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Learning of foraging area-specific marking odor by ants (Hymenoptera, Formicidae)

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ABSTRACT

It is known that ants learn visual and olfactory elements present in their foraging area through operant conditioning (associative learning) while they forage and find food. However, how they learn the specific odorous marking of their foraging area is still unknown. Working on four colonies of *Myrmica rubra* LINNAEUS 1758 and two of *M. sabuleti* MEINERTS 1861, we showed that young ants that did not yet have the knowledge of a specific odor, become imprinted with it after being briefly in contact with it, even in the absence of older congeners or any rewards. Naïve young ants can even be artificially imprinted with an alien marking odor.

KEYWORDS: callow ant, Dufour gland, imprinting, *Myrmica rubra*, ontogenesis, Y-maze

INTRODUCTION

Ants live in an odorous world and communicate with one another essentially through odors. In many ant species, among others, there exist a nest odor, an entrance odor and an area-marking odor (e.g. for the ant *Myrmica rubra* LINNAEUS 1758) [1, 2]. Ants also use several environmental, visual and olfactory elements which help them in navigation [3, 4, 5, 6, 7, 8, 9, 10]. Ants also have an alarm odor, a recruiting odor and a trail following odor. All this is well documented [11]. Recently emerged ants (callow ants) do not know every species or colony specific odors [12]. It has been proven that they soon learn their nest odor through habituation and/or imprinting [13]. It has also been shown that they learn the entrance odor through imprinting and acquire the knowledge of the external (outside) visual aspect of their nest entrance through operant conditioning (or associative learning) [14]. How they learn to follow a trail [15] and to exhibit the alarm reaction [16] has also been studied. Of course, in the process of becoming older and while foraging and collecting food, ants progressively memorize visual and olfactory elements, temporarily or permanently present in their foraging area, and use them for navigation [3-10].

Foragers of *Myrmica* ant species mark the area surrounding their nest via discontinuous small deposits of their Dufour gland content. The marking is done with the non-volatile part of the gland secretion [17, 18] which is a species specific mixture of alcanes and alcenes. The area-marking of *M. rubra* differs, for instance, from that of *M. sabuleti* MEINERTS 1861. The Dufour gland of *M. rubra* essentially contains heptadecene, α-farnesene and pentadecane while that of *M. sabuleti* essentially contains bishomofarnesene, homofarnesene, α-farnesene and very small amounts of alcanes [19, pages 63, 64]. Inside the nest as well as very near the nest entrance, such a secretion is not deposited. At these places, other marking odors are used [20, 1, 2, 21]. Young ants that have never left their nest and/or have never moved far from the nest entrance, have never perceived the odor of their foraging area and thus, probably, do not know that odor.

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The aim of the present work is to examine how young workers, 6 to 9 months old, that have never foraged, acquire the knowledge of their area-marking odor, using the ant *M. rubra* as a model and the species *M. sabuleti* for checking the findings. In the 'Discussion' section, the results will be compared to similar findings in other animal species.

MATERIALS AND METHODS

Collection and maintenance of ants

The work was conducted on five colonies of *M. rubra*, labeled I, II, III, IV and V. Three of them were collected at Marchin (Condroz, Belgium) and two of them in the Aise valley (Ardenne, Belgium); all of them were found on grass land. The work was also performed on two colonies of *M. sabuleti*, labeled I and II, collected in an old quarry, one at Höge Materlingen (Ardenne, G D of Luxembourg) and one at Olloy/Viroin (Ardenne, Belgium). The biology of these two species is now well known; their eye morphology, subtended angle of vision, visual perception, visual and olfactory conditioning, navigation system, and recruitment strategy have been analyzed in the course of many years [a summary is presented in 22].

The collected colonies contain a queen, brood and about 500 workers. From March to May, several workers emerged and they were about 9 months old in December or January, when the present experiment was undertaken. They were darker than when they were about 3 months old, but lighter than older workers and are expected to live for nearly three years [23]. The colonies were maintained in the laboratory in artificial nests made of one to three glass tubes half-filled with water, with a cotton-plug separating the ants from the water. The glass tubes were deposited in trays (42 cm x 27 cm x 7 cm), the sides of which were covered with talc. The trays served as foraging areas, as food was delivered in them. The young ants were observed each day; they were always staying inside the nest, and never moved outside on the foraging area. The colonies were fed with sugar-water provided *ad libitum* in a small glass tube plugged with cotton, and with cut *Tenebrio molitor* larvae served twice a week on a glass-slide (Fig. 1A). Temperature was maintained at 20 ± 2 °C and humidity at about 80%, this remaining constant over the course of the experiment. The lighting had a constant intensity of 330 lux when caring for the ants (e.g. providing food, renewing nesting tubes), training the ants and testing them. During the other time periods, the lighting was adjusted to 110 lux.

Experimental apparatus and methods

Obtaining the area-marking odor of ants

Pieces of Whatman® paper n° 1 of different dimensions were deposited in the foraging area of colonies I, II, III and IV of *M. rubra* between the ants' nest tubes and food sites. They were kept in place for three days, and the four colonies were duly cared for during that time period, but without cleaning the trays (Fig. 1A). The foragers often walked on the deposited Whatman pieces of paper; doing so, they marked the paper with the specific foraging area odor. Small pieces (2 cm x 2 cm) of these marked papers were cut and used for testing ants in an adequate apparatus (see below). While the inside of the nest was marked at a colonial level with the cuticular lipids of ants, the outside foraging area was marked at a specific level with discontinuous spots of the Dufour gland content [24, 17].

Testing the ants

Young ants move slowly, with hesitation; they are not inclined to forage and to walk for long distances. On the other hand, the odor to be tested is an area-marking one: it is a non volatile odor, detectable only when being close to it. Ants must be tested in choice apparatuses, as in Y-mazes. But the decision zone of these mazes must be small and the presented odor must not be far from the tested ants. Consequently, test experiments were performed in small Y-mazes built with strong white paper as those previously used in [25]. They were deposited in a small tray (22 cm x 15 cm x 5 cm), and their sides were covered with talc to prevent the ants from vertically escaping (Fig. 1B). In such an apparatus, the ants do not deposit their trail pheromone (since they are not going from a food source to their nest) but they may deposit other chemicals, such as their cuticular lipids. So, as a precaution, the floor of each apparatus was changed between tests. For control experiments, the Y-apparatus was left empty. For test experiments,

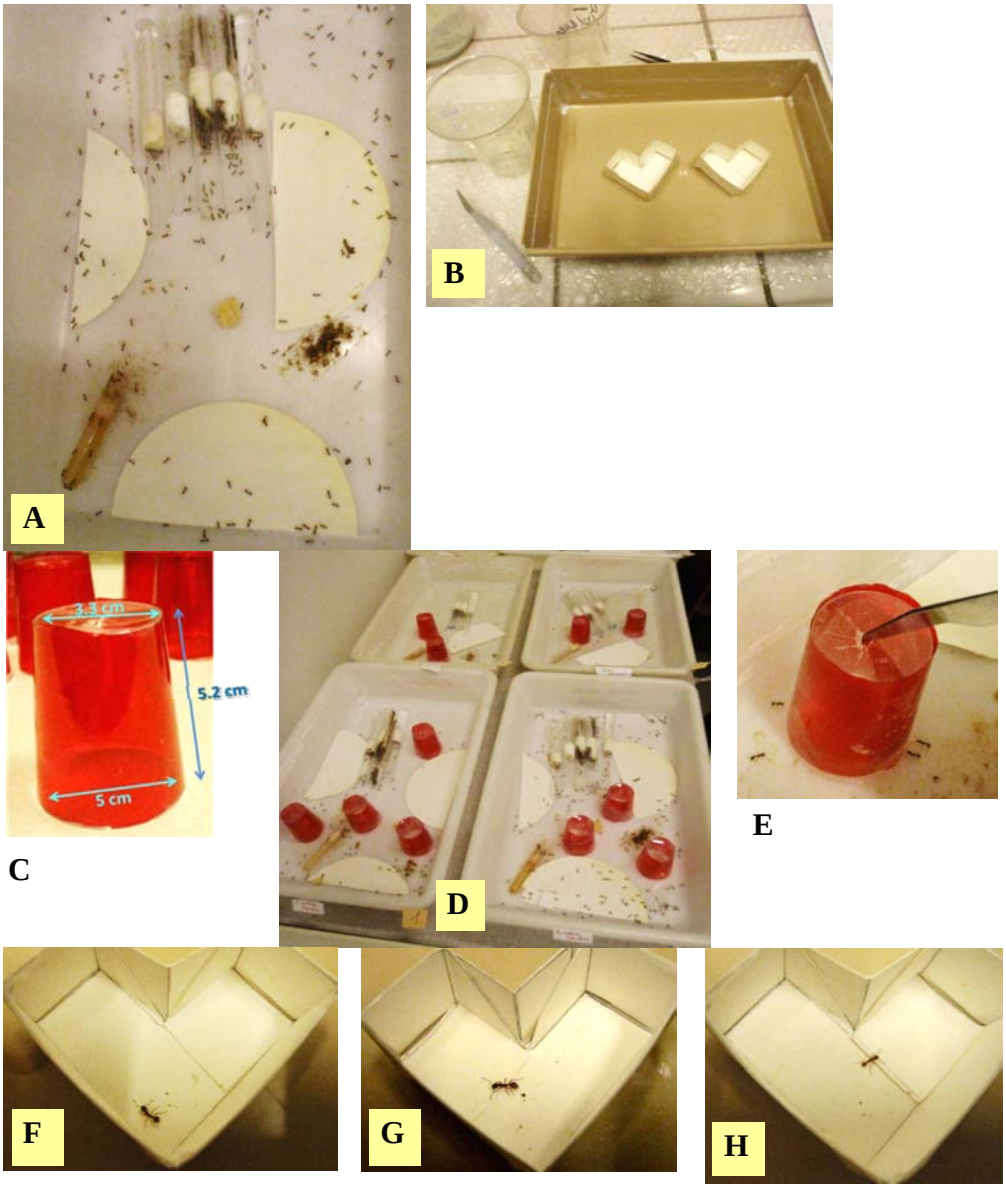

Fig. 1. Experimental apparatus and reaction of the ants. **A**: one of the four used *Myrmica rubra* colony with Whatman paper on the foraging area. After three days, the paper became marked with the foraging area-marking odor of the ants, and pieces (2 cm x 2 cm) of this marked paper were set in one branch of Y-mazes in which ants were tested. **B**: the Y-mazes (test apparatus, in a small tray) in which ants were tested one by one, and the two polyacetate glasses where ants were kept before and after testing. **C**: the reversed brandy glasses covered with red cellophane paper used for examining how ants learn their area-marking odor. **D**: the four *M. rubra* colonies with the reversed brandy glasses in their foraging area, i.e. the design prepared for experimenting naïve young ants that have never left their nest tubes. **E**: placing a naïve young ant (taken out of its nest tube) inside a reversed brandy glass lying in the foraging area of a *M. rubra* colony. **F**: a young naïve *M. rubra*, that has never been in contact with its species foraging area-marking odor, taken out of its nest tube and tested: the ant did not move towards the marked piece of paper (on the right) and even avoided it. **G**: a young naïve *M. rubra* worker taken out of its nest tube, placed for 50 min on its marked foraging area, under a reversed glass, then tested: the ant moved towards the marked piece of paper (on the left). **H**: a young naïve *M. sabuleti* worker taken out of its nest tube, placed for 50 min on a *M. rubra* marked foraging area, under a reversed glass, then tested: the ant also moved towards the marked piece of paper (on the right).

the Y-apparatus was provided, in one of its branch, with a piece (2 cm x 2 cm) of the Whatman paper which had previously been deposited in the foraging area of a *M. rubra* colony (Fig. 1F, G, H) and had thus been marked with the area-marking odor of that species. A thin pencil drawn point indicated the 'entrance' of each branch of the Y. Two identical apparatus were simultaneously used. The marked piece of paper was placed in the left branch of one of the two Y-apparatus and in the right branch of the other apparatus. Each ant was tested three times: once in one of the apparatus, then in the other, then again in the first apparatus, as detailed below (Experimental protocol). The use of two apparatus allowed presenting the cue on the left as well as on the right of the ants without relocating the cue. Such an experimental design has already been used in [25].

Examining the learning of area-marking odor by ants

Reversed polyacetate brandy glasses (base: diameter = 5 cm; top: diameter = 3.3 cm; height: 5.2 cm) were used for isolating naïve young workers in *M. rubra* foraging areas. As ants perceive the red color as almost black, the glasses had their outside covered with red cellophane paper. The sides were slightly covered inside and outside with talc to prevent the ants from climbing up. A hole was pierced in the center of the circular top of each reversed glass through which three to four naïve young ants (see details below) could be placed inside the glass. Doing so, these naïve ants were not rewarded, did not see or olfactorily perceive *M. rubra* foragers but stayed, for 50 min, on a *M. rubra* marked foraging area. The modified brandy glasses are shown in Fig. 1C, D and E.

Planning of the experiment

Six different experiments were performed successively:

1) First, a control experiment was done using ten foragers of each *M. rubra* colony and empty Y-mazes i.e. not provided with a piece of area marked paper.

2) Secondly, for checking if foragers know their foraging area odor, ten foragers of each *M. rubra* colony were tested in Y-mazes provided, in one of their branches, with a piece of area marked paper.

3) Thirdly, for examining if callow ants natively know their foraging area odor, 15, 10, 8 and 7 naïve young workers (that have never left their nest tube) belonging to *M. rubra* colonies I, II, III and IV, respectively were taken out of their nest and tested in Y-mazes provided, in one of their branches, with a piece of *M. rubra* area marked paper. Later on, as a supplementary control experiment, young workers of the *M. sabuleti* colony II were tested in Y-mazes provided with an unmarked white paper in one of their branches.

4) Fourthly, for studying how callow ants acquire the knowledge of their forging area odor, in a short time and without being rewarded, 15, 10, 8 and 7 *M. rubra* naïve young workers, belonging to colonies I, II, III and IV, respectively, were taken out of their nest tubes, and three to four of them were placed inside 4, 3, 2 and 2 reversed glasses placed in the foraging area of colonies I, II, III and IV, respectively (Fig. 1D). They were kept there for 50 min. After this isolation, they were tested as explained below, in the Y-mazes provided, in one of their branches, with a piece of *M. rubra* area marked paper, and were finally placed back into their initial nest tubes.

5) Fifthly, a check experiment was performed using callow ants of another species. Twenty four naïve young workers of the *M. sabuleti* colony I (that have never left their nest tube) were taken out of their nest and three to four of them were placed inside three reversed glasses kept in the foraging area of *M. rubra* colonies I and II, for 50 min. These *M. sabuleti* callow ants were not rewarded, did not see or olfactorily perceive *M. rubra* foragers but stayed, for 50 min, on an area marked with the foraging area odor of *M. rubra* species. After this isolation, these callow ants were, one by one, tested in the Y-mazes provided, in one of their branches, with a piece of *M. rubra* area marked paper, and were finally placed back in their initial nest tubes.

6) Finally, a supplementary control experiment was performed on *M. rubra* callow ants belonging to colony V. Twenty such callows were taken out of their nest and placed, for 50 min, inside five reversed glasses (four ants per glass) kept on unmarked paper (Whatman® n°1). They were then tested in Y-mazes provided, in one of their

branches, with a piece of *M. rubra* area marked paper.

Experimental protocol

For conducting the experiment, the ants to be tested were removed from their colony and placed in a polyacetate glass with its sides covered with talc. They were then tested one by one, as explained below, in 2 Y-maze apparatus duly prepared for the experiment, i.e. either having nothing in their branches (control experiment) or provided with pieces (2 cm x 2 cm) of Whatman paper naturally marked with the area-marking odor of *M. rubra*, one piece in the left branch of one Y-maze and another identical piece in the right branch of the other Y-maze (Fig. 1F-paper on the right, 1G-paper on the left, 1H- paper on the right). Each ant was tested three times: once in one of the apparatus, then in the other one, then again in the first apparatus. Half of the ants were initially tested in the Y-maze provided with the odorous paper in its left branch and the other ants were initially tested in the Y-maze provided with the odorous paper in its right branch, this being randomly decided before experimenting. Each time, the ant to be tested was gently transferred from the polyacetate glass to the area lying between the two branches of one of the Y-apparatus and the branch chosen by the ant was recorded. Then the ant was transferred to the other Y-maze, on the area lying between the two branches and again, the branch chosen by the ant was recorded; the ant was then once more transferred to the first Y-maze and the branch chosen by the ant was again recorded. After these three tests, the ant was placed in another polyacetate glass until all the removed ants had been tested. At the end of the experiment, the ants were put back at their initial location (the old ants, on their foraging area and the young ants, inside their nest tube). Such an experiment allowed recording the number of times the ants turned left or right in the empty Y-apparatus (control) as well as the number of times the ants chose the marked branch of the Y-maze (Table 1). Finally, for each kind of experiment, the total number of choices of the marked and the unmarked branch of the Y-mazes could be established. It was statistically compared to that expected under the null hypothesis, according to which ants navigate the Y-apparatus at random, using the non-parametric goodness-of-fit χ^2 test [26, p 45-51]. While doing so, the Bonferroni correction must not be applied. Responses were considered as non-significant when $P > 0.05$.

RESULTS

Control experiment (Table 1, line 1)

Foragers of *M. rubra*, tested in empty mazes, went either to the right or to the left branch without any preference. Even if the numbers of choices were not the same for each side and for each of the four colonies e.g. 15 ‘right’ and 15 ‘left’ choices, the sum of the scores amounted to 60 choices for each branch of the mazes, a result of course statistically similar to that expected if ants randomly navigated the mazes. This showed that the Y-maze test had no bias.

Experiment on foragers (Table 1, line 2)

Foragers of *M. rubra*, tested in mazes provided with the foraging area odor of that species in one of their branches, oriented themselves towards this branch of the mazes. They moved for a short time on the area lying between the two branches of the mazes, turned in narrow circles, moved their antennae and then in general walked towards the marked area. The obtained result, 94 choices (78.33%) for the marked area *vs* 26 choices for the unmarked one, was statistically different from that expected if ants had no preference for one or the other branch of the mazes ($\chi^2 = 38.53$; df = 1; $P < 0.001$).

Experiment with naïve young *M. rubra* workers (Table 1, lines 3, 4)

Myrmica rubra young workers (that have never left their nest tube) were tested in Y-mazes provided with the species area odor in one of their branches. They moved slowly, cautiously, apparently avoiding the marked area (Fig. 1F). The young naïve workers of each of the four used colonies seldom chose the marked branch of the Y apparatus. Among the 120 recorded choices, only 40 (33.33%) were for the marked branch, while 80 were for the unmarked branch of the Y-mazes. Such a result, 40 *vs* 80 compared to 60 *vs* 60, was statistically significant ($\chi^2 = 13.34$, df = 1, $P < 0.001$).

Such avoidance might be due to the paper itself. So, a supplementary control experiment was performed using *M. sabuleti* young workers and unmarked paper instead of marked paper.

Table 1. Number of ants that have chosen, during the three tests, the right and the left branches of Y-mazes (*control*) or the marked (with *Myrmica rubra* area-marking odor) and the unmarked branches of Y-mazes (lines 2 to 7). The experimental protocol is detailed in the 'Materials and Methods' section and partly illustrated in Fig. 1. The statistical method is explained in the 'Materials and Methods' section and is detailed in the 'Results' section; df = 1, level of probability set at $P < 0.05$.

Ants tested; experiments made	Initial colony	No. of tested ants	No. of ants that have chosen the branch right, marked		left, unmarked	
M. rubra foragers; empty mazes; control	I	10	13		17	
	II	10	18		12	
	III	10	17		13	
	IV	10	12		18	
		Total: 40	Total: 60	$\chi^2 = 0$; $P > 0.99$	60	NS
M. rubra foragers; mazes with one branch marked with *M. rubra* area-marking odor	I	10	25		5	
	II	10	23		7	
	III	10	24		6	
	IV	10	22		8	
		Total: 40	Total: 94	$\chi^2 = 38.5$; $P < 0.001$	26	S
M. rubra young naïve ants; mazes with one branch marked with *M. rubra* area-marking odor	I	15	16		29	
	II	10	11		19	
	III	8	7		17	
	IV	7	6		15	
		Total: 40	Total: 40	$\chi^2 = 13.34$; $P < 0.001$	80	S
M. sabuleti young ants; mazes with unmarked paper in one branch; supplementary control	II					
		Total: 20	Total: 31	$\chi^2 = 0.07$; $P > 0.70$	29	NS
M. rubra young ants placed on their area odor for 50 min; mazes with one branch marked with that odor	I	15	34		11	
	II	10	25		5	
	III	8	18		6	
	IV	7	15		6	
		Total: 40	Total: 92	$\chi^2 = 34.13$; $P < 0.001$	28	S
M. sabuleti young ants placed on *M. rubra* area odor for 50 min; mazes with one branch marked with that odor	I	12	29		7	
		12	28		8	
		Total: 24	Total: 57	$\chi^2 = 24.5$; $P < 0.001$	15	S
M. rubra callows placed on unmarked paper for 50 min; mazes with one branch marked with *M. rubra* area odor	V	20				
			Total: 22	$\chi^2 = 4.27$; $P < 0.05$	38	S

The tested *M. sabuleti* young workers went equally towards the empty branch of Y-mazes and the branch provided with an unmarked white paper ($\chi^2 = 0.07$, df = 1, $P > 0.70$). This shows that an unmarked paper does not induce avoidance, and that the previously observed avoidance was not induced by the paper, but by its odor.

Experiment with young *M. rubra* workers placed, for 50 min, in contact with the area-marking odor of *M. rubra* (Table 1, line 5)

The same experiment as above was conducted, but the tested *M. rubra* young ants were initially placed, for 50 min, inside reversed brandy glasses placed in the foraging area of *M. rubra* colonies.

During this isolation, callow ants behaved unusually: they quickly moved for one or two minutes, then stopped and rested. In the course of the subsequent test, unexpectedly, the young ants in general chose the marked branch of the Y-mazes. They moved to their right, then to their left, or walked in circles, thus perceiving the marked piece of paper deposited in one branch of the Y apparatus. Then, they mostly oriented themselves towards the marked paper (Fig. 1G). Most of the ants of the four used colonies chose the marked branch of the Y apparatus. *In fine*, among the 120 recorded choices, 92 (76.67%) were for the marked branch of the Y-mazes. Such a result (92 *vs* 28 compared to 60 *vs* 60) was statistically significant ($\chi^2 = 34.13$; df = 1; $P < 0.001$).

Experiment with young *M. sabuleti* workers placed, for 50 min, in contact with the area-marking odor of *M. rubra* (Table 1, line 6)

The same experiment as explained just above was performed using 24 young *M. sabuleti* workers that had never left their nest tube. During their isolation, these callow ants quickly moved for a few minutes, then stopped and rested. After their isolation, the young *M. sabuleti* ants, tested three times in Y-apparatus, turned towards their right, then towards their left or moved in circles on the area lying between the two branches of the Y-mazes and, thereafter, in general oriented themselves towards the branch provided with the marked piece of paper (Fig. 1H). This occurred for the two series of 12 ants tested three times and the result was 57 choices (79.17%) for the marked branch vs 15 choices for the unmarked branch of the Y-mazes. Such a result (57 *vs* 15 compared to 36 *vs* 36) was statistically significant ($\chi^2 = 24.5$; df = 1; $P < 0.001$).

Experiment with young *M. rubra* workers placed, for 50 min, on an unmarked (blank) paper (Table 1, line 7)

An experiment, identical to the previous one, was conducted on twenty young ants of colony V that had never left their nest tube, and had been placed, for 50 min, on an unmarked paper. In the Y-mazes, a branch of which contained paper marked with *M. rubra* area odor, these young ants seldom went towards the marked paper. In general, they moved towards the paper but soon turned away from it; they seemed to be recognizing the paper but not its odor. Finally, these ants chose 22 times (36.67%) the marked area and 38 times (63.33%) the empty branch. Such a result (22 *vs* 38 compared to 30 *vs* 30) was statistically significant ($\chi^2 = 4.27$; df = 1; $P < 0.05$).

DISCUSSION

The present result is valid for *Myrmica* species, which marks its foraging area by depositing spots of its Dufour gland content, and should be examined in other ant species.

The time of life at which ants became imprinted with their area-marking odor depends on the demographic state of the colony. It occurs earlier or later according to the presence of a few or many foragers in the colony, respectively.

The foraging area odor of a species does not change in the course of a worker's life. Acquiring the knowledge of this odor through imprinting is adequate since knowledge acquired in this way does not vanish in the course of time but remains permanent. On the contrary, the visual and the olfactory elements located in the foraging area may change over the course of time and are adequately learned through operant conditioning [3, 4, 5], a kind of learning which can be forgotten and replaced [13]. Indeed, ants go on learning throughout their life, through classical and operant conditioning (associative learning) as well as latent learning [27].

Jaffe and co-authors [28, 29] already showed that ants possess nestmate odors, area-marking odors and territorial marking odors. The authors presumed that the recognition as well as the learning processes of these odors may be similar. The work of Jaisson [30] and the present one are in favor of such a hypothesis.

Imprinting is an event actually known to occur in several animal species (birds, rats, sheep, monkeys, human beings, social insects etc.). Large amount of information can now be found on this topic: for instance in [31, 32, 33, 34, 35, 36, 37, 38]. Habituation has also been demonstrated in insects [13, 39, 40].

As a matter of fact, what is currently known about the ontogenesis of the cognitive abilities of ants is that young ants become habituated and/or imprinted

with their nest odor while they are living inside their nest [13]. Ants acquire, at least partly, kin recognition during their larval life as well as just at their emergence [41]. After that, they become imprinted with their nest entrance odor when they come into contact with the entrance and learn the visual aspect of their nest entrance, through operant conditioning, when they leave their nest, and re-enter it [14]. Later on, they become imprinted to their area-marking odor when they forage for the first time [present work]. They then learn the trail following behavior [15] and the alarm reaction of the species [16]. Finally, they learn, through operant conditioning, several visual and olfactory cues that allow them to navigate [3, 4, 5].

CONCLUSION

The present work shows that:

1. Ant foragers very well know their area-marking odor and orient themselves towards it.

2. Naïve young workers, 6–9 months old, that have never left their nest, do not know their area-marking odor. They even try to avoid contact with it; a supplementary control experiment showed that this avoidance was not due to the paper but to its odor. This result agrees with the behavior of ants that are less than 6 months old: they move inside the nest, sometimes up to the entrance and then, move back inside the nest.

3. When the young ants were kept in contact for a short time (less than one hour) with the area-marking odor of their species, in the absence of any congener and without having been rewarded (e.g. by receiving food, seeing congeners or seeing their nest entrance), they recognize the odor perfectly, seek contact with it and orient themselves towards it. Such an observation shows that, in the course of a critical time period, young ants become imprinted with their area-marking odor, most probably while moving a short distance from their nest entrance, for the first time; the behavior of callow ants, placed in contact with the foraging area odor, is also in favor of such a presumption.

4. The latter statement was confirmed by the observation that young workers of a given species (that have never left their nest and thus not yet have had the knowledge of their area-marking odor) rapidly ‘learn’ the area-marking odor of a foreign species, simply by being in contact with it, in the absence of any foragers and any reward, apparently *via* imprinting with that alien marking odor.

5. It was observed that young ants kept for 50 min on an unmarked paper went on avoiding their species foraging area odor (which they have never encountered), but accepted the paper free of odor (which they have once encountered).

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CONFLICT OF INTEREST STATEMENT

We affirm that we have no conflict of interest concerning the present subject.

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