Idiosyncratic route-based memories in desert ants, Melophorus bagoti: How do they interact with path-integration vectors?

Martin Kohler, Rüdiger Wehner *

Institute of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Received 24 December 2003; revised 10 May 2004; accepted 25 May 2004

Available online 13 August 2004

Abstract

Individually foraging desert ants of central Australia, Melophorus bagoti, exhibit amazingly precise mechanisms of visual landmark guidance when navigating through cluttered environments. If trained to shuttle back and forth between the nest and a feeder, they establish habitual outbound and inbound routes, which guide them idiosyncratically across the natural maze of extended arrays of grass tussocks covering their foraging areas. The route-based memories that usually differ between outbound and inbound runs are acquired already during the first runs to the nest and feeder. If the ants are displaced sideways of their habitual routes, they can enter their stereotyped routes at any place and then follow these routes with the same accuracy as if they had started at the usual point of departure. Furthermore, the accuracy of maintaining a route does not depend on whether homebound ants have been captured at the feeder shortly before starting their home run and, hence, with their home vector still fully available (full-vector ants), or whether they have been captured at the nest after they had already completed their home run (zero-vector ants). Hence, individual landmark memories can be retrieved independently of the state of the path-integration vector with which they have been associated during the acquisition phase of learning. However, the ants display their path-integration vector when displaced from the feeder to unfamiliar territory.

© 2004 Elsevier Inc. All rights reserved.

Keywords: Desert ants; Landmark guidance; Melophorus; Path integration; Route memories

1. Introduction

It has often been reported that central place foragers such as bees and ants follow fixed routes when performing their round-trip journeys through cluttered environments (for reviews see Collett, Graham, & Durier, 2003; Collett & Zeil, 1998; Wehner, 1981, 1992). However, there are only very few studies, in which such stereotyped routes have been recorded in detail (ants: Baader, 1996; Fresneau, 1994; Wehner, Harkness, & Schmid-Hempel, 1983; Wehner, Michel, & Antonsen, 1996), or in which the visual spatial memories involved have been investigated by either displacing the animal or manipulating part of the route (ants: Fourcassié, Henriques, & Fontella, 1999; Schmidt, Collett, Dillier, & Wehner, 1992; Wehner et al., 1996; maze experiments in honey bees: Collett, Baron, & Sellen, 1996; Collett, Harland, & Collett, 2002; Srinivasan, Zhang, Berry, Cheng, & Zhu, 1999; Srinivasan, Zhang, & Bidwell, 1997; Srinivasan, Zhang, & Lehrer, 1998; Zhang, Bartsch, & Srinivasan, 1996).

Here, we present the results of a systematic study of route-based memories in the Australian Red Honey Ant, Melophorus bagoti. These ants inhabit the arid low-shrub and grassland desert of central Australia (Christian & Morton, 1992; Conway, 1992; Wehner, Wehner, & Cheng, 2003). There the foraging areas of these large desert ants are covered by irregular arrays of grass tussocks, which vary only quantitatively in size.
and to a lesser extent in shape but not qualitatively in figural aspects or in colour. As the space between these tussocks consists of hard desert soil devoid of any other vegetation, the ants’ foraging ground forms a labyrinthine system of similarly sized and shaped landmarks and interconnected corridors. We have used this natural maze-like setting to first enquire about how stereotyped and idiosyncratic the routes actually are that the ants follow while shuttling back and forth between the nest and a given feeding site. With these descriptive data at hand, we then ask how the ants’ route memories might be organized.

We already know from studies on North African desert ants, *Cataglyphis fortis*, that ants can associate steering commands, so-called “local vectors,” with particular landmark scenes, so-called “snapshots” (Bisch-Knaden & Wehner, 2001; Collett, Collett, Bisch, & Wehner, 1998). Similarly, honey bees studied in small-scale laboratory devices can link particular flight directions to particular visual cues (maze experiments: lit. cit. above). In the context of route-based memories the question arises how strongly the memorized links of a landmark chain, i.e., the acquired local views and the local vectors associated with them are tied together. Are the local views of landmark scenes stored in a numerical order, so that the ants get primed to approach scene $S_n$ only after they have experienced scene $S_{n-1}$? Under natural conditions the environmental constraint that $S_{n-1}$ always precedes $S_n$ would suffice to retrieve the right memory at the right time. Furthermore, are the local views necessary to retrieve the associated local vectors, or can more global cues activate the retrieval process as well? For example, the sequence of landmark views could be linked to corresponding states of the ant’s global path-integration vector. Again we know from studies in *Cataglyphis* that this global vector is continually updated even if the ants follow habitual landmark routes that deviate from the direction of the global vector (Sassi & Wehner, 1997), and that the snapshot characterizing the nesting site is retrieved only after the homing ant has run off its global vector (Wehner et al., 1996). Finally, to what extent can the ant’s path-integration system be decoupled from the route-based system of navigation?

In the present account, we address these questions by displacing ants from their feeding or nesting sites to different locations along or outside the routes to which they have become familiar in a number of preceding foraging runs. In particular, two groups of ants are subjected to the same displacement paradigms: (i) ants that have been captured at the feeding site, so that their home vector is still fully available within some kind of working memory, and (ii) ants that have already completed their home run and by this have reset their path-integration system to zero. The way of how these two groups of ants behave in otherwise identical experimental situations should inform us about how strictly route-based memories are linked to path-integration vectors.

2. Materials and methods

2.1. Field site

All experiments were performed in the central Australian grassland next to the Simpson’s Gap Visitor Centre (23.43°S, 133.44°E), 17 km west of Alice Springs (Northern Territory). The area is covered by tussocks of Buffel grass, *Cenchrus ciliaris*, which are distributed uniformly ($R = 1.32$ as calculated from the distribution of 213 tussocks within a randomly selected $10 \times 10 \text{m}^2$ area; this value of $R$ is significantly different, with $p < .001$, from a random distribution characterized by $R = 1.0$; theoretically the $R$ values range from 0 for a clumped distribution to 2.15 for an ideally uniform distribution; Clark & Evans, 1954). The sizes (heights about 10–60 cm) and distributional patterns of the tussocks were such that the foraging ants had to wind their ways around them while walking on sandy surfaces of clay loam. In addition to the *Cenchrus* tussocks, there were some widely dispersed trees of *Acacia estrophiolata* (Ghost gum) and *Hakea eyreana*. During most of the experiments surface temperatures ranged from $40^\circ$ to $70^\circ$C.

2.2. Species

Similar to *Cataglyphis* in the Afro-Asian deserts and *Ocymyrmex* in the Namib desert, the Australian *M. bagoti* is a thermophilic scavenger foraging for dead arthropods at extremely high temperatures (Christian & Morton, 1992; Wehner, 1987; Wehner et al., 2003). Above ground activity ceases during the winter months (Christian & Morton, 1992). Of the 29 species and subspecies described for this Australian endemic genus (Shattuck, 1999) *M. bagoti* is the largest and apparently best heat adapted species. As is the case for all *Cataglyphis* species studied intensively in navigation experiments (*C. bicolor*, *C. fortis*), *M. bagoti* has not been observed to employ trail pheromones, not even when many ants were trained to the same feeder (B. Muser, S. Sommer, S. and R. Wehner, unpublished observations). Furthermore, as shown later in this account, individual ants exhibit different paths when proceeding from nest to feeder, and from feeder to nest, and the inbound and outbound paths of individual ants are usually different from each other.

2.3. Field experiments

2.3.1. Recordings

The study area was mapped by a gridwork of lines (grid width 1.0 m), within which the outlines of all...
 individually labelled ants (see Table 1 ). In all five experimental paradigms. In total we recorded 604 control and experimental runs. Whenever possible, each particular ant was tested in various series of displacement experiments. Displacement occurred either in the ant’s full-vector state (displacement from the feeder immediately after the ant had grasped a food item and was about to start its homebound run) or in the ant’s zero-vector state (after the homing ant had arrived at the nest site and was to enter the colony). Note that as in our previous work the terms “full-vector state” and “zero-vector state” refer to the output of the ant’s path integrator (stored vector state minus current vector state). Of course, even in a “zero-vector ant” that has returned to its point of departure the path-integrator state. Of course, even in a “zero-vector ant” that has just returned to its point of departure the path-integrator state (from which it can be loaded down, with reversed sign, for subsequent outbound runs (for recent reviews on path integration in insects see Collett & Collett, 2000; Wehner, 1992; Wehner, Gallizzi, Frei, & Vesely, 2002; Wehner & Srinivasan, 2003). Full-vector and zero-vector ants were displaced to various release sites either along their habitual route or sideways of it. The different displacement paradigms are outlined in Fig. 1. In all cases the ants continuously carried their food item indicating that they were strongly motivated to return to the nest. At least one control run was inserted between any two experimental runs. Whenever possible, each particular ant was tested in all five experimental paradigms. In total we recorded the trajectories of 604 control and experimental runs of 48 individually labelled ants (see Table 1 ).

Fig. 1. Experimental paradigms: Displacements along the habitual route (left) and sideways (right). The numbers 1.1, etc. refer to the experimental series described in the text. N (filled square): nesting site; F (open square): feeding site; filled circle: release site. Heavy arrow-headed lines: displacement of full-vector ants. Thin arrow-headed lines: displacement of zero-vector ants. Dashed lines: beeline of inbound/outbound route.

2.3.3. Experiments

After the ants had completed their sets of control runs, they were tested in various series of displacement experiments. Displacement occurred either in the ant’s full-vector state (displacement from the feeder immediately after the ant had grasped a food item and was about to start its homebound run) or in the ant’s zero-vector state (after the homing ant had arrived at the nest site and was to enter the colony). Note that as in our previous work the terms “full-vector state” and “zero-vector state” refer to the output of the ant’s path integrator (stored vector state minus current vector state). Of course, even in a “zero-vector ant” that has just returned to its point of departure the path-integrator state (from which it can be loaded down, with reversed sign, for subsequent outbound runs (for recent reviews on path integration in insects see Collett & Collett, 2000; Wehner, 1992; Wehner, Gallizzi, Frei, & Vesely, 2002; Wehner & Srinivasan, 2003). Full-vector and zero-vector ants were displaced to various release sites either along their habitual route or sideways of it. The different displacement paradigms are outlined in Fig. 1. In all cases the ants continuously carried their food item indicating that they were strongly motivated to return to the nest. At least one control run was inserted between any two experimental runs. Whenever possible, each particular ant was tested in all five experimental paradigms. In total we recorded the trajectories of 604 control and experimental runs of 48 individually labelled ants (see Table 1 ).

2.4. Statistical analysis

Path density plots were computed for individual ants subjected to a particular experimental paradigm. As each particular ant would walk at a steady pace with nearly constant speed, the path density plots show how much time, on average, an ant has spent within each unit square during its outbound or inbound runs. In detail, the path density plots were obtained by transferring the digitized data (using GEDIT for DOS and GEDIT for WINDOWS) to a square grid of lines (grid width 20 cm). As an example, let us assume that in a particular test situation, an individual ant had to run four times from the nest to the feeder. Then, for each unit square, the ratio of the lengths of all segments of the ant’s four paths covering that unit square to the total lengths of all the ant’s four paths was computed. The ratios of all square pixels were then used to design false-colour density plots (see Åkesson & Wehner, 2002). These vivid graphical representations show how often an ant tested in a particular experimental paradigm has traversed a particular part of its foraging area, i.e., how persistently it has stuck to a particular route (see Fig. 3B, Table 2).

To test for differences in the spatial layout of the paths of different ants, or of the same ant in different experimental paradigms, we employed the following procedure (compare Fig. 2): First the deviations $d$ of the ant’s locations $L$ from the straight line connecting the nest $N$ and the feeder $F$ were determined (in 0.5 m bins along the nest-food line $= \overline{NF}$; $l$ is the projection...
of L on NF; the 0.5-m bin size was used in all cases, even if different NFs were used in different experiments). Values of d were taken as positive or negative depending on whether the points L were located to the right or left of NF, respectively. They are not independent but by necessity arranged in an order (d1, d2, d3, . . . , d19) thus defining each individual path by a series of 19 successive values. A doubly repeated-measures Analysis of Variance was used to compare variances within or between individuals separately for each experimental series and nest. As an example, this procedure is described in detail in the Results (Table 2). The 19 d values (path) and the in- and outbound journeys (inout) were repeated within individuals, and the numbers of runs per individual are the replicates. This type of repeated-measures ANOVA takes into account the problem of pseudoreplication (Ende, 1993). Specifically, the interindividual variance (individual) divided by the intraindividual variance (error individual) follows an F distribution and provides a measure of the idiosyncrasy of the route taken. In experimental series 2.1 and 2.2 (Fig. 8) statistics of circulary distributed data (Batschelet, 1981) were applied in addition.

3. Results

3.1. Idiosyncrasy of outbound and inbound routes

The most striking result of recording the foraging (outbound) and homing (inbound) paths of individual ants is that once an ant has discovered a renewable food source, in our case, an experimentally established feeding site, it follows amazingly stereotyped routes to and from that site. Two examples are given in Figs. 3 and 4. These routes differ much more strongly between individual ants than within, suggesting idiosyncratic foraging (individual-effect in Table 2 for nest No. 1: F16,51 = 29.362, p < .001; the corresponding values for nest No. 2 are: F6,35 = 37.908, p < .001). Except for some usually minor deviations the ants' routes are kept constant over the entire recording period. For example, the ant whose inbound paths are portrayed in Fig. 4 was observed over a time period of 13 days. Given the array of grass tussocks covering the area between nest and feeder the ants are not able to take the direct route connecting nesting and feeding sites. By running within the system of inter-tussock alleys, the paths significantly deviate from this beeline route (path-effect in Table 2 for nest No. 1: F18,918 = 152.135, p < .001; nest No. 2: F32,1120 = 9.262, p < 0.001; Figs. 3 and 4). Furthermore, these paths differ between individuals (path * individual-effect in Table 2 for nest No. 1: F288,918 = 8.802, p < .001; nest No. 2: F192,1120 = 14.542, p < .001).

By applying the repeated-measures Analysis of Variance statistics to the 136 runs of the 17 ants...
mentioned above, two additional conclusions can be
drawn. First, in the vast majority of cases, outbound
and inbound routes differ within individual ants (in- out-effect in Table 2 for nest No. 1: $F_{1,51} = 7.801$,
$p = .007$; nest No. 2: $F_{1,35} = 6.218$, $p = .018$, 42 runs
in 7 ants, i.e., 3 outbound and 3 inbound runs per ant). Second, in addition, these inbound/outbound differ-
ences differ between individuals (inout * individual-eff-
ct in Table 2 for nest No. 1: $F_{16,51} = 13.793$, $p < .001$;
nest No. 2: $F_{6,35} = 3.371$, $p = .010$).

In those cases in which an ant’s trajectory passes
through the border area of a polygon depicting a grass
tussock, either the diverging branches of the tussock
have not reached the ground or the tussock flattened
out at its border. In any way, these cases do not mean
that the ant had made its way through the tussock, i.e.
climbed into that piece of vegetation. It always remained
on the flat ground. Furthermore, due to the pixel size of
$20 \times 20 \text{cm}^2$ the pixels by necessity had to overlap, at least
partially, with the outlines of the tussocks.

Note that all the “control runs” described above have
been performed by the ants in succession immediately
after the ants had encountered the feeder for the first
time. The experiments to be described next were started
only after the ants had completed these control runs (4
outbound and 4 inbound runs per ant at nest No. 1; 3
outbound and 3 inbound runs per ant at nest No. 2;
as described above, there are no differences in the con-
clusions drawn from the ants of either nest). Further
control runs were inserted into the experimental series
(see below), so that in most ants more than 9 outbound
as well as more than 9 inbound runs were recorded over
periods of about 10 days.

3.2. Displacements to locations along the familiar route

In all experiments described in this and the following
section the ants’ trajectories are compared to the trajec-
tories of the pre-experimental control runs performed in
the very same ants. These pre-experimental runs are al-
ways used as references for the experimental runs.

In a first series of experiments (series 1.1) ants that
had returned from the feeder to the nest (zero-vector
ants) were captured at the nest entrance and displaced.
back to the feeder. Upon release, they immediately followed their habitual inbound routes (Fig. 5). Their trajectories are statistically indistinguishable from the control routes recorded in the same individuals (nest No. 1: \(F_{1,8} = 0.250, p = .631, N = 21\) runs of 13 ants; nest No. 2: \(F_{1,3} = 0.019, p = .899, N = 9\) runs of 6 ants). It is especially astounding that, with one single exception, the ants did not display any search behaviour at all after they had been released at the feeding site.

The second set of experiments (series 1.2) differed from the first one in that the zero-vector ants were displaced to, and released at, a location midway between the nest and the feeder. Again, with only one exception, all 15 ants (26 runs) tested this way directly channelled into their familiar route (Fig. 6), even though prior to entering their route they had not experienced the first half of it (nest No. 1: \(F_{1,9} = 0.815, p = .390, N = 18\) runs of 9 ants; nest No. 2: \(F_{1,2} = 6.164, p = .131, N = 8\) runs of 6 ants). The one exceptional ant mentioned above first returned to the feeder rather than to the nest (again along its habitual outbound route), turned around and without hesitation followed its habitual inbound route.

These two series of experiments clearly show that Melophorus ants maintain their strict route-bound courses even if their path integrator has been reset to

![Fig. 5. Inbound runs of two zero-vector ants after displacement from the nest N to the feeder F; experimental series 1.1. (A) Ant P7: four runs shown in orange, (B) ant S1: one run shown in black. The control runs are underlain in grey: 9 and 11 runs in (A) and (B), respectively. Throughout this and the following Figs. 3–9 a particular colour of a trajectory refers to a particular ant (e.g., orange to ant P7).](image)

![Fig. 6. Inbound runs of two zero-vector ants after displacement from the nest N to a location midway between nest N and feeder F; experimental series 1.2. (A) Ant F1: one run shown in red, (B) ant H2: two runs shown in black. Control inbound runs are depicted in grey: 7 and 13 runs in (A) and (B), respectively.](image)
zero state, and that they can do so not only from the location at which they usually start their homebound courses, but also from an arbitrary location along their familiar route. Hence, even though route memories are acquired in such a way that each part of the route corresponds to a particular state of the ant’s global vector, it can be decoupled from these vector states.

To further investigate the possible coupling of vector states and route memories, we next released ants captured at the feeder rather than at the nest (“full-vector ants”) and released them at their familiar route midway between the nest and the feeder (series 1.3), i.e. at the same locations at which they had been released in series 1.2 as zero-vector ants. Now these ants still loaded with their full (100%) vector state experienced that part of their landmark route, which they had previously passed after having already run off the first 50% of their home vector. Nevertheless, the inbound routes of these full-vector ants did not differ from those of the zero-vector ants (Fig. 7; nest No. 1: $F_{1,5} = 3.068$, $p = .140$, $N = 14$ runs in 7 ants; nest No. 2: $F_{1,1} = 0.040$, $p = .875$, $N = 5$ runs in 4 ants), nor did they differ from the control inbound runs (nest No. 1: $F_{1,7} = 2.167$, $p = .184$; nest No. 2: $F_{1,1} = 0.058$, $p = .850$).

Fig. 7. Inbound runs of two full-vector ants after displacement to a location midway between nest $N$ and feeder $F$; experimental series 1.3. (A) Ant $F1$: two runs shown in red, (B) ant $H6$: 4 runs shown in blue. Grey lines depict control inbound runs: 7 and 20 runs in (A) and (B), respectively.

Fig. 8. Trajectories of homing ants that had been transferred to a location (filled circle) sideways of their habitual inbound routes. The trajectories were cut when the ants’ trajectories had reached the 2-m circle. Grey polygons depict the tussocks around the release site. (A) Full-vector ants, i.e., ants displaced from the feeder ($N = 16$). (B) Zero-vector ants, i.e., ants that had arrived at the nest and were displaced to the release site ($N = 20$). Open circles mark the intersection of the runs with the 1- and 2-m circles. The red arrow heads indicate the ants’ mean headings. Their positions along the black line provide a measure of the dispersion ($0 < \tau < 1$) of the data (0 and 1 mean that the data are randomly distributed or all oriented in the same direction, respectively). If the red arrow head lies beyond the small mark at the black line (what is the case in both the 1- and the 2-m circle), the data are uniformly distributed ($\tau < .001$, Raleigh test). The feeder–nest homing direction is 147°. In the full-vector ants (A), it is just included within the 99% confidence interval (2-m circle: 115.32°–147.68°), whereas in the zero-vector ants (B) the directional choices do not differ significantly from a random distribution (2-m circle: $p = 0.14$).
In no case did the ants overshoot their nesting site, even though upon reaching that site they had run off only 50% of their home vector. Hence, in comparing series 1.2 and 1.3 (see Figs. 6 and 7), an unexpectedly clear result emerges: full-vector ants and zero-vector ants completely coincide in the precision of their route-based homing behaviour, even if they are released somewhere along their habitual routes rather than at the usual starting point of the route. This implies that whatever the state of the ant’s global vector is, the route-based memories are retrieved and used in an almost unerring way. What then is the rule the global vector plays in Melophorus ants when they are foraging and homing in cluttered environments? This question is addressed in the following section.

3.3. Displacements to locations outside the familiar route

If full-vector ants are displaced sideways from their familiar route as sketched out in Fig. 1 (series 2.1), they are supposed to first rely on their path-integration system and start to run off their home vector. Indeed, in most of the 23 runs recorded in 11 ants the displaced animals selected their proper homeward course, even though their journeys now led them through novel territory covered by a novel array of tussocks (Fig. 8A). However, the individual runs varied in the distances covered by the ants in the direction of the vector course. In some cases, the ants ran off their home vector completely (see Fig. 9A, run No. 5; Fig. 9B), but in most cases they broke off their vector course at an earlier stage, moved...
towards their familiar landmark corridor, entered it, and followed it in its habitual way (e.g. Fig. 9A runs Nos. 1–4). If an ant was displaced repeatedly to the same point of release, as was the case in the ant of which five homeward trajectories are shown in Fig. 9A, it behaved differently with respect to when and where it would enter its familiar route, but no systematics could be detected yet in the way these differences occurred over time. In a few cases, the ants even performed some search loops close to the point of release, but the occurrence of one or another initial search loop was a rather rare event as compared to what happened if the same type of displacement experiment was performed with zero-vector ants.

In fact, all zero-vector ants displaced in series 2.2 to the very same site to which they had been displaced in their full-vector state exhibited extensive search-loop patterns about the point of release (Figs. 8B and 10). Finally, however, all of the 27 homebound trajectories recorded in 13 zero-vector ants displaced laterally from their familiar route again ended up, sooner or later, within their route. This is borne out by the repeated-measures Analysis of Variance, which results in highly significant differences between the trajectories of the displaced zero-vector ants and their control inbound runs, if the first parts of the trajectories are considered (d values for $l = 15–8$: $F_{1,12} = 9.174, p = .010$). However, no differences occur in the second parts of the homebound trajectories ($F_{1,12} = 1.180, p = .299$). In two out of 20 cases the search movements about the release point were followed by a run sideways to the route in the direction towards the nest rather than along the route itself (Fig. 10C). Most surprisingly, these “parallel runs” recapitulated the gross geometrical features of the control runs. However, in comparing the initial behaviour of the laterally displaced zero-vector ants with that of the full-vector ants (series 2.1), clear-cut differences emerge. The full-vector ants cover much larger distances parallel to their route than the zero-vector ants (occasionally) do.

4. Discussion

Route fidelity based on visual landmark memories is widespread among ants. Even trail-laying species such as wood ants (Formica species: Rosengren, 1971; Rosengren & Fortelius, 1986), the giant predatory ants of neotropical forests (Paraponera clavata: Harrison, Fewell, Stiller, & Breed, 1989), the seed-harvesting ants of arid grassland environments (Pogonomyrmex barbatus: Hölldobler, 1971, 1976), and the carpenter ants of deciduous forests (Camponotus modoc: David & Wood, 1980) rely on visual landmarks the more heavily, the more frequently they have travelled their route. Actually, it is only by visual information that ants can determine the polarity of a trail (Klotz, 1987). Furthermore, trail following is a slow process. In all cases mentioned above, i.e., in Paraponera, Pogonomyrmex, and Camponotus, the ants’ walking speed increases substantially when visual rather than chemical guidance starts to dominate the ants’ navigational performances.

Most conspicuously, however, visual landmark memories are involved in route fidelities of solitarily foraging ants. Wherever such fixed routes have been observed in solitary foragers, e.g., in some rainforest ponerines (Fourcassie et al., 1999; Fresneau, 1994) or in a low-shrub desert formicine (Cataglyphis: Wehner et al., 1983, 1996), trail pheromones could be excluded as navigational aids, but how the visual information defining the route is acquired and used has remained largely elusive.

In the present account we have tackled this question in desert ants of central Australia, M. bagoti. These large formicine ants forage individually within a labyrinth of irregular arrays of similarly sized and shaped grass tussocks and inter-tussock alleys. The latter consists of bare sand ground. Even though we have not recorded yet the interommatidial divergence angles of the compound eyes of M. bagoti, we can assume that they will be in the size order of those of Cataglyphis bicolor. Then, from the sizes of the tussocks (see Material and methods) and the inter-tussock distances (see, e.g., maps in Fig. 3) we can conclude that the array of tussocks experienced by the ants must have created highly resolvable and contrast-rich retinal images. Within this conspicuous maze-like system of walkways the foraging ants select their idiosyncratic routes from the nest to an experimentally installed feeder and—usually in a different way—back to the nest. These routes are maintained with amazing accuracy over the entire period of time in which the feeder is visited. In using these routes the ants might rely on chain-like sequences of memories of learned visual patterns linked to specific motor commands and primed by internal or external contextual cues.

The most likely candidate for an internal cue is the state of the ant’s path integrator. As shown by the current experiments, in which the ants have been displaced from the feeder to a location outside their habitual route (series 2.1), the path integrator is working, even if the path-finding ant relies on landmarks in negotiating its way through the array of tussocks. Nevertheless, there is no indication whatsoever that Melophorus links particular landmark scenes to particular states of its path integrator. First, if zero-vector ants, which have already run off their path-integration vector, are displaced back to the feeder and released there (series 1.1), they follow their familiar route with the same accuracy as if their path integrator had not been reset to zero state (control runs). Second, if full-vector ants, i.e. ants which have been captured at the feeder, are displaced to some point
along their route (e.g. midway between nest and feeder: series 1.3), they are as accurate in keeping their familiar route as zero-vector ants are in the same situation (series 1.2). If their sequential landmark memories were strictly associated with corresponding states of their path integrator, in the experiments of series 1.3 the memories retrieved by particular states of the integrator would be inappropriate, since now landmark memories and vector states are out of phase.

On the other hand landmark memories could be linked in such a way that the matching of one memorized snapshot activated the next—and the steering command leading to it. As it is well known that honey bees (e.g., Chittka, Kunze, Shipman, & Buchmann, 1995; Collett, Fry, & Wehner, 1993; Collett et al., 2002; Srinivasan et al., 1997, 1998; Zhang, Lehrer, & Srinivasan, 1998, 1999) and desert ants (e.g., Andel & Wehner, 2001; Bisch-Knaden & Wehner, 2001; Collett et al., 1998) can attach local vectors to views of particular landmark scenes, a string of such landmark-cum-vector associations continuously linking local views to local movements could, in principle, guide the animal along its route. Matching one snapshot would recall the vector leading to the next, and so forth. Note, however, that as shown in the present study an ant can enter its route and properly channel itself into it, at arbitrary places (for a preliminary study in Cataglyphis bicolor see Wehner, 1990). Nevertheless, once the ant has started to move along its landmark corridor, the sequential coherence of memory retrievals is re-established. Hence, one should take a closer look at the details of the ant’s behaviour once the “lost” forager has hit its familiar route again.

Finally, more distant landmarks could act as external primers for memory retrievals (for honey bees see Collett, Fauria, Dale, & Baron, 1997; Collett & Kelber, 1988; Menzel, Giurfa, Gerber, & Hellstern, 2002). As at our study site some middle-sized trees occur at larger distances from the ants’ routes, these trees could provide panoramic cues enabling the ants to move in the general direction of the route and to approach the particular landmarks along the route from the proper direction. This hypothesis is supported by the behaviour of zero-vector ants displaced laterally from the route (series 2.2). Having performed some search loops about their point of release, these ants invariably moved towards the route rather than, for instance, in the direction opposite to it. The same behaviour was observed in the laterally displaced full-vector ants (series 2.1). Once released, however, these ants did not engage in search behaviour but immediately followed their vector course before they turned towards the route (see, e.g., Fig. 9), but never towards the other side, i.e., away from the route. Obviously, in the case of the full-vector ants, distinct landmarks present at the ant’s horizon skyline have been able to override vector navigation. This conclusion can also be drawn from extensive series of displacement experiments performed in wood ants, Formica japonica, which seem to select and maintain their homeward courses by means of panoramic skyline cues rather than by relying on vector navigation (Fukushi, 2001). In the present account, Fig. 10C provides an illustrative example. It depicts two inbound runs of a zero-vector ant released at a location outside the ant’s habitual route. In one run (No. 2) the ant approached and entered the route just after it had completed its initial searches, but in the other run (No. 1) it moved parallel to the route along a path that reflected the overall geometry of the route. Distant landmark cues provide the only information that could have guided the ant by, for instance, retrieving the proper local vector even if the local landmark views are inappropriate.

In M. bagotti, which forages in cluttered semi-desert environments, keeping a familiar landmark route seems to be the predominant way of navigation. As indicated by both the control runs and the experimental runs, the memorized landmark views (snapshots) are recalled and matched with amazing accuracy. Near-by landmarks such as the grass tussocks provide high-motion parallax cues and are used for establishing the fine-grain structure of the path. More distant landmarks, which give rise to more slowly changing low-motion parallax information seem to define the general geometrical features of the path, first of all its polarity. They are the most likely contextual cues that prime the local view-based landmark memories.

One of the most intriguing questions that remains to be tackled is how a route-following ant “dissects” and compartmentalizes its route. While steadily moving along its route Melophorus experiences continuous self-induced visual flow fields consisting of a kaleidoscopic blend of fast- to slow-moving parts of its visual scene. What temporal filters and mechanisms might be used by the ant to relegate particular aspects of this flow-field information to particular information channels, and what use does the navigating ant finally make of these different kinds of visual information?

A first step towards answering such questions will be to enquire about how the ants learn a particular route in the first place. In this context it is worth mentioning that at our study site some routes, or segments of a route, are chosen by the ants more frequently than others. At present we have not yet mapped out the complete three-dimensional structure of the ants’ environment, but with such topographic information at hand, we might be able to deduce from the ants’ behaviour some of the rules applied by the animals in selecting their paths. For example, as ants try to balance the angular elevations of two landmarks on either side of their route (Heusser & Wehner, 2002), they would move closer to the smaller of two objects. On the other hand, they might get attracted by a comparatively large visual signpost (wood ants:
Graham, Fauria, & Collett, 2003; honey bees: Chittka et al., 1995); or they might pass a particular landmark on the side that is closer to their global-vector course, or they might pass it on the side that enabled them to deviate as little as possible from their former course. Furthermore, if some landmarks happened to be rather close together the ants might be more likely to detour the entire group of objects rather than meander around the individual objects. Such pre-programmed rules governing the ants’ spatial behaviour might help us to understand how ants segment their routes and how they learn, retrieve, match, and string together the sequences of snapshots used in following their routes.

Acknowledgments

We are very grateful to Christina Brand, M.Sc., for her continuous cooperation in the field. We also thank Dr. Ken Cheng, Dr. Markus Knaden, and Stefan Sommer, M.Sc., for stimulating discussions, Dr. Wolf Blanckenhorn for his expert advice in the statistics of the repeated-measures Analysis of Variance, the Swiss National Science Foundation as well as the Human Frontier Science Program for financial support, and the Parks and Wildlife Commission, Northern Territory, for permitting us to carry out this research project within the West MacDonnell National Park, Australia.

References


