Running the distance: robustness of embodied distance measurement despite social interference in fiddler crabs

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Abstract

Path integration (PI), a spatial memory process, is an essential navigation strategy. Through PI, animals integrate their movements during foraging into a ‘‘home vector” that allows direct return to the origin. In humans, feedback from body movement contributes to readout of the home vector: physical estimation by walking toward the origin improves people’s ability to identify the origin point. However, how such feedback affects home vector readout in other animals remains unclear. Here, we suggest that leg movement feedback contributes to a robust readout of the home vector against errors induced by social behavior in fiddler crabs. Depending on whether they engaged in territorial behavior before homing runs, fiddler crabs altered their response to visual cues (fake burrow entrances) placed along their homing path. When social behavior was absent, the crabs showed a clear transition in behavior, initially suppressing visual cues in favor of PI but prioritizing visual cues as they approached their burrow. But when social behavior was present, this clear transition was disrupted, suggesting that error was induced into the internal estimation of burrow locations when the crabs attempted to interact with visual cues. Nevertheless, when crabs ignored the fake burrow entrance, they returned to their masked true burrow with equal precision regardless of the presence or absence of social behavior. These results suggest that the internal estimation of burrow location during the return is subject to induced errors, whereas the physical estimation is not, and feedback from leg movement contributes to robust distance measurement.

Keywords: navigation, fiddler crab, path integration, embodied memory, *Austruca perplexa*

Introduction

Many animals, including humans, use a spatial memory system for navigation known as path integration (PI), through which an animal's movements are summed to form a single "home vector" that enables direct return to the origin point [1, 2]. When measuring distance, animals generally use some sort of idiothetic sensory information [3–6], i.e., information created by and derived from an animal's own locomotion. In humans, walking itself can be the source of information not only when measuring distance during outbound journeys (i.e., forming the home vector) but also when returning to the origin point (i.e., reading it out) [7–9], suggesting that PI is an embodied memory process [10]. Moreover, physical estimation by walking toward the origin improves people's ability to identify the origin point [9]. Although the home vector can be read out without feedback from body movement, such feedback contributes to its readout for an effective return.

In other animals, how does feedback from body movement contribute to reading out the home vector? Desert ants use PI to return to their nest when they find food while foraging on a featureless saltpan. They also sometimes must access PI memory to estimate the nest location partway through the return path, when comparing and interacting with other information, such as visual cues [11–14]. Could physical estimation by walking toward the origin improve their ability to identify the origin point compared to internal estimation partway through the return path? If so, body movement feedback could contribute to reading out the home vector. Specifically, this feedback contributes to not only monitoring the traveled distance during the return (via stride integration [3, 4]) but also calibrating the desired travel distance. However, it is hard to compare the accuracy of these two processes because of the difficulty of directly assessing the accuracy of estimation in nonhuman animals. One alternative would be to investigate situations that affect these two processes differently, e.g., where an error occurs in the internal estimation partway through the return path but not in the physical estimation.

Fiddler crabs are potentially suitable for studying this difference, as their frequent engagement in social behaviors likely introduces errors into PI [15, 16]. When threatened, these crabs can run back to their burrows precisely despite generally lacking visual contact with them due to perspective foreshortening [17–22]. They traditionally have been considered to do this by relying exclusively on PI (e.g., [17, 21]). In our

previous experiments, we investigated how fiddler crabs respond when PI and visual cues are in conflict [23, 24]. By masking true burrows (the goal of PI) and placing fake entrances (visual cues) at various distances along their homing paths, we found that fiddler crabs only responded to visual cues located near their burrow; otherwise, they ran up to the masked true burrow, ignoring the fake entrance [24]. This implies that crabs exhibit a clear transition where they initially suppress visual cues in favor of PI memory, but switch to prioritizing visual cues as they approach their burrow.

In this study, to explore whether and how social behavior influences PI and its interaction with visual cues, we observed escape responses of fiddler crabs that started during territorial behavior (Fig. 1). Adopting our previous approach [24], we additionally placed a conspecific contained in a transparent cup in the vicinity of the focal crab's burrow and located a fake entrance along the homing path of the focal crab engaged in territorial behavior (Methods). Under this social condition, we found that the clear transition observed in the non-social condition in our previous study [24] was disrupted. This suggests that error was induced by social behavior into the internal estimation of burrow locations, which is used in interactions with visual cues during homing runs. Nevertheless, we also confirmed that, when crabs did not respond to the fake entrance, they could return to the masked burrow location just as precisely under the social condition as under the non-social condition. These results suggest that the internal estimation of burrow location during the return path is subject to induced errors, but the physical estimation is not, and that feedback from leg movement contributes to robust distance measurement.

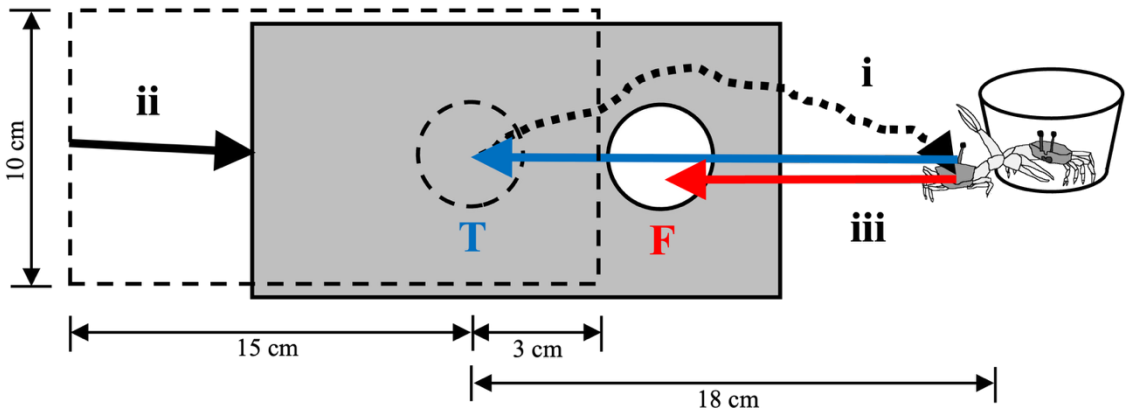

Figure 1. Experimental paradigm. After the focal crab had emerged from its own true

burrow (on which a fake entrance cut into a cork sheet was superimposed) and moved toward a transparent cup containing a conspecific to engage in territorial behavior (i), the sheet was translocated so that the true burrow was masked and only the fake entrance was shown (ii). The focal crab ran back to the masked true burrow or fake entrance when it was startled (iii; blue or red arrow, respectively). Dashed circle (T): true burrow; solid circle (F): fake entrance.

Results & Discussion

After being threatened while engaging in territorial behavior, fiddler crabs rushed back and stopped abruptly at the fake entrance ("F event," Methods) or the masked true burrow ("T event"). In Fig. 2A and B, we show the distribution of fake entrance locations during F and T events, in a reference frame where we defined the positions of the true burrows as the origin and situated the direction from the starting point of the run to the true burrow to be from right to left along the x-axis. It is clear that the distributions of the T and F events under the social condition (the present study; Fig. 2B) overlap more compared to the non-social condition (our previous study [24]; Fig. 2A). We then calculated the probability of occurrence of a T event in relation to the distance between the true burrow and the fake entrance along the x-axis (the x-coordinate of the fake entrance in the reference frame described above), as well as the curve fitted by sigmoid functions (Fig. 2C and D). Although there was no significant difference in the threshold of the logistic curve (i.e., the distance of 50% probability) between conditions (social: 44.18 mm; non-social: 43.43 mm, Bootstrap test, $p = 0.854$), the social condition had a significantly shallower slope than under the non-social condition (0.075 vs. 0.20, Bootstrap test, $p = 0.008$). These results suggest that social behaviors disrupt the clear transition observed in the non-social condition, i.e., from initially suppressing visual cues in favor of PI memory to later prioritizing them. Taking previous research into account [15, 16], social behaviors seem to introduce errors in PI (i.e., the internal estimation of the true burrow location), which interacts with visual cues.

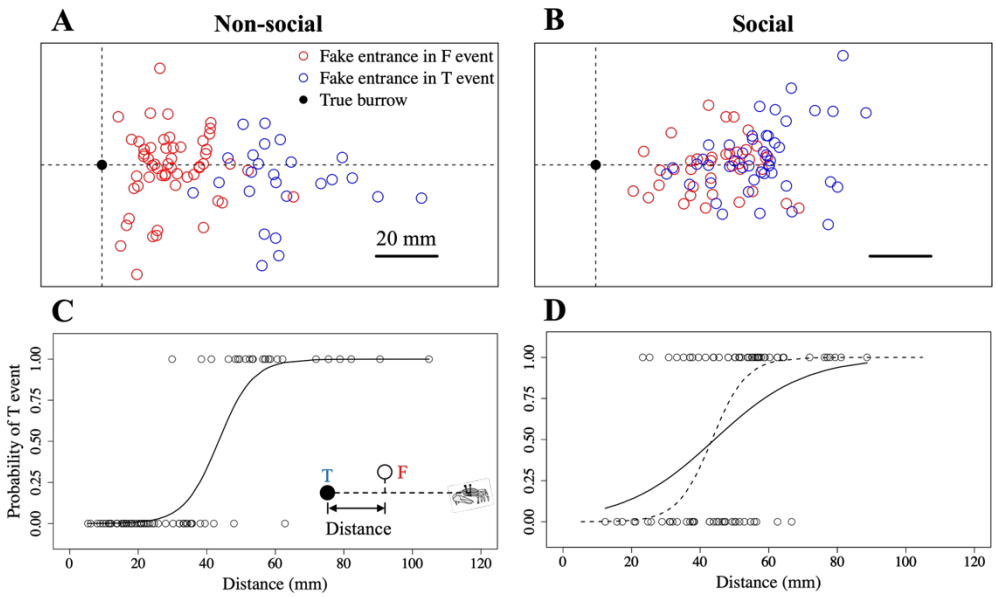

Figure 2. Burrow selection in relation to true burrow to fake entrance distance. Left and right panels show non-social and social conditions, respectively (experiments without and with territorial behavior). (A and B) Location distribution of fake entrances during F events (returned to fake entrance, red circles) and T events (returned to true burrow, blue circles). Black filled circles indicate true burrow locations. The direction from the starting point of the run to the true burrow is normalized to be right to left. (C and D) Probability of occurrence of a T event in relation to the distance between the true burrow and fake entrance. Open circles represent individual trials: T events (1) and F events (0). Solid lines represent best-fit sigmoid functions for each condition. The dashed line in Fig. D shows the non-social sigmoid curve for comparison. The inset in Fig. C illustrates how the distance between the true burrow and the fake entrance is determined (see main text for details). Left panels are adopted from ref. [24].

How much error does social behavior introduce into the internal estimation of the true burrow location? To examine this, we conducted a simulation using data from the non-social condition, where we added artificial errors to the location of true burrows (the goal of PI), with the errors normally distributed with various values of standard deviation (σ). When we calculated the slope of the fitted sigmoid curve using the x-distance between this modified burrow and the fake entrance for each σ, we identified that the slope with a σ of 18 mm closely matches that of the social condition (see Methods and Fig. S1).

Does social behavior also induce error when crabs physically run up to the masked true burrows? To address this, we determined "homing error" during T events (returned to masked true burrow) by calculating the distance between the position of the masked true burrow and the crab's position when it stopped. If social behavior also induces error in the physical estimation, this homing error should be larger under the social condition than under the non-social condition. However, we found no significant difference in homing error between the social and non-social conditions (Welch's *t*-test, $N_{social} = 46$, $N_{non\text{-}social} = 25$, $t = 0.29$, $p = 0.77$, Cohen's $d = 0.068$) (Fig. 3). Moreover, we estimated a "predicted error" by adding Gaussian noise with the estimated σ of 18 mm to the true burrow position of the non-social data and calculating the distance between this simulated true burrow location and the crab's position when it stopped (Methods). We then observed that the homing error under the social condition was significantly smaller than this predicted error (Welch's *t*-test, $N_{social} = 46$, $N_{predicted} = 25$, $t = -4.42$, $p = 0.00023$, Cohen's $d = -1.32$) (Fig. 3). This implies that the crabs successfully returned to the masked true burrow even under the social condition, and that social behavior does not influence homing error in the physical estimation while running to the burrow. Taken together, these results suggest that the two readout processes of the home vector are differently influenced by social behavior: the internal estimation of the burrow location during the return path is subject to induced errors, but the physical estimation is not.

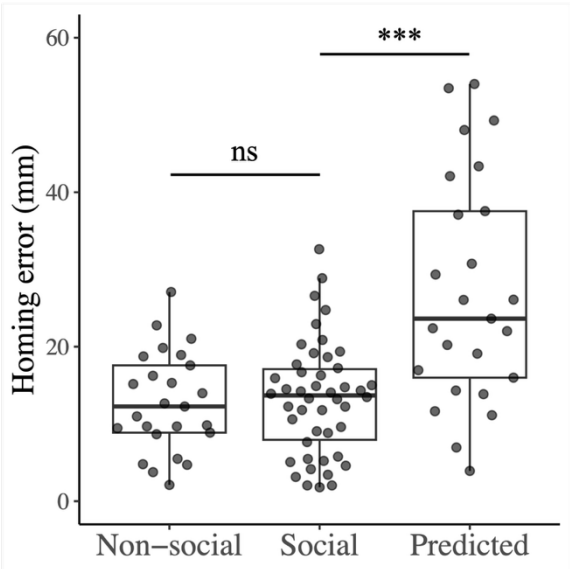

Figure 3. Homing error during T events (return to masked true burrow). Homing error was calculated as the distance between the position of the masked true burrow and

the crab's position when it stopped. Homing error in the social condition (center) did not differ significantly from that in the non-social condition (left, $p > 0.05$) but was significantly smaller than the predicted error (right, $p < 0.001$). Predicted error was calculated by adding Gaussian noise with an estimated standard deviation of 18 mm to the true burrow positions from non-social data and calculating the homing error with this modified burrow location. Each data point represents a trial. Box-and-whisker plots show the median (thick central line), interquartile range (box), and 1.5× the interquartile range (whiskers). ns, not significant.

Our findings provide insights into how social animals have evolved complex navigational systems to handle the inevitable interplay between navigational cues and social behavior. As has been well documented, fiddler crabs can start their homing run even when they cannot see their burrow [17–22]. This requires crabs to estimate their burrow location even in the absence of body movement. In other words, the home vector can be read out without body movement as some sort of internal representation that signals the location of the burrow before initiating the homing run. Perhaps this internal representation is also used to compare and interact with visual cues, i.e., to decide whether to respond to these cues, and social behavior induces error into it. On the other hand, information from leg movements can also contribute to reading out the home vector, and this information is presumably primarily used to decide when to stop running and is not influenced by social behavior. Hence, when crabs decide to ignore visual cues (i.e., T events) regardless of whether the decision is correct, they can return just as precisely to the masked true burrow even after engaging in territorial behavior. In other words, if feedback from leg movements plays no role in deciding when to stop, and if that decision relies solely on the internal representation, the homing error under the social condition would be expected to be larger than that under the non-social condition. Yet this was not the case.

During homing runs, fiddler crabs appear to measure the traveled distance by integrating "strides taken," as has also been observed in desert ants [3, 4], rather than using linear acceleration or optic flow [22]. Our results suggest that feedback from leg movement also contributes to calibrating the "strides to be taken" or the remaining desired travel distance, which is compared with the traveled distance to decide when to stop. In

other words, the desired travel distance (the length of the home vector) becomes apparent only when it is exhausted; otherwise, it is not directly available and must be estimated, for example, by comparison with other information (e.g., visual cues).

What kind of motor output might serve as the "stride length" that is used to measure the traveled distance and presumably calibrate the desired travel distance? Fiddler crabs measure distance perfectly well even when using fewer than the full complement of walking legs, such as when two legs are involved in carrying a mud ball [22]. In this case, only six of the usual eight walking legs are used. This would require each leg to have different joint angles and muscle tension than is normal, and hence to produce a different proprioceptive output. Therefore, to achieve a successful return, information from leg movement is likely filtered to provide, instead of all the nuances of actual performance, a more "abstract" indication of stride size [22]. The dynamics of whole-leg movements appear to be relevant to the measure of stride length, rather than the specific details of individual legs [7]. This implies that whole-leg dynamics are used as a computational resource, specifically a physical reservoir [25], which stores the spatial information and contributes to measuring distance.

Methods

Field experiments were conducted in August 2023 during the daytime from 2 h before to 2 h after low tide on a colony of fiddler crabs (*Austruca perplexa* H. Milne Edwards, 1852) in a tidal flat on Iriomote Island, Okinawa, Japan (24°24′N, 123°48′E). We recorded all experiments from above by using a Panasonic HC-WX990M-K camcorder (3840 × 2160 pixels, 30 frames per second) fixed to a tripod. Immediately after the camera was set up, we conducted each experimental trial on an arbitrarily chosen individual in the colony with up to 4 repetitions.

Experimental Procedure

The experimental procedure was adopted from our previous study [24], with revisions to some details to introduce territorial behavior between a focal and conspecific male (Fig. 1). We created a fake entrance by cutting a 1.5-cm-diameter hole at a distance of 3 cm from the edge of a 10 × 18 cm cork sheet, to which a plastic sheet of the same size was

attached for reinforcement (total thickness, 2 mm). The sheet was attached to a fishing line on the two corners closest to the fake entrance, allowing an observer to pull the sheet towards them.

Before starting trials with each focal male, we captured another male with a burrow at least 2 m away from the focal male's burrow and placed it in a transparent plastic cup (base diameter 7 cm, height 4.5 cm) with 2–3 mm of water to display it as a decoy in the trials.

Before starting each trial, the fake entrance was superimposed on the true burrow entrance with the focal crab in it. We observed that the crabs emerged from this modified burrow entrance, foraged, engaged in homing behavior, and defended the burrow in a similar manner to what is observed under natural conditions. We placed the transparent plastic cup containing a conspecific male 18 cm from the true burrow, on the shorter side of the sheet from the fake entrance. After the focal crab emerged from and left its burrow, it immediately approached the decoy crab in most cases and engaged in territorial behavior, which involved touching its claws to the cup containing the decoy crab (Fig. 1(i)). An observer, sitting on a chair 2 m away, then translocated the sheet to allow the fake entrance to be shown at various distances along the homing path of the focal crab and the true entrance to be covered by the sheet (Fig. 1(ii)). The sheet translocation was performed slowly to avoid disturbing the focal crab. Then, the focal crab was startled by the observer getting up from the chair, and it ran back to the masked true burrow or to the fake entrance (Fig. 1(iii)).

In total, 94 trials were conducted with 50 crabs. In 10 of the 94 trials, the crab was caught by the edge of the sheet; these trials were excluded. The remaining 84 trials (involving 47 crabs) were used in the following analysis.

Data analysis

From the recorded footage, we recorded the start and end points of an escape run as well as the locations of the true burrow and of the fake entrance after translocation by using image-processing software (Library Move-tr/2D ver. 8.31; Library Co. Ltd., Tokyo, Japan). We used a reference frame in which the location of the true burrow was defined as the origin, and the direction from the starting point of the run to the true burrow was normalized to be right-to-left along the x-axis. We first checked if the fake entrance was

translocated outside the area where the crab could fully see it, that is, the area within 4 cm of the home vector (i.e., whether the absolute value of the y-coordinate of the fake entrance was smaller than 4 cm in the reference frame described above). This was done because the visual contact distance of *A. perplexa* to its burrow is limited owing to perspective foreshortening, so that the crab can fully perceive the burrow entrance, regardless of its body size, only when it is within about 4 cm [24, 26, 27]. We confirmed that in all 84 trials, the fake entrance was translocated within this area.

If the stopping point was closer to the fake entrance than to the masked true entrance, we considered that the crab had reverted to the fake entrance and labelled these trials "F events." Alternatively, when the stopping point was closer to the masked true entrance than to the fake entrance, we considered that the crab had run back to the true burrow and labelled these trials "T events."

We calculated a sigmoid function obtained from logistic regression to evaluate the relationship between the probability of a T event, P_T, and the distance between the true burrow and the fake entrance along the x-axis (the x-coordinate of the fake entrance in the reference frame described above), D,

$$P_T = 1/[1 + \exp(-\beta_0 - \beta_1 D)],$$

where β_0 and β_1 are the intercept and steepness parameters, respectively.

To estimate how much error social behavior introduces to PI, we conducted a simulation by using data from the non-social condition [24], where we virtually displaced the true burrow locations (i.e., the origin in the reference frame described above) by using normally distributed errors with various values of standard deviation (σ). As a result, the simulated coordinate of the true burrow (x_{sim}, y_{sim}) was calculated as

$$(x_{sim}, y_{sim}) = (\sigma Z_x, \sigma Z_y),$$

where Z_x and Z_y are Gaussian random numbers with mean 0 and standard deviation 1. Using this simulated coordinate of the true burrow and its distance to the fake entrance along the x-axis, we calculated the slope of the fitted curve for each σ ranging from 0.5 to 25 mm (in increments of 0.5 mm), averaged across 100 simulation trials, to identify

which value of σ matched the data observed under the social condition (Fig. S1).

Statistical analysis

To compare the threshold ($-\beta_0/\beta_1$) and slope (β_1) of the fitted logistic regression models between conditions, bootstrap resampling (1000 iterations) was performed, and p values were computed by doubling the proportion of samples in which the estimated difference between conditions crossed zero. Welch's t-tests were used to test differences of homing error between the social condition, non-social condition, and predicted error. When making multiple comparisons, p values were adjusted by using the false discovery rate control [28]. All statistical analyses were conducted in R version 4.4.1 (The R Foundation for Statistical Computing, Vienna, Austria).

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Author contributions

H.M. conceived the study, analyzed the data, and wrote the first manuscript draft; H.M. and T.T designed and performed the experiments and contributed to writing the final version.

Declaration of interests

The authors declare no competing interests.

Data and materials availability

All data needed to evaluate the conclusions of the paper are present in the paper and/or the Supplementary Materials.

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