



Sensorimotor sequence learning in the ant *Gigantiops destructor*

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In several ant species, foragers venture outside the nest individually to collect food at a remote location, relying on memorized views of the surroundings to find their way. Although sensorimotor learning has been described previously in bees and a few ant species, its potential importance for navigation has often been underestimated. Motor memories independent of landmark identification could nevertheless prove useful for ants such as the tropical species *Gigantiops destructor* that forages in visually complex environments. We tested the sensorimotor learning ability of these ants using unmarked Y-mazes of increasing difficulty: constant-turn mazes, simple and double alternation mazes and irregular mazes. In the absence of visual cues, the ants were able to learn not only motor displacement rules but also route-specific patterns of movement. The ants' preference for simple navigation strategies was also demonstrated by their tendency to use a simple repetitive motor rule different from the rule they were expected to learn. These findings suggest that relying on different sensorimotor memories eliminates the need to form, store and retrieve numerous landmark views along foraging routes, which are potentially cognitively demanding and time consuming in naturally cluttered environments.

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Desert ants and wood ants foraging in cluttered environments are able to learn, retrieve and match sequences of identified landmark views to guide them between their nests and familiar feeding sites (Fukushi & Wehner 2004; Kohler & Wehner 2005; Harris et al. 2007; Narendra et al. 2007a, b). To optimize travel efficiency, ants should also sequence together the different memorized views by associating them with stored local vectors that indicate precisely where and how far to go to reach the next stage of their idiosyncratic outbound and inbound routes (Collett & Collett 2004; Wehner et al. 2006). This navigation strategy might thus appear a demanding cognitive task for animals such as tropical ants, which face complex arrangements of similar topographic features (e.g. trees, bushes or stones) that act as landmark beacons or as barriers and obstacles to locomotion in their natural habitat.

This is notably the case of the Neotropical ant *Gigantiops destructor*, which is known for foraging within the very cluttered Amazonian rainforest without the help of

chemical information (Beugnon et al. 2001). This solitary forager follows familiar landmark routes repeatedly, preying mostly on termites. The typical distance of foraging area from the nest is 2–20 m (Beugnon et al. 2005). If the food source is not depleted, a forager ant can come back to the same spot several times a day during a 5-week period (Chagné & Beugnon 2001).

Way-finding in *Gigantiops* ants implies an accurate recognition of at least two locations, the nest and feeding site, and the representation of spatial relations between these locations (Beugnon et al. 2005). In this central-place foraging species, precise identification of familiar visual landmarks is crucial both at the beginning and at the end of the foraging journey (Macquart et al. 2006). To drastically reduce the memory load of spatial information when navigating, we hypothesized that ants could rely on more economical strategies, especially when en route to the goal along the different one-way routes of their foodward and homeward journeys (Macquart et al. 2006). Among them, the motor learning hypothesis states that animals may learn individual site-specific serial motor programs that increase their ability to move rapidly, safely and efficiently in a home range containing obstacles or barriers to locomotion (Stamps 1995; Srinivasan & Zhang

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2004). This hypothesis emphasizes procedural (motor) rather than cognitive (encoding and storing complex featural and configural information) routines for processing spatial information. Ants can use such egocentric procedural instructions when confronted with either a single detour along a route (Bisch-Knaden & Wehner 2001) or several detours (Macquart et al. 2006). They can maintain a constant direction relative to their previous walking direction along barriers without encoding their visual features (e.g. shape, colour, size and pattern). In laboratory conditions, *G. destructor* foragers en route to a goal rely on a simple visuomotor routine consisting of an ordered succession of right and left detours around unspecified landmarks. In this way, an unusual landmark can be used as an acceptable beacon to be detoured around on a given side if it occurs in the right context along the foraging route (Macquart et al. 2006).

In the present work, we investigated the role played by sensorimotor learning during navigation in *G. destructor*. We tested whether and how ants could learn different patterns of locomotor movement (algorithmic behaviour) by selecting the appropriate right and left detours along a route independent of specific visual landmarks marking each choice point. This hypothesis, difficult to test in natural environments, can be investigated in the controlled conditions of the laboratory by using unmarked mazes in which the orientation choices of the animals can be recorded precisely.

To control the ants' motivation for maze learning we tested them during the inbound journey during which maze patterns are learned in a more regular and efficient manner than during the outbound journey (Schneirla 1953). We confronted homing ants with a series of Y-choice points presented in a linear succession of identical chambers in the absence of specific visual cues (Fig. 1a, b).

We trained marked ants with forced turns to make them learn different sensorimotor rules of increasing complexity such as repetition, simple and double alternation and randomization of right and left detours. The way in which segments of a familiar route can be encoded as sensorimotor programs independent of identified visual cues provides additional insights on how *Gigantiops* ants might learn to move quickly and accurately in complex habitats where many topographic features are alike. Consequently, our work further elucidates a model species that has not been studied extensively to date in a context in which ant navigation studies have focused on only three genera: the desert ants *Cataglyphis* spp. and *Melophorus bagoti* and the wood ant *Formica rufa*. It also extends the validity of the 'slalom racer hypothesis', formulated primarily for *Gigantiops* (Macquart et al. 2006), to all animals that forage in cluttered terrains. This hypothesis assumes that ants can learn a group of discrete locomotor patterns (i.e. learn to systematically bypass an obstacle on the same side without individual recognition of its visual features) if it

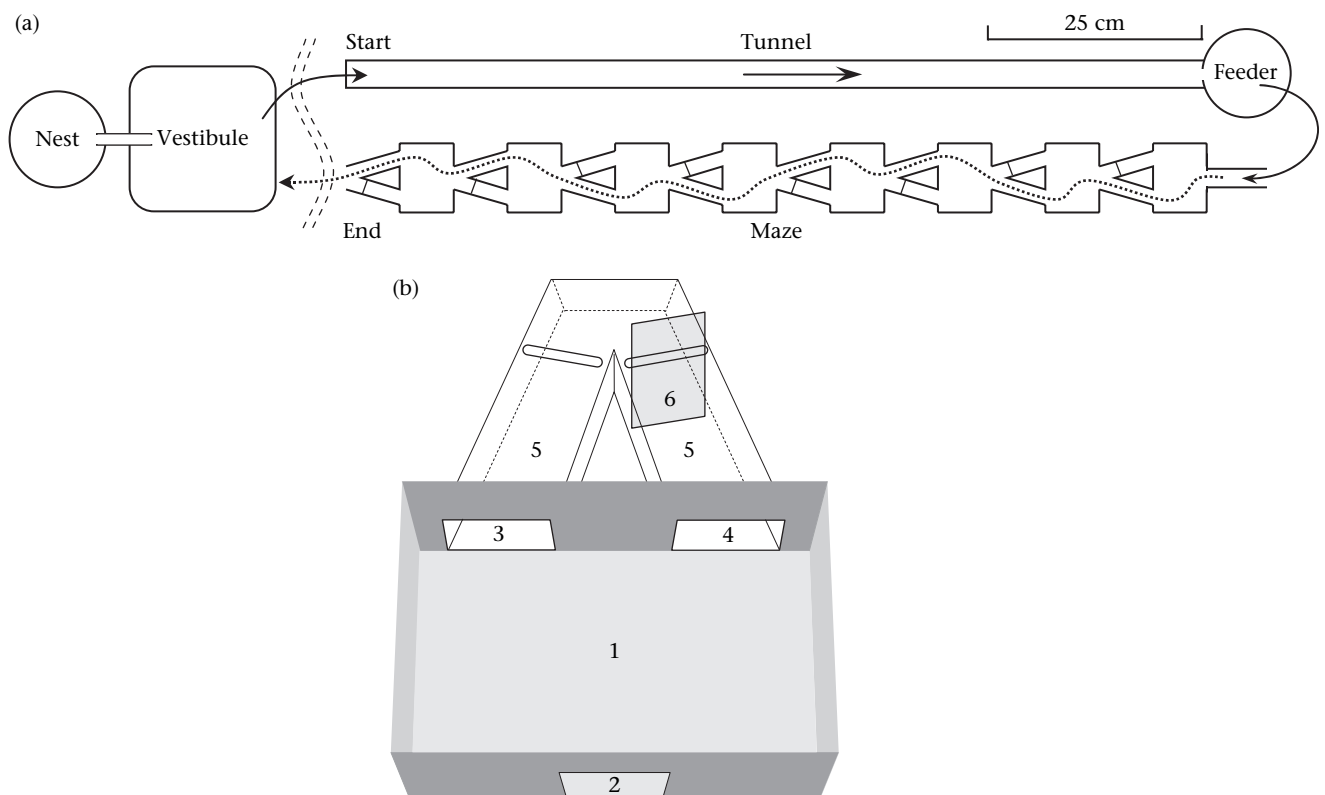


Figure 1. (a) Experimental set-up. Foragers taken from the vestibule walked in a straight tunnel towards a feeder. After prey capture, ants were transferred to the start of a linear homing Y-maze (illustrating here a double alternation sequence). Ants coming out of the maze were reintroduced in the vestibule, from which they went back to the nest to deposit the prey before the next trial. Only one ant at a time was introduced in the set-up. (b) Detail of a maze chamber and its associated V-shaped tunnel. (1) Maze chamber; (2) chamber entrance; (3) correct exit; (4) wrong exit; (5) V-shaped tunnel; (6) transparent sliding door (shaded in the figure).

is encountered at the expected location. Ants could then sequence together the successive basic motoric programs into an idiosyncratic site-specific serial program as a kind of signature route (Macquart et al. 2006). Such a procedure would relieve animals of cognitive demands imposed by learning and remembering numerous visually identified landmarks when en route to a goal.

METHODS

Observations were made on 11 colonies of *G. destructor* collected in French Guiana in April 2004 and October 2005. They were reared in Toulouse, in laboratory conditions at 28°C, with high humidity (70% RH) and a 12-h light/dark cycle. Each colony was housed in an artificial plaster-of-Paris nest (15 cm diameter) connected to a square plastic chamber or vestibule (27 × 27 × 10 cm³) containing water and honey. The typical size of a colony ranged 17–133 workers (Beugnon et al. 2001) but each colony included only a few specialized foragers because only one to three ants forage for prey during a 3-month period of time under laboratory conditions (Macquart et al. 2006).

Dichotomic Maze

The set-up of the maze (Fig. 1a) was the same as that in previous studies conducted on *Cataglyphis cursor* (Chameron et al. 1998). Foodward and nestward runs were performed individually. Ants departed from the vestibule outside their nest and walked straight towards a feeder containing prey (*Drosophila melanogaster*) through a 120-cm-long Fluon-coated plastic tunnel. The homing runs were performed in a maze consisting of a series of 5–10 identical chambers, depending on the experiment. The lateral walls of the chambers were opaque plastic to block visual cues at each side. All chambers had one entrance and two exits and were connected by V-shaped tunnels equipped with sliding doors (Fig. 1b). These chambers and tunnels are independent elements that can be combined to form mazes of variable length. In each V-shaped tunnel, depending on the experiment, either one or both branches were kept open. In the former case, one exit of a chamber led the ants to the subsequent chamber and the other exit was a dead end. This allowed for the design of simple or complex maze configurations, depending on the arrangement of the open exits in the successive chambers. Because all chambers were identical and offered the same visual configuration, only egocentric cues would enable the ants to make the correct choices along the maze.

Experimental Procedure

The aim of our study was to test whether ants could learn to detour correctly in successive identical chambers of the maze. Foraging ants were individually marked on the thorax with enamel paint drops. Marked individuals always returned to the nest through the maze: they climbed on a twig introduced in the feeder and were released singly in the first chamber of the homing maze.

As each forager entered the nest after a trial to deposit the prey, it had to come out spontaneously to be used in the following trial. This method allowed us to follow the foraging rhythm of the ants and ensured sufficient motivation. Consecutive trials were separated by at least 10 min even if a forager entered the vestibule before this time interval. In most experiments, the sample size decreased along the trials mainly because some ants stopped foraging and remained inside the nest.

Performance Measurement

The learning score (LS), that is the percentage of correct choices in the maze, was calculated for each ant on each trial during the learning phase: $LS = (\text{number of correct choices} \times 100) / \text{number of boxes}$. The LS values thus range from 0% (wrong choice in each box) to 100% (correct choice in each box). For a given sensorimotor task, a curve thus shows the evolution of the mean LS (mean of the different scores of the ants trained at the task) from trial to trial (see, e.g. Fig. 2a).

The time spent in the maze was recorded for each trial (time recording started when the ant entered one of the two exits in the first chamber and stopped when the ant found the correct exit in the last chamber). As for the learning scores, curves show the evolution of the mean time spent in each type of maze from trial to trial (see, e.g. Fig. 2b). The different types of experiments conducted are described below.

Repetition Learning

These experiments were conducted in an eight-chamber maze, with all open exits on the same side (constant-turn maze). Ants were trained in a right-turn maze (RRRRRRRR; $N = 12$) and in a left-turn maze (LLLLLLLL; $N = 12$). Immediately after being trained for repetition on a given side, ants were tested on the opposite side ($N = 11$) to test whether the learning of a new sensorimotor task was impaired by the previous training: five right-trained ants were retrained in a left-turn maze and six left-trained ants were retrained in a right-turn maze.

Alternation Learning

In this series of experiments, either simple or double alternation sequences had to be learned. In the simple alternation task, the opened exits were alternated from one chamber to the next (eight-chamber zig-zag maze). Depending on the departure side, ants were presented with a LRLRLRLR sequence ($N = 10$) or its mirror equivalent RLRLRLRL ($N = 9$). In the double alternation task, either a LLRRLRLR sequence ($N = 13$) or its mirror equivalent RLLRRLRL ($N = 11$) was used, depending on the departure side.

Irregular Sequence Learning

In contrast to the mazes described above, here ants ($N = 16$) were trained on several irregular mazes in which

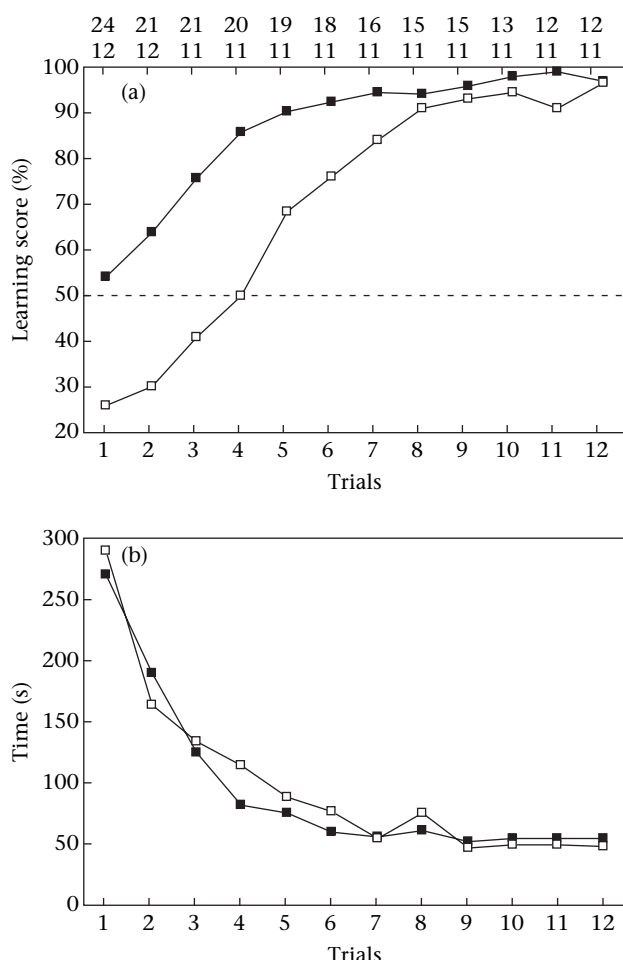


Figure 2. Progressive learning in constant-turn mazes. (a) Learning score as a function of trials. (■) Learning scores of the ants on their first task in a constant-turn maze (because training side had no significant effect (see text), the RRRRRRRR and LLLLLLLL groups were pooled on the figure). (□) Learning score of the ants tested on the reverse task (the data were pooled because there was no significant difference (see text) between the two groups). (---) Theoretical random performance. Numbers at the top of the graph indicate sample sizes for both tasks (upper line: first task; lower line: reverse task). As for all graphs, values obtained with less than five ants are not plotted. Note that the graph represents the performance in the whole maze (eight chambers), so that each correct (or wrong) choice in a chamber represents a 12.5% increase (or decrease) of the LS. (b) Time spent in the maze as a function of trials. (■) Times recorded during the first task in constant-turn mazes (RRRRRRRR and LLLLLLLL groups pooled). (□) Times recorded during the reverse task (LLLLLLLL and RRRRRRRR groups pooled).

the sequences contained no obviously regular pattern of turns. To reduce the task complexity, each ant was assigned a particular sequence of five turns instead of eight, e.g. RLRL, LLRL or RLLR. Navigating accurately through the maze required the learning of the entire sequence of turns. The sequences were pseudo-randomly designed: we excluded those containing three or more consecutive turns on the same side because they could simplify the task (e.g. a RLRL sequence would be retained whereas a RLLR sequence would not).

Extended Mazes

As soon as the learning scores reached an arbitrary value of 75% (i.e. six successful choices of eight on a given homing run), the choices of the ants were examined in extended mazes including additional chambers. The ants trained in constant-turn mazes and alternation mazes were presented with two additional chambers to test whether the turns in the extensions were treated as continuations of the maze sequence, which would indicate the learning and extrapolation of simple sensorimotor rules. For repetition, simple and double alternation tasks, the expected choices would be RRRRRRRR (or L...LL), RLRLRLRL (or L...LR) and RLLRLLRR (or L...LL), respectively. In contrast, the specificity of the sequences learned in the irregular mazes was tested in extended mazes with five additional chambers in which the ants were not expected to repeat the sequence of turns made in the first five chambers.

Control Tests

To test for any hidden irregularity within or outside the maze for each experimental condition, we first analysed the choice made by the ants in the first chamber on their first homing run ($N = 93$). Then, as for the rule extrapolation tests, the following control tests were conducted for each sensorimotor task as soon as the learning scores exceeded 75%. First, the blocking doors were taken off to check that the ants' choices were not specifically influenced by the open or closed exits ('opening test'; $N = 27$). Second, the maze was rotated by 90° anticlockwise to test for the influence of extra-maze landmark cues ('rotation test'; $N = 27$). Third, the chambers were shuffled to eliminate possible visual or olfactory intramaze cues ('shuffle test'; $N = 15$). The shuffle test was not performed after training in constant-turn mazes because each chamber required the same directional choice.

Data Analysis

Learning trials

In constant-turn mazes, we analysed the evolution of the LS within trials and investigated whether the ants' performance was influenced by departure side (left-turn or right-turn maze) and/or by previous training in a mirror configuration. The data were analysed with a three-way ANOVA (three factors: departure side, new configuration and repeated measures: trials). In alternation mazes, the effects of departure side (left or right) and alternation type (simple or double) on training performances were analysed with a three-way ANOVA (three factors: departure side, alternation type and repeated measures: trials). In irregular mazes, the training performances obtained in the different five-chamber configurations were pooled and analysed with a repeated-measures ANOVA.

For all tasks, ANOVAs were complemented with Helmert contrasts to determine speed of learning and asymptote level.

Control tests

For each ant, the score (percentage of correct choices) obtained during each control test (S_{test}) was compared to the score obtained during the preceding trial in training conditions ($S_{\text{reference}}$) by calculating $\Delta S = S_{\text{test}} - S_{\text{reference}}$.

We first looked for an influence of the training type or test type on ΔS . There were three control test types (opening, rotation and shuffle) for each training type, except for repetition trainings (two control test types, no shuffle test; see above), which had to be analysed separately. The results in alternation and irregular mazes were thus analysed with a two-way ANOVA (two factors: training type and test type) and the results in repetition mazes were analysed with a t test.

After verifying that ΔS was influenced neither by the training type nor by the test type, a t test was used to look for a difference between ΔS mean and a fictive nil mean.

RESULTS

Repetition Task (Constant-turn Mazes)

A repeated-measures ANOVA showed a significant increase in the ants' successful performance from trial to trial on the first task (Fig. 2a; $F_{11,220} = 66.15$, $P < 0.0001$). Ants made random choices on their first trial (mean LS = 54.1%) but rapidly learned to turn on the correct side. There was no effect of the training side ($F_{1,20} = 0.31$, $P = 0.58$): the ants learned the right-turn maze as well as the left-turn maze.

During the first homing trips, ants explored the maze for about 5 min (Fig. 2b), climbing on every side of the chambers or trying to progress through dead ends. Travel time decreased rapidly after this exploration phase (less than 1 min): as the ants became familiar with the chambers' configuration, any wrong choice was corrected by a U-turn leading directly to the adjacent open exit. This resulted in a fast progression, and the loss of time caused by wrong turns had a minor influence on the total time spent in the maze.

After their training on a given side, the ants were tested in extended constant-turn mazes including two additional chambers. Ants made correct choices in these additional chambers (Table 1: 95.2% of correct choices), turning in the same direction as in the previous chambers. This suggests that they learned a sensorimotor repetition rule during their training and were able to extrapolate this rule in the maze extensions.

When retrained in a mirror configuration, the ants first applied the previous sensorimotor rule: they systematically turned in the wrong direction, which resulted in low performance scores (Fig. 2a), especially on the first trial (mean LS = 23.8%). They finally learned this reverse task (repeated-measures ANOVA: $F_{11,220} = 6.09$, $P < 0.0001$), but the performance improvement was significantly slower than that for the preceding task ($F_{1,20} = 29.07$, $P < 0.0001$), suggesting that the previously learned sensorimotor rule was hindering the learning of the new rule.

Using Helmholtz contrasts, the differences between trials become nonsignificant after trial 8 ($P > 0.05$), indicating that the group reached asymptote of learning at this stage.

Alternation Tasks (Zig-zag Mazes)

Data analysis consisted of a three-way ANOVA (three factors: alternation type, maze configuration, repeated measures). The only significant effect concerned the repeated measures ($F_{11,264} = 15.60$, $P < 0.0001$), indicating an improvement of the LS across trials (Fig. 3a). Note, however, that the higher scores (LS around 85%) were not as good as those in the repetition task (LS reaching 100%). Alternation type (simple or double), departure side and interaction had no effect (respectively, $F_{1,24} = 0.03$, $P = 0.86$; $F_{1,24} = 1.13$, $P = 0.29$; $F_{11,264} = 0.17$; $P = 0.99$), which means that (i) double alternations were learned as well as simple alternations and (ii) for a given task, a maze configuration was learned as well as its mirror equivalent. Helmholtz contrasts show that the differences between trials become nonsignificant after trial 7 ($P > 0.05$), indicating that the group reached asymptote of learning at this stage. As for the repetition tasks, the time spent in the maze decreased rapidly during training (Fig. 3b), the ants navigating about four times faster through the maze once they knew its spatial configuration.

When tested in extended mazes after the learning phase, the ants trained in simple alternation mazes obtained good scores in the two additional chambers (Table 1: 72.2% of correct choices), with better scores in the first chamber (88.8% correct) than in the second chamber (55.5%). The ants trained in double alternation mazes obtained medium scores in the additional chambers (Table 1: 42.8% of correct choices) because high scores in the first chamber (71.4%) were counterbalanced by poor performance in the second chamber (14.3%). In both cases, the ants' directional choices in the first additional chamber followed the same logic as in the preceding part of the maze, which

Table 1. Performance in additional chambers of extended mazes

	Constant-turn mazes (%)	Simple alternation mazes (%)	Double alternation mazes (%)	Irregular mazes (%)
Score in the additional chambers	95.2	72.2	42.8	52.7
Score in the first additional chamber	100	88.8	71.4	
Score in the second additional chamber	90.5	55.5	14.3	

Extended constant-turn mazes (two additional chambers): $N = 21$ ants; extended simple alternation mazes (two additional chambers): $N = 9$ ants; extended double alternation mazes (two additional chambers): $N = 7$ ants; extended irregular mazes (five additional chambers): $N = 11$ ants. All exits were opened in the additional chambers. Percentages represent proportions of correct choices.

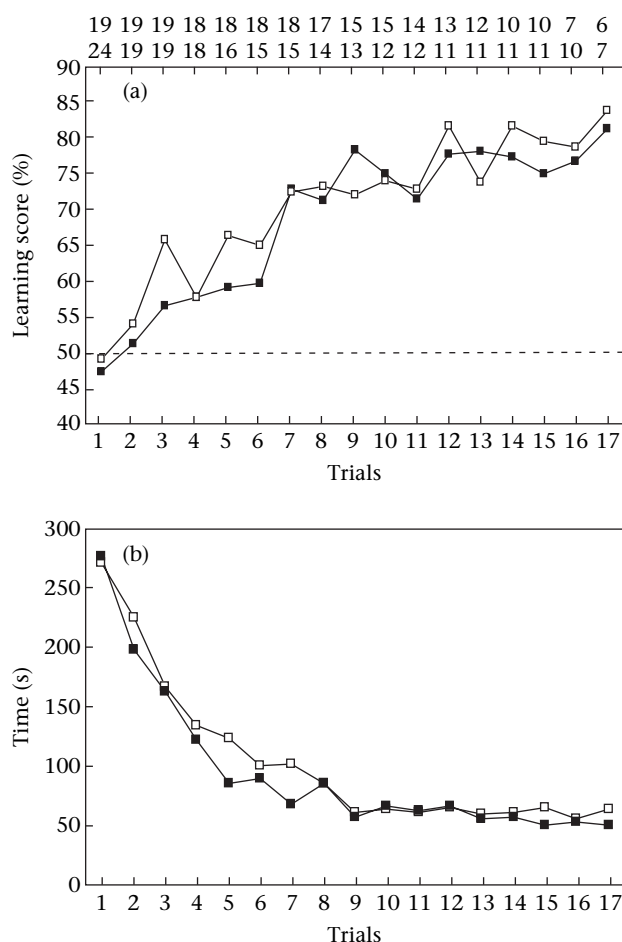


Figure 3. Progressive learning in alternation mazes. (a) Learning score as a function of trials. (■) Learning scores for the simple alternation task (because departure side had no significant effect (see text), the RLRLRLRL and LRLRLRLR groups were pooled on the figure). (□) Learning scores for the double alternation task (because departure side had no significant effect (see text), the RRLRLRL and LLRLRLRL groups were pooled on the figure). (---) Theoretical random performance. Numbers at the top of the graph indicate sample sizes for both tasks (upper line: simple alternation; lower line: double alternation). Note that the graph represents the performance in the whole maze (eight chambers), so that each correct (or wrong) choice in a chamber represents a 12.5% increase (or decrease) of the LS. (b) Time spent in the maze as a function of trials. (■) Times recorded in simple alternation mazes (RLRLRLRL and LRLRLRLRL groups pooled). (□) Times recorded in double alternation mazes (RRLRLRL and LLRLRLRL groups pooled).

suggests that they started extrapolating a sensorimotor displacement rule. Scores in the second additional chambers decreased with the complexity of the motor rules (from repetition to double alternation).

Irregular Mazes

In contrast to the previous experiments, ants were trained in a maze requiring the learning of specific sequences of turns without an elementary subpath. To facilitate such a complex learning task, ants were trained on five-chambered mazes. The ants' learning scores were at chance levels on the

first trial (mean LS = 46.2%) and increased significantly across the following trials (Fig. 4a; repeated-measures ANOVA: $F_{11,88} = 7.82$, $P < 0.0001$). Helmoltz contrasts show that the differences between trials become nonsignificant after trial 2 ($P > 0.05$): this early asymptote of learning might be due to the reduced number of chambers used in this task. The shorter maze could also explain the rapid drop in travel time observed between trial 1 (204 s spent in the maze) and trial 2 (96 s) (Fig. 4b).

When tested in an extended irregular maze, including five additional chambers, the ants did not repeat the learned sensorimotor sequence in the extension and made random choices (Table 1: 52.7% of correct choices). This result suggests that, despite the reduced number of chambers, ants presented with an irregular sequence learn the specific chain of turns instead of a simple locomotion rule.

Control Tests

The choices of naïve ants in the first chamber were equally distributed between both exits (left exit: 45 choices; right exit: 48 choices), showing that neither extra-maze visual cues nor hidden intramaze irregularities influenced the ants.

In constant-turn mazes, test type had no influence on the difference in ΔS in test scores and training scores ($t_{26} = 1.82$, n.s.). Similarly, in alternation and irregular mazes, neither the experiment type (two-way ANOVA: $F_{2,32} = 0.17$, n.s.) nor the test type (two-way ANOVA: $F_{2,32} = 0.49$, n.s.) had a significant influence on ΔS . These results allow for the analysis of all test performances simultaneously, that is computing a general ΔS for all experiments and all tests. This analysis shows that, in all experiments, the performance of the ants was not affected when all exits were opened, when the maze was rotated by 90° or when the chambers were shuffled (difference between test scores and training scores: $\Delta S = -0.01 \pm 0.65$; t test of the difference with a theoretical mean of 0 errors: $t_{68} = -0.18$, n.s.). This indicates that no visual cues (e.g. light reflection on the sliding doors) or odorant cues (e.g. hypothetical odour plumes or air flux) were used for solving the maze. This was indirectly confirmed by the systematic choice of the closed exits when the ants were tested in a mirror maze just after a repetition training.

DISCUSSION

We explored the ability of the solitary forager *G. destructor* to navigate through a multiple Y-maze and to learn the appropriate locomotor rules. *Gigantiops* ants learned very rapidly to detour on the same side at each stage of a multiple Y-maze. Similarly, in the absence of specific visual cues, bees can learn to fly rapidly through a maze in which every turn must be made in the same direction (Zhang et al. 2000). Ants also learned the simple sequential alternation rule, in which they had to systematically alternate between left and right along a route, even though this sensorimotor pattern was harder to learn than the repetition rule. The performance of *Gigantiops* is comparable to those of bees trained in a zig-zag maze, which they learned nearly as well as a constant-turn maze (Zhang et al. 2000).

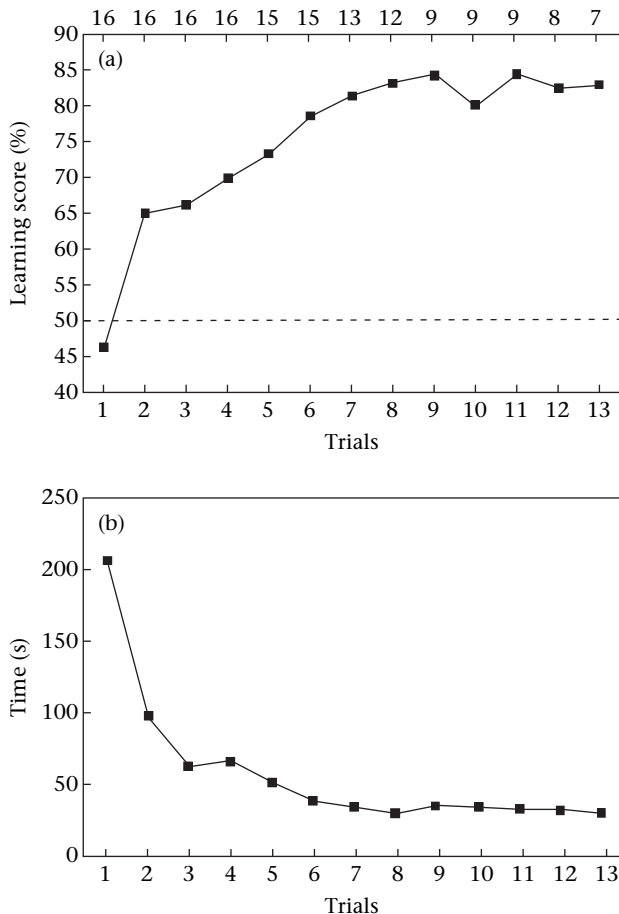


Figure 4. Progressive learning in irregular mazes. (a) Learning score as a function of trials. (---). Theoretical random performance. Numbers at the top of the graph indicate sample size. Note that the graph represents the performance in the whole maze (five chambers), so that each correct (or wrong) choice in a chamber represents a 20% increase (or decrease) of the LS. (b) Time spent in the maze as a function of trials.

The tendency to 'turn on the same side' therefore appears to prevail over alternation behaviour in *Gigantiops*. By contrast, spontaneous alternation behaviour (SAB), that is the tendency for animals to alternate their choices of T- or Y-maze arms, is common across many vertebrates and invertebrates (Tolman 1925; Hughes 2004). However, studies of SAB in insects are conflicting (Lester 1968) and limited (Hughes 1989; Zhang et al. 1996, 2000). For example, the fruit fly *D. melanogaster* shows sequential repetition when freely tested in a multiple T-maze (Murphey 1965) and sequential alternation when forced to turn between a first and a second choice point (May & Wellman 1968). Despite Schneirla's (1929) conclusions, the ants *Formica subintegra* and *Camponotus noveboracensis* did not alternate spontaneously when forced turns were experienced prior to a free choice (Dingle 1962). This suggests that a strong tendency for repetition behaviour is common to several ant species, including *G. destructor*.

Ants were able to learn both the constant-turn and the zig-zag rules and extrapolate them successfully to negotiate extensions of the unmarked linear mazes. Indeed, when presented with a greater number of Y-choices

compared to training, ants persisted in the corresponding learned motor rule, with high scores for sequential repetition but lower scores for alternations. Similarly, flying bees trained to negotiate a maze in which every turn was made in the same direction (repetition) or in which the correct turns alternated between right and left (alternation) applied the corresponding learned rules when tested in extended versions of the training mazes (Zhang et al. 2000).

It is well known that ants gauge the distance they travel during their foraging excursions (Thiélin-Bescond & Beugnon 2005; Collett et al. 2006; Wittlinger et al. 2006, 2007). Moreover, distance estimation in *Gigantiops* ants can interact with sensorimotor tasks (Chevarin 2006). This could explain why scores in the second additional chambers were always lower than scores in the first chambers. Ants were also able to learn a randomized sequence of alternation decisions when homing in fixed irregular mazes. Ants mastered this complex sensorimotor learning rather quickly, even though this was theoretically much harder to learn than simpler constant right-turn or left-turn tasks.

Contrary to the extended zig-zag and constant-turn mazes, in which ants persisted in the corresponding alternation and repetition motor rules, ants tested in the extended irregular mazes did not persist in their fixed learned routine and displayed random choices out the additional exits. This implies that the ants memorized the entire and unique sequence of turns that was necessary to navigate through each irregular fixed maze successfully. The same conclusion was drawn in studies of flying bees, which acquired a sequence of motor commands describing the correct path through an unmarked irregular maze (Collett et al. 1993; Zhang et al. 1996).

We therefore confirmed the prediction of the motor learning hypothesis that animals must be able to perform basic sensorimotor patterns before sequencing these together to form site-specific motor programs (Stamps 1995). Our findings are also in accordance with those found in flying bees, except that bees appear to learn irregular (random) mazes nearly as well as zig-zag (alternation) mazes (Zhang et al. 2000). Also *Gigantiops* ants appear more skilled than rats at learning a double alternation maze (Hunter & Hall 1941). To our knowledge, such a complex sensorimotor task has never been tested in any other insect species.

Zhang et al. (2000) indicated that two bees trained on variable irregular mazes could apply a constant-turn rule even if this led them to meet a number of dead ends en route. Although this requires further investigation, we made similar observations: ants displayed repetition behaviour during their training in alternating and irregular mazes instead of changing direction in the appropriate chambers. This led the ants to dead ends, but each error was immediately corrected by a U-turn in the chamber towards the adjacent open exit. Unlike bees, the constant-turn strategy was observed in a majority of ants. However, the occurrences of repetition behaviour were scattered among each ant's trials and the main strategy consisted of learning the expected sensorimotor tasks, reducing the number of errors. Taken together, these results show that ants can develop individual strategies to solve complex navigation tasks.

These alternative strategies lighten the memory load of the individuals that use them because constant-turn rules were the easiest to learn. Thus, the hypothesis that reduced memory demands balance the costs of meeting dead ends may explain the apparent widespread use of these basic strategies among insects.

In conclusion, sensorimotor learning may allow the solitary forager *G. destructor* to learn and follow complicated familiar routes in its complex rainforest habitat, in addition to using visual information (Beugnon et al. 2001, 2005). One could predict (Chevarin 2006) that different motoric acts learned independent of identified visual cues could be primed by the distance travelled (i.e. turning left after a certain distance travelled since the start of the homebound journey) and/or according to the number of choice points bypassed (i.e. turn right at the third choice point). All else being equal, the consistency shown by desert ants in choosing a particular detour side around an inconspicuous barrier could be also considered a sensorimotor program (Bisch-Knaden & Wehner 2001). The role of procedural knowledge in ant navigation could, therefore, be more important than assumed previously (Knaden et al. 2006).

These findings suggest that sensorimotor routine memories in ants could eliminate the need to recollect numerous landmark views along their routes, a task that appears cognitively demanding in naturally cluttered environments containing many similar topographic features. Our slalom racer hypothesis (Macquart et al. 2006), which predicts that *Gigantiops* ants must be able to form site-specific locomotor programs independent of landmark identification, may thus permit accurate, rapid and safe route navigation with a reduced spatial memory load and a reduced processing time. Reducing travel time along familiar routes presents a high adaptive value in this ant species by lowering the risk of predation by lizards, mantids and spiders (Beugnon et al. 2005). By reducing the number of landmark-recognition-triggered responses, sensorimotor learning appears to be a much simpler and faster form of navigation along a familiar route. Such situation-dependent spatial knowledge should certainly apply to many other invertebrate and vertebrate species (Stamps 1995).

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