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Backtracking behaviour in lost ants: an additional strategy in their navigational toolkit

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Ants use multiple sources of information to navigate, but do not integrate all this information into a unified representation of the world. Rather, the available information appears to serve three distinct main navigational systems: path integration, systematic search and the use of learnt information—mainly via vision. Here, we report on an additional behaviour that suggests a supplemental system in the ant's navigational toolkit: 'backtracking'. Homing ants, having almost reached their nest but, suddenly displaced to unfamiliar areas, did not show the characteristic undirected headings of systematic searches. Instead, these ants backtracked in the compass direction opposite to the path that they had just travelled. The ecological function of this behaviour is clear as we show it increases the chances of returning to familiar terrain. Importantly, the mechanistic implications of this behaviour stress an extra level of cognitive complexity in ant navigation. Our results imply: (i) the presence of a type of 'memory of the current trip' allowing lost ants to take into account the familiar view recently experienced, and (ii) direct sharing of information across different navigational systems. We propose a revised architecture of the ant's navigational toolkit illustrating how the different systems may interact to produce adaptive behaviours.

1. Introduction

Animals use multiple sources of information to navigate [1]. In ants, information appears to be exploited by separate guidance systems rather than being integrated into a unified representation of space [2]. The ant navigational toolkit is well known for encompassing three main strategies: path integration (PI), systematic search and the use of learnt information from different sensory systems [3–7]—mainly views. Based on a celestial compass and an inbuilt step-counter, PI continuously provides egocentric information about the direction and distance to the nest and enables the foraging ant to return to it by the shortest direct track [8,9]. However, PI is prone to cumulative errors [10,11], so that ants also learn the visual scenery perceived along their trips. This typically leads to the development of habitual idiosyncratic routes that enable ants to navigate robustly between the nest and food sources by means of learnt views [12–15]. Route-views can also enable homing from novel locations if familiar distal information is still available [16,17], but when neither PI nor views are sufficient for homing, ants rely on an emergency plan: a systematic search pattern consisting of gradually extending loops [18,19].

Recently, *Melophorus bagoti* ants have been shown to display a behaviour that seemed different from those three known strategies [20]. *Melophorus bagoti* ants with artificially occluded eyes but functional ocelli can still use their celestial compass [21]. But instead of heading in the home direction according to PI, those ants headed opposite to the direction they were recently travelling before their compound eyes were painted. In other words, they backtracked. However, this behaviour was observed only when the compound eyes were artificially covered, so that it could well be the result of 'relic' mechanisms from flying ancestors, never expressed in natural conditions [20].

Here, we show that such backtracking behaviour is actually observed in natural conditions—with untreated ants—and thus represents a part of the ant's navigational toolkit. We first describe the conditions in which ants backtrack, then explain its ecological function and discuss why the mechanisms involved raise fundamental questions about the cognitive architecture underlying ant navigation. Finally, we propose a simple architecture to explain how the different navigational systems may interact to produce navigational behaviour in ants.

2. Material and methods

(a) Experimental site and animals

Experiments were performed with Australian desert ants *M. bagoti*, approximately 10 km south of Alice Springs. The study site is a typical habitat of *M. bagoti*. It is laced with trees and buffel grass tussocks, providing an abundance of visual cues for navigating. The thermophilic *M. bagoti* is a solitary foraging ant that does not lay chemical trails but relies heavily on vision while travelling through its habitat [22]. Foragers usually scavenge during the heat of the day for roasted dead insects, seeds and sugary plant sap [23,24].

(b) Training and testing procedures

Foragers were trained to follow a route to a feeder containing cookie crumbs and located either 8 or 16 m away from the nest entrance. The route (1.5 m wide) was constructed with 10 cm-high wooden planks dug into the ground that prevented the ants from escaping without hindering or limiting their view of the surrounding panorama (for details, see [17]).

Across all experimental conditions, training and testing were conducted in a similar manner. Ants that were sufficiently experienced to reach the feeder were subjected to one and only one of the experimental conditions. Ants loaded with a cookie were released to home along the route and captured either just before they were about to enter the nest (zero-vector (ZV) ants) or at variable locations along the route, depending on the condition. In addition, a group of 'no route' ants were trained along the 8 m route but did not undertake a foraging trip before being tested. Instead, those ants were provided with food close to the nest (within a 10 cm circle) before being tested. Ants that emerged from their nest and picked up a food item were immediately captured and tested. Regardless of the experimental condition, each tested ant was transferred individually in a dark plastic tube to one out of three release points located at least 50 m away from the training route and hence presenting unfamiliar surroundings to the ants. All tests were conducted on clear sunny days to ensure that the ants could rely on their celestial compass. At each release point, a goniometer (1.2 × 1.2 m) was used to record their initial headings at 0.6 m. To guarantee proper homing motivation, only ants that clutched their food item were tested. Overall, approximately 730 ants—from three different nests—were tested.

(c) Data analyses

Circular statistics were used to analyse the ants' headings [25]. *V*-tests were used to determine whether ants were significantly oriented given a predicted direction, and Rayleigh tests were used in the absence of a predicted direction. *S*-tests were used to reject hypothetical directions. Finally, Watson–Williams tests were used compare the mean directions of two different groups. Bonferroni corrections were applied in cases of multiple tests.

3. Results

(a) Description of the backtracking behaviour

Ants homing from the feeder were captured just before reaching their nest so that the state of their PI vector was zero (i.e., ZV ants). ZV ants were then transported in a tube and released at one of three different test locations at least 50 m away from the nest, all presenting an unfamiliar environment. At all three distant release points, the ants' initial direction (recorded at 0.6 m) was significantly directed eastward when the homing route pointed westward ($ps < 0.003$, *V*-tests; figure 1*a*) and westward when the homing route pointed eastward ($ps < 0.001$, *V*-tests; figure 1*b*). In other words, ZV ants released on unfamiliar terrain headed first towards the compass direction opposite to the homing route they had just travelled: they backtracked.

To control for the potential role of the scenery perceived at the distant release points, we then tested ants that were provided with cookies just a few centimetres from their nest entrance, so that they travelled no route at all. At all three distant release points, their initial direction was oriented neither towards the east ($ps > 0.403$, *V*-tests) nor towards the west ($ps > 0.423$, *V*-tests; figure 1*c*), showing that the scenery perceived at the unfamiliar release points did not by itself drive the backtracking direction taken by ants having homed along a route. This confirms that backtracking behaviour is triggered only if ants have travelled a route before capture, and that the direction of backtracking is based on an absolute compass, most likely the ants' celestial compass.

These experiments were replicated on two other nests, with similar results (nest 2 backtracking: $p < 0.001$, *V*-test; nest 3 backtracking: $p < 0.001$, *V*-test; no route: $p = 0.851$, Rayleigh test) confirming the same pattern of backtracking (see the electronic supplementary material, figure S1).

Overall, this shows that ZV ants keep information about the compass direction of the route they just travelled and backtrack if the perceived scenery becomes suddenly unfamiliar. It has to be noted that the ants did not backtrack for very long (2.1 m ± 0.8 m; $n = 23$; see the electronic supplementary material, figure S2) before turning and displaying the typical systematic search observed in unfamiliar surroundings [10,18,19].

(b) Ants backtrack in the absence of ocelli input

Ants with ocelli covered by opaque paint during both training and test still backtracked when captured close to their nest and released on unfamiliar terrain ($p < 0.001$, *V*-test; figure 1*d*). Headings were no more scattered than with functional ocelli (*S*-test on scatter: $p = 0.5948$). This reveals that the compass information necessary for backtracking can be mediated by the compound eyes alone.

(c) Ants backtrack towards the last portion of the foraging route

Ants store foodward vectors to return to a profitable feeder on subsequent trips [26,27]. We tested whether the backtracking direction was based on such a foodward vector, or whether it was based on the last portion of the travelled route only. Ants were trained to home from a feeder via a two-legged route, captured just before reaching their nest (i.e., as ZV ants) and released on the distant test field
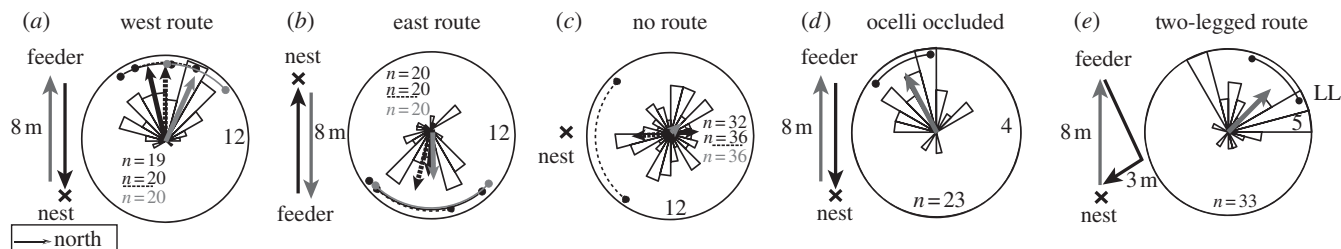
3

Figure 1. Zero-vector ants backtrack when released on unfamiliar terrain. (*a,b*) Headings of homing ants captured just before reaching their nest (zero-vector ants) and released at three different distant unfamiliar release points after an 8 m foraging route towards the west (*a*) or the east (*b*). At all three distant release points, ants did not display random choices but backtracked towards the feeder compass direction. (*c*) Headings of ants captured close to the nest with no foraging route and released at the three distant release points. Such ants were oriented neither towards the nest nor towards the feeder compass direction. (*d*) Headings of homing ants with occluded ocelli captured just before reaching their nest. (*e*) Headings of ants after a two-legged inbound route. Ants did not head towards the feeder, but showed a bias towards the last leg of travel (for statistical details see text). All circular histograms (figures 1–3) show the ants' headings after 0.6 m in sectors of $15°$, with the same conventions. Grey arrow, outbound route; black arrow, inbound route. Black cross denotes capture location of the homing ants. The number on the circle's edge (e.g. 12 in (*a*)) indicates the scale for the histogram, so that the centre is 0 and the radius extends to 12 ants per sector in (*a*). Arrow within the histogram represents the mean vector and arc the 95% CI of distribution. Different arrow styles refer to the three different release points.

(figure 1*e*). Their heading direction was indeed different than the one taken by ants having homed from the same feeder but along a straight route ($p = 0.004$, Watson–Williams test). With the two-legged homing route, ants did not backtrack towards the feeder (figure 1*e*; $p = 0.001$, S-test, rejecting the feeder direction), but rather towards the last leg of the route travelled (figure 1*e*; $p = 0.130$, S-test, not rejecting the last-leg direction).

(d) Ants backtrack only if captured close to their nest

Full-vector ants (FV ants; i.e., those captured at the beginning of their homing trip) are well known for heading along the direction dictated by their PI vector when released on unfamiliar terrain [16,28,29]. By contrast, we showed here that ZV ants (i.e., captured at the end of their homing trip) head in the opposite direction (figure 1*a,b*). We thus investigated at which stage of the homing route ants would switch from heading according to their PI vector to backtracking if the perceived scenery becomes unfamiliar.

Whether the route was 8 or 16 m long, homing ants captured 8 or 4 m before their nest headed along their PI compass direction when released on unfamiliar terrain (figure 2 upper panels; PI direction: $ps < 0.001$, V-tests; backtracking direction: $ps > 0.999$, V-tests). By contrast, backtracking behaviour was observed when ants were captured just before entering their nest (figure 1*a,b*) and also when captured 1 m before their nest entrance (figure 2 lower panels; PI direction: $ps > 0.995$, V-tests; backtracking direction: $ps < 0.005$, V-tests). Ants captured 2 m before their nest, however, displayed random heading on unfamiliar terrain (figure 2 middle panels; PI direction: $ps > 0.128$, V-tests; backtracking direction: $ps > 0.723$, V-tests). The heading distributions were not bimodal ($ps > 0.206$, bimodality V-tests), suggesting that the ants were not following either the PI vector or the backtracking vector. Instead, such random headings might indicate integration of the two opposite directions dictated by PI and backtracking, or alternatively, the start of systematic search on the spot.

Overall, 2 m before the nest appeared to be a key distance, at which ants released on unfamiliar terrain neither backtracked nor followed their PI but headed randomly. Ants headed according to their PI vector if captured before that point (i.e., further away from the nest) and backtracked if captured after that point (i.e. closer to the nest).

It has to be noted, however, that when ants had experienced a route of only 2 m long, they followed their PI when captured at 2 m (i.e., as FV ants), displayed random headings when captured at 1 m, and backtracked only when captured closer to the nest (see electronic supplementary material, figure S3).

(e) Ants do not backtrack if they have not seen the nest surroundings before capture

We have shown that ants backtrack on unfamiliar terrain only if they have been captured at the end of their homing route (i.e., less than 2 m from to their nest). So what information did the ants use to estimate how close to the nest they were?

A first hypothesis would be that they use the current odometric state of their PI. To test this hypothesis, we captured ants halfway along their homing route (4 m) and released them again at the feeder (8 m). Such ants immediately resumed homing towards the nest and were captured again halfway along their route (4 m) so that they had travelled the first half of the route twice. These ants walked, in total, 8 m in the nest direction. Their PI state after their second capture was thus zero. When released on the test field, such ZV ants did not backtrack ($p = 0.594$, V-test) but performed random heading directions (data not shown; $p = 0.970$, Rayleigh test). This shows that information about the nest distance before capture is not purely based on the current state of PI.

A second hypothesis would be that backtracking is driven by the view perceived before being captured and displaced. We modified the previously described manipulations in two ways and tested them on another nest. As for the previous group, the ants ran twice the first half of their homing route so that their PI vector was in a zero state. Before being released on the distant test field, however, these ZV ants were released for 3–5 s either halfway along their route where they had just been picked up (figure 3*a*) or close to their nest so that they could see the nest surroundings before being tested (figure 3*b*). In the latter case, the nest was covered by a 0.6×0.6 m wooden board to ensure that ants could neither enter nor smell the nest. After the 3–5 s, the ants were recaptured and released at the distant release point. Interestingly, the ants that saw the nest surroundings before being captured backtracked (figure 3*b*; $p < 0.001$, V-test), whereas the ants that saw the middle of the route
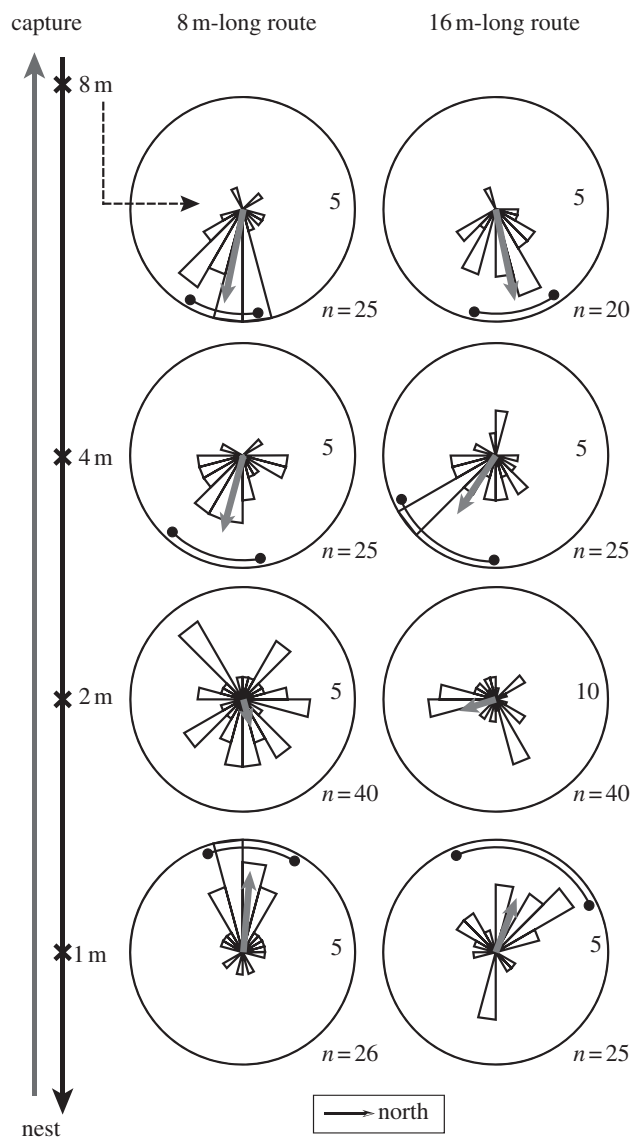
Figure 2. Ants' headings on unfamiliar terrain when captured at different stages of the inbound route. Ants homing from a feeder located either at 8 or 16 m were captured at different locations along their homing route and released on unfamiliar terrain. Ants captured at 8 and 4 m headed towards the nest direction. When captured at 2 m, ants showed non-directional choices but when captured at 1 m ants backtracked towards the feeder direction (for statistical details, see text). See legend of figure 1 for symbols.

before capture showed the undirected headings that we would expect of ants entering into a systematic search (figure 3a; $p = 0.405$, V-test). This suggests that backtracking behaviour is triggered on unfamiliar terrain only if ants have perceived the scenery of the nest surroundings before capture.

(f) Ants do not backtrack if they still have a significant residual path integration vector

We investigated here whether ants would backtrack if they have seen the nest surroundings before capture, but still had a significant residual PI vector. For this purpose, we captured ants at the feeder (FV ants), released them halfway along the route (at 4 m), let them run the last 4 m of the route and captured them just before they entered their nest for testing. Such ants had seen the nest surroundings before capture but had run only half of their homing vector and thus possessed a 4 m-long residual vector. When released on unfamiliar terrain,

these ants did not backtrack (figure 3c; $p = 0.970$, V-test), but followed the direction of their current PI vector (figure 3c; $p < 0.001$, V-test), showing that a short residual vector is necessary for backtracking to dominate behaviour.

Overall, ants backtrack only if (i) they are on unfamiliar terrain, (ii) their PI vector presents a small scalar value, and (iii) they have recently experienced the familiar surroundings near the nest.

4. Discussion

Melophorus bagoti lives in a cluttered visual environment and relies heavily on the visual panorama to navigate [22,30,31]. Even though the visual panorama is mostly learnt along stereotypical routes [12–15], ants can recognize familiar surroundings and rely on views quite far away from their habitual route [15,16] even if they had never been to that actual location before [17]. The visual knowledge of an ant can thus be described functionally as a large catchment area (i.e., familiar terrain), from any location from which the ant can robustly walk back to its nest (dashed area of figure 4b).

However, navigating ants may sometimes end up in totally unfamiliar terrain, particularly in cluttered environments where the scenery changes significantly with displacement. In natural conditions, this might happen if they have strayed accidentally, been displaced by a gust of wind, or simply when departing for the first time from a newly discovered feeding site. For such cases, it could be suspected that ants have evolved navigational strategies that are tuned to increase their chances of getting back to familiar terrain. In this work, we investigated such strategies by capturing homing ants in different contexts along their homing route, releasing them in totally unfamiliar terrain, and observing their initial direction.

(a) Functional reasons: strategies for getting back to familiar terrain

Functionally, backtracking behaviour maximizes the chances of getting back to familiar terrain. Backtracking is triggered when the homing ant has arrived near her nest, but then views become unfamiliar, suggesting some uncontrolled displacements (figure 1a,b). Because one side of the nest is more familiar to her (the side between nest and feeder), and the current unfamiliar visual evidence suggests that she is not on that side, the chances are that she is beyond the nest in the feeder-nest direction (yellow area in figure 4b), so that backtracking becomes an adaptive solution. The distance remaining on the return route before displacement is an important determinant. If the ant is still far from the nest, then the sudden appearance of an unfamiliar view suggests displacement to the side of the familiar route or beyond the feeder, providing no reason for backtracking (blue area in figure 4b). In this case, the best chance of recovering a familiar view is to travel in the feeder-nest direction, as dictated by the PI (figure 2, 8 m and 4 m). If ants are captured 2 m before the nest and released on unfamiliar terrain, they display random heading (figure 2, 2 m), as backtracking and following the PI vector appear equally good options (red area in figure 4b). Similar functional considerations apply to the case of a 2 m outbound distance (see electronic supplementary material, S2).
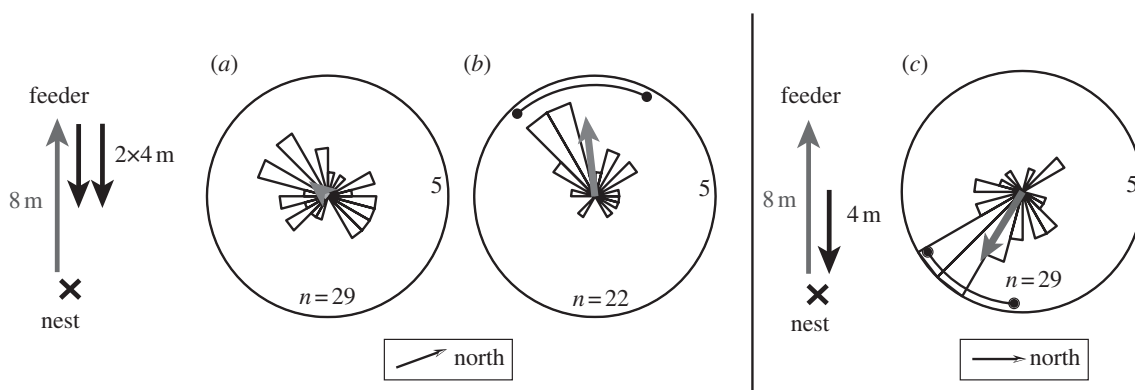
Figure 3. Mechanisms of ants' backtracking on unfamiliar terrain. (a,b) Ants were captured halfway home, released at the feeder, and captured again halfway home, so that their path integrator state was zero. Ants were then quickly released for 3–5 s at the middle of the route again (a) or at the nest vicinity (b) before being captured again and released on unfamiliar terrain, where their headings were recorded. Ants that perceived the nest surrounding before capture (b) backtracked towards the feeder compass direction, whereas those that had perceived the middle part of the route (a) showed no directional preferences. (c) Ants were captured at the feeder and released at the middle of the homing route, so that their path integrator state was half the feeder–nest vector when they reached the recapture point close to the nest before being released on unfamiliar terrain. Ants followed the direction of their residual path integrator vector and did not backtrack towards the feeder (for statistical details, see text). See legend of figure 1 for symbols.

If the evidence favours backtracking (i.e., current view unfamiliar, resulting PI vector close to zero and view near nest recently sighted), the backtracking direction should be back along the last-leg travelled, and not back towards the feeder (figure 1e). That is because it is only views along the homeward route that trigger homing behaviour, not views along an outbound route to the feeder that differs from the last leg [32].

Overall, this provides convincing evidence that the strategy used by *M. bagoti* when on unfamiliar terrain is remarkably flexible in choosing between the PI direction, backtracking or random search, and well adapted to increase the chance of getting back to familiar terrain (figure 4b). The decision-making process takes into account the ant's distance from the nest when she lost track of the familiar surroundings (figure 2), the overall length of the route (see electronic supplementary material S2 and figure S3) and the compass direction of the last travelled segment (figure 1e). We now discuss possible mechanisms underlying such a strategy.

(b) Mechanistic implication: remembering the direction just travelled

The backtracking behaviour of the ants implies that the compass direction recently travelled is memorized (figure 1e). Recently, ocelli have been shown to play such a role in *M. bagoti* [24]. However, covering the ocelli did not abolish or alter the backtracking behaviour observed here (figure 1d), so that compass information from the compound eyes is sufficient to remember the direction just travelled. It is unclear how compass information from ocelli and compound eye may interact.

(c) Mechanistic implication: remembering information about the recent views experienced

From a mechanistic point of view, the most intriguing result is that ants backtracked on unfamiliar terrain only if they had seen the nest surroundings before being displaced (figure 3a,b). This point raises three important questions about the minimum cognitive architecture necessary to explain ant navigation.

First, how does the familiar scene perceived before capture impact on behaviour after release? It was believed that navigating ants used the visual surroundings by comparing long-term stored representations with the view currently perceived [28,33]. Our results now suggest that some information derived from views is also stored in a type of 'memory of the current trip', allowing ants to modulate their behaviour according to the scene they recently experienced.

Second, how do ants know that the scenery perceived before capture was the one at the nest? Ants are believed to use views to know 'what to do', but not 'where they are' [2,33–35]. Results here suggest that ants can somehow obtain—from the use of views—information about their proximity to the nest. Following the bottom-up tradition of seeking the simplest explanation in terms of cognitive mechanisms [36], we suggest below a parsimonious explanation. Given the ontogeny of foraging behaviour (i.e., learning walks and repeated runs around the nest), it is likely that the ants' knowledge of the visual surroundings is most accurate around the nest. The degree of familiarity [37] of the scenery perceived might thus be higher around the nest than further away along the route. Therefore, ants may simply store in short-term memory information about the familiarity of the scenery experienced in the current trip, and follow their backtracking vector only if (i) the current scenery is totally unfamiliar, (ii) PI vector is close to zero, and (iii) familiarity experienced before capture was highest.

Third, the triggering of backtracking seems to involve the recognition of or at least some degree of familiarity with views recently experienced, which implies a direct connection to the visual-matching system. Until now, such a direct interaction between different navigational systems has not been required to explain past results of ant navigation. Instead, the different systems—which could be considered as independent modules—were thought to interact only indirectly at the motor output [38]. The present results, however, imply at least one direct interaction between such modules (figure 4a, grey arrow).

(d) A scheme of the ant's navigational toolkit

Several lines of evidence show that ants do not integrate different sources of information into a unified representation
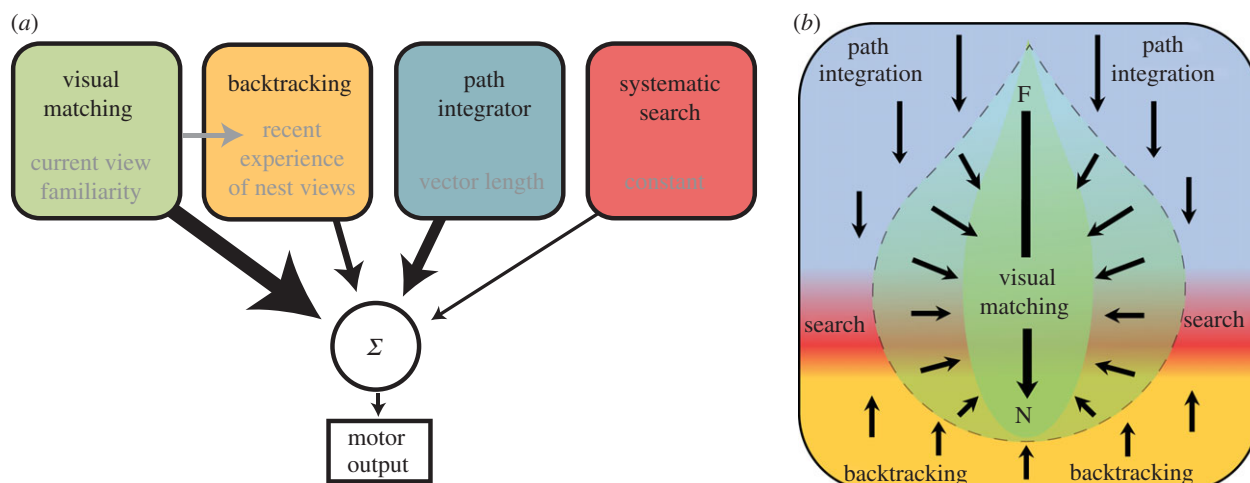
Figure 4. Integration of the different systems of the ant navigational toolkit. (*a*) This scheme illustrates how the four navigational systems (visual matching, backtracking, path integration and systematic search) might be integrated into an appropriate navigational behaviour. We assume that all four systems are not alternatively switched on and off, but are always active and integrated and weighted according to their final excitatory power ($\sum$). The influence of each navigational system on the final behaviour depends on both its own excitatory level (grey text) and the strength of its connection (black arrow thickness) with the output. The grey text indicates what parameter determines the excitatory level of a given navigational system. The strength of the connections (black arrow thickness) is only illustrative but reflects the relative influence of the different systems at their maximum excitatory level observed in *M. bagoti* ants. The grey arrow represents the direct interaction between the inputs to visual-matching and backtracking necessary to explain the present results. (*b*) The colours of this scheme illustrate the relative influence of the different navigational systems as a function of the ant's position after a displacement away from her habitual route (central arrow). The relative influences of the navigational systems are based on the scheme presented in (*a*), assuming that the homing ant was at the closest location possible along its familiar route before displacement. The dashed line delineates the familiar terrain, outside of which visual-matching has a negligible remaining influence on the behaviour. The arrows indicate the resulting direction dictated by the different modules influencing behaviour at that position.

of space, a so-called cognitive map [32,39–41]. Instead, PI, visual-matching and systematic search seem to act as separate modules, competing only at the motor output [2,38]. Indeed, Collett [42] has recently shown that PI and visual-matching are simultaneously active and not sequentially switched on and off. Their relative influence on the final behaviour is weighted according to the precision of the directional output of each module. The more precise the directional output of a module is, the more influence on the final behaviour it has [42]. The present results are consistent with this view, but also extend it.

First, as backtracking behaviour cannot result from the three known main systems (i.e., visual-matching, PI and systematic search), we consider backtracking as a fourth system on its own (figure 4*a*). Such a backtracking system would maintain compass information from the direction recently travelled.

Second, the relative influence of the different modules on the final behaviour may not depend solely on the precision of their output pattern but also on both the current and recent situations. As we have seen, backtracking is effected only if the ants have recently perceived the nest surroundings, but are now on unfamiliar terrain (figure 3*b*). The other modules of the ant's navigational toolkit might also be weighted by particular parameters, namely the current visual familiarity for visual-matching, and the current PI vector length for PI (see grey text in figure 4*a*). Such parameters can be seen as proxies for estimating the functional reliability of the module's outputted direction. For instance, the PI vector length is a good proxy for the functional reliability of the direction outputted by PI. If the PI vector is long, then the nest is surely somewhere in that direction. This would explain, for instance, why PI has little influence when close to the nest (figure 2) even though its directional output is probably

accurate. Similarly, visual-matching is a reliable strategy on a familiar route but not on unfamiliar terrain—where it may output wrong directions owing to fortuitous matches of the current scene to remembered scenes [17,37]. By weighting visual-matching according to the current view familiarity, its influence would be very high—and hence dominate behaviour—on a familiar route but very low on unfamiliar terrain. In this manner, the more reliable its information, the more a module is excited, and thus the more strongly the module influences behaviour. Because it serves as an emergency plan, we suggest that systematic search is continuously excited but weakly weighted, so that it dominates behaviour only when the other navigational systems are not excited at all, that is, when the ant is on unfamiliar terrain, has a small PI vector length and has not recently experienced the view of the nest surroundings. Some results, however, suggest that the influence of systematic search may increase with time spent in unfamiliar terrain [43]. Such a temporal factor deserves more investigation, and some discussion is given in electronic supplementary material S2.

Our third suggestion regarding the navigational toolkit is about differences between species. Natural selection is likely to have adjusted the initial weightings of the various modules for a given species. For instance, *M. bagoti* in its visually cluttered environment appears to weight visual-matching more than it weights PI when compared with the salt-pan ant *Cataglyphis fortis* when tested under similar conditions [44,45]. More strikingly, in *Gigantiops desturctor*—which has evolved in the rainforest where the canopy obstructs most of the sky—the influence of PI is minimal even when foragers are captured far away from their nest and released in an open landscape [29]. It has to be noted that some animals—at least vertebrates—can also adapt such weights appropriately with experience [1]. These weights can be seen as the connection

strength of each module's output with the summator ($\sum$) that determines directional output (thickness of black arrows in figure 4a). In our model, they act as fixed multipliers and do not vary with the current situation (see the electronic supplementary material, table S1).

Our scheme is of course far from encompassing the whole complexity of the ant navigational toolkit. Evidently, the model does not tackle how sensory input feeds the different strategies, but only how these are integrated and weighted for the final behaviour. In addition, the model lacks any rigorous quantification of the weights or excitatory levels of the different modules and their excitatory parameters, our current numbers being only rough and ready. Nonetheless, it shows that this simple architecture can be extended to explain past results obtained in ant navigation and provides clear predictions (see electronic supplementary material S2) that could be easily tested and that we hope will stimulate future research dedicated to unravelling the mechanisms underlying ant navigation.

5. Conclusion

We showed here that *M. bagoti* ants foraging along a familiar route and displaced to unfamiliar terrain do not simply engage in a systematic search, but use a well-adapted strategy to head first in a direction that increases the chance of returning to familiar terrain. Notably, ants backtrack towards the last travelled direction if they were close to their nest before losing track of the familiar surroundings. Some hints in the past literature suggest that such a backtracking behaviour may well be a rather general phenomenon in insects (see fig. 2 of [46] and fig. 7 of [47]). In *M. bagoti*, the control of this behaviour involves the current view of unfamiliar terrain, odometric information from the PI, and, notably, information about the most recently travelled compass direction and the recently experienced familiar view before displacement. We still favour the idea that ants do not integrate information into a unified representation of space. Instead, this work highlights how robust and flexible navigational decisions can arise from simple interactions within a distributed system.

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