{x}=0.06$, S.D.=0.24 , N=15; 4: $\bar{x}=0.51$, S.D.=0.28 , N=2; 5: $\bar{x}=0.44$, S.D.=0.42 , N=51; 6: $\bar{x}=0.51$, S.D.=0.46 , N=23; 7: $\bar{x}=0.69$, S.D.=0.31 , N=3; 8: $\bar{x}=0.26$, S.D.=0.15 , N=13). Standard error bar of individual marked with number 8 did not overlap with mean of individuals 2~7.
Discussion

Two types of error can be uncured during path integration, random and systematic. Error in measurement or synaptic noise in the calculation process causes random error, while an incorrect integration process (i.e., the vector summing algorithm) is thought to cause systematic error (Maurer & Sequinot 1995). No sensor or integration system is perfect, thus every real-life navigational system contains some degree of random error. Systematic error, on the other hand, may or may not be present in a navigational system and must be quantitatively predictable from some aspect of the animal’s excursion path prior to its homing run. From the results presented, we found evidence that homing error of *U. pugilator* is both quantitatively predictable and makes the characteristic "inward" errors as observed in other path integrating animals (Etienne & Jeffery, 2004).

While we found significant correlation with homing error for all variables among those which missed the burrow, but only angular range was significantly different between excursions which missed the burrow and those that did not. Angular range was also the only variable to have significant correlation with homing error when all 256 excursions were analyzed (i.e., including those with homing errors of less than 8 mm). We did find significant correlation with homing error for all variables among the excursions which missed the burrow, but some of these may be artifacts, i.e., they may not actually be causal to homing error but appear to do so because of their high correlation with angular range. For instance, excursions with larger angular range would more likely require longer path length, and also result in larger departure-return difference, and a longer path length would more likely need longer excursion time. Among the variables measured, angular range was the best predictor of homing error in
terms of the variation explained by regression analysis and was the only variable to have significant correlation after other variables were controlled for (r=0.45, T_{41}=3.25, P=0.002). Finally, we found that errors are significantly more likely to be inward rather than outward ($\chi^2_{1}=11.26$, $P<0.001$), which is consistent with systematic errors in other path integrating animals. Thus, *U. pugilator*'s homing paths show predictable inward homing error bias, or systematic error.

We did observe a significant difference in homing error among the individuals tested (Single Factor ANOVA: $F_{7,249}=3.16$, $P=0.003$; Fig. 7), however it may be expected that one individual may have more accurate homing than others, just as a person may be better at finding his/her way in a maze than others. There was no significant difference among the individual for inward-outward error bias ($\chi^2_{5}=3.43$, $P>0.5$).

Systematic and random error in foraging fiddler crabs has been previously examined. Fiddler crabs align their transverse body axis with their burrow direction during foraging, and so give a constant readout of where they believe their burrow to be (Land and Layne, 1995; Zeil 1998). In a 2003 study, Layne *et al.* measured *U. rapax*'s body axis during excursions with large angular range, and analyzed the relationship between their body-burrow orientation and time spent foraging, path length, and amount of body turns. They found no evidence of systematic error, at least as it might be detected in a bias in body-burrow orientation (Layne *et al.*, 2003a).

One factor that may have contributed to this lack of evidence for systematic error may be *U. rapax*'s foraging behavior. A large systematic homing error is detrimental to an individual's survival, and animals may minimize the effect of such error by their
measurement or computational strategy. For example, desert ants *Cataglyphis fortis* make about equal amounts of right and left turns, so that the systematic errors on either side eventually cancel out (Müller & Wehner, 1988). It was noted that *U. rapax* often make foraging excursions with a large angular range, generally much more frequently than in *U. pugilator*. Considering angular range was the best predictor for homing error in *U. pugilator*, it is possible that *U. rapax* has some sort of strategy to reduce systematic error caused by increasing angular range. Further examination of *U. rapax*'s homing error with a larger sample size may be helpful to understanding in this matter.

There have been many studies on systematic error in path integrating animals and the study presented here makes some notable additions to our knowledge of the nature and production of systematic error. First, most of the previous studies on systematic errors restricted the animal’s outward path (Bisetzky, 1957; Gorner, 1958; Müller & Wehner, 1988; Seguinot et al., 1993). As mentioned above, large systematic homing error affects an animal’s chances of survival and so should be minimized by natural selection (Benhamou & Poucet, 1996). This makes observation of systematic error in freely moving animals difficult. However, by recording a large number of excursions, we were able to collect a large enough sample size to detect the existence of systematic error in freely moving animals.

There is another factor which makes the study presented here unique, but the path integration model of Müller and Wehner must first be described. The only existing path integration model which incorporates and fits inward systematic error strikingly well is one created by Müller and Wehner to describe the behavior of the desert ant. The model recursively calculates the home vector in a simple, but faulty, arithmetic equation
(Müller & Wehner, 1988). The direction of the home vector in the model is calculated using the following equation:

\[ \phi_{n+1} = \phi_n + \frac{k(180^\circ + \delta)(180^\circ - \delta)\delta}{l_n} \]

where \( \phi_n \) and \( l_n \) is direction and magnitude of home vector after \( n^{th} \) step, respectively. \( \delta \) is direction of animal’s movement for \( n+1^{th} \) step in reference to the home vector (Fig. 8A). \( k \) is the fitted constant \((k=4.009 \times 10^{-5} \text{ deg}^{-2})\) and each step has arbitrary unit length of 1. The difference between equation above and mathematically correct \( \phi_{n+1} \) calculation (i.e. systematic error of the model due to \( \delta \)) has a maximum value around \( \delta=125^\circ \) (Fig. 8B). When \( \delta \) is positive, the \( \phi_{n+1} \) produced by the model is greater than those if the integration process is not faulty. This sort of faulty integration process could, in theory, explain the inward error seen in many animals.
Fig. 8. (A) Illustration to describe variables in systematic error model adapted from Müller & Wehner (1988). After the n\textsuperscript{th} step, the home vector has a direction of $\varphi_n$ and distance of $l_n$. For the n+1\textsuperscript{th} step, the animal deviates from home vector direction by an angle $\delta$ and, after n+1\textsuperscript{th} step, the home vector has direction of $\varphi_{n+1}$. (B) The difference between correctly calculated $\varphi_{n+1}$ and $\varphi_{n+1}$ estimated by the faulty arithmetic model by Müller & Wehner (Angular error= $\varphi_{n+1}$ estimated by the model - correctly calculated $\varphi_{n+1}$) is plotted assuming sufficiently large $l_n$. 
Unlike other species whose systematic error has been investigated, fiddler crabs do not have to turn their bodies in order to change their direction of travel – as discussed earlier, this allows them to keep their body axis aligned with the direction of their burrow while they travel in virtually any direction (Zeil, 1998; Layne et al., 2003a). One of reasons *Cataglyphis fortis* does not exhibit large systematic error in natural navigation is because the ants rarely make sharp backward turns (Müller & Wehner, 1988). The independence of body turns and travel direction in fiddler crabs has important consequences for controlling errors despite using idiothetic information. This has to due with an important difference between measuring travel direction idiothetically versus allothetically. For animals that walk almost exclusively forward (which is almost all of them), those that use allothetic cues can measure changes in heading as *direction*, whereas those that use idiothetic cues must measure *turns*. Measuring any one direction of travel against, e.g., the sun’s azimuth, is likely to generate the same error as any other direction, because direction has no magnitude. However, large turns are likely to generate larger errors than small turns. In fact, fiddler crabs make very few body turns and actively oppose any attempts by researchers to impose body turns (Layne et al. 2003b). By minimizing turns, an animal using idiothetic cues may out-perform one using allothetic cues. By walking in any direction relative to their body axis, fiddler crabs have considerable freedom in heading direction (frequently with δ around 125°), without reflecting body turns and errors associated with the body turns – more freedom, in fact, than if another, forward-walking animal were to use idiothetic cues.

Fiddler crabs do make some body turns, however. In order to orient their body axis to toward the burrow means that the body must constantly turn in small increments.
In excursions with large angular range, the amount of body rotation should also be large. In fact, the continuous body rotation and lack of visual information may explain the systematic inward homing error. If fiddler crabs have a bias toward turning its body more than it intended, and in nature rely on visual flow to correct the unintended body rotation, or if they underestimate the body turns they do make, then the accumulated angular homing error in light-free environment would be inward, similar to what the model by Müller & Wehner explains. In fact, Merkle et al. discusses the possibility of systematic underestimation of body axis rotation causing the characteristic inward error (Merkle et al., 2005). Unfortunately, the infrared video we collected does not have high enough resolution for reliable measurement of body rotations. The experiment also does not have clear starting point for homing runs, which makes the application of the model difficult.

The ability of an animal to reach its home is often crucial to its survival. *U. pugilator* uses its burrow as a central point for feeding, courtship, mating, rehydration, and predator escape (Zeil & Layne, 2002). They have developed unique local navigational strategy that minimizes or reduces body rotation, which is only possible due to their omnidirectional movement. We have presented support for a predictable inward homing error bias, i.e. a systematic error. The fact that the previous study (Layne et al. 2003a) failed to find conclusive support for systematic error in daylight leads one to think that vision plays an important role in preventing unintended body rotation, or accurately estimating body rotation, intended or not. Further study on the body orientation’s effect on homing error with and without visual information may help elucidate this matter.
References


