Path integration in desert ants, *Cataglyphis fortis*

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ABSTRACT Foraging desert ants, *Cataglyphis fortis*, continually keep track of their own positions relative to home—i.e., integrate their tortuous outbound routes and return home along straight (inbound) routes. By experimentally manipulating the ants' outbound trajectories we show that the ants solve this path integration problem not by performing a true vector summation (as a human navigator does) but by employing a computationally simple approximation. This approximation is characterized by small, but systematic, navigational errors that helped us elucidate the ant's way of computing its mean home vector.

Ever since Darwin (1) suggested that animals might be able to navigate by a system of "dead reckoning," or path integration, similar to that used by mariners at sea, a plethora of species, including spiders (2–8), crustaceans (9), insects (10–13), birds (14, 15), and mammals (14, 16), has been shown to employ such systems of navigation. Path integration means that the animal is able to continuously compute its present location from its past trajectory and, as a consequence, to return to the starting point by choosing the direct route rather than retracing its outbound trajectory (Fig. 1).

Nothing is known, in invertebrates and vertebrates, about how such path integration systems work. Investigators have focused on what sensory systems are involved in providing the animal with the necessary information about its rotatory and translatory movements (visual information: refs. 17–19; proprioceptive information: refs. 4, 6, 14, 16), but there are no data available on how such information is handled and used by the animal's path integration system. Jander (10) surmised that integrating all angular deviations over time completely solved the problem, but simple calculus shows that it does not. Mittelstaedt (7, 20) assumed that the animal integrated the components of motion along two mutually perpendicular directions. As human navigators know, this kind of vector summation is indeed a correct solution to the path integration problem, but whether animals behave according to that scheme has not been tested yet in any species.

In the present account we show that ants do not perform a true vector summation but instead use some rather simple formalism in integrating their foraging paths. First, we describe that ants trained and tested under well-defined experimental conditions exhibit small, but consistent, navigational errors. Second, we use these errors, and the systematics behind them, to derive the ant's approximate way of solving the navigational problem. Third, we conclude that due to the geometrical properties of the ant's natural foraging trajectories, the approximate solution fulfills the animal's overall navigational needs sufficiently well.

MATERIALS AND METHODS

Saharan desert ants, *Cataglyphis fortis* (21), were trained to walk in narrow plastic channels along angular trajectories

from the nest, N, to an artificial feeder, F (Fig. 2A). The length of the channels ($5.0 \leq a, b \leq 10.0$ m) and the angular distances between them ($0° \leq \alpha \leq 180°$) could be varied systematically. When the ants had reached the feeder, they were captured individually within small glass flasks and transferred to the test area where they were released <1 min after capture. The test area, a hard sandy plain, was painted with a grid of white lines that allowed us to record the ant's path on a reduced scale. In some experiments the homing ant was accompanied by a small vehicle loaded with optical equipment to shield off the sun and/or modify the pattern of polarized light in the sky (ref. 17; for further details, see *Results*). Statistics of circularly distributed data (22) were used for analyzing the ants' homeward courses. All experiments were performed in southern Tunisia near the village of Maharès (34.58°N, 10.50°E) during July and August 1985 and 1986.

RESULTS

Two-Leg Trajectories. When an ant is trained to walk along the two-leg trajectory depicted in Fig. 2A (outbound path $N \rightarrow F$; $a/b = 2$; $0° \leq \alpha \leq 180°$) and then released within the open test field, it immediately sets out in its homeward direction—or what it "thinks" is its homeward direction. In fact, the homeward courses of the ants deviate significantly and systematically from the true homeward direction, with the error angle ε depending on the turning angle α (Fig. 2B) and the ratio a/b of the lengths of the two legs of the path (not shown here).

This striking result is independent of what kind of celestial compass the ants are allowed to use while walking within the channels: the sun compass, the polarization compass, or both compasses simultaneously. The former can be excluded by screening the sun; the latter can be excluded by painting out the dorsal rim areas of the ant's eyes (19). The dorsal rim area of the eye contains the insect's compound polarization filter, which is necessary for deriving compass information from celestial patterns of polarization (23, 24).

Some experimental complications arise when the ants rely on their polarization compass. Due to the way this compass works (19, 23, 25) compass errors must occur whenever the slit-like celestial window seen by the ants walking within the channels does not run parallel or perpendicular to the solar vertical—e.g., the symmetry plane of the skylight pattern. However, as the insect's polarization compass is now known in considerable detail, any possible error angle introduced by the polarization compass can be computed and thus taken into account. No compass errors occur, of course, whenever the ants use the sun compass.

The mere fact that ants, when integrating a path, exhibit significant (and under some conditions quite substantial) navigational errors shows that the ants do not solve the path integration problem in its complete form. Instead, they resort to what could be called a shortcut, or approximate, solution. In trying to unravel this approximation we started with the assumption (13) that the ants might simply be computing
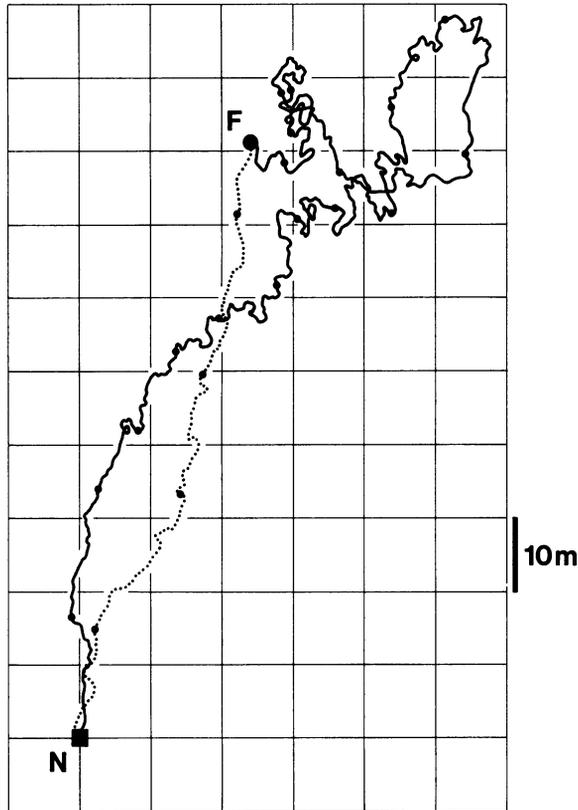
FIG. 1. Foraging trip of an individual ant, *Cataglyphis fortis*. Outbound and inbound trajectories are depicted by solid and stippled lines, respectively. *N*, nest; *F*, location of food item found by the searching ant. The length of the outbound path is 354.5 m; the maximal distance from the nest is 113.2 m. Time marks (small filled circles) are given every 60 s.

iteratively the arithmetic mean of all angles steered, with each angle weighted by the distance the ants have covered in

that direction. Such a distance-weighted mean-direction hypothesis can be formulated as follows (see Fig. 2*C*):

$$\varphi_{n+1} = \frac{l_n\varphi_n + \varphi_n + \delta}{l_n + 1} = \frac{\varphi_n(l_n + 1) + \delta}{l_n + 1} \qquad [1a]$$

$$l_{n+1} = l_n + 1 - \frac{\delta}{90°}. \qquad [1b]$$

In this equation φ_n is the direction in which the ant has covered the distance l_n (in unit lengths) after the nth step and δ is the angle about which the ant has turned and therefore ($\varphi_n + \delta$) the direction in which it proceeds for another unit length (e.g., the length of an ant's stride). φ_{n+1} and l_{n+1} denote the direction and distance, respectively, after the ($n + 1$)th step. As l_n is much larger than the unit length, Eq. 1a can be transformed (for $l \to \infty$) to

$$\varphi_{n+1} = \varphi_n + \frac{\delta}{l_n}. \qquad [2]$$

If this formalism is applied for all two-leg trajectories tested in our experiments, one obtains a reasonably good fit between the model and the experimental results for $90° \le \alpha \le 120°$, but the fit deteriorates increasingly as α approaches $180°$ (see Fig. 2*B*). A complete fit between the data and the model can be obtained by modifying Eq. 2 in the following way:

$$\varphi_{n+1} = \varphi_n + k\frac{(180° + \delta)(180° - \delta)\delta}{l_n}. \qquad [3]$$

In this new version of the model the ant is assumed to take its previous homeward course ($\varphi_n + 180°$) as the reference vector (see Fig. 2*C*). The deviation of the new course ($\varphi_n + \delta$) from this reference vector can be determined approximately by multiplying the two possible angular differences—i.e., ($180° + \delta$) and ($180° - \delta$). Moreover, the difference between these two values (i.e., 2δ) informs the ant about the exact amount and the sign of the turn. Thus, the product of all three terms is an approximate measure of the influence the ($n + 1$)th step has on the ant's homeward course. This
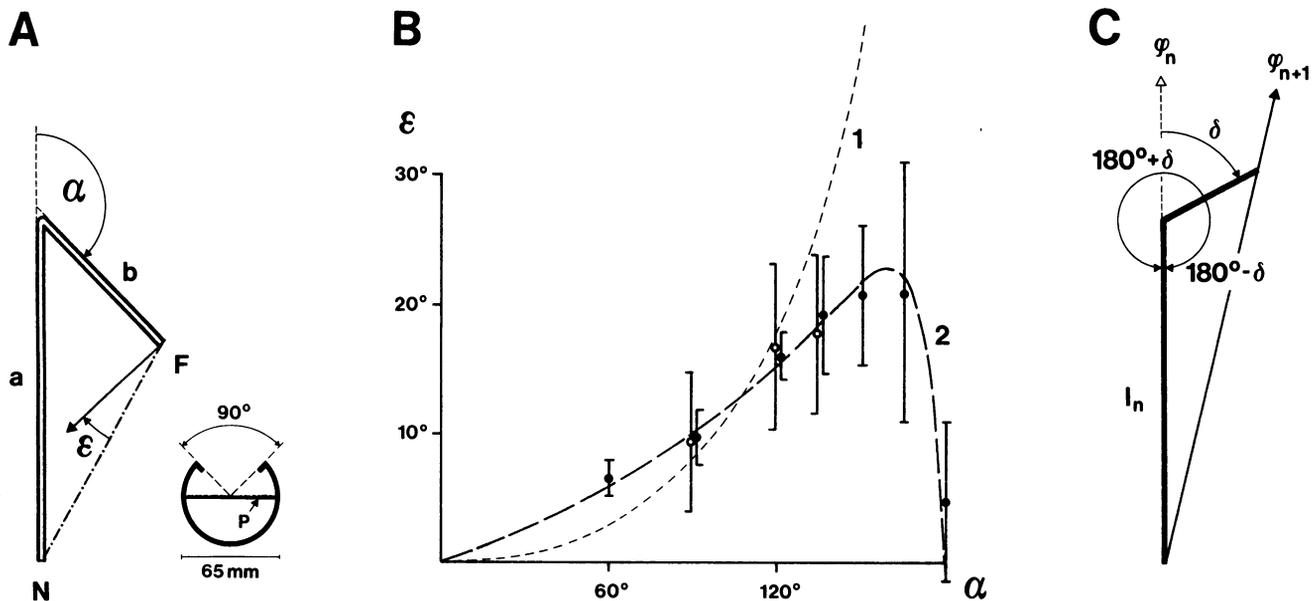
FIG. 2. Results of the two-leg experiments. (*A*) Experimental set-up. *N*, nest; *F*, food source; *a* and *b*, length of first and second segment of the training route, respectively; for cross section of the training channels, see *Inset*; *P*, platform on which the ants walked; α, turning angle; ε, error angle as recorded from homing ants captured at *F* and released in the open test area. (*B*) Results. Error angles (ε) plotted for different turning angles (α). $a = 10$ m; $b = 5$ m. The ants were allowed to use either their sun compass (O) or their polarization compass (●) system. Confidence limits are given for $P = 0.99$. The data include 1412 experiments performed with 310 ants. Curves 1 and 2 depict the error angles as calculated due to Eqs. 2 and 3, respectively. (*C*) Interpretation. φ_n and φ_{n+1} denote the ant's mean direction after its nth and ($n + 1$)th step, respectively; l_n, distance covered by the ant after the nth step; δ, angular difference between φ_n and the direction of the ant's ($n + 1$)th step.

product is normalized by k so that it maximally reaches 90° (in Eq. 3 the fitted constant is $k = 4.009 \times 10^{-5}$ deg^{-2}) and distance-weighted by l_n. The curve computed from Eq. 3 is depicted in Fig. 2B. It is statistically indistinguishable from the experimental data (see confidence limits for $P = 0.99$).

In principle, this procedure is very similar to what the insect does when using visual landmarks for navigation (piloting): it tries to match a stored "snapshot" of the visual scene with the current scene (26, 27). In the case of piloting the match is achieved when the ant is at home. In the case of path integration, the match tells the ant that it is on its direct homeward course.

Three-Leg Trajectories and Natural Foraging Paths. In the experiment described in Fig. 3 a third leg ($\alpha_2 = 90°$, $c = 5.0$ m) is added to the training array used so far ($\alpha_1 = 90°$). When the ants who have walked along this three-leg trajectory are displaced to the open territory of the test field, they deviate by $\varepsilon = 30.8°$ from the true homeward direction (length of mean orientation vector r = 0.96, $P < 0.001$, Stephens test; ref. 22). The actual error angle ε cannot be discriminated statistically from the deviation ε_m as predicted by the model ($\varepsilon_m = 33.7°$, $P >> 0.1$, Stephens test; ref. 22).

Finally, and most importantly, the model describes what occurs under natural conditions when the ant performs its outward journey within its normal foraging area. If such an outbound path is biased toward one direction, as is the case in the path shown in Fig. 4, the ant's home trajectory deviates from the true homeward direction ($P < 0.01$, Stephens test) by an angular amount exactly as predicted by the model ($P > 0.1$, Stephens test; $n = 14$).

DISCUSSION

The ant's approximate solution outlined in *Results* has been found to agree with all experimental data we have at hand. In addition, results obtained in bees (28) and spiders (6) in quite different behavioral contexts are in accord with the model we propose. Hence, the question arises how the ant can afford to use an approximate rather than correct way of computing its homeward course. How does *Cataglyphis* cope with this potentially dangerous situation?

First, the situation is not all that bad. The ant's path integration system yields relatively large errors only when the

FIG. 4. Natural foraging path of an ant. N, nest; F, location where the ant found a food item. In the experiment, the ant was displaced from F to F'. After release, its homing direction was recorded (see *Inset*). Black arrow, direction of the nest; white arrow, ant's homing direction as computed from Eq. 3; ε, error angle by which the ant's trajectory deviates from the true home direction (N).

ant performs sharp backward turns. A survey of the ant's actual foraging trajectories shows that such turns rarely occur. Second, errors resulting from, say, a 150° turn to the left and a 150° turn to the right are equal in amount but opposite in sign and thus cancel each other out. Again, as one can learn from surveying the ant's natural foraging trajectories, *Cataglyphis fortis* turns as often to the right as to the left, so that an overall directional bias is unlikely to develop. It is only in such rare cases as the one depicted in Fig. 4, in which turns to one side significantly outweigh those to the other, that the homeward courses computed by the ants should deviate from the true direction toward home—and, as shown above, this actually occurs. Nevertheless, due to some powerful backup systems, including the use of landmarks (29) and a systematic search strategy (12), ants are not lost even in such rare cases.

The more general message to be derived from our results is that ants, within the framework of their overall navigational capabilities, can afford to use some simple formalism in solving a complex navigational task. What appears, at least to the human designer, as an incomplete solution to the underlying mathematical problem is, in fact, a well-designed strategy in coping with a problem that the insect—rather than the human navigator—had to solve during its evolutionary history.

FIG. 3. Example of a three-leg experiment. For definitions and conventions, see the legend to Fig. 2. $a = 10$ m; $b = c = 5$ m. The heavy black bars depict the homing directions of ants trained to walk from N to F and then released in the test field. The data are from 88 experiments performed with 20 ants. Black arrow, mean homing direction of the ants; white arrow, home direction as computed due to the model (Eq. 3).

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