

Trail geometry gives polarity to ant foraging networks

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Pheromone trails are used by many ants to guide foragers between nest and food^{1–4}. But how does a forager that has become displaced from a trail know which way to go on rejoining the trail? A laden forager, for example, should walk towards the nest. Polarized trails would enable ants to choose the appropriate direction, thereby saving time and reducing predation risk. However, previous research has found no evidence that ants can detect polarity from the pheromone trail alone^{3,5–7}. Pharaoh's ants (*Monomorium pharaonis*) produce elaborate trail networks throughout their foraging environment⁸. Here we show that by using information from the geometry of trail bifurcations within this network, foragers joining a trail can adaptively reorientate themselves if they initially walk in the wrong direction. The frequency of correct reorientations is maximized when the trail bifurcation angle is approximately 60 degrees, as found in natural networks. These are the first data to demonstrate how ant trails can themselves provide polarity information. They also demonstrate previously unsuspected sophistication in the organization and information content of networks in insect societies.

Ants use chemical, visual and even magnetic cues to orient themselves correctly in their foraging environment^{4,9}. Some pheromone-trail-following ants readily correct their course, when displaced, by using their memory of environmental cues (landmarks and sun compass)^{3,10,11}. For example, in the common garden ant *Lasius niger*^{10,11} movement of visual cues by the experimenter results in course adjustments by the ant, while in the Argentine ant *Linepithema humilis*¹¹ and *La. fuliginosus*³ pheromone trails are always followed, regardless of whether visual cues are moved. Thus ants using external orientation cues can readily determine direction when on a trail. However, species that are principally guided by the chemical trail itself may find reorientation harder. One solution would be to follow the trail to its conclusion at nest or food, and then reorientate if necessary. But making such long trips to determine directionality would be costly. A better solution would be to have polarized trails.

Previous experimental studies, however, found no evidence of intrinsic polarity in pheromone trails^{3,6,7,10}. These studies assumed that polarity information contained in trails must take the form of a pheromone concentration gradient. However, pheromone concentration is not the only mechanism that could polarize trails. In particular, trail geometry could supply this information. Ant foraging trails are often thought of as a single line, but in fact most trail-laying ants produce complex trail networks branching throughout their foraging environment^{8,12–15}, suggesting that network geometry could provide polarity information. Acosta *et al.*¹⁶ studied networks of three species of leafcutter ants (*Atta sexdens*, *A. capiguara* and *A. laevigata*) and one seed harvester ant (*Messor barbarus*), and found that they shared one common geometrical feature—the mean angle between trail bifurcations as they branch out from the nest is 50–60°.

Our results show that Pharaoh's ant colonies (*Mo. pharaonis*) produce similar networks (Fig. 1a–c) with a mean bifurcation angle of 53° (Fig. 1c). Pharaoh's ants readily form trail networks, even before discovering food, which highlights their reliance on pheromone trails for orientation^{8,17}.

Information inherent in trail bifurcations could be used by

foragers to determine trail polarity. For example, ants encountering a 60° bifurcation while travelling away from the nest would have a choice of two paths, each deviating by approximately 30° from their current heading. Returning foragers would also have a choice of two paths but, in contrast to outbound ants, one deviates by only a small amount (30°) from the current heading while the other deviates greatly (120°). The trail making a large deviation would lead away from the nest whereas the one with a small deviation only would lead to the nest.

In experiment 1, we determined whether individual Pharaoh's ant foragers could reorientate when placed onto a natural and complete trail network lacking other ants, if they were initially walking the wrong way. Our results clearly show that they can. Most of the foragers (70%) reoriented themselves (75%, $n = 20$, of fed foragers; and 65%, $n = 20$, of unfed foragers), which is highly significant when compared to the 12.5% ($n = 40$) that reoriented in the control group (χ^2 test, degrees of freedom, d.f. = 1, $P = < 0.001$). Corrections to routes took the form of reorientations (U-turns or large deviations) at a trail bifurcation (53.6%, $n = 28$) or U-turns following a bifurcation (46.4%, $n = 28$), which suggested that bifurcations are important.

In experiment 2, we obtained strong support for the geometry hypothesis. In this experiment we allowed individual ants (fed or unfed) to walk along experimental straight or bifurcating trails. Tests conducted on straight trails showed that any reorientations occurring were as likely to be correct (R_c) as incorrect in relation to the polarity of the trail when it was originally formed (R_i), that is, 7% versus 6% ($R_c:R_i = 1.17$). These course changes were all U-turns and occurred at a low frequency (6.5%, $n = 200$). In addition, 17.5% of ants left the trail altogether. In contrast, a single trail bifurcation (55°) facilitated many more course corrections, and so

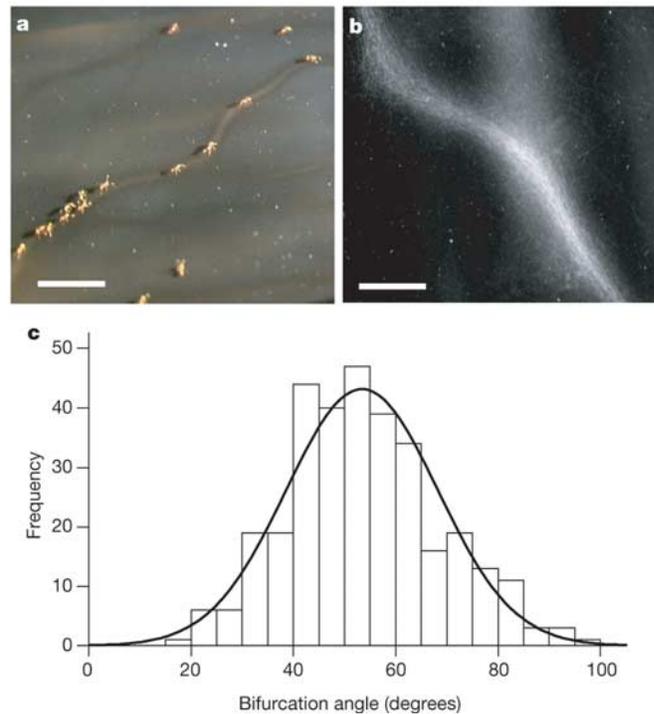


Figure 1 Pheromone trail networks of Pharaoh's ants on a smoked glass surface. **a**, Part of a network showing bifurcations to smaller trails (scale bar, 1 cm). **b**, Close-up of a single bifurcation (scale bar, 0.5 cm). **c**, Analysis of bifurcation angles from four separate trail networks: mean angle = 53.4°, s.d. = 14.8°, $n = 321$; mean distance between bifurcations = 2.9 cm, s.d. = 2.3 cm, $n = 485$. Solid line, normal distribution curve.

presumably provided much more information. 43% of fed ants ($n = 100$) made U-turns upon meeting the bifurcation point when walking in the 'wrong' direction: that is, away from the nest (Supplementary Table 1). Conversely, only 8% of fed ants walking the 'correct' way made U-turns or other corrections that led to them incorrectly heading away from the nest. This is similar to the 'background' U-turn frequency observed on straight trails (6.5%). Data from unfed ants are very similar. 47% ($n = 100$) made course corrections at the bifurcation point when moving the 'wrong' way: that is, towards the nest. Again, only 8% walking the 'correct' way made incorrect course changes. Overall, correct course changes (R_c) occurred far more frequently than incorrect ones (R_i), producing a correct to incorrect ratio ($R_c:R_i$) of 5.63 (45%:8%). Note that although only 45% of ants corrected their orientation at a single bifurcation, real networks contain many bifurcations and many opportunities for course correction.

To control for the possibility that alternative orientation cues might confound our results, these experiments were repeated in two alternative positions, by rotating the test trail sections through 90° and 180° relative to their original position when established. The results were not significantly different to those obtained in the original position. (For the straight trail: 90° rotation, χ^2 test, d.f. = 3, $P = 0.054$, $R_c:R_i = 0.6$; 180° rotation, χ^2 test, d.f. = 3, $P = 0.064$, $R_c:R_i = 1.17$. For the bifurcating trail: 90° rotation, $\chi^2 = 1.185$, d.f. = 3, $P = 0.553$, $R_c:R_i = 6.33$; 180° rotation, $\chi^2 = 4.565$, d.f. = 3, $P = 0.102$, $R_c:R_i = 4.06$.) These results confirm that Pharaoh's ants making course corrections while walking on trails use pheromone trails for orientation, rather than external cues. They also confirm that straight sections of the trails are not polarized.

The above trials used experimental trail bifurcations of 55° to investigate course corrections at the natural angle of trail bifurcations. However, it was also important to investigate reorientation at additional bifurcation angles. In particular, the trail-geometry hypothesis predicts that the ability of ants to correctly reorientate will diminish as the angle approaches 120° . This is because a bifurcation of 120° is symmetrical and conveys no polarity information. Using the same methods as above, we studied angles of 30, 45, 60, 75, 90, 105 and 120° . Results for correct and incorrect reorientations are presented in Fig. 3a and reorientation ratios ($R_c:R_i$) in Fig. 3b. The relationship is highly nonlinear

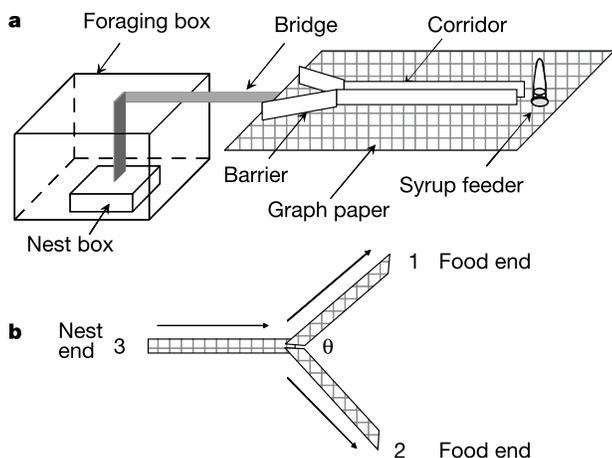


Figure 2 Experimental set-up used to form straight trails and assembly of trail bifurcations. Foraging ant traffic was constrained to produce straight pheromone trails on paper (a), which were cut into sections (b) and reassembled to form the requisite trail bifurcations with variable angle $\theta = 0-120^\circ$. Start locations were designated as 3, the nest direction (left) and 1 or 2, the food directions (right). Arrows show that the original direction to food on the trail was preserved when bifurcations were prepared.

($r^2 = 0.016$; analysis of variance, ANOVA, d.f. = 8, $F = 0.11$, $P = 0.749$) but fits with high statistical significance to a quadratic curve ($R^2 = 0.923$; ANOVA, d.f. = 8, $F = 36.16$, $P < 0.001$). Bifurcation angles from $30-90^\circ$ were highly effective, with $R_c:R_i$ ratios ranging from 3.28 at 30° to a maximum at 60° ($R_c:R_i = 5.8$), then declining to 4.26 at 90° . As predicted, the ratio of 1.03 at 120° was not significantly different to that of a straight trail (1.17), demonstrating an absence of polarity information at 120° (χ^2 test, d.f. = 1, $P = 0.952$). Angles close to 60° also minimized the proportion of ants leaving the trail. The quadratic curve fitted to trail-leaving frequency ($R^2 = 0.729$; ANOVA, d.f. = 8, $F = 8.71$, $P = 0.019$) showed (Fig. 3c) that angles in the range $33-97^\circ$ had the lowest leaving rates (14–15%).

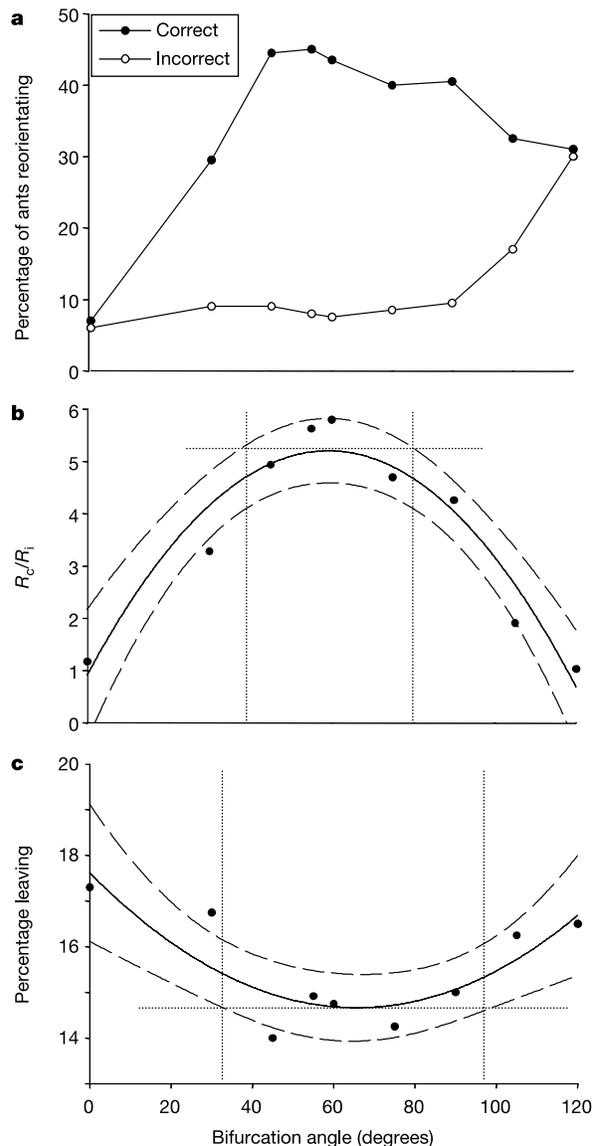


Figure 3 Outcomes of individual trail following tests using straight (0°) and bifurcating ($30-120^\circ$) trail sections. **a**, Percentage of foragers making correct and incorrect reorientations. For each point $n = 200$, except at 0° where $n = 100$. **b**, Ratio of correct to incorrect reorientations ($y = -0.0012x^2 + 0.1449x + 0.9175$) with 95% confidence interval (dashed lines, $36-81^\circ$). **c**, Percentage of individual ants departing from test trails at each angle where $n = 400$ for angles $30-120^\circ$ and $n = 200$ for 0° ($y = -0.0007x^2 + 0.0933x + 17.625$) with 95% confidence interval (dashed lines, $33-97^\circ$). (Dotted lines show the 95% confidence intervals for the angles with the maximum ratio, in both **b** and **c**.)

The branching geometry of Pharaoh's ant trails enables individual foragers moving in the wrong direction to reorient themselves. With bifurcations close to the natural angle the effect is strong both in the ratio of correct to incorrect reorientations (about 5:1) and in the proportion of ants who reorient themselves at a single bifurcation (~45%). Our results also support the geometric prediction that straight trails and those bifurcating at 120° do not result in adaptive course corrections.

The physicist Feynman speculated that a system of pheromones laid in a linear pattern of A-B-space-A-B-space might provide polarity information¹⁸. Realistically, however, such a system could only work for trails laid by one ant, because the message would be lost when trails were overlaid. Pheromone gradients could, in principle, provide polarity information but seem not to be used by ants, perhaps because they are unreliable. Trails nearer the nest should have higher pheromone concentrations caused by greater traffic. But the reverse can be true, particularly when a food source is newly discovered. In fact, the trail bifurcation system that we have discovered is reliable and much simpler.

Our results show that bifurcation angles similar to those found in natural networks (~60°) give the best reorientation ratios. Other natural transport and communication systems with branching, such as plant roots or cardiovascular systems, are thought to have evolved to minimize energy expenditure in resource distribution^{19–23}. Similarly, trail bifurcations of approximately 60° may actually optimize the flow of ants through the network, particularly in a natural situation where traffic is bi-directional²⁴. Thus, trail networks could have been evolutionarily optimized to achieve an efficient flow of resources to the nest and ants may exploit this emergent property of networks in orientation. The geometry of these trail networks constructed by Pharaoh's ants provides a subtle and previously unsuspected source of information, enabling the colony to forage more efficiently. □

Methods

Study species

Study colonies of Pharaoh's ants (*Mo. pharaonis*) contained 1,200–2,500 workers, brood at all stages and multiple queens (12–50), and were housed in wooden nest boxes (11 cm × 8 cm × 2 cm high) held within a large plastic foraging box (45 cm × 30 cm × 15 cm high) in a climate-controlled room (24 ± 2 °C, relative humidity = 30%, light/dark ratio 12 h:12 h). *Mo. pharaonis* has monomorphic workers, ~2 mm body length, and nest-mate recognition is absent in this unicolonial ant⁴. Frequent splitting and combining of the colonies made the six study colonies genetically similar. Colonies were given fresh water ad libitum and fed daily with mealworm (*Tenebrio*) larvae, weekly with apple sauce, and monthly with dried egg yolk.

Quantifying the geometry of trail networks formed on smoked glass

Sheets of toughened glass (39.2 cm × 27.6 cm) were held over a wax candle flame to coat them with a fine layer of soot. A colony was then given access to one edge of a smoked sheet via a drawbridge. A syrup feeder was placed at the opposite edge. Colonies were allowed to forage for 2 h, which was sufficient time to establish trail networks covering the glass sheet. The ants were shaken off and the trail networks, visible as lines where the soot had been worn away (Fig. 1), were traced onto transparent plastic and the bifurcation angles measured.

Individual forager reorientation on smoked glass trail networks (experiment 1)

In each orientation trial individual forager ants were collected from the floor of their colony's foraging box and put into one of two internal states, 'unfed' or 'fed', as follows. A group of 25 ants were held for 2–2.5 h in an empty plastic box (unfed), or in a box containing three 1 M sucrose solution feeders. Of the ants with access to food only those with "a visibly enlarged gaster, which appeared striped because all the abdomen was distended, exposing the inter-segmental membranes"²⁵ were defined as fed. We placed single fed or unfed ants on a natural trail network (smoked glass, as above) from which the ants had been removed within the previous 10 min. Each ant was oriented on a trail facing the 'wrong' direction (that is, away from the nest) when fed and facing towards the nest when unfed. Twenty ants in each of the two states were observed until they reached either the feeder or the drawbridge via the trail network. We noted how many fed and unfed ants correctly reoriented on the trail network and where they did this relative to trail bifurcations. Control samples of 20 ants in each of the two states were also placed on trails facing the 'correct' direction and their destinations recorded.

Individual trail bifurcation tests (experiment 2)

To construct experimental bifurcations we constrained the foraging of *M. pharaonis*

colonies using plastic barriers to form straight pheromone trails on a piece of paper leading from the nest to a syrup feeder. We temporarily linked a colony box to a foraging arena (140 cm × 70 cm) with a drawbridge. Part of the arena was covered with two A4 (29.5 cm × 21.0 cm) sheets of ECF (eucalyptus chlorine-free) paper photocopied with a 2-mm grid. Two polycarbonate strips (60 cm × 4 cm × 0.5 cm thick), coated with Fluon to prevent ants from climbing them, were placed on the paper to form a 4-mm-wide corridor leading to the syrup feeder, which was held within a section of Fluon-coated plastic pipe (8 cm in diameter). A total of 2,000 ants were counted passing the mid-point of the corridor (both directions combined) before ants were shaken from the paper. The 60 cm × 0.4 cm section along which the ants had walked and deposited trail pheromone was cut from the paper. Experimental bifurcations were constructed (except for 0°, which was a 30 cm straight trail) using three 15-cm trail sections, by cutting their tips to form the appropriate angle (30°, 45°, 55°, 60°, 75°, 90°, 105°, 120°), then securing the cut pieces of paper with adhesive tape to a fresh sheet of backing paper (Fig. 2). Because trails decay rapidly²⁶ we used trail bifurcations for a maximum of 20 min after the ants forming the trail had been removed from the paper. For each angle we tested 100 individual ants starting at the nest end (position 3) and 50 ants at each of the two food ends (positions 1 and 2), for each state (unfed and fed, as detailed in experiment 1). For straight trails we used only 50 ants in each state at each end. Trail decay limited separate trials to 20–50 ants on each occasion so data from several trials were pooled per bifurcation angle. To control for visual and magnetic cues, we repeated experiments for straight trails and 55° bifurcations but with the trail set-up rotated through 90° and 180° relative to the standard position.

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