Maze negotiation by a myrmicine ant (Hymenoptera: Formicidae)

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Abstract

After spatial conditioning to two differently coloured cues, *Myrmica sabuleti* MEINERT, 1861 workers correctly negotiated a maze provided with the two coloured markers, both from the entrance to the exit and in the reverse direction. When the two markers were replaced by differently coloured ones, the ants failed to negotiate the maze. This suggests that, in nature, these ants can find their way using a few memorised landmarks rather than by learning entire trajectories. This supports a combined "snapshot" and "sketchmap" model.

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Introduction

In many ant species, foragers move all around the surroundings of their nest, apparently randomly, looking for food. These surroundings are commonly marked with specific pheromones. After detecting food, they return to their nest, often laying down a chemical trail. They then recruit nestmates from the inside and / or the vicinity of the nest. This requires foragers to localise themselves with regard to the nest, memorise at least partly their trajectory, recognise the directions of their movement and evaluate the distances they travel. They can estimate such walked distances using odometry (CAMMAERTS 2005a). They can also memorise some of their locomotor reactions (MACQUART & al. 2006b) and use distant, stable cues for orienting themselves (for example SALO 1998). Odorous markings of areas help them because such markings are stronger and / or different close to the nest (CAMMAERTS & CAMMAERTS 1998, 1999, 2001). As soon and as long as possible, however, ants use visual landmarks and cues present along their path. They memorise them and associate them with the subsequent locomotor reactions. This use of visual cues by foragers has been extensively studied (KLOTZ & REID 1993, CHAMERON & al. 1998, NICHOLSON & al. 1999, COLLETT & al. 2003, HARRIS & al. 2005, GRAHAM & COLLETT 2006, MACQUART & al. 2006a). Several of these studies used mazes. Note that, since SCHNEIRLA (1929), mazes were and are still used for other purposes briefly reviewed in the "Discussion". As for the present purpose – the study of the use of visual cues – MACQUART & BEUGNON (2007), for instance, recently tested foragers of *Gigantiops destructor* (FABRICIUS, 1804) in a maze, whereby the correct path involved a succession of choices between right and left directions. A narrow black marker was displayed to the ants when the correct path was to the right, a broad black marker when it was to the left. *Gigantiops destructor* foragers rapidly learned to correctly negotiate the entire maze.

In this situation, as in many other experimental ones, the ants (as well as other insects) are trained, then tested in the same apparatus – a maze with or without visual cues. They must concurrently learn the distance to walk, the visual elements to take into account, the direction to choose and the locomotor reactions to perform. Another approach would be to dissociate these elements. Doing so would better agree with natural situations because, in the field, certain elements may change: food sources are seldom located at the same places within the colony foraging area, the exact position of several elements (pieces of flowers, leaves, small stones) may somewhat change, the nest itself may be relocated in the same environment, and the form and dimension of the nest and of other neighbouring structures may vary. Several cues, however, will remain unchanged. Do the foragers permanently forget previously memorised paths and do they continuously learn entire new trajectories or, on the contrary, can they use acquired knowledge of stable cues, of unchanging elements, when they must forage in a somewhat modified environment?

To answer these questions, we trained ants in front of two different markers that had to be associated with two different locomotor reactions. We then tested the ants in a maze adequately provided with these two markers.

Most previous work on foragers' orientation concerns species with large eyes and good vision. *Gigantiops destructor* is a case in point. Is the situation different for the very numerous species with relatively small eyes and poor vision? *Myrmica sabuleti* MEINERT, 1861 is such a species. We have used that species as a model for some time now. *Myrmica sabuleti* older workers forage and recruit nestmates (CAMMAERTS & CAMMAERTS 1980). They clearly also use their visual perception while foraging (M.-C. Cammaerts, unpubl.). They can distinguish several black elements from one another, they are sensitive to the dimen-

sions of perceived elements, their minimum angle of vision is 5° 12', they see very well above them, and they are sensitive to the orientation of perceived elements. Apparently, however, they see their environment with convexity (CAMMAERTS 2004a, 2006). They can discriminate colours (CAMMAERTS 2007), and the light threshold to do so is lower (CAMMAERTS & CAMMAERTS in press) than the one required for perceiving forms (CAMMAERTS 2005b). An ongoing morphological study (M.-C. Cammaerts & al., unpubl.) shows that these workers have smaller eyes than other species. These ants can acquire classical conditioning as well as spatial learning (CAMMAERTS 2004b). They can also be spatially conditioned (CAMMAERTS 2004c). Operant conditioning (a simpler experimental method) is also possible on *M. sabuleti* workers, whereby meat as a reward yields the best results (CAMMAERTS 2004d). Differential operant conditioning can also successfully be used (CAMMAERTS 2006, 2007). Consequently, we performed differential as well as spatial operant conditioning on *M. sabuleti* workers using meat as a reward and two differently coloured elements as conditional stimuli. We also tested these workers before and after their conditioning in mazes provided with the two differently coloured elements used during conditioning. Thereafter, we evaluated the precision of the ants' response, testing them in mazes provided with somewhat modified markers. Finally, we examined whether ants accustomed to walk in one direction, seeing elements in front of them, can correctly use these elements to return the same way. For this purpose we tested ants in mazes provided with adequate markers, but admitted them through the exit of the mazes and observed their movement towards the entrance.

Material and methods

Collection and maintenance of ants

The experiments were performed on two large colonies of *M. sabuleti* collected at Höhes Martelingen (Grand Duchy of Luxembourg, 49° 49' 30" N, 5° 45' 00" E), then divided in two experimental colonies, each one containing one or two queens, brood and about 500 workers. Each experimental colony was maintained in the laboratory, nesting in two or three glass tubes half-filled with water. A cotton-plug separated the ants from the water. The glass tubes were deposited in a tray (37 cm × 52 cm × 8 cm) serving as a foraging area (Fig. 2). The borders of this area were covered with talc and food was delivered inside. It was on these foraging areas that ants were trained using appropriate apparatus and were tested in mazes.

Food consisted of sugared water offered in a small glass tube plugged with cotton, as well as of dead cockroaches deposited on a glass slide. This meat food was withheld four days before an experiment and never offered during an experiment because it served as a reward during the training phases.

The temperature was 20°C ± 1°C; the humidity was high and constant; the lighting, obtained using a dimmer and five OSRAM concentra 60 W lamps, had a constant intensity of 1,500 lux.

Experimental apparatus

Experimental apparatus used to train the ants: The ants of each colony were trained using an apparatus made of a glass slide, a reward and a cube provided with two markers. The glass slide (2.6 cm × 7.6 cm) served to support the reward at one end and the cube at the other end so that the distance between the two objects was 4 cm. The reward was a young cockroach (1.5 cm to 2 cm), killed by freezing, tied to the glass slide with an insulated copper wire. The cube (five of its faces) (2 cm × 2 cm × 2 cm) was built with strong white paper (Steinback ®) kept in position using glue. Two differently coloured square pieces of paper (1.5 cm × 1.5 cm) (Canson ®), one blue, the other yellow, were glued on two opposite faces of the cube. Figure 1 shows how pieces of paper of the given dimensions were cut and folded to construct such a cube (see also cubes in Fig. 1).

Maze used to test the ants: Each maze was built of strong white paper (Steinback ®). It consisted of a floor free of talc and of walls covered with talc. There was no ceiling, allowing optimum aeration and observation. The floor width and wall height were 2 cm. The distance between two successive turns inside the maze was 4 cm. Figure 1 shows the four pieces of strong white paper drawn, cut, folded and assembled using glue in order to build a maze; this maze must then be provided with the appropriate square pieces of coloured paper. This involved gluing square pieces (1.5 cm × 1.5 cm) of blue or yellow paper (Canson ®) on the walls, inside the maze, in front of each choice point: a blue square when the correct path was to the right, a yellow square when the correct path was to the left. Mazes dotted with such markers can be seen in Figure 2. Of course, no meat was placed in the mazes; these apparatus were devoted to tests and the ants, consequently, never deposited a trail. Nevertheless (see the "Discussion"), the bottom of each maze was covered by an appropriately cut piece of paper renewed between each experiment.

Experimental protocol

The entire protocol consisted, for each of the four ant colonies, successively, of

+ a control experiment during which the ants were admitted into the maze through the entrance,
+ another control experiment during which the ants were admitted into the maze through the exit,
+ a six-day training period,
+ a first test (ants admitted through the entrance),
+ a three-day training period,
+ a second test,
+ a second three-day training period,
+ a third test,
+ a one-day training period,
+ a test in mazes provided with modified markers,
+ a one-day training period,
+ and a test during which the ants were admitted through the exit of the maze.

The training phases consisted of placing a training apparatus on the foraging area of each used colony and providing these apparatus with food. This meat was tied to the glass slide 4 cm away from the cube, and positioned on the right of the blue square and (at the same time) on the left of the yellow square. The apparatus was variously oriented and relocated on the foraging areas 9, 3 and 1 times during the 6-day period, the two 3-day periods and the two 1-day periods of training, respectively. Meat was then renewed as necessary.
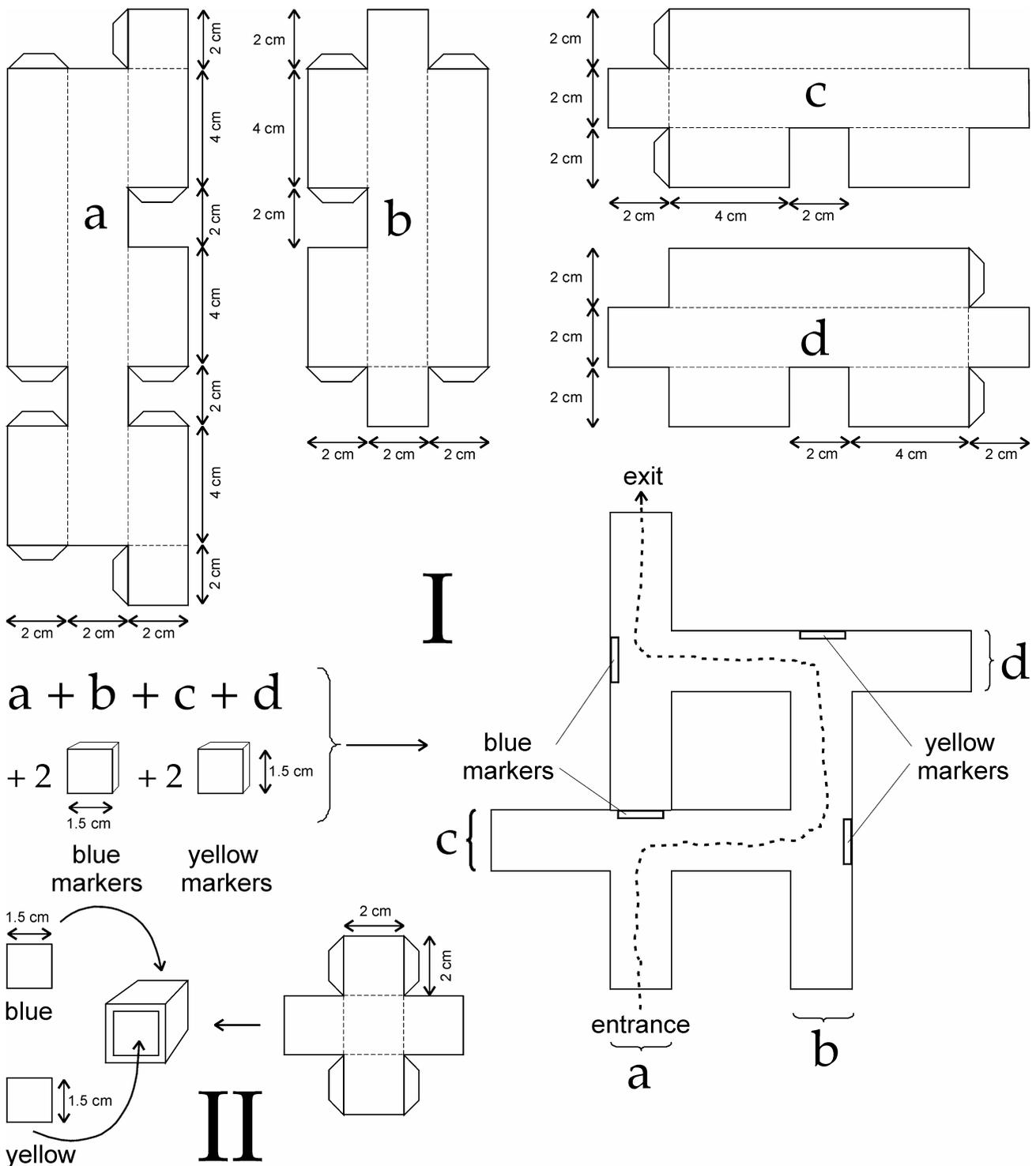
Fig. 1: (I) The maze inside of which the ants were tested and its construction. (II) The experimental apparatus used to condition the ants. Maze and apparatus were built in white strong paper. The stepped bold line inside the maze indicates the correct way.

Each **control and test experiment** was conducted exactly in the same way. To conduct such an experiment on a colony, a maze was deposited in the tray of the respective colony and 10 ants were, one by one, allowed to enter the maze through its entrance or gently placed inside of it very near the entrance. Their movements were then observed and quantified as detailed below. Each tested ant was allowed to go out of the maze through its exit or was gently taken out of it. It was then isolated in a polyacetate glass whose borders had been covered with talc, until ten foragers were tested, in order to avoid testing the same animal twice.

As mentioned above, a test was also conducted using **mazes provided with modified markers**. The modification consisted in replacing the blue squares by violet ones and the yellow squares by green ones. The violet and the
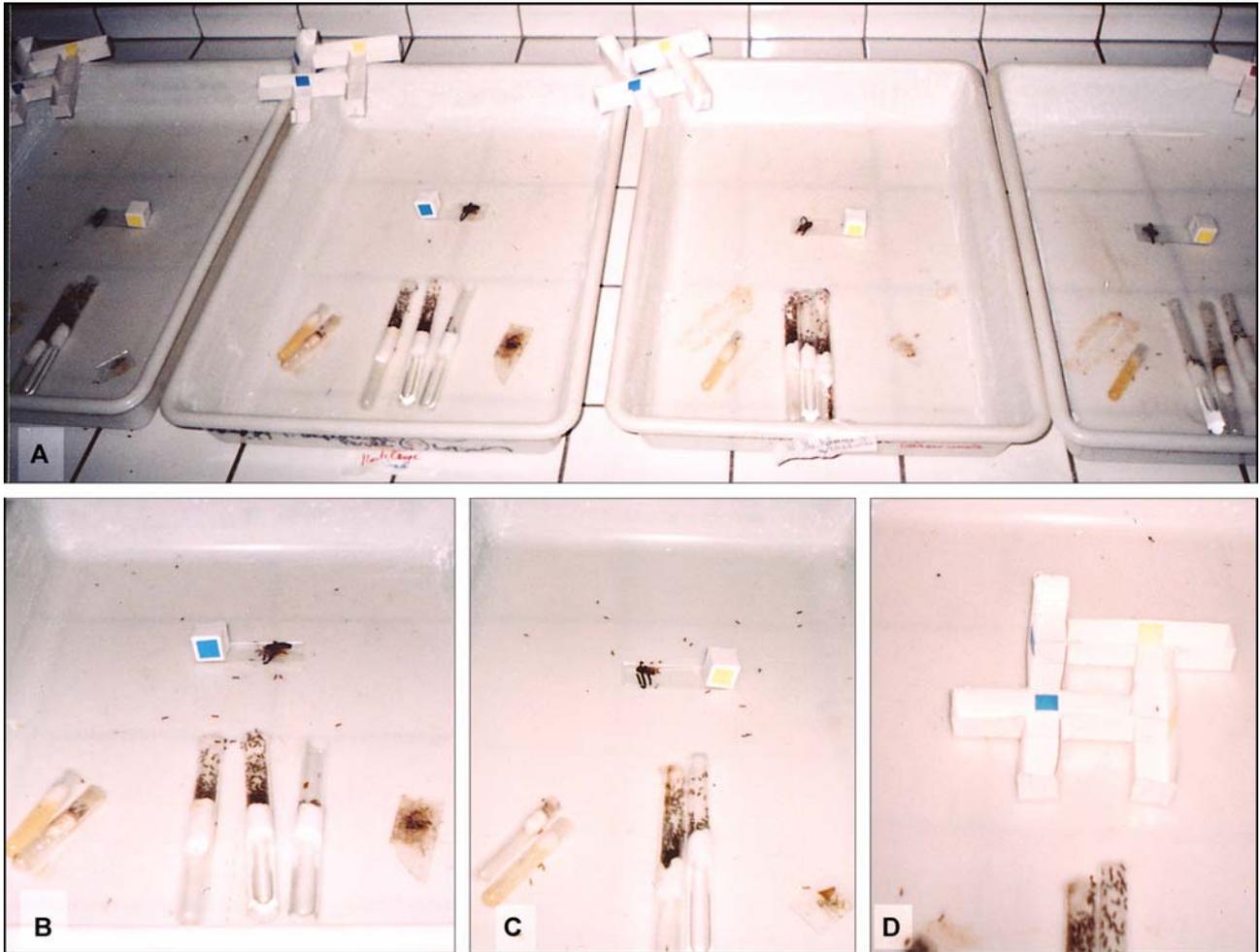
Fig. 2: Effect of differential spatial operant conditioning to two differently coloured markers on ants' travelling along a maze provided with these markers. (A) Experimental colonies of *Myrmica sabuleti* used. An experimental apparatus allowing the ants' conditioning can be seen in the tray of each colony. A maze provided with adequate markers lays on the borders of the tray of the three left colonies. A maze with differently coloured markers can be seen on the borders of the tray of the colony located on the right. (B, C) Differential spatial operant conditioning to a blue and a yellow square (conditioning at the same time: see "Material and methods"). (D) Test on an ant in a maze provided with the blue and the yellow markers. The ant is giving a second correct choice having just turned to the left in front of a yellow marker.

green squares were made of coloured strong paper (Canson ®) (1.5 cm × 1.5 cm) and glued on the walls of the mazes just like the blue and the yellow squares had been (Fig. 1A on right).

The control and the test experiments in which the ants were admitted into the mazes through their exit were performed using unchanged mazes (i.e., mazes with blue and yellow markers). The mazes were deposited into the ants' trays just like when ants were admitted through the entrance. The experiments were conducted exactly like the preceding ones and the ants' response was quantified in the same way (see below).

The blue, yellow, violet, and green papers used are those previously employed for studying colour discrimination in *M. sabuleti* workers. The spectra of the light reflected by these papers are given in CAMMAERTS (2007).

Quantification of the ants' movement

For each ant entering a maze, the ants' choice of direction (correct / incorrect) was recorded at each turn. When the

ants were admitted through the entrance, the correct choices were to go to the right in front of a blue square and to the left in front of a yellow one. When the ants were admitted through the exit, the correct choices were to turn 90° (to the left near a blue square and to the right near a yellow one), while the wrong choices were to move straight ahead. At the end of an experiment performed on one colony (i.e., on ten ants), the total number of correct choices (among the forty potential ones) as well as the number of ants having made no, one, two, three or four correct choices while turning in the maze were established. Four correct choices corresponded to successful negotiation of the maze. The results obtained for each of the four colonies were pooled (Tabs. 1 and 2).

For each experiment (made on four colonies), the distribution of the total number of ants having made no, one, two, three and four correct choices was compared to the corresponding control distribution using the non-parametric χ^2 test (SIEGEL & CASTELLAN 1988).

Tab. 1: Responses of *Myrmica sabuleti* workers moving in a maze provided with two coloured markers. I: before conditioning, II to IV: after 6, 9 and 12 days of spatial conditioning in front of the two markers set in the maze, respectively, V: in a maze provided with two differently coloured markers.

Experiment	Colony	Numbers of correct responses	Numbers of ants having given				
			0	1	2	3	4 correct responses
I	1	8 / 40	4	4	2	0	0
control	2	8 / 40	3	6	1	0	0
	3	8 / 40	3	5	2	0	0
	4	8 / 40	4	4	2	0	0
	all	**32 / 160**	**14**	**19**	**7**	**0**	**0**
II	1	31 / 40	0	0	2	6	2
after 6 days	2	31 / 40	0	0	2	5	3
of conditioning	3	31 / 40	0	0	3	3	4
	4	31 / 40	0	1	2	3	4
	all	**124 / 160**	**0**	**1**	**9**	**17**	**13**
III	1	36 / 40	0	0	0	4	6
after 9 days	2	34 / 40	0	0	1	4	5
(that is 3 more	3	35 / 40	0	0	1	3	6
days) of	4	35 / 40	0	0	0	5	5
conditioning	**all**	**140 / 160**	**0**	**0**	**2**	**16**	**22**
IV	1	36 / 40	0	0	0	4	6
after 12 days	2	36 / 40	0	0	0	4	6
(that is again 3	3	37 / 40	0	0	1	1	8
more days) of	4	37 / 40	0	0	1	1	8
conditioning	**all**	**146 / 160**	**0**	**0**	**2**	**10**	**28**
V	1	12 / 40	2	6	0	2	0
in the presence	2	12 / 40	4	1	4	1	0
of differently	3	12 / 40	3	3	3	1	0
coloured	4	12 / 40	1	6	3	0	0
markers	**all**	**48 / 160**	**10**	**16**	**10**	**4**	**0**

Results
Experiments using unchanged mazes and ants' admission through the entrance (Tab. 1, I to IV)

Control experiments (Tab. 1, I): Based on the results of the four experiments performed on the four different colonies, each time on ten ants, these ants (before any conditioning) made only 32 correct choices out of the 160 potential ones. The ants' score was thus 2 / 10. This result was identical in each of the four used colonies. The 32 correct choices resulted from 14 ants that made no correct choice, from 19 ants that made one correct choice and from seven ants that made two correct choices. No ants made three or four correct choices.

Test experiments (Tab. 1, II to IV): After six days of training in front of the two markers and then being presented with the maze, the 40 tested ants made a total of 124 out of 160 correct choices. This corresponded to a score of 7.5 / 10. Again, this result was identical for each of the four colonies and therefore reliable. This time, no ant made no correct choice, and only one made one correct choice. Moreover, nine ants made two correct choices, 17 made three, and 13 made four correct choices, the latter corresponding to an entirely correct negotiation of the maze. The distribution of these numbers of choices statistically differed from the control (P < 0.001).

After three more training days, the ants' score was 8.75 / 10 (140 correct choices among 160 encountered ones), the same result being obtained for each of the tested colonies. No ant made no or one correct choice; two ants made two correct choices; 16 and 22 made three and four correct choices, respectively, while moving through the maze. This distribution differed significantly from the control (P < 0.001).

After three more training days, the ants slightly increased their previous score and exhibited a total of 146 out of

Tab. 2: Responses of *Myrmica sabuleti* workers moving in a maze provided with two coloured markers, from the exit towards the entrance of the maze, I: before and II: after a 13-day period of spatial operant conditioning to the two coloured markers.

Experiment	Colony	Numbers of correct responses	Numbers of ants having given				
			0	**1**	**2**	**3**	**4 correct responses**
I control	1	9 / 40	2	7	1	0	0
	2	9 / 40	4	3	3	0	0
	3	8 / 40	3	6	1	0	0
	4	8 / 40	4	4	2	0	0
	all	**34 / 160**	**13**	**20**	**7**	**0**	**0**
II after a 13-day period of conditioning	1	27 / 40	0	1	2	6	1
	2	24 / 40	1	1	2	5	1
	3	26 / 40	0	2	2	4	2
	4	25 / 40	1	0	3	5	1
	all	**102 / 160**	**2**	**4**	**9**	**20**	**5**

160 correct choices. The photograph shown in Fig. 2D was then taken. This score of 9.125 / 10 was almost the same in each colony. This time, no ant made no or one correct choice, two ants made two correct choices, ten ants made three correct choices, and 28 ants moved correctly through the maze (four correct choices). These values statistically differed from the control (P < 0.001).

Experiments using modified mazes (Tab. 1, V)

When the blue and the yellow markers in the mazes were removed and replaced by violet and green ones, respectively, the ants hesitated at each choice point. They turned their head and body several times to the left and to the right; then, they often moved in one direction and after that in the opposite one. They finally moved slowly in the maze. Ultimately, the 40 tested ants made a total of 48 out of 160 correct choices, i.e., a score of 3 / 10. Here, ten ants made no correct choice, 16 ants one correct choice, and ten ants two correct choices. Only four ants made three correct choices and no ant performed an entirely correct trajectory. This distribution was not identical to, but nevertheless not statistically different from the control (df = 2, $\chi 2$ = 1.96, 0.30 < P < 0.50). This behaviour and movement in a maze with colours altered from those presented during the training phases confirm two previously reported abilities: the ants can visually distinguish blue from violet and yellow from green (CAMMAERTS 2007), and operant conditioning is successful and precise in these insects (CAMMAERTS 2004d).

Experiments with ants' admission through the exit (Tab. 2)

During the control experiments, movement resembled that of ants admitted through the entrance before any conditioning. The 40 tested ants made a total of 34 of 160 correct choices, a score of only 2.125 / 10. This reflects 13 ants making no correct choice, 20 ants with one correct choice and seven ants with two correct choices. No ant made three or four correct choices (Tab. 2, I).

After a 14-day period of conditioning, the 40 tested ants made a total of 102 correct choices. This surprising score of 6.375 / 10 reflects only two ants making no correct choice, four ants with one correct choice, nine with two, 20 ants with three, and five ants with four correct choices (Tab. 2, II). Recall that for making a correct choice, the ants must display a different motor response than when moving from the entrance towards the exit. They had to neglect the straight way and to turn 90° either to the left (near a blue square) or to the right (near a yellow square). Note that, during these test experiments, the movement all along the maze differed from that of ants admitted through the entrance. This time, the ants very often turned back on their path, generally until the previously correctly travelled point of choice. There, they turned 180° and moved again towards the entrance. This behaviour apparently helped the ants to find their correct way back through the maze. Indeed, doing so allowed the ants to briefly see the cues as they would have seen them if admitted through the entrance of the maze.

Conclusion

The present work reveals three facts:

1. After having been trained, for several days, to turn right in front of a blue square and left in front of a yellow square, *M. sabuleti* workers were able to successfully negotiate a maze (a rather complex apparatus different from that used for training) provided with the two coloured squares.

2. When the two coloured markers in the maze were replaced by two differently coloured ones, the ants exhibited a clear hesitating behaviour and ultimately did not successfully negotiate the maze.

3. After having been trained for several days in front of two coloured markers, *M. sabuleti* workers correctly moved from the exit towards the entrance of a maze provided with the two markers. Their score of 6.375 / 10, though low, was significantly different from the control value (2.125 / 10).

Discussion

Based on the first fact above, we can conclude that, in nature, foragers can probably isolate and use a few memorised landmarks to find their way within their foraging area, even if several other elements have changed.

The second fact again underlines (CAMMAERTS 2007) that this species can distinguish colours. This also demonstrates very precise learned associations between certain landmarks and locomotor reactions. Consequently, in nature, they will not (potentially incorrectly) respond to somewhat changed landmarks, but will continue to correctly respond to unchanged markers.

As for the third fact above, we observed that the ants moving towards the entrance turned many times and often briefly moved towards the exit. This apparently helped them to correctly move through the maze. This strategy allowed them to repeatedly see the learned markers as they had seen them during training. This suggests that, during training, the ants have learned that, for going away from the training experimental apparatus and foraging again or coming back to their nest, they had to move for a time, the coloured markers staying behind them. In nature, foraging requires moving away from as well as back to the nest. Our present results suggest that ants can negotiate their way in both directions using learned visual markers.

Four elements of our experimental protocol allow us to rule out several alternative interpretations. Firstly, all experiments (control and tests) were conducted in the same way, making the results comparable. Secondly, during the tests, no meat was offered and therefore no trail pheromone was deposited. To account for potential deposition of small amounts of Dufour's gland content, a piece of white paper was set in each maze and renewed between each experiment. Thirdly, the behavioural status of all the tested ants was always identical (simple foraging / orientation; no nestmates recruited or congeners followed). Fourthly, the numbers of ants having made 0, 1, 2, 3, or 4 correct choices, obtained for each experiment based on the response of each tested ant, were not normally distributed: we thus used non-parametric χ^2 tests to statistically compare distributions.

Mazes have been used for several purposes, also involving ants. SCHNEIRLA (1929) already used them to study ants' learning performances. Mazes were then used to study ants' visual perception abilities (for example, VOWLES 1965). Then, after partial success, mazes were used to more closely examine orientation faculty (e.g., CHAMERON & al. 1998, MACQUART & al. 2006b, MACQUART & BEUGNON 2007). The present work further addresses these issues. In the mean time, mazes were applied to study not only the ants' ability to memorise sequences of turns, but also their capability of passing the information on to nestmates. Thanks to their studies of maze learning, REZNIKOVA & RYABKO (1986, 1994, 2003) and RYABKO & REZNIKOVA (1996) revealed how many bits of information ants can memorise and pass on to congeners and at what rate. Recently, again using ants' maze learning, REZNIKOVA (2008) went a step further and proposed an objective quantitative method to investigate the communication and cognition in highly social animals. Finally, mazes have also been employed to analyse certain characteristics of ant learning performances: for example, KARAS & UDOLAVA (2001) studied the role of different motivations in the successfulness of maze learning.

Contrary to the process usually applied to test ants in mazes, we dissociated the memorisation of visual cues and their use for correctly negotiating a maze. This may reflect what occurs in nature. Indeed, over time, a few visual elements in a foraging area may remain unchanged and therefore still be valid, while others may vary (in dimension, location, etc). This makes it more useful for ants to "learn" a few stable cues than to memorise an entire complex trajectory in which some markers may soon become unusable.

During our experiments, the ants acquired conditioned responses to two cues in one situation, then exhibited their responses in another situation. Based on this result, we deduce that ants will still be able to recognise a few unchanged cues despite changes in their natural foraging area. They will correctly respond to these cues and so find their way. Ants would be able to "know", to "feel", or to "realise" that a cue is likely to be still valid based on complementary information: the distance walked to reach it, its orientation, its illumination, its position with regard to distant, motionless cues, etc. Accordingly, ants may well select a few useful landmarks among the very numerous ones present all along their trajectories. This concept is deducible from the experimental work of FOURCASSIE & al. (1999) on *Dinoponera gigantea* (PERTY, 1833). It was also developed by HARRIS & al. (2005) working on wood ants, and was then extended, by HARRIS & al. (2007), to the use of certain characteristics (e.g., width) of the landmarks. More recently, COLLETT & al. (2007) observed that ants displayed to a rather unfamiliar site could still reach their goal. These authors concluded that ants memorised and used a few unchanged landmarks, which is in agreement with our own deduction.

In the present work, we presented vertical cues. We know, however, that *Myrmica* workers also see below, laterally and above them (CAMMAERTS 2004a). This calls for conducting a separate experiment presenting cues to the ants in a horizontal plane above them. In nature, ants are known to use such cues because they look up to the canopy (examples: *Pachycondyla tarsata* (FABRICIUS, 1798), see HÖLLDOBLER 1980; *Odontomachus bauri* EMERY, 1892, see OLIVEIRES & HÖLLDOBLER 1989, *Formica polyctena* FOERSTER, 1850; see SALO 1998).

Another bit of information gained in this study is that foragers searching for the correct path often briefly reverse their direction. Such events essentially occurred when the ants were admitted through the exit of the mazes. Here, the ants might check their acquired landmark information. These observations and interpretations agree with (but are not identical to) those of GRAHAM & COLLETT (2006). Those authors reported that wood ant foragers frequently retrace their steps for a short distance, thereby probably acquiring their landmark information. In our opinion, *M. sabuleti* workers in our tests retraced their steps not to acquire landmark information, but probably to check that they had correctly responded to and were still moving according to their acquired landmark information.

This and other behaviours we observed here support the two hypotheses proposed for explaining ants' (and bees') success in correctly orienting themselves: the "snapshot" (CARTWRIGHT & COLLETT 1982) and the "sketchmap" (BEUGNON & al. 1996). Accordingly, during training, *M. sabuleti* workers learned that meat is lying a short dis-

tance to the right of a blue square or, conversely, to the left of a yellow square: they behaved according to the "snapshot" model. But they also memorised the relations between nest, food and cues because, while moving towards the exit, they turned right in front of a blue square and left in front of a yellow square, and while moving towards the entrance, they turned 90° when being near a cue. This behaviour reflects the "sketchmap" model. The two proposed models are therefore apparently complementary and not exclusive, whereby foragers rely on them alternately.

As reviewed by PASSERA & ARON (2005) and summarised in the present "Introduction", visual cues are the key elements used by foragers to correctly orient themselves. The new information gained in the present paper is that *M. sabuleti* workers, though having poor vision, can memorise a few visual cues and associate them with simple locomotor reactions. These ants use this learning to find their way from the nest to a food site as well as for returning. This learning and its use is precise: the ants do not respond to somewhat modified cues. Chemical stimuli may also be used (PASSERA & ARON 2005). We will therefore undertake chemical operant conditioning on *M. sabuleti* workers, and subsequently test them in mazes provided with chemical cues. After that, ants will be tested in mazes concurrently provided with chemical and visual cues. Indeed, in nature, ants are simultaneously confronted with these two kinds of cues. The present work therefore partly solves the problem of how ants negotiate their path: it shows how ants with poor vision (a myrmicine) use visual elements to do so and opens the issue of the use of odorous sources.

Acknowledgements

Zusammenfassung

Nach räumlicher Konditionierung auf zwei verschiedene Farben fanden Arbeiterinnen von *Myrmica sabuleti* MEINERT, 1861 den korrekten Weg durch ein mit Markierungen der beiden Farben ausgestattetes Labyrinth, und zwar vom Eingang zum Ausgang und in umgekehrter Richtung. Wenn aber die beiden Farbmarkierungen durch solche anderer Farben ersetzt wurden, fanden die Ameisen den Weg durch das Labyrinth nicht. Unsere Ergebnisse erlauben den Schluss, dass diese Ameisen in ihrer natürlichen Umgebung ihren Weg anhand weniger, ins Gedächtnis eingeprägter Landmarken finden anstatt durch das Erlernen des gesamten Wegverlaufs. Das entspricht einer Kombination des "Snapshot"- und des "Sketchmap"-Modells der Orientierung.

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