Ants' learning of nest entrance characteristics (Hymenoptera, Formicidae)

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Abstract

Young workers, experimentally removed from their nest and set in front of it, are not very good at finding the nest entrance and entering the nest. I examined how young ants learn their nest entrance characteristics, dealing only with the entrance *sensu stricto*, not with its vicinity. I observed that young ants have the innate behavior of trying to exit and re-enter their nest. I found that they are imprinted with the nest entrance odor while they are still living inside their nest and that they learn the visual aspect of their nest entrances, thanks to operant conditioning, when they exit their nest and succeed in re-entering in the course of their first short trips outside.

Introduction

In an ant colony, young individuals never leave the nest; they stay inside it where they perform duties. They are then 1–9 months old and are not dark pigmented as are their older congeners. Ants 1–2 years old go on working inside the nest, but move outside each time many foragers are required. Very old ants essentially move outside the nest. Foragers are able to return to their nest, locate the entrance, and enter it without difficulty. They can do so rapidly even after a major disturbance, for instance due to sexual swarming or the presence of a large living prey (personal observation). However, while studying the spatiotemporal learning ability of differently aged ants (Cammaerts, 2013*b*), I observed that the isolated 3–9-month-old workers, obliged to leave their nest to find water and food, initially had difficulty in locating and recognizing an entrance and, therefore, in re-entering their nest. After a few days, they did so more easily. This observation highlighted the fact that young workers must learn, or be conditioned to their nest vicinity and to their nest entrance characteristics.

How ants locate their nest entrances has already been widely studied. They use several visual and olfactory elements such as panoramic cues, landmarks, and learned odors, memorized while walking (displaying a 'learning' walk) all around the vicinity of their nest and their nest entrances. *Cataglyphis fortis* workers pinpoint their nest entrances using olfactory cues (Steck *et al.*, 2009). Desert ants (*C. fortis, Ocymyrmex robustior, and Melophorus bagoti*) use memory of the distance walked from the nest, path integrator, visual cue recognition, and some innate searching behavior (Narendra, 2007*a*,*b*; Merkle & Wehner, 2010; Müller & Wehner, 2010; Wehner & Müller, 2010; Schultheiss & Cheng, 2011; Schultheiss *et al.*, 2013). It can thus be stated that young ants learn the location of their nest entrance thanks to innate behavior (walking around it and memorizing perceptions) and operant conditioning (or associative learning), being rewarded each time they correctly approach the place where their nest entrance is located.

In the present work, I focused on learning of the characteristics of the nest entrance itself, *sensu stricto*, the chemical and visual aspects of the hole through which ants must enter. Indeed, although the systems used by ants in locating their nest entrances, and the learning of these systems, are rather well documented, the step preceding the acquisition of these different cognitive capabilities – i.e., the 'entering' of the nest and the learning of the nest entrance characteristics – is not yet known.

I examined this question on the ant *Myrmica rubra* Linnaeus, 1758 whose nest entrance is known to be chemically marked with the workers' labial gland content deposited with the legs (Cammaerts & Cammaerts, 1999). A nest entrance not

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only has a particular odor but also possesses a given visual aspect which, if memorized, may help the foragers to find it. This has been clearly observed in the ant *Manica rubida* (Cammaerts & Cammaerts, 1987). In the ant *M. rubra* also, each nest entrance has a given aspect. This species inhabits grassland, open lands, and borders of paths and gardens; it nests in the earth, under stones, in grass roots or in dead branches. The nest entrances are almost horizontally-oriented holes, with a given shape and several kinds of visual and olfactory material. The workers are very sensitive to many chemicals (Cammaerts *et al.*, 2012*a*). They have a visual perception of middle quality: their eye morphology has been examined (Rachidi *et al.*, 2008), their subtended angle of vision measured (5°10′; Cammaerts, 2011), their visual perception studied (they distinguish filled shapes, Cammaerts, 2013*a*). They have better vision than the ant *Myrmica sabuleti* and can distinguish colors (yellow, green, and blue in particular), see UV light and perceive perspective as can *M. sabuleti* (Cammaerts, 2004, 2007*a*, *b*). To enter their nest quickly and easily, *M. rubra* workers have to recognize their nest entrance in its surroundings very precisely, through the perception of olfactory and visual elements. Young ants must learn to do this.

Hence, the present work deals with the mechanism(s) underlying the learning of the olfactory and visual aspects of nest entrances in the ant *M. rubra.* What has been comprehensively demonstrated is that very young workers are imprinted with their nest odor (Bos & D'Ettore, 2012). Such a mechanism might also be present in the acquisition of knowledge of the nest entrance characteristics. On the other hand, ants forage using olfactory and visual elements memorized thanks to operant conditioning (Cammaerts & Rachidi, 2009; Cammaerts *et al.*, 2012*b*, Cammaerts, 2012*a*). This mechanism may also play a role in the learning of some nest entrance characteristics. Moreover, some innate behavioral elements very probably also exist in such a cognitive acquisition. This study will constitute a step further in the understanding of the ontogenesis of the ants' complex cognitive abilities.

Material and methods

Collection and maintenance of ants

The experiments were performed on three colonies of *M. rubra*, labeled I, II, III, two collected at Marchin (Condroz, Belgium) and one from the Aise valley (Ardenne, Belgium), all found on grassland. These colonies contained a queen, brood and about 500 workers. From March to May, several workers emerged and were thus about 4–6 months old in September, when the experiment was undertaken. They were not as dark as the older workers and expected to live for up to 3 years (Cammaerts, 1977). The colonies were maintained in the laboratory in artificial nests made of one to three glass tubes half-filled with water, a cotton-plug separating the ants from the water. The glass tubes were deposited in trays (42 cm × 27 cm × 7 cm), the sides of which were covered with talc. The trays served as foraging areas, food being delivered in them. The ants were fed with sugar-water provided *ad libitum* in a small glass tube plugged with cotton, and with cut *Tenebrio molitor* served twice a week on a glass slide (fig. 1a). Temperature was maintained at 20° ± 2°C, humidity at about 80%, this remaining constant over the course of the experimentation. The lighting had a constant intensity of 330 lux when caring for the ants (e.g., providing
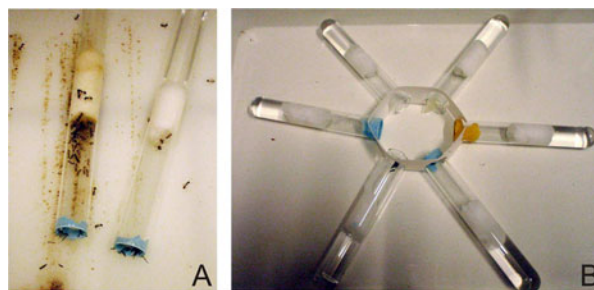

Fig. 1. Experimental material. (a) One colony maintained in two nest tubes, duly marked with blue and thyme; (b) the experimental apparatus used to test the ants.

food and renewing nesting tubes), training the ants and testing them. During the other time periods, the light was dimmed to 110 lux.

Experimental material and apparatus

For each colony, the entrance of the ants' nest (the border of each glass tube) was covered with blue paint (® enamel, to a depth of 2–3 mm) in which a few pieces of thyme were inserted (fig. 1a). No experiment was then conducted. The colonies were meticulously maintained for six days and young workers located inside the nest were carefully observed.

Experiments were performed after 6, 9, and 12 days on young workers (located inside the nest, aged 3–9 months) and then on foragers located in the foraging area or near the nest. The experiments were conducted in an experimental apparatus deposited in a tray (34 cm × 23 cm × 4 cm) (fig. 1b). This apparatus was built as follows. A piece of very strong white paper (Steinbach®, 20 cm × 2 cm) was used to form a circular enclosure with a perimeter of 18.84 cm and a diameter of 6 cm. This enclosure can be stood up (fig. 1b). Near the lower border, six equally spaced holes (diameter = 1.6 cm) were cut and, in each hole, a glass tube (= a test tube, diameter = 1.5 cm, length = 10 cm) was inserted, half filled with water, and plugged with cotton. The experimental apparatus thus offered six nest entrances circularly located and equally distant. The entrance of each of the six test tubes was marked differently (fig. 1b, Table 1). One entrance was unmarked (the control entrance), one was marked with blue color, one with pieces of thyme, one with blue color and pieces of thyme, one with yellow color, and one with pieces of onion. The piece of hard white paper was covered with talc to prevent the ants from climbing it.

It has been shown that, before any conditioning, *M. rubra* workers do not have any preference for the color blue or yellow, nor for thyme or onion (Cammaerts, 2012*a*). It has also been demonstrated that, when conditioned to thyme and onion using aqueous extracts, these ants respond to the odor of these two elements (Cammaerts, 2012*a*).

Experimental protocol

The nest entrances of the three colonies were marked with blue color and pieces of thyme. Inside the nests, several young workers, 6–8 months old, were living, while several foragers were moving in the foraging area, returning from time to time to their nest. Experiments were conducted on the young workers 6, 9 and 12 days after marking the nest entrances, as

Table 1. Number of ants, of three colonies (I, II, and III), having entered an unmarked test entrance (= control) or one marked with a color and/or an odor (fig. 1b), their initial nest entrance being marked with thyme and blue color (fig. 1b). n = number of ants tested from each colony; T = total number of ants tested. The total numbers of ants found in each test tube were statistically analyzed using the non-parametric χ^2 goodness-of-fit test (Siegel & Castellan, 1989), the results being detailed in the text, 'Results' section.

Tested workers	Colony n	Control	Blue	Thyme	Blue + thyme	Yellow	Onion
Young							
After 6 days	I 15	4	0	10	1	0	0
	II 13	4	1	7	1	0	0
	III 20	3	3	7	7	0	0
	T : 48	11	4	24	9	0	0
After 9 days	I 14	1	2	7	3	1	0
	II 11	3	2	5	1	0	0
	III 18	0	5	5	5	1	2
	T: 43	4	9	17	9	2	2
After 12 days	I 14	1	2	2	6	3	0
	II 15	2	7	2	2	2	0
	III 16	2	1	9	2	1	1
	T: 45	6	10	13	10	6	1
Foragers	I 11	0	4	3	4	0	0
	II 13	1	6	3	3	0	0
	III 11	0	3	2	6	0	0
	T: 35	1	13	8	13	0	0

well as on the foragers after 14 days. I did not mark the young ants; they were not numerous (see Table 1) and not as dark as older ants; I simply collected and tested all of them. To conduct an experiment, ants were gently removed from their colony, placed in a polyacetate cup (with talc-covered sides), and then transferred to the experimental apparatus enclosure, in front of the six differently marked and circularly located entrances. The ants had to be tested all together because, in the used experimental apparatus, a young ant, isolated, stayed nearly motionless and scarcely made a choice. Some conspecific collaboration between tested ants may thus have occurred. The movements of the tested ants and their successive choices were observed until they stopped moving between different test tubes and stayed inside them. At that time, their final location in different test tubes was recorded (Table 1).

Between the experiments conducted 6, 9, and 12 days after the entrances of the initial nest tubes had been marked, the positions of the six test tubes in the experimental apparatus were changed to prevent the ants from learning the entrance positions, for instance, via panoramic cues. Moreover, the initial positions of the six test tubes were different for colonies I and II on the one hand and for colony III on the other. After each experiment, the ants were removed from each test tube of the experimental apparatus, placed in a polyacetate cup, and then put back in their foraging area, very near their nest entrance. They were observed until they behaved exactly as they did before having been removed from their nest and tested. All the young ants entered their nest within 2–8 min (this delay corresponds to some 'learning' walk exhibited by the young ants) while the foragers immediately entered the nest or continued to forage as normal.

Actually, this experiment enabled me to examine the relative proportions of entrance choices made by young workers who had previously never left the nest, young workers who had previously only left the nest once or twice, and foragers who had used the nest entrances many times (proportions given in the 'Results' section). Each time, the numbers of ants observed inside the six test tubes were statistically analyzed using the non-parametric χ^2 goodness-of-fit test (Siegel & Castellan, 1989, p. 45). The ants'

distribution among the six test tubes, as well as the ants' preference for one, two, or three of these tubes was statistically analyzed, the obtained results being then compared to the expected random outcomes.

Results

Young ants

Young workers 6–8 months old, still living inside the nest, from time to time moved toward the nest entrance then returned to the inside of the nest. This behavior was exhibited without any apparent benefit, probably instinctively, previous to their first outside trip.

When tested for the first time (that is after 6 days of life in their initial nest tube duly marked), in the course of a life period during which they have never gone out of their nest, the young workers immediately went inside the test tube marked with thyme (Table 1, first part). It was particularly obvious, especially for the ants of nest I, which were younger than those of nests II and III. On average, for the three nests, 50% of the young tested chose the 'thyme' marked entrance and 18.8% chose the 'thyme + blue' marked entrance. No ant chose the 'yellow' or the 'onion' marked entrance, probably because tested young ants have never encountered such cues and found them odd. The distribution of the tested young ants inside the six test tubes differed statistically from the expected random outcomes (= 8 ants in each tube; df = 5, χ^2 = 51.26, and $P < 0.001$). Moreover, the fact of finding 24 ants in the 'thyme' marked test tube, as well as zero ants in the 'yellow' and the 'onion' marked tubes, also differed statistically from the randomly expected number of ants in these test tubes (eight in each tube; $P < 0.001$).

When put back in their initial foraging area, the young workers immediately tried to re-enter their nest, but encountered some difficulties in finding the entrance and generally walked in meandering patterns. They often followed a conspecific path for entering the nest. The facts of 'being motivated' for 'going back home' and 'entering the nest' are,

very probably, instinctively exhibited behavior, even if not very efficiently performed at the beginning.

During the second experiment, conducted 9 days after marking the initial nest entrance with the color blue and thyme, many young workers (which had passed through their nest entrance once over a short period) again entered the test tube entrance marked with thyme (39.5% of the ants did so) and also the 'blue + thyme' marked nest tube (21% of the ants made this choice) as well as the 'blue' marked one (21% of ants behaved in this manner) (Table 1, second part). Only 4.6% of the tested young workers chose the 'yellow' and the 'onion' marked entrances. The young tested ants' distribution inside the six test tubes differed statistically from the expected random outcomes (7.17 ants in each test tube; df = 5, $\chi^2 = 23.18$, $P < 0.001$). The fact of finding 17 ants in the 'thyme' marked test tube (instead of 7.17), 26 ants in the 'blue' and the 'thyme + blue' marked test tubes (instead of 14.34), 26 ants in the 'thyme' and the 'thyme + blue' marked test tubes (instead of 14.34) was also statistically significant ($P < 0.01$). Finally, the presence of four ants in the 'yellow' and the 'onion' marked test tube (instead of 14.34) was also very significant ($P < 0.001$).

After the experiment, when put back in their initial foraging area very near their nest entrance, the young workers tested did not forage but only tried to enter the nest. They moved briefly in the vicinity of the entrance, remained still for several seconds looking for the entrance *sensu stricto* and then entered the nest. These behaviors seem to have been instinctively performed.

The third experiment, performed 12 days after marking the initial nest entrance, concerned young workers which had already passed through their nest entrance twice during their life. Many of them again entered the test tube with the entrance marked with thyme (29% of the ants did so) (Table 1, third part). However, this time, 22.2% of these young workers went through the 'blue + thyme' marked entrance and 22.2% went through the 'blue' marked entrance. Again, only very few ants entered a test tube with an entrance marked 'yellow' (13.3%) or 'onion' (2.2%). The tested ants' distribution inside the six test tubes differed slightly from the expected random outcomes (7.5 ants in each tube; df = 5, $\chi^2 = 11.92$, and $P < 0.05$). The presence of 33 ants in the 'blue', the 'thyme', and the 'blue + thyme' marked test tubes (instead of 22.5 ants) as well as seven ants in the 'yellow' and the 'onion' marked test tubes (instead of 15) was statistically significant ($P < 0.01$).

When placed back in their initial foraging area, the young workers again tried to enter their nest as quickly as possible (and could do so more rapidly than in the two previous similar situations) and stayed inside.

Hence, in the course of the three experiments conducted on the young workers, the proportion of choices of the 'thyme' marked entrance decreased, equaling 50, 39.5 and then 29% successively, while that of the 'blue + thyme' marked entrance varied little (18.8, 21, and 22.2% successively) and that of the 'blue' marked entrance increased (equaling 8.3, 21, and 22% successively), primarily between the first and second experiment (Table 1 first, second, and third parts). On the other hand, young workers seemed to present the instinctive (innate) behavior of approaching the nest entrance when inside the nest (but without exiting), similar to when they are outside, of 'searching' for the location of the nest and its entrance *sensu stricto* (a brief period since they are returned close to the nest). In the latter case, the ants passed through the entrance, entered the nest, and remained inside.

Foragers

As for the foragers tested in the experimental apparatus 14 days after marking of the initial nest entrances, they moved more rapidly than the young workers. They entered different test tubes several times and finally appeared to choose primarily the 'blue' and 'blue + thyme' marked entrances (37% of these ants chose each of these two entrances) (Table 1, last part). They also often went through the 'thyme' marked entrance (22.9%) but none (0%) stayed inside the test tubes with an entrance marked with yellow or onion. The ants' distribution inside the six test tubes differed statistically from the expected random outcomes (5.83 in each tube; df = 5, $\chi^2 = 34.28$, $P < 0.001$). The presence of 34 ants in the 'blue', the 'thyme', and the 'blue + thyme' marked test tubes (instead of 16.9) and that of zero ants in the 'yellow' and the 'onion' marked test tubes (instead of 11.7) were also statistically significant ($P < 0.001$).

Discussion

The aim of the present work is to discover how ants learn their nest entrance characteristics. Indeed, it has often been observed that, even after a major disturbance, ants are able to rapidly re-enter their nest, while it has also been observed that young workers are unable to do so. Working on *M. rubra* and using blue color as well as thyme odor as entry characteristics, I found that young ants which had never previously left their nest reacted strongly to the odor of their nest entrance, whereas those which had previously left their nest once or twice continued to react to that odor, and also reacted to visual characteristics. The middle aged foragers primarily reacted to the visual aspect of their nest entrance, but also, to a lesser extent, to its odor.

It can thus be presumed that the nest entrance odor is 'learned', during the first months of an ant's life, by imprinting, when these ants move within their nest and approach the entrance; such an imprinting may be ineluctable, rapid, and persistent. As for the visual aspect of the entrance, it is learned later on, when the ants exit their nest and try to re-enter. This learning of the visual characteristics of the nest entrance probably occurs thanks to operant conditioning, the ants' 'trying to enter their nest' being rewarded with the return itself.

I estimated that pieces of thyme were more appropriate than any odor from aqueous or hexane extracts for marking the artificial nest entrances because the odor must persist unchanged during 13 days, must be set at exactly the same time as the blue color, and must be located only and precisely where the blue color was. On the other hand, in a previous work on the species, I showed that ants effectively used the odor and not the sight of pieces of thyme (Cammaerts, 2012*a*).

Different ants' reactions, behavior, and task performance results, appear to be a combination of three systems of cognitive ability acquisition, as stated by Graham *et al.* (2010): (1) specific innate behavioral elements acquired through heredity; (2) behavioral elements acquired thanks to imprinting processes during a short, sensitive, critical time period, often at an early stage of life (Fielde, 1903, Plateaux, 1960, Jaisson, 1991). This may even occur before adult emergence, but usually occurs just after emergence. However, some imprinting can also occur later, during adult life, an individual remaining capable of being imprinted during different stages of its life (Bos & D'Ettore, 2012); (3) behavioral

elements learned thanks to classical conditioning and/or operant conditioning (Giurfa, 2007) with possibly, not necessarily, some prior imitation.

These differently acquired elements are not in contradiction. On the contrary, they not only complement one another, but also interact in the elaboration of entire complex behaviors, these behaviors being as well adapted as possible to the individual's life and circumstances (Bos & D'Ettorre, 2012). It is as if some enhancement results from the existence of different mechanisms allowing behavioral acquisitions.

In the present work, focusing on the learning of nest entrance characteristics, I detected (1) innate behavior: at a given stage of their life ants try to exit their nest, and once outside they instinctively try to return and re-enter their nest; (2) imprinting acquisition of the odor of the nest entrances; (3) operant conditioning allowing the learning of the visual aspect of the nest entrances. These three mechanisms cooperate and enhance the learning of the nest entrance characteristics so that, finally, the ants' entering their nest becomes very efficient.

The critical time at which the latter two learning mechanisms occur depends on the colony population and on its demographic status: if there are a lot of old ants in the colony, it will occur later; if there are only a few old workers in the colony, it will occur earlier.

Each cognitive ability young ants must acquire is 'learned' in a precise order, during a precise critical time period. I presume that young ants 'learn' the nest odor first, then the entrance odor, followed by the visual aspect of the entrance, and thereafter the visual aspect as well as the odor of the nest vicinity. The following 'learning' step may be that of the area marking odor.

The nest entrance odor is produced by workers depositing labial gland content with their legs. This odor changes very little over time. Odor recognition is adequately acquired by imprinting since knowledge acquired in this manner is generally permanent. Effectively, old workers, imprinted with their nest entrance odor while young, continue to respond to it and to mark their nest entrance with it, throughout their life. The visual aspect of the nest entrances may change over the course of time: the dimension, materials and shapes of entrances may change somewhat with the seasons and even completely change when nest relocation occurs. It is appropriate that such visual aspects are learned through operant conditioning as this process allows previous knowledge to be replaced (Stroeymeyt et al., 2010). Hence, even though imprinted with colony-specific labial gland content odor indicating correct nest entrances, individuals go on being able to continuously update their learning of the visual aspect of their nest entrances thanks to operant conditioning occurring throughout their life when they forage and re-enter their nest.

Learning and memorizing are indissociable. M. rubra is known to have a rather short olfactory memory and a rather longer lasting visual memory (Cammaerts, 2012b). Memories concerning nest entrances are continuously reinforced in the course of the ants' exiting and re-entering the nest via the entrances. Memory leads to costly protein synthesis (Guerrieri et al., 2011). Nevertheless, memory can be changed (Margulies et al., 2005). Nest relocation is thus possible but costly from all points of view, and hence only occurs when highly necessary (Cammaerts & Cammaerts, 2000).

In conclusion, the ants must learn all required social cues, tasks, and behavior. They acquire the knowledge of their nest odor thanks to imprinting (Bos & D'Ettorre, 2012). The present work deals with the learning of the nest entrance sensu stricto characteristics and shows that entrance odor (due to workers' labial gland content deposits) is recognized thanks to imprinting, while the visual aspect of the entrances is learned thanks to operant conditioning. Underlying these two mechanisms, there are innate behaviors, the ants having the instinct to exit and re-enter the nest. Throughout their lifetimes, ants can learn various visual characteristics of their nest entrances thanks to new operant conditioning.

My next tasks will be to research how ants acquire the knowledge of their foraging area marking, and later on of their trail pheromone and their alarm pheromone, as well as of the trophallaxis process, since young workers possess none of this knowledge (Cammaerts, 2013b).

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