

Report

Path Integration Controls Nest-Plume Following in Desert Ants

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Summary

The desert ant *Cataglyphis fortis* is equipped with sophisticated navigational skills for returning to its nest after foraging [1, 2]. The ant's primary means for long-distance navigation is path integration, which provides a continuous readout of the ant's approximate distance [3] and direction [4] from the nest [5]. The nest is pinpointed with the aid of visual [6–8] and olfactory landmarks [9–11]. Similar landmark cues help ants locate familiar food sites. Ants on their outward trip will position themselves so that they can move upwind using odor cues to find food [12]. Here we show that homing ants also move upwind along nest-derived odor plumes to approach their nest. The ants only respond to odor plumes if the state of their path integrator tells them that they are near the nest. This influence of path integration is important because we could experimentally provoke ants to follow odor plumes from a foreign, conspecific nest and enter that nest. We identified CO₂ as one nest-plume component that can by itself induce plume following in homing ants. Taken together, the results suggest that path-integration information enables ants to avoid entering the wrong nest, where they would inevitably be killed by resident ants.

Results and Discussion

Foraging *Cataglyphis fortis* ants preferably approach their nest from downwind during the final few centimeters of homing (Figure 1A), suggesting nest-derived plume-following behavior (for visualization of the nest-derived plume see Movie S1 available online). When approaching the nest from downwind, ants pinpointed the nest entrance either straight or on a counter-turning walking track (Movie S2).

In order to systematically compare ants that approach the nest from downwind and upwind, we trained ants to a feeder and displaced them downwind or upwind, respectively (Figure 1B; for details, see Experimental Procedures). Following their path-integration vector, we saw that homing ants reached a fictive nest position that was either downwind or upwind of the nest entrance. When starting their nest search upwind of the nest entrance, ants usually exhibited characteristic loops, whereas ants approaching the nest from downwind tended to pinpoint the nest entrance on a rather straight route (Figure 1B; for example runs, see Figure 1Biv).

Are the plumes that the ants follow nest-specific, or do ants also follow plumes of foreign conspecific colonies? We covered two nests with circular arenas that allowed the ants

to leave and enter their nests via a central opening (Figure 2A; for details, see Experimental Procedures). To exclude any nest-defining cues other than nest odor, we installed circular barriers (height, 0.1 m; Ø: 3.4 m) surrounding the arenas. A U-shaped aluminum channel (length, 2 m) pointing away from the arena was dug into the ground and led the ants under the barrier toward the feeder. After about 30 min, the ants learned to enter the channel and pinpoint the feeder. Homing ants had to pass along the channel, climb onto the arena via a sand ramp, and locate the nest entrance in the center of the arena. The visually identical arena setups allowed us to transfer ants from the feeder of their own setup to a setup connected either with a foreign nest or with no nest (no-nest control). Homing ants were thus tested in a familiar visual surrounding but with their own nest-derived plume, a foreign plume, or no plume. Whereas only 16% of the ants ended up at the fictive nest entrance in the control, 71% (73%) of the ants pinpointed the nest after the first contact with their own (foreign) nest-derived plume (Figure 2B). Thus, plume-following behavior was not restricted to the plume of the home nest. Ants approached the nest upwind with a zig-zag movement (see Movie S2) that resembled the movement of flying insects following plumes [13–17]. Plume-following moths, for instance, exhibit movements in a zig-zag fashion to relocate the odor plume when it is lost [17].

We next asked whether we could elicit plume following in *C. fortis* with a single plume component. Increased CO₂ concentrations have been reported within the nests of leaf-cutting ants [18], and CO₂ has been shown to be involved in the social behavior of different ant species (e.g., the localization of buried nest-mates) [19, 20]. By measuring the CO₂ concentrations, we found increased levels at nest sites (median 352 ppm; n = 18) compared to control sites (279 ppm; n = 13; Mann-Whitney test, p < 0.001; for details, see Experimental Procedures). When we tested ants in the absence of any natural nest odor (no-nest control) but provided them with an artificial CO₂ plume that mimicked the concentration emanating from a nest, the presence of CO₂ was sufficient to induce plume-following behavior in 62% of the homing ants (Figure 2B). When the CO₂ concentration was increased to about twice the values measured at the nest sites, it was no longer attractive (data not shown). CO₂ was probably not the only volatile emanating from the nest. However, its high volatility and its diffusion characteristics (due to its weight, CO₂ usually accumulates at ground level) predestine this molecule as a nest cue for homing ants.

Our results suggest that nest-derived plumes are not nest-specific and that CO₂ is one of the active compounds inducing plume-following behavior in homing ants. Trusting a single cue that is not nest-specific is dangerous. As is true for other ants [21, 22], *C. fortis* reacts extremely aggressively toward non-nest-mates that enter the nest vicinity [23, 24]. In order to quantify the costs of following the wrong plume, we—by displacement of homing ants to foreign nests—encouraged homing foragers to enter a foreign nest. This procedure resulted in the death of 13 out of 27 displaced ants, whereas the remaining 14 ants, which also entered the foreign nest, were able to escape after initial contact with resident ants

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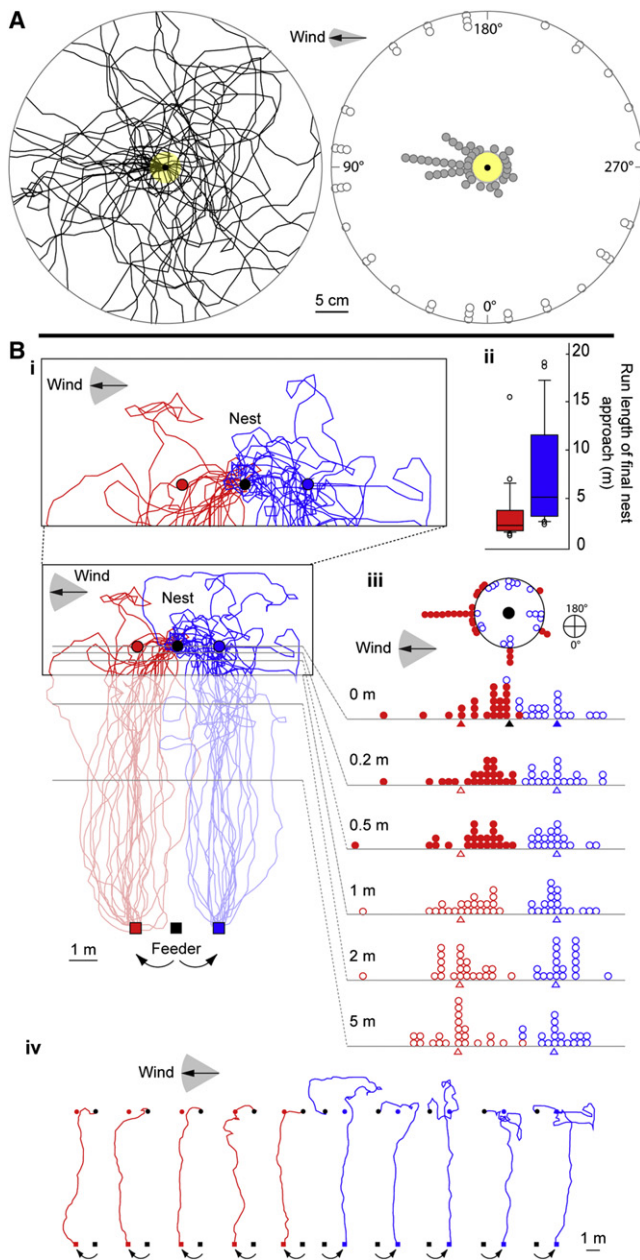


Figure 1. Homing Ants Follow Nest-Derived Odor Plumes

(A) Final nest approach during natural foraging ($n = 40$ ants). Homing trajectories (left) and angular distribution (right) of ants (gray circles; arranged in 15° sectors) approaching their nest (filled black circle). Wind direction, ranging from 75° to 105° . At outer circle ($\varnothing 25$ cm), ants are not aligned with plume (gray empty circles; Rayleigh test, $p > 0.05$; mean vector, 50° ; length of mean vector, 0.1). At inner circle ($\varnothing 2.5$ cm; shown by yellow filled area), ants are aligned with plume (gray filled circles; Rayleigh test, $p = 0.001$; mean vector, 98° ; length of mean vector, 0.4). For visualization of nest-derived plume, see [Movie S1](#).

(B) Nest approach after displacement.

(Bi) Homing trajectories of ants approaching the nest (black circle) from downwind (red paths, $n = 23$ ants) or upwind (blue paths, $n = 19$ ants). Nest-to-feeder distance was 10 m. Curved arrows depict the displacement. Red (blue) square depicts release point after 1.5 m downwind (or upwind) displacement from feeder. Red (blue) circle indicates path-integration (PI) defined nest position after downwind (upwind) displacement.

(Bii) Box plot representation of median and interquartile ranges of run lengths of final parts of the homing runs (within the black rectangle in Bi); whiskers, 90th and 10th percentiles; circles, outliers. Approaches from

(for details, see [Experimental Procedures](#)). Following foreign nest-derived plumes was thus shown to be dangerous and behavior that ants would likely avoid.

Consequently, we asked whether *C. fortis* foragers experienced foreign nest-derived plumes under natural conditions, and, if they did, whether such contacts inevitably caused the death of the forager. Alternatively, the ants might have developed a counter-strategy that allowed them to home successfully. Using GPS, we tracked foraging ants in their natural habitat. Two out of 20 ants crossed the nest-derived plumes of neighboring nests during their homing efforts ([Figure 3A](#); for details, see [Experimental Procedures](#)) but did not respond to the plumes. Foragers came into contact with plumes from foreign nests but responded with a counter-strategy that circumvented the fatal error of entering the wrong nest. There were two major differences between the arena experiments and the freely foraging ants. The first was that the state of the path integrator corresponded to a position close to home in the arena experiments and to a position far from home for the freely foraging ants. The second difference was that the visual surroundings were the same for the foreign and natal nests in the arena experiments but differed in the freely foraging ants.

We next tested whether the state of the path integrator helped the ants to distinguish their own nest from a foreign nest. We performed an experiment in which ants were equipped with path-integration vectors of variable lengths when exposed to the plume of their own nest. We trained the ants in the open field to feeders that were placed at different distances ([Figure 3B](#); for details, see [Experimental Procedures](#)), captured the ants at the feeder and released them close to their home nest. Although displaced from the feeder to a position close to the nest entrance, ants that entered the nest-derived plume still had path-integration vectors of different lengths available. All ants that—at the time of plume contact—had run off their path-integration vector responded to the plume ([Figure 3Bi](#)). When the ants still were equipped with a long vector, few entered the nest; in other words, the majority ignored the nest-derived plume and relied instead on the vector information ([Figures 3Bii and 3Biii](#)). Therefore, ants seemed to follow the nest-derived plume only when the home vector indicated that they were close to home. The inclusion of path integration might ensure that homing ants do not follow the wrong nest-derived plumes, which would likely be fatal (see above).

Subsocial shield bugs (*Parastrachia japonensis*) face similar navigational tasks as the ants mentioned above. Like *C. fortis* foragers, the bugs use path integration to find their way back

downwind were significantly shorter (Mann-Whitney test, $p < 0.001$).

(Biii) Statistical analysis of homing paths. Black arrowhead depicts nest position. Filled red (blue) arrowhead depicts fictive nest position of ants displaced downwind (upwind). Open arrowheads indicate paths as defined by path integration. Circles depict positions where the ants crossed the gray lines shown in (Bi). Filled circles depict positions where the ants deviated from the path as defined by path integration (Wilcoxon signed rank test, each $p < 0.05$). Open circles depict positions where ants did not deviate from path as defined by path integration ($p > 0.05$). Inset figure shows circular distribution of ants entering a circle (radius, 0.2 m) surrounding the nest entrance (filled red circles, data significantly directed, Rayleigh test, $p < 0.001$, mean vector, 82° , length of mean vector, 0.6; open blue circles, data not directed, $p > 0.05$; mean vector, 204° ; length of mean vector, 0.2).

(Biv) Example runs of ants approaching the nest from downwind (in red) and upwind (in blue), respectively (paths also shown in Bi).

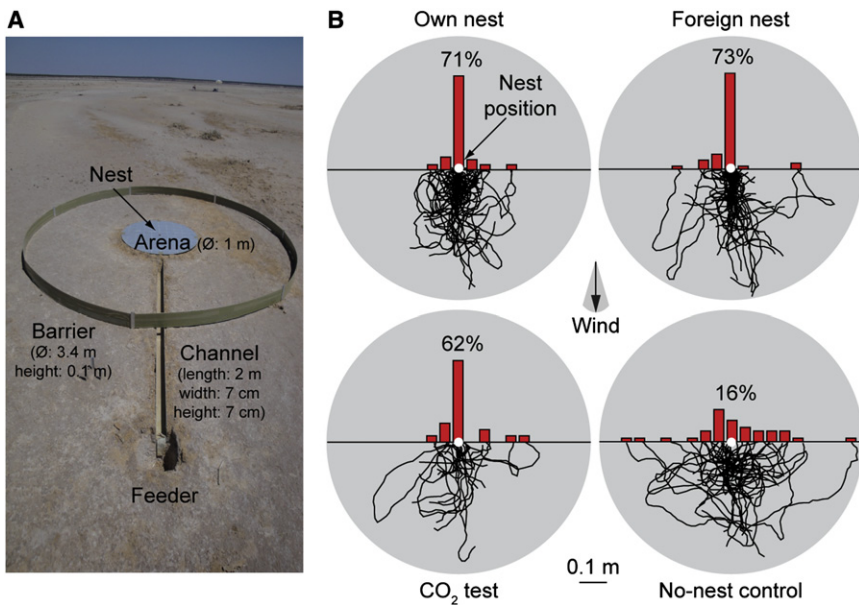


Figure 2. Plume Following Is Not Nest-Specific and Can Be Induced by CO₂

(A) Experimental setup: circular arena with central opening (3 cm) placed on top of the nest and a surrounding barrier to exclude remote nest-defining visual cues. Aluminum channel dug into the ground leads ants to an artificial feeder. Ants leave the nest by the central opening, pass the channel, and get cookie crumbs at the feeder. (B) Nest approach of ants captured at the feeder and released either at the same feeder (own nest), at a setup connected to another nest (foreign nest), at a setup not connected to any nest (no-nest control), or at a setup not connected to any nest but equipped with a CO₂ plume (CO₂ test). Gray circles depict circular arenas (Ø: 1 m). Black lines show paths from 2 s before the first plume contact until the ants reached either the nest position (white circle) or a fictive line orthogonal to the wind direction crossing the central opening (own nest, n = 52, median distance when passing the nest: 0 cm; foreign nest, n = 44, median distance: 1 cm; no-nest control, n = 37, median distance: 7 cm; CO₂ test, n = 21, median distance: 2 cm). Runs were normalized to wind direction. Histograms depict line crossings in 5 cm bins. Numbers above bars depict percentage of ants that crossed the line at the nest position. No-nest control differed significantly from conditions in which ants were tested either with own nest, foreign nest, or CO₂ plume (Kruskal-Wallis test and Dunn's multiple comparison tests, p < 0.05). There was no difference between the latter three test conditions (p > 0.05). For details, see [Experimental Procedures](#). For example run, see [Movie S2](#).

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to the nest, which they pinpoint using chemical cues [25]. In contrast to *C. fortis* ants, the bugs react to the chemical cues from their own nest even when the path integrator tells them that they are far away from home. However, because the bugs are able to discriminate their own from foreign nests by chemical cues, they do not run the risk of entering the wrong nest [26].

In addition to chemical cues, ants use visual landmarks to pinpoint the nest entrance [6, 7]. Similar to our results for nest-odor cues, ants ignore nest-defining visual cues when the path-integration vector indicates that they have not yet

arrived in the vicinity of the nest-entrance hole [26]. Our results suggest that, apart from informing foragers about their position relative to the nest, path integration seems to play a crucial role in preventing foragers from being killed by following ambiguous nest cues.

Experimental Procedures

Experimental Site and Ant Species

Field experiments with the desert ant *C. fortis* were performed during early June and mid-August 2010 in a flat salt pan near the village of Menzel Chaker (Tunisia).

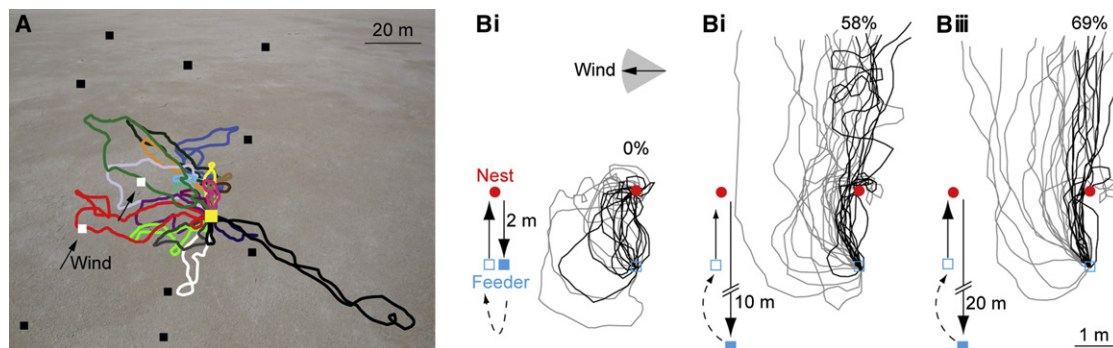


Figure 3. Path Integration Controls Plume-Following Behavior

(A) Foraging runs of 20 ants from a single nest (yellow square) tracked with GPS. Different colors represent different foraging runs. Black and white squares indicate foreign nests whose plumes (white) or were not (black) crossed by tracked foragers. Crossing the nest plume was assumed to have occurred when an ant passed the nest less than 0.3 m downwind. The mean minimum distance between neighboring nests was 23 m; the mean maximum foraging distance was 28 m.

(B) Experimental paradigm in which we set path integration in conflict with the nest-derived plume. Ants trained from nest (red circle) to feeder (blue square; nest-to-feeder distance; Bi, 2 m; Bii, 10 m; Biii, 20 m) were displaced from feeder (dashed arrows) and released along training route 2 m away from the nest (release point, open blue square). Ants followed their path-integration vector (black arrows) and reached the nest-derived plume with a home-vector length of 0 m (Bi), 8 m (Bii), or 18 m (Biii). Black trajectories depict ants that passed the nest in less than 0.3 m distance in downwind direction (Bi, n = 12 ants; Bii, n = 13 ants; Biii, n = 13 ants). Gray trajectories depict ants that passed the nest more than 0.3 m distance in a downwind direction (Bi, n = 9 ants; Bii, n = 17 ants; Biii, n = 15 ants). Numbers above trajectories depict the percentage of ants that passed but rejected the plume and followed the path-integration vector (chi-square test for trend, p < 0.05).

Experiments

Ants Follow the Plume of Their Nest

We first video-recorded the final part of the ants' homing runs in the vicinity of a nest entrance during natural foraging. A thin thread attached to a needle and placed close to the nest entrance continuously informed us about wind direction. Recorded traces were transferred to paper and digitized using Graph Click (version 3.0). A circle (\varnothing : 1 m; 45° segments) painted on the ground served as a reference. The positions of the homing ants when crossing two fictive circles with radii of 25 cm and 2.5 cm were recorded and the angular distributions were analyzed using Oriana 3 (used throughout the analyses of the circular data). The directionality of the data was examined using the Rayleigh test.

We next trained foraging ants to visit an artificial feeder containing cookie crumbs at a distance of 10 m in the open and flat salt pan; the nest-to-feeder direction was orthogonal to the wind direction (see Figure 1B). After at least half a day of training, we captured ants at the feeder and displaced them 1.5 m either downwind or upwind of the feeder. We recorded homing runs on paper until the ants entered the nest. A grid (mesh width, 1 m) on the ground served as a reference. Ants displaced in such a way still had their path-integration vector available and reached a fictive nest position that was located downwind or upwind of the nest, respectively. Here and everywhere else in the following experiments, the ants were tested individually and only once. Homing traces were digitized and the run lengths of final parts of the traces (i.e., within the black rectangle in Figure 1Bi) were calculated by Gedit Graphics Editor and Run Analyzer [27]. Run lengths of upwind approaches were compared with those of downwind approaches using the Mann-Whitney test (GraphPad InStat, version 3.06, was used throughout the statistical analyses of the noncircular data). The positions where the ants (displaced either upwind or downwind) crossed horizontal lines at 5 m, 2 m, 1 m, 0.5 m, 0.2 m, and 0 m away from the fictive nest positions were measured in order to see whether the ants' homing paths differed from the path of the vector course (see gray lines in Figure 1Bi). The Wilcoxon signed rank test was performed to analyze whether the data differed from 0 (direct line between release point and fictive nest position). In addition, the angular distribution of the final nest approach was measured at 0.2 m from the nest and the directionality of the data was examined using the Rayleigh test.

Foreign Nest-Derived Plumes Induce Plume-Following Behavior

An aluminum arena (\varnothing : 1 m) was placed on the flat desert ground on top of the nest entrance so that ants were forced to leave and enter the nest solely through a central hole in the arena (\varnothing : 0.03 m). The arena established a homogeneous and defined area around the nest entrance and excluded any nest-defining cues other than nest odor. An aluminum channel (U-shaped cross-section; length: 2 m, width: 0.07 m, height: 0.07 m) dug into the ground led the ants to a feeder containing cookie crumbs (see Figure 2A). Within an hour, all foraging ants of a nest had learned this procedure. The arena was surrounded by a 0.1 m high circular barrier (\varnothing : 3.4 m) to prevent ants from using remote nest-defining visual cues. A thin thread attached to a needle and placed close to the nest entrance provided continuous information about wind direction. Smoke (produced by an air flow tester, Draeger Safety AG, Luebeck, Germany) released from the central hole of the arena allowed us to visualize the nest-derived plume and confirmed that the wind close to the nest entrance was not turbulent in the presence of the surrounding barrier, i.e., the plume was straight (see Movie S1). Based on the visualization with smoke, we defined the odor plume as a straight line originating at the nest. Preliminary observations of ants tested in the arena that was connected to their own nest revealed that homing ants almost always made immediate turns toward the nest when they passed the nest downwind in less than 0.3 m distance, whereas they did not do so when passing the nest farther away. This suggests that the functional reach of the potential plume lies around 0.3 m. Consequently, we assumed a nest-derived plume of 0.3 m length in subsequent experiments. Identical setups at different sites allowed us to video-record the homing performances of ants returning from the feeder to either their own nest, to a foreign nest, or to a no-nest control. In order to suppress any contact with resident ants during testing, a net covered the nest entrance. The testing of ants under different conditions was randomized. The video-recorded homing paths were recorded on paper from shortly before the ants had their first contact with the odor plume (as defined by the filmed position of the thin thread) and lasting until they either reached the nest position or crossed the fictive line as shown in Figure 2B. Because the nest entrance on the arena was visually inconspicuous homing ants did not always reach the nest directly but missed the entrance by few centimeters. At that time, the path-integration vector was run off and the ants started a nest search until they finally reached the nest plume [28, 29].

A grid (mesh width, 0.1 m) painted on the arena served as a reference. Run directions were normalized to wind direction. The absolute values of the distances between crossing positions and nest entrance were analyzed using the Kruskal-Wallis test with Dunn's multiple comparison tests.

Risk of Following the Plume of a Foreign Nest

In an additional experiment, we let the ants return to the foreign nest but used no net to cover the entrance hole, i.e., the ants were not prevented from entering the foreign nest. We marked the ants at the feeder with a color dot on their gaster, displaced them to a foreign nest, tracked the number of test ants entering the nest, and observed the response of resident ants. We counted ants that were directly attacked and pulled deeper into the nest. Test ants that did not reappear at the surface after 2 hr were considered dead.

CO₂ Triggers Plume-Following Behavior

Carbon dioxide released from nests was measured either 2 cm downwind of the nest entrances at ground level or at the same height in a nest-free area (using a Telaire 7001 CO₂ measurement device).

In the absence of any nest, using the same arena setup as described previously, we provided ants with an artificial CO₂ plume that mimicked the concentration emanating from a nest. CO₂ was released out of the central opening of the arena (around 500 ppm measured 2 cm downwind of the opening) using a tube connected to a CO₂ bottle.

State of the Path-Integration Vector Controls the Response to the Nest Odor

Natural foraging runs: All *C. fortis* nests in an area of approximately 100 m × 100 m were localized with a GPS measurement device (GARMIN eTrex Vista HCx). Foraging runs of 20 ants of a nest located centrally were GPS-tracked, i.e., one of us carried the GPS device with an activated path-recording function and followed foraging ants at a distance of 2 m. Due to the flatness of the area, the GPS always received input from at least 12 satellites, resulting in an accuracy of about 2 m. When ants passed close to the vicinity of neighboring nests, we immediately measured the minimum distance between the path and the nest entrance and recorded the actual wind direction. GPS-recorded foraging runs were analyzed graphically, and mean minimal distances between neighboring nests ($n = 12$) and maximal foraging distances of ants ($n = 20$) were measured.

Conflict of path integration vectors and plume-following behavior: Foraging ants were trained from the nest to a feeder located 2 m, 10 m, or 20 m away from the nest with the nest-to-feeder direction being orthogonal to wind direction (Figure 3B). After at least half a day of training, we captured ants at the feeder and released them along the training route 2 m away from the nest (in the 2 m training paradigm, the ants were captured and released at the feeder). When entering the plume, the ants' home-vector length was either 0 m (training distance: 2 m), 8 m (training distance: 10 m), or 18 m (training distance: 20 m). Homing runs of ants were recorded on paper until the ants either entered the nest or overshot the nest entrance for more than 4 m; runs were then digitized. A grid (mesh width, 1 m) on the ground served as a reference. Only ants that passed the nest downwind (i.e., on the side of the nest-derived plume) were recorded, and we only considered ants that crossed the plume within the functional reach of 0.3 m in the analyses. The number of ants that entered the nest after contact with the odor plume was counted, and the data were analyzed with a chi-square test for trends.

Supplemental Information

Supplemental Information includes two movies and can be found with this article online at doi:10.1016/j.cub.2012.02.029.

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