

Are ants sensitive to the geometry of tunnel bifurcation?

Grégory Gerbier · Simon Garnier · Cécile Rieu ·
Guy Theraulaz · Vincent Fourcassié

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Abstract The ability to orient and navigate in space is essential for all animals whose home range is organized around a central point. Because of their small home range compared to vertebrates, central place foraging insects such as ants have for a long time provided a choice model for the study of orientation mechanisms. In many ant species, the movement of individuals on their colony home range is achieved essentially collectively, on the chemical trails laid down by their nest mates. In the initial stage of food recruitment, these trails can cross each other and thus form a network of interconnected paths in which ants have to orient. Previous simulation studies have shown that ants can find the shortest path between their nest and a food source in such a network only if there is a bias in the branch they choose when they reach an asymmetrical bifurcation. In this paper, we studied the choice of ants when facing either a symmetrical or an asymmetrical bifurcation between two tunnels. Ants were tested either on their way to a food source or when coming back to their nest, and either in the presence or in the absence of a chemical trail. Overall, our results show that the choice of an ant at a tunnel bifurcation depends more on the presence/absence of a trail pheromone than on the geometry of the bifurcation itself.

Keywords Ants · Argentine ant · *Linepithema humile* · Orientation · Trail network

Introduction

Ant colonies use a variety of foraging strategies to exploit the food sources present in their foraging area (Beckers et al. 1989; Traniello 1989). In some species, food collection is achieved exclusively by solitary individuals, while in others it is achieved mostly collectively, by thousands of workers travelling along well-defined foraging trails (Hölldobler and Wilson 1990). These trails emerge from a succession of pheromone deposits, first by the scouts that have discovered the food source and that have returned to the nest, then by the workers that are recruited by these scouts from inside the nest. In species of ants forming large colonies, such as army ants, leaf-cutting ants or seed-harvesting ants, simultaneous mass recruitment to several food sources can lead to the emergence of a system of dendritic foraging trails centered on the nest (Hölldobler and Möglich 1980; Vasconcelos 1990; Gotwald 1995; Kost et al. 2005). In some species, the workers lay a chemical trail more or less permanently and a network of interconnected exploratory trails can also emerge as a result of mass recruitment to a new area (*Linepithema humile*: Aron et al. 1989; *Monomorium pharaonis*: Fourcassié and Deneubourg 1994).

While moving within a network of chemical trails, ants are faced with a succession of bifurcations, and at each of these bifurcations they have to make a choice as to which trail they will take next. As several trails can sometimes lead to the same food source, at least in the initial stage of a network, the length of the path followed by an ant within a network depends on the choice it makes at each bifurcation. Using an artificial network of galleries in which several interconnected paths can be used to reach a single food source, Vittori et al. (2006) have shown that ants choose one of the shortest possible paths in the network with a

G. Gerbier · S. Garnier · C. Rieu · G. Theraulaz · V. Fourcassié (✉)
Centre de Recherches sur la Cognition Animale,
UMR CNRS 5169, Université de Toulouse,
118 route de Narbonne, 31062 Toulouse cedex 4, France
e-mail: fourcass@cict.fr

probability that is significantly much higher than that given by a random orientation. Computer simulations show that the choice of one of the shortest paths in such a network can emerge only if an intrinsic bias, i.e. a bias in the absence of a chemical trail, is introduced in the choice of the ants when they face asymmetrical bifurcations (Vittori et al. 2006): ants should preferentially choose the branch that deviates less from their initial direction, which is actually what is observed in real experiments (Vittori et al. 2006). This means that ants are able to measure in one way or another the deviation they make from their initial direction when choosing a branch. This has indeed been demonstrated by Jackson et al. (2004) in an elegant experiment on the Pharaoh's ant *Monomorium pharaonis*. These authors have shown that the workers of this species can use the differences in the geometry of the bifurcations they face to orient within a network of foraging trails. In a system of dendritic foraging trails centered on the nest, an ant exiting the nest and moving to the food sources located at the periphery of the network generally faces symmetrical bifurcations, i.e. the two trails that follow a bifurcation deviate by the same angle from the original direction of the ant. An ant coming back to its nest on the other hand face asymmetrical bifurcations: the trail leading to the nest that follows the bifurcation deviates less from the original direction of the ant than that leading to another food source. This geometric property of trail networks is used by ants to find their way in a network: when unfed ants going to a food source face an asymmetrical bifurcation, they have a high tendency to make a U-turn and come back to their point of departure, while fed ants coming back to the nest do the same when they face a symmetrical bifurcation.

This paper describes a simple experiment carried out in order to understand the mechanisms that generate the bias observed in ants at asymmetrical bifurcation when they orient in a system of multiple interconnected galleries such as that used in Vittori et al. (2006). As in Jackson et al.'s (2004) experiment, we tested the behaviour of ants at a symmetrical or asymmetrical bifurcation in two different motivational contexts: either when they were unfed and exploring the environment, or when they had just fed and were returning to their nest. We assumed that if ants use the geometry of the bifurcations to orient in a network of foraging trails, as shown by Jackson et al. (2004), they should be more sensitive to the geometry of a tunnel bifurcation in the presence than in the absence of trail pheromone. We thus tested ants in two different experimental set-ups (in the presence and in the absence of a trail pheromone signal) and compared their orientation performance. The aim of our study was not to replicate, in the Argentine ant, Jackson et al.'s (2004) experiment on the measurement of the geometry of trail bifurcation by the Pharaoh's ant. The experimental set-up we used was indeed completely different

from that used by Jackson et al. (2004). In our experiment, ants moved in an enclosed tunnel system, whereas in Jackson et al.'s (2004) experiment, ants moved on strips of paper and could leave the trail at any moment. Our aim was specifically to investigate the origin of the orientation bias observed in Argentine ant when workers reach an asymmetrical bifurcation in a tunnel network.

Methods

Biological material

A total of 15 experimental colonies of the Argentine ant *Linepithema humile* (Formicidae, Dolichoderinae), each containing 2,000 workers without queen or brood were used in the experiments. The ants were collected near Narbonne on the French Mediterranean coast where *L. humile* is considered as an invasive species with unicolonial habit (the species forms a gigantic colony extending along the Mediterranean coast from Italy to Portugal and individuals mix freely among physically separated nests: Giraud et al. 2002). The ants were housed in artificial plaster nests ($\varnothing = 10$ cm) and had access to an external foraging area. They were reared in an experimental room at a constant temperature of 25°C under L: D 12: 12 conditions and fed twice a week with a mixture of eggs, carbohydrates and vitamins (Bhatkar and Whitcomb 1970) and with *Musca domestica* maggots.

Experimental set-up and protocol

The orientation of the Argentine ant workers was tested in a series of alternatively inverted Y-mazes whose branches deviated by an angle of 60° (Fig. 1). The PVC plate in which these mazes were carved could slide between two other PVC plates that were fixed. A transparent PVC plate fixed on the two lateral plates and covering the whole set-up prevented the ants from escaping the maze. Small access galleries were carved in one of the fixed plate, while in the other fixed plate small circular chambers ($\varnothing = 20$ mm), each with a 15 mm long and 5 mm wide access gallery, were carved. The depth of the galleries and chambers were 5 mm. During a test, the central plate of the set-up was slit so that each branch of a maze coincided with one access. To prevent the use of external visual cues, the whole set-up was surrounded by white tissue, which also ensured an indirect and diffuse lighting. On its way to the food an ant could face either a symmetrical (S) or an asymmetrical bifurcation (A), and on its way back it could face again either a symmetrical (S) or an asymmetrical (A) bifurcation. This makes four combinations of tests possible for the foodbound and nestbound trip: S–S, A–A, S–A and A–S.

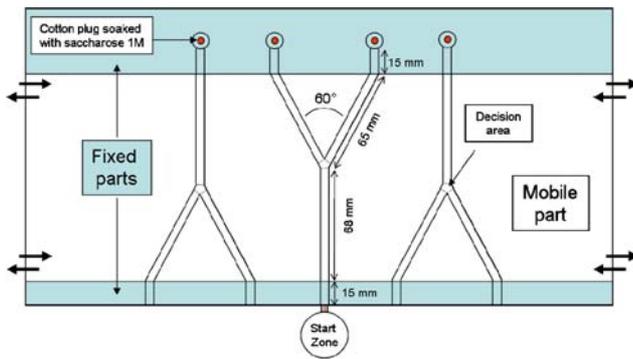


Fig. 1 Experimental set-up. The mazes used in the experiment were carved in a PVC plate that could slide between two other PVC plates that were fixed. A transparent PVC plate fixed on the two lateral plates and covering the whole set-up prevented the ants from escaping the maze. Small access galleries were carved in one of the fixed plates, while in the other fixed plate small circular chambers ($\varnothing = 20$ mm) in which food was placed were carved. The depth of the galleries and chambers were 5 mm and the width of the galleries 5 mm. During the test, the central plate of the set-up was slit so that each branch of a maze coincided with one access on the lateral plates

A test was started by collecting an ant in the foraging area of its colony and by gently depositing it in a small Petri dish placed in front of an access gallery (“START” in Fig. 1). A food source (a small piece of cotton soaked with a 1 M solution of sucrose) was placed in each circular chamber (during symmetrical foodbound tests) or in only one of them (during asymmetrical foodbound tests). We waited until the ant found the food source and, after it had fed on it, until it went back to its point of departure. Each ant was thus tested successively in an unfed (foodbound trip) and then in a fed (nestbound trip) state. For both trips, the following data were recorded:

- Initial choice: the first branch chosen after the ant crossed the bifurcation for the first time. A branch was considered as chosen when the ant reached and moved beyond an area we called “decision area” (Fig. 1). Note that an ant could enter the decision area and make a U-turn to go back toward its point of departure. In that case, the initial choice of the ant corresponded to the branch by which it entered the maze.
- Final choice: the first branch extremity reached.
- Whether or not the ant made a U-turn on the branch chosen after crossing the bifurcation for the first time. Spontaneous U-turns occurring before an ant reached the bifurcation for the first time were not considered.

We made two series of tests: one with an unmarked set-up and the other with a marked one. In the first series of tests, ants were tested in mazes in which no chemical trail had been deposited before. The bottom of the galleries was made of PVC. Each maze was used once and then washed with alcohol before being reused. Ants were thus tested in

different mazes on their way to the food and back to the nest. Therefore, had the ants laid down a pheromone trail during their outbound trip, this manipulation should prevent them from using it when returning to the nest. In the second series, pieces of paper on which a fresh chemical trail had been deposited were placed before the tests at the bottom of the maze galleries. To avoid the effect of trail decay, the same pieces of papers were used during only 20 min. The trail pheromone duration of *L. humile* is indeed estimated to be close to 30 min (Deneubourg et al. 1990). This allowed us to test on average three ants. The six pieces of paper (three for the access galleries and one for each branch of the maze) that were used to cover the bottom of the maze were cut from a piece of paper that had been marked during 30 min by workers of a colony of the Argentine ant travelling between their nest and a food source (1 M saccharose solution). This duration was sufficient to ensure that the paper was marked homogeneously.

When ants were tested in marked set-ups with a different type of bifurcation in their food- and nestbound trips, the same maze was used, whereas when they were tested with the same type of bifurcation on both trips, two adjacent mazes were used. If ants lay down a trail during their outbound trip, they could theoretically use it during their return trip when the same maze was used. However, the pieces of paper that were placed at the bottom of the tunnels had been marked by ants during 30 min. They were thus saturated by trail pheromone and it is highly unlikely that ants could be able to perceive their own trail against this saturated background to orient on it during their return trip. Besides, no individual trail idiosyncrasy has ever been shown in the Argentine ant. When two adjacent mazes were used, the pieces of paper that were placed in the two mazes were marked by two different experimental colonies. Since the Argentine ant is uniclonal (Tsutsui et al. 2000; Giraud et al. 2002) workers of one colony readily follow a trail laid by another colony. Two adjacent mazes were used in both cases during tests in unmarked set-ups.

A total of 50 ants were tested in each set-up (marked and unmarked) for each combination of bifurcations an ant could encounter on its way to the food and back to the nest (S-S, S-A, A-S, A-A). Each ant was tested once and was excluded from the experimental colonies after being tested.

Statistical analysis

A χ^2 test for contingency tables was used to compare the proportion of ants choosing each of the three branches of the set-up in their initial and final choice. A binomial test was used to test the random character of the initial and final orientation of the ants between the two branches they faced after crossing the bifurcation. A χ^2 test for contingency tables was used to compare the proportion of ants making

U-turns in the three branches of the mazes. A Yates correction was applied to all χ^2 statistics.

Results

The results are presented graphically in Fig. 2. There were four combinations of bifurcation types an ant could face on its outbound and nestbound trip during a test: S–S, S–A, A–S and A–A. Since there were no significant differences in the performance of the ants when they faced the same type of bifurcation, either in their foodbound or their nestbound trip, the data for each identical bifurcation in the foodbound and nestbound trip were pooled. For example, the data for the symmetrical bifurcation faced by ants in their outbound trip in the S–S and the S–A tests were pooled. This increased the sample size to 100 ants for each type of bifurcation for the foodbound and nestbound trip.

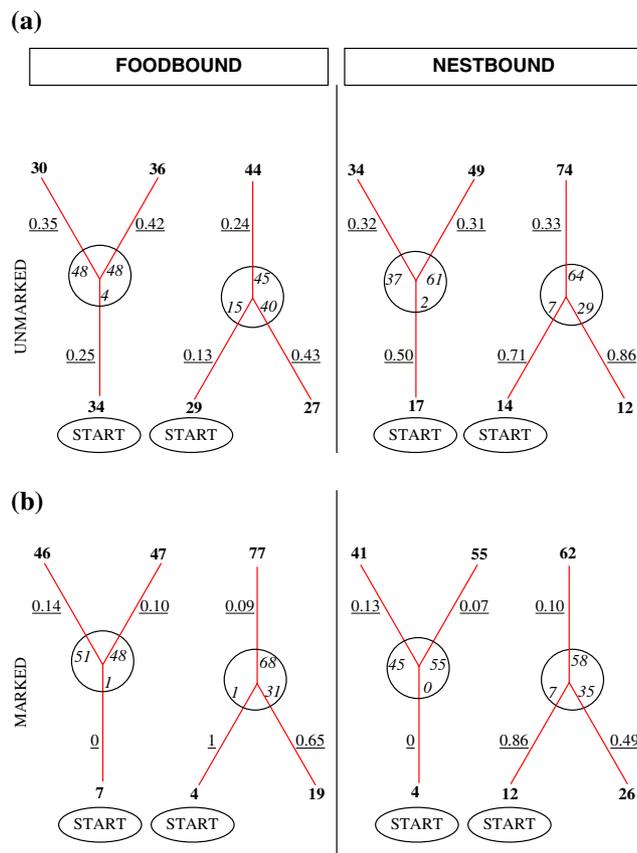


Fig. 2 Proportion of ants selecting each branch of the maze in their initial choice (*numbers in italic*) and in their final choice (*numbers in bold*) in (a) an unmarked set-up (b) a marked set-up. The proportion of ants making a U-turn on each branch of the maze after reaching a bifurcation for the first time is indicated by underlined numbers. For asymmetrical bifurcations, the data for the two possible branches of departure have been collapsed on the same branch. The movement of the ants is always from bottom to top. $N = 100$ ants for each bifurcation

Foodbound trip (unfed ants)

Independent of whether the set-up was unmarked (Fig. 2a) or marked (Fig. 2b), both the initial (binomial test: $P = 1$ and $P = 0.84$, respectively) and the final ($P = 0.54$ and $P = 1$, respectively) choice of the unfed ants that crossed a symmetrical bifurcation were not different from random. In the unmarked set-up, however, one-third of the unfed ants that faced a symmetrical bifurcation went back to their point of departure to exit the maze (Fig. 2a), while this proportion decreased to 7% in the marked set-up (Fig. 2b; $\chi^2 = 22.61$, $df = 2$, $P < 0.001$).

The results for asymmetrical bifurcations differed between the two set-ups. In the unmarked set-up, unfed ants chose equally between the two branches that followed the bifurcation (binomial test: $P = 0.66$), while their final choice was slightly, but not significantly, biased towards the branch that deviates the less from their direction of origin (binomial test: $P = 0.06$). In the marked set-up, ants expressed a significant preference in their initial and final choice for the branch that deviated by an angle of 30° over the branch that deviated by an angle of 120° (binomial test: $P < 0.001$ for both choices). The proportion of ants that went back to their point of departure to exit the maze was also higher in the unmarked set-up than in the marked set-up ($\chi^2 = 29.33$, $df = 2$, $P < 0.001$).

In both set-ups, when unfed ants faced a symmetrical bifurcation, the proportion of U-turning ants was not significantly different on the two branches that follow the bifurcation ($\chi^2 = 0.18$, $P = 0.67$; $\chi^2 = 0.04$, $P = 0.84$, for the unmarked and marked set-up, respectively; $df = 1$). When unfed ants faced a marked asymmetrical bifurcation, a much greater proportion of ants made one or several U-turns on the branch of the bifurcation that deviated by an angle of 120° than on the branch that deviated by an angle of 30° ($\chi^2 = 31.29$, $P < 0.001$, $df = 1$).

Nestbound trip (fed ants)

In the unmarked set-up, fed ants facing a symmetrical bifurcation did not choose randomly between the two branches of the bifurcation: the right branch was initially preferred (binomial test: $P = 0.02$). In the final choice, however, no preference was expressed (binomial test: $P = 0.12$). In the marked set-up on the other hand, ants did not express a significant preference for either branch they faced at a symmetrical bifurcation, both in their initial and final choice (binomial test: $P = 0.31$, $P = 0.18$, respectively). As in the foodbound trips, more ants came back to their point of departure to exit the maze in the unmarked set-up than in the marked set-up ($\chi^2 = 9.05$, $df = 2$, $P = 0.011$).

In both set-ups, fed ants facing an asymmetrical bifurcation chose preferentially the branch that deviated less from

their initial direction. A slightly higher proportion of ants exited the maze by the branch that deviated by 120° in the marked set-up than in the unmarked set-up ($\chi^2 = 6.37$, $df = 2$, $P = 0.041$).

In both set-ups, the proportion of fed ants that made one or several U-turns after crossing an asymmetrical bifurcation was higher on the branches that deviated by 120° than on the branch that deviated by 30° ($\chi^2 = 20.68$, $P < 0.001$ and $\chi^2 = 15.51$, $P < 0.001$ for the unmarked and marked set-up, respectively; $df = 1$).

To further test the effect of the bifurcation geometry on the ants' behaviour, we categorized the final choice of the ants as correct or incorrect according to the criterion defined by Jackson et al. (2004). This criterion is based on the geometry of the bifurcation unfed and fed ants should encounter in a network of natural foraging trails. Unfed ants that faced a symmetrical bifurcation (i.e. the correct geometry in natural trail network), made a U-turn and exited by the entrance branch of the maze were considered as making an incorrect choice. Similarly, fed ants that faced an asymmetrical bifurcation, made a U-turn and exited by the entrance branch of the maze or by the branch that deviated by 120° were also considered as making an incorrect choice. Conversely, unfed ants that faced an asymmetrical bifurcation, made a U-turn and exited the maze by the entrance branch of the maze or by the branch that deviated by 120° were considered as making a correct choice. The same was true for fed ants making a U-turn at a symmetrical bifurcation and exiting the maze by the entrance branch. We then computed the ratio of correct to incorrect choice for each set-up (marked and unmarked). A confidence interval for this ratio was computed by a non-parametric bootstrap method (Manly 1991).

We found a ratio of correct to incorrect reorientation of $1.22 (\pm CI_{0.95} 0.34)$ for the unmarked set-up and a ratio of $0.60 (\pm CI_{0.95} 0.56)$ for the marked set-up. Both ratios are not significantly different from unity, which means that workers of the Argentine ant made as many correct as incorrect choices in the set-ups in relation to the geometry of natural trail network.

Discussion

Overall, our results confirm the fact observed by Vittori et al. (2006) that the workers of the Argentine ant do make biased choice at asymmetrical bifurcations: ants chose preferentially the branch that deviates less from their original direction. This was true in all cases except for unfed ants exploring an unmarked set-up for which the bias was only marginally significant.

In the unmarked set-up, the ant dispersion was generally more important than in the marked set-up. More ants came

back to their point of departure. This is particularly true for unfed ants that tended to exit the maze evenly by the three branches of the maze. The difference between unfed and fed ants could be explained by the fact that unfed ants could be more prone to exploration than fed ants. Unfed ants initially chose equally between the two branches that follow a bifurcation. However, about a third of them on average made a U-turn after crossing the bifurcation and came back to their point of departure. Fed ants on the other hand had a higher forward tendency and their behaviour was close to that observed for both unfed and fed ants in a marked set-up.

In the marked set-up, independent of whether they were unfed or fed, ants had a high forward tendency. Few ants made a U-turn at the bifurcation and came back to their point of departure. When facing an asymmetrical bifurcation, they initially tended to choose the branch that deviated less from their original direction. Moreover, those ants that chose the branch that deviated more had a high tendency to make a U-turn.

The fact that the number of ants making one or several U-turns was always much higher on the branch that deviated the more in asymmetrical bifurcations is intriguing. How did ants sense that they made too high a deviation from their original direction? The first mechanism one could think of is based on the use of the external visual cues that ants find in their surroundings. However, this mechanism can be dismissed because we took care to place the set-up in an environment as featureless and homogenous as possible, in terms of visual cues, contrast as well as lighting conditions. Besides, the Argentine ant is known to have poor visual discrimination capabilities (Aron et al. 1993). Ants could also use a compass to assess the deviation of their course. In the absence of a visual compass such as that provided by the sun or the polarized light of the sky (Müller & Wehner, 2007), the only compass that could be used by the ants in our experiment is the magnetic compass. However, although the use of magnetic cues for orientation has been demonstrated in a few species of ants (*Formica rufa*: Camillepe and Stradling 1995; *Oecophylla smaragdina*: Jander and Jander 1998; *Atta colombica*: Banks and Srygley 2003) no evidence of magnetic orientation has hitherto been provided in the Argentine ant. Finally, ants could be able to integrate their course deviations by using an egocentric system of reference, based on the idiothetic (kinaesthetic) cues they perceive while they change their walking direction. This type of orientation has already been described in other ant species (*Cataglyphis fortis*: Bisch-Knaden and Wehner 2001). Additional experiments in darkness and in the absence of magnetic field should be performed to test this hypothesis.

Our results show that fed and unfed workers of the Argentine ant, contrary to those of the Pharaoh's ants (Jackson et al. 2004), did not react differentially to the

geometry of the bifurcations. Whereas Jackson et al. (2004) found a ratio of correct to incorrect reorientation of 5.80 for a bifurcation with two trails diverging by an angle of 60°, the values we found for the same bifurcation angle for Argentine ants moving in tunnels were not significantly different from unity, independently of whether ants travelled on a marked or an unmarked set-up. In the marked set-up, 77% of unfed ants arrived at the food source, although they had to cross an asymmetrical bifurcation to do so. In the same way, 96% of fed ants crossed a symmetrical bifurcation without making a U-turn and chose one of the two branches that followed the bifurcation. In both cases, had the ants reacted to the geometry of the tunnel bifurcation in the same way as the Pharaoh's ants on natural foraging trails in Jackson et al.'s (2004) experiment, they should have made a U-turn and come back to their point of departure.

There are at least two explanations that can be provided for the discrepancy observed between our results on the Argentine ant and those of Jackson et al. (2004) on the Pharaoh's ant. One may be due to a difference in the experimental set-ups that were used and the other to a difference in the foraging behaviour of the two species.

In Jackson et al. (2004) ants moved on plane strips of paper, whereas in our experiments they moved within galleries carved in a PVC plate. This could make a difference in the choice of the ant in front of a bifurcation. First, because of their natural wall-following tendency (Dussutour et al. 2005), the forward tendency of the ants moving within the galleries could be accentuated. Second, ants may be able to assess more easily the angle of a bifurcation when moving on a plane surface than when moving within tunnels, by rotating their body and scanning the ground with their pairs of antennae.

Finally, an alternative explanation for the discrepancy between the Argentine ant and the Pharaoh's ant behaviour could be that the Argentine ant, contrary to the Pharaoh's ant, does not use a network of foraging trails, or that the networks formed by the two species in their natural settings have different geometry. Preliminary experiments show that foragers of the Argentine ant, in the same way as those of the Pharaoh's ants (Fourcassie and Deneubourg 1994), are able to form spontaneously networks of exploratory trails. Whether or not these networks have the same characteristics as those of the Pharaoh's ant, however, remains to be investigated.

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