

Article

Eye Movement Reflexes Indicate the Homing Direction in the Path-Integrating Fiddler Crab, *Uca pugilator*

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Abstract: As animals execute essential behaviors like foraging, they must orient with respect to the space around them, requiring some neural/behavioral mechanism for spatial navigation. One such navigation mechanism is path integration, whereby animals recall their starting point by creating a memory-stored home vector. In some animals, this is stored in an egocentric frame of reference; however, it remains unclear what comprises this in animals' spatial memory. The fiddler crab *Uca pugilator* makes an excellent model to investigate the nature of the egocentric frame of reference because they appear to path integrate using self-motion cues to form an egocentric vector. We hypothesized that the home vector direction is governed by the optokinetic system, since the eye-body angle explicitly reflects the deviation of the body axis from home direction as optokinetic eye movements stabilize the eyes against body rotation. To test this hypothesis, we monitored eye and body movements during foraging excursions of crabs showing varying degrees of visual stabilization. We found that crabs with good eye stability had more accurate home vectors than those with poor eye stability, and the quantitative degree of stability accurately predicted the crabs' perception of home direction. These results suggest that eye movement reflexes may establish the homing direction in path integrating fiddler crabs.

Keywords: arthropods; fiddler crab; *Uca pugilator*; spatial orientation; navigation; path integration; homing; eye movements; optokinetic system



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1. Introduction

The study of animal behavior enhances our understanding of essential aspects of animal activity, such as how animals respond to stimuli and move within their environment [1]. This latter aspect, locomotion, is required by many animals to perform behaviors integral for their survival [2]. When animals move to perform essential activities, they do so with respect to the space and objects around them, a phenomenon known as spatial orientation, a major manifestation of which is navigation [3]. Navigation is fundamental in that an accurate system of navigation is required for activities that occur on a frequent basis such as visiting foraging sites, searching for mates, taking shelter from predators, and locating and returning home [4].

Animal navigation employs the use of sensory cues, and the information provided to the senses is categorized based on an important distinction—it is treated either as allothetic or idiothetic in nature, and the distinction depends on its source [5]. The former type has its source external to the animal, independent of posture or movement, while the latter is sourced internal to the animal or produced by the animal's own movements [6,7]. Thus, allothetic navigation consists of orienting or moving relative to a landmark, or a celestial or earth-based cue [5,8]. Most animals that have been studied use one or another allothetic cue to navigate. On the other hand, navigation by idiothetic cues implies the monitoring of self-motion [6]. The idea that animals could use their own distance and direction measurements in the absence of landmarks was proposed by Charles Darwin in 1873 [9] and more formally defined and named path integration about a century later by

Mittelstaedt and Mittelstaedt [6,7]. In path integration, the animal integrates linear and rotational movements and creates a single, memory-stored vector pointing to the start of the path. As its name implies, the process continuously updates this vector (Figure 1) and allows the animal to return home on a straight line (a “bee line”) after a sinuous trip [10]. Path integration can use allothetic cues [11,12], but so can other navigation strategies; it is the only strategy possible if using idiothetic information.

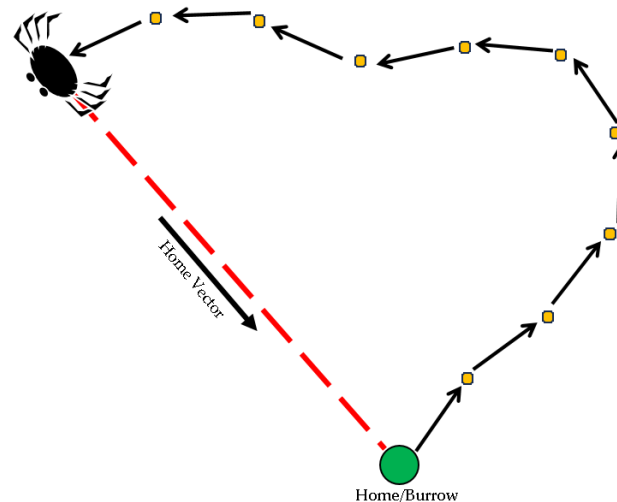


Figure 1. Illustration of a path-integrating fiddler crab on a foraging excursion. The path has been arbitrarily discretized into small motion vectors, which are continuously summed to form a single vector which points back to the starting location, i.e., the home vector.

An important consequence of the distinction between allothetic or idiothetic sensory information used by navigating animals is that it suggests which type of spatial frame of reference the animals possess, that is, the coordinate system in which they define their home vector [13]. As with the source of sensory cues, there are two major categories: exocentric and egocentric frames of reference [13–15]. An exocentric frame of reference is based in coordinates relative to the position or orientation of elements in the environment [13,16]. The nature and mechanism of this frame of reference seems intuitively clear, as it is referred to tangible features. On the other hand, an egocentric frame of reference specifies coordinates relative to the animal’s “self” [8,10,13,16]. It is not intuitive or clear what specifically constitutes this egocentric frame of reference, or in other words, what is an animal’s directional “self”.

In this study, we investigated the basis of an egocentric frame of reference through examining the path integration system of the Atlantic sand fiddler crab, *Uca pugilator* (Bosc, 1802). These crabs are short-range, central-place foragers [17] that move to and from their burrows during critical activities such as foraging, burrow defense, and courtship [18–20]. In all of these situations, they can recall their burrow location, and there is strong evidence they do so by idiothetic path integration [21] (but see [22,23] for evidence of allothetic path integration by Australian fiddler crabs). *U. pugilator* are close relatives of another American species, *Uca rapax* [17,24], whose homing errors after being passively translated, or rotated on a disk, are consistent with idiothetic path integration [21], and not with allothetic path integration. A detailed analysis of frame-by-frame responses to imposed disk rotation showed that *U. rapax* total movement on the disk—self-translation, self-rotation, imposed translation, imposed rotation—and then subsequent homing direction—was best reproduced by two versions of an idiothetic path integration model, and was not accurately reproduced by two other idiothetic models nor any of three allothetic path integration models. The behavior and homing errors of *U. pugilator* mirror those of *U. rapax* after translation and rotation (unpublished data), and we therefore assume they possess the same path integration mechanism. Therefore, to create the home vector, *U. pugilator* must

measure and encode movements relative to some self-derived spatial reference. Given their unique propensity to align their transverse axis with the home direction [21,22,25], an obvious candidate for the frame of reference is the animal's body axis. However, the spatial reference cannot be strictly equal to the body axis since the latter is often not well aligned with home, but the crab's concept of its home direction remains correct.

An alternative to the body axis *per se*, since it explicitly reflects the deviation of the body axis from home direction, is horizontal eye position. Fiddler crabs have highly mobile, compound eyes that are able to rotate in three dimensions somewhat independently of the body [4,26,27]. They exhibit optokinetic eye movements that stabilize the eyes against body yaw rotation through a combination of slow-phase and fast-phase eye movements, the latter being homologous to the human nystagmatic fast phase [28–30]. For the purpose of this paper, we define a saccade as the fast phase of nystagmus, i.e., the fast flick eye rotations that can precede, co-occur with, or succeed body rotations [31]. We hypothesize that the home vector is controlled by, or a product of, the optokinetic system, since the eye–body angle explicitly reflects the deviation of the body axis from home direction as optokinetic eye movements stabilize the eyes against body rotation. The body axis may indeed form the ego-basis of the coordinate system if the crab adjusts its vector to account for bodily deviations from the home direction. If the eyes are well stabilized, we assume they maintain this angle with the body, interspersed with large, fast saccades. We also assume the path integrator accounts for these saccades by a form of spatial updating [32], but any very small and/or slow eye movements are assumed to be, in large part, drift in the optokinetic system that the path integrator does not account for, and which, therefore, leads to homing error. We examined the orientation of the eyes during foraging, and digitally removed large saccades to create time series of a fictive eye orientation called eye* (eye-star). This contains drift that is not accounted for by the path integrator, as well as small eye movements that may be accounted for, such as microsaccades. We hypothesized that the angle between eye* and the burrow direction is proportional to path integration homing errors (though not equal, due to its inclusion of an unknown amount of “known” eye movement, and also due to the effect of body translations).

2. Materials and Methods

Experiments were carried out at the University of Cincinnati, from fall of 2019 through spring of 2023 on animals purchased from livebrineshrimp.com (Oak Hill, FL, USA).

2.1. Laboratory Setting

Fiddler crabs were housed in a circular 1.5-meter diameter stainless steel tank, containing sand 8" deep from fiddler crab natural habitat in North Carolina. Brackish water (~25 ppt, made from Instant Ocean) was pumped in and out of the arena to create pseudo-tidal rhythm. The crabs were fed once every other day with tropical fish flakes (Omega One Goldfish flakes). Both male and female crabs were used for this study, and were randomly chosen. When fiddler crabs were acclimated, as indicated by natural behaviors such as digging their own burrows, foraging, courtship, and burrow defense (which took between five and 120 min), experiments were conducted during pseudo low tide during both day and night (lab lights on and off, respectively). *Uca pugilator* are both day and night active [17,33]. Tide and temperature are the prime determinants of their activity, with highest levels reached when temperatures are at least 25 °C, day or night [33]. In our experiments, the lab temperature was maintained at 26 °C.

2.2. Experimental Procedure

Foraging excursions were videotaped from above at 30 frames/s using a Sony HDR-HC1 camcorder with infrared night vision capability, which allowed us to obtain footage in darkness. To monitor fiddler crab eye movements, a flag made of flexible thermal paper (~5–7 mm × 1 mm) was glued onto the medial, non-visual surface of one eyestalk, and extended backwards above the carapace (Figure 2a). To track body movements, white

reflective paint was used to mark the two lateral tips, i.e., the left and right side, of the fiddler crab's carapace (Figure 2a).

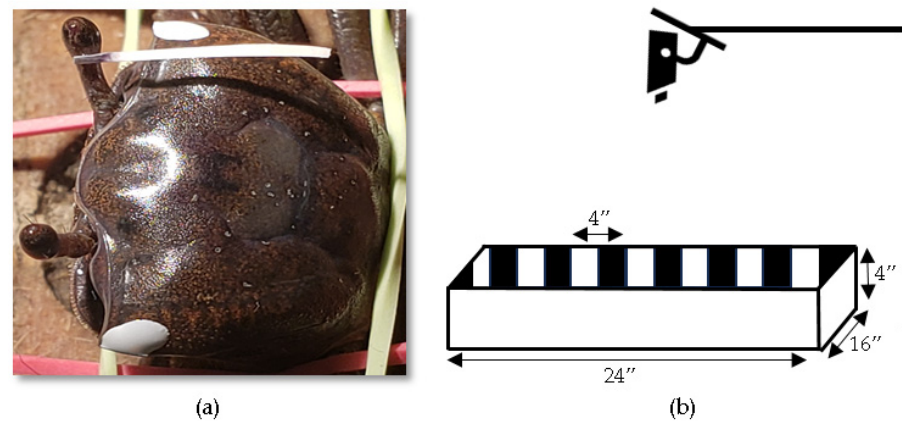


Figure 2. (a) Eye flag and carapace points used to track eye and body movements in the fiddler crab; (b) illustration of experimental arena with black and white stripes in the surround.

The animals were placed into an experimental arena ($24'' \times 16'' \times 4''$), constructed on top of the sand in the holding tank, the walls of which were made of Sintra[®] and had vertical black and white stripes alternating with a spatial period of four inches (Figure 2b). Foraging excursions were recorded with the room lights on ($N = 30$) and off ($N = 42$). The idea was to induce a range of visual stability, which would be compared with theoretically variable homing errors.

2.3. Digitization and Data Analysis

The video recorded foraging excursions were digitized using custom MATLAB code (The MathWorks, Natick, MA, USA). A total of 72 fiddler crab foraging excursions were processed with video software and digitized ("clicked") by hand. All paths were digitized at 10 frame intervals (three times per second). At each frame, the two painted dots on the carapace and two ends of the eye flag were clicked to obtain the crab's body and eye positions. Sections of the path within two body lengths of the burrow were excluded from analysis, to avoid the region within which crabs can simply view and approach/orient to the burrow entrance. All path data were standardized so that the crab faced clockwise relative to the radial direction of the burrow (as in Figures 6 and 7).

The crab's body and eye orientations were computed from the slope of the lines connecting these points (Figure 3). The eye–burrow angle was calculated between a line from the eye flag's proximal end to the burrow, and a line from the flag's proximal end to its distal end (Figure 3). Because fiddler crabs have panoramic vision [34,35], and do not visually fixate on objects (for the only exception, see [26]), the eye flag cannot be said to indicate where the crab is "looking". If the eyes do have a special relationship with the burrow direction, this is assumed to be established during the beginning of the foraging excursion. Therefore, for the eye flag, all angles were normalized to this part of the excursion, i.e., the eye orientation in the first frame was set to zero and all subsequent eye-related angles are relative to this orientation.

Saccades were identified and removed from the eye orientation time series of each path (see Figure 4 for an example). Saccade identification was performed using subjective judgement in combination with quantitative filters. This is because, first, crabs perform behaviors that have the velocity profile of saccades but are not (e.g., the crab cleans its eye with its maxilliped [36]), and second, the beginning and end of saccades are often slow enough to avoid detection by velocity alone. Therefore, each case must be examined manually and compared with the corresponding video footage to identify real saccadic movements. Removing saccades from the eye orientation trace created a fictive form of eye orientation we call eye* (eye-star).

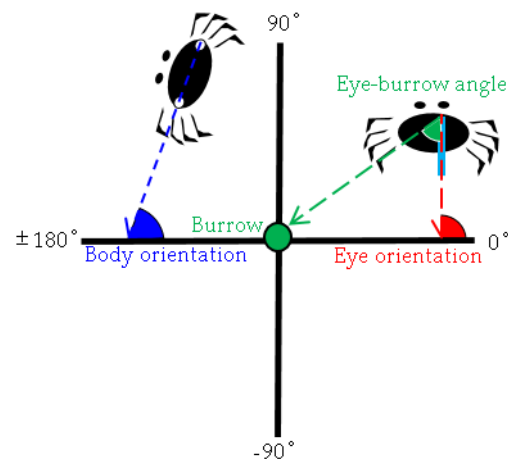


Figure 3. Illustration of body orientation, eye orientation, and eye-burrow angles.

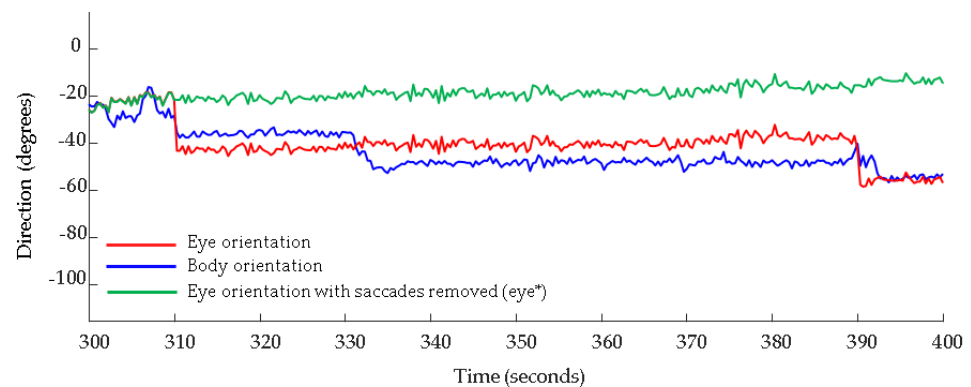


Figure 4. Example time series of body orientation (blue), eye orientation (red), and eye orientation with saccades removed, i.e., eye* (green).

To illustrate what eye movements take place and the effect of saccade removal, the foraging behavior of a crab near its burrow is shown in an exaggerated, schematic form in Figure 5. Two possible ways a crab may carry its eyes, not mutually exclusive, are exemplified in the two panels, each with a crab advancing counter-clockwise around its burrow. First, we consider an idealized crab with perfect eye movements, as indicated by the red dashed lines. In one case (Figure 5a), after the crab establishes a relationship between its eye and the burrow (a.1), the eyes are then stabilized during body rotation (which is small but random) and translation (a.1→a.2). Eye orientation is unaffected, but the eye–burrow angle is changed by the translation. This angle is known by the path integrator in the brain, and the home vector (not shown) remains accurately pointed at the burrow. The eye–burrow relationship is then restored with a large saccade during the next step (a.2→a.3). The path integrator accounts for this, as well as the effect of additional translation, so, the home vector remains true to the burrow.

Now consider a perhaps more realistic crab with imperfect eye movements, indicated by the gray dashed lines. A lack of optokinetic stability causes the first step (a.1→a.2) to incur a 10° error in eye orientation (α), of which the path integrator is unaware, though it is aware of the eye–burrow angle change due to translation. This 10° error becomes an uncorrectable, inherent part of the eye orientation, and the crab now believes the burrow lies at position β , and the foraging crab will orient itself around this point. The error remains through the next translational step and large saccade (a.2→a.3); these are accounted for by the path integrator, though note that the latter brought the eye in line with the false burrow location β . If we were able to isolate the eye movements unknown to the path integrator (errors) from the rotational (saccades) and translational factors that are known and accounted for, by identifying and digitally removing the latter from the time series,

we would be left only with errors, predicting the crab will home to location β (light green dashed line). We can do this with large saccades (that is, digitally remove them), but we are not yet able to accurately identify and remove the effect on the eye–burrow angle of translations. Thus, we removed the large saccades to produce eye* (dark green dashed line) as our prediction, knowing that this deviates from the crab's own sense of the burrow location by an amount dictated by translation. Eye* does not contain the translations, but its angle with the burrow direction does. Keep in mind that all of the movements and angles in Figure 5 are highly exaggerated.

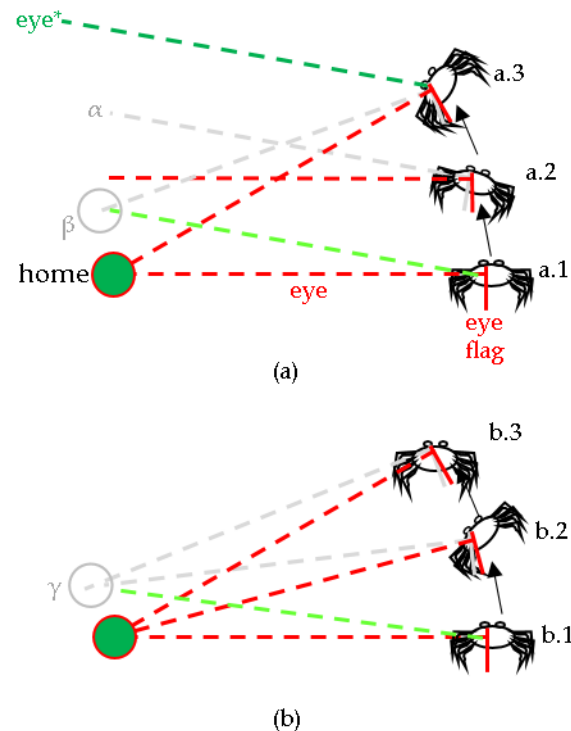


Figure 5. Two possible ways fiddler crabs may move their eyes while foraging counter-clockwise around their burrow: coarsely punctuated rotation (a) or fine rotation (b). During step a.1→a.2, eyes are stable during body rotation and translation. From a.2→a.3, a saccade restores eye orientation with home. From b.1→b.2→b.3, small saccades or smooth rotations maintain constant eye–burrow relationship. Red dashed lines: idealized eye movements lacking errors. Gray dashed lines: eye movements that incur an error during first step. Green dashed lines: homing direction predicted from eye stabilization errors only (light green), and from eye stabilization errors plus translations (dark green = eye*). Circles: real burrow (red, green filled) and false burrow (gray, unfilled). The Path Integrator knows about: 1. eye–burrow angular deviation due to translation (a.1→a.2); 2. large saccade (a.2→a.3); 3. small or smooth rotations maintaining eye–burrow relationship (b.1→b.2→b.3). The Path Integrator does not know about 4. stabilization errors (a.1→a.2; b.1→b.2). We can digitally remove (2) large saccades to give eye*, a time series containing small/smooth rotations plus errors, and the final eye*–burrow angle also contains the effect of translations.

Another possible way the eyes of a foraging crab may move is illustrated in Figure 5b. Again, these are not mutually exclusive with Figure 5a. Here, an idealized crab maintains the eyes' relationship with the burrow (red dashed lines) throughout both body rotations and translations (b.1→b.2→b.3). This is accomplished by either smooth rotations or very small saccades (microsaccades), though we cannot tell which, and neither are distinguishable from stability errors (shown in gray dashed lines that bring the false burrow to position γ) so we cannot digitally remove them. However, the assumption is that the function of these is to oppose errors and maintain a constant eye–burrow relationship, so their presence

in the time series will tend to remove the effects of translations on our final eye*–burrow angle (compare $a.1 \rightarrow a.2$ with $b.1 \rightarrow b.2$).

The eye*–burrow angle and the homing errors for each path were calculated. The homing error was determined by first identifying the point in the animal's path when they appeared to change from "homing" to a specific location to searching for a burrow not found; this was dubbed the "search" point and was invariably characterized by a large ($>60^\circ$) change in egocentric walking direction. Second, we identified the point in the path that separated foraging from homing behavior, that is, the point immediately prior to their relatively straight, concerted journey home. This point was dubbed "home time" and was characterized by the onset of lateral walking that continued until the search point. The posture of the animal at this point, where theoretically they display their concept of their home direction, is clearly crucial to their homing direction and our prediction of it. It was important, therefore, that the point immediately prior to the homeward journey be selected as home time. Homing error was the angle between the line connecting "home time" with "search", and the line connecting "home time" and the real burrow.

Homing error values and eye* values were tested for normality (D'Agostino's K^2 normality test) and linear regression analyses were conducted to examine the relationship between these variables. The F-test was used to compare the fit of the linear regression model between homing error and eye*–burrow angle. Also, our prediction was that the linear regression would produce a unity slope, i.e., the quantitative degree of eye*–burrow angle would equal the quantitative predictor of the homing error angle. Therefore, we also performed a Student's t -test to compare the slope of the model prediction of the regression analyses to the obtained slope-intercept.

3. Results

A total of 72 fiddler crab foraging excursions were analyzed for this experiment. These ended with homing errors between 0° and 65° (see Figures 6 and 7 for examples). We used lights-on and lights-off conditions to induce a range of eye stabilities, and we found lower standard deviation in the eye–body angle with the lights on ($x = 6.92$, $N = 30$) than with the lights off ($x = 10.34$, $N = 42$; Student's t -test, d.f. = 71, $t_{\text{stat}} = -2.25$, $p = 0.0255$). However, this cannot be strictly interpreted as better stability in the light, since low variability in this angle can be a sign of poor stability under some conditions. Also, there was no difference in homing errors between lights on ($x = -2.42$) and lights off ($x = -2.69$) conditions (Student's t -test, d.f. = 71, $t_{\text{stat}} = 0.09$, $p = 0.92$); nor any difference in eye*–burrow angle (lights-on $x = 8.45$, lights-off $x = 6.17$, d.f. = 71, $t_{\text{stat}} = -0.49$, $p = 0.63$).

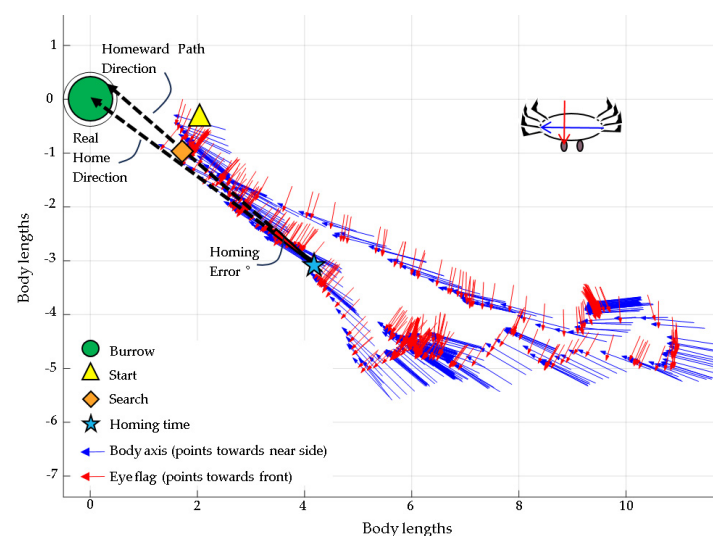


Figure 6. Example of a foraging excursion where the animal made $<5^\circ$ homing error (essentially no error). Crab inset in top right shows body and eye orientations relative to the burrow.

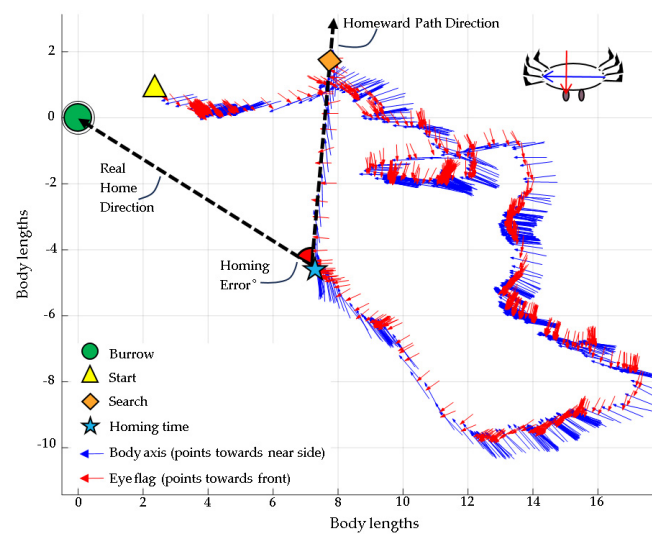


Figure 7. Example of a foraging excursion where the animal made a $\sim 65^\circ$ homing error. Crab inset in top right shows body and eye orientations relative to the burrow.

For each foraging excursion, saccades were identified and removed, and the eye*–burrow angle was computed at home time. This was then regressed against the animal’s corresponding homing error (Table 1; Figure 8). It was found that eye*–burrow angle was a significant predictor of homing error ($y = 0.82x + 8.72$; $R = 0.57$, $F_{1,70} = 34.3$, $p < 0.0001$), indicating that fiddler crabs with good eye stability had more accurate home vectors than those with poor eye stability. One of the points appeared to exert disproportionate weight on the regression. To determine its effect, this point was removed and the regression analysis was repeated. This modified regression exhibited a slightly diminished trend in the relationship ($y = 0.66x + 8.88$, $N = 71$; $R = 0.44$; $p < 0.001$), but the statistical interpretation remained the same, i.e., eye*–burrow angle significantly predicted homing error.

Table 1. Regression relationship between homing error and eye*–burrow angle.

	<i>Df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Significance F</i>
Regression	1	4217.20	4217.20	34.32	$p < 0.0001$
Residual	70	8601.87	122.88		
Total	71	12,819.07			
	<i>Coefficients</i>	<i>Standard Error</i>	<i>t Stat</i>	<i>p-Value</i>	
Eye*–burrow angle	0.40	0.07	5.86	$p < 0.0001$	

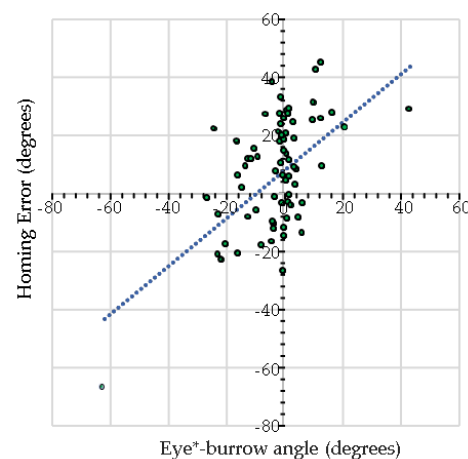


Figure 8. Regression relationship between the eye*–burrow angle and the homing error angle.

In addition, we performed a Student's *t*-test to compare the slope of our model prediction with the actual results that we obtained. We hypothesized that the slope of the linear regression would be equal to 1, i.e., the eye*–burrow angle would equal the homing error angle. We did not see a significant difference between the predicted slope ($m = 1$) and the actual slope ($m = 0.82$; Student's *t*-test, $t = 0.11$, $p = 0.91$), indicating that the homing error can be explained by the eye*–burrow angle.

4. Discussion

To recall the location of a position in space from memory, it is required that spatial information be based in some frame of reference [13,15,16,37]. The basis of an exocentric frame of reference seems to be instinctively clear, as the spatial information is independent of the organism's position, but rather tied to external environmental information [13,38–41]. However, it remains unclear, in a navigation context, what constitutes an egocentric frame of reference.

Fiddler crabs tend to orient their transverse axis of their body towards home and, combining this with the fact that they run fastest laterally, there has been speculation that the home direction is tied to their body axis [21,22,25,35]. However, this cannot be strictly true because even when the body axis is not well aligned with home, the crab's concept of its home direction remains relatively accurate. We hypothesized that the body axis may play a key role in the basis of the crab's coordinate system, only if the crab can continuously account for the bodily deviations from the home direction. That led us to investigate the role of eye position during path integration, since, theoretically, the optokinetic system could provide those required body deviations from a set point. The idea is that the optokinetic system stabilizes the eyes during bodily oscillations and, thus, continuously holds the body–home-angular deviation; the eyes only intentionally rotate to maintain the correct relationship with the home direction. In effect, the eyes, and not the body, form the spatial reference for the home vector. A testable corollary to this is that if the optokinetic system does a poor job of stabilizing the eyes, i.e., if the eyes are allowed to drift, then the spatial reference and the home vector will also drift, and the animal will make a homing error that is predictable from this drift.

We found that the eye*–burrow angle computed at home time was a quantitative predictor of homing error. That is to say that crabs with eyes that were poorly stabilized had inaccurate home vectors and crabs with eyes that were well stabilized had more accurate home vectors. These results are indicative of the mechanics of the optokinetic system. If the optokinetic system is leaky [42], this could cause the spatial coordinate system to wander or shift. This is tantamount to the path integrator failing. In a similar vein, if the animal did not make large saccades but had a small homing error, perhaps the eye maintained its special relationship with the burrow direction by performing microsaccades or a kind of smooth tracking (Figure 5b, this is a hypothetical possibility, as these movements have not been described for these animals). While microsaccades and large saccades exhibit similar kinematics, they differ in their order of magnitude [43,44]. These smaller eye movements are subtle to detect and, to us, indistinguishable from drift. If the animal performed them, we can assume they have either or both of the following related functions: to counteract drift by bringing the eye back to the correct position [45], or to alter eye orientation so as to maintain the eyes' special relationship with the burrow direction (see Figure 5b) and, if each cause visual updates comparable to those produced by larger saccades, maintain the home vector's spatial reference. In either case, they should reduce, not increase, the apparent drift away from the "correct" eye orientation. The main culprits for changing the eye–burrow angle in a way the crabs' path integrator accounts for and cannot yet be isolated from the data are translational movements combined with stable eyes (Figure 5a). A step to further explore these mechanisms would be to examine the microsaccades (or smooth rotations) at a much finer scale through sampling at higher temporal and spatial resolution, and by developing a method for identifying and isolating the effect of translations. This would

shed more light on the biological functions of visual stabilization and its possible role in maintaining a spatial frame of reference.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse11091719/s1>.

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