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Use of olfactory and visual cues for orientation by the ant *Myrmica ruginodis* (Hymenoptera: Formicidae)

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Abstract

Myrmica ruginodis NYLANDER, 1846 foragers were differentially conditioned to two olfactory and two visual cues. The ants were then placed in mazes provided with either olfactory cues, or visual cues, or with successively or alternatively set visual and olfactory cues. In the latter case, the ants scored consistently higher in front of visual cues. The conditioned ants perfectly negotiated mazes provided with correct visual cues and wrong olfactory ones, but moved incorrectly through mazes provided with wrong visual cues and correct olfactory ones. *M. ruginodis* foragers thus primarily used visual cues to orient themselves when traveling, neglected olfactory cues and continued to respond to visual cues even if they became obsolete. However, when responding to olfactory cues, the ants responded to the actual odor and not to the visual perception of the odorous object, and were able to discriminate amongst the odors. *M. ruginodis* workers also distinguished differently colored cues. Unexpectedly, they failed to respond to the lower vertical part of the learned visual cues and responded entirely to the upper part of these cues. This means that when foraging or traveling, their main field of visual perception is above them and not in front of them. Under conditions of low light intensity (< 5 lux), *M. ruginodis* workers could no longer respond to visual cues. In such instances, they relied on odorous elements to find their way and did so better than under high light intensity. They responded to olfactory cues under low light intensity, even if wrong visual cues were added and even if the olfactory cues were incorrectly set in the mazes. In the latter case, the ants progressively stopped responding to the obsolete olfactory cues. The navigation system of *M. ruginodis* differs from that of *M. sabuleti* MEINERT, 1861 and is in agreement with the typical environment of the species and the morphology of the eyes.

Key words: Conditioning, foraging, learning, visual perception, olfaction.

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Introduction

Ants forage and orient themselves to the surroundings of their nests using trail and scent marking pheromones in combination with visual cues, according to the snapshot or sketchmap model (COLLETT & GRAHAM 2004, COLLETT & al. 2007). To some extent, they are also able to utilize components of odor (PASSERA & ARON 2005).

For example, the foragers of *Myrmica sabuleti* MEINERT, 1861 primarily use odors to negotiate their trajectories (CAMMAERTS & RACHIDI 2009), although they are able to use visual cues in the absence of olfactory ones (CAMMAERTS & LAMBERT 2009). If the olfactory cues are incorrectly set in a maze, the ants initially respond to them but soon cease and switch to the available (correct) visual elements (CAMMAERTS & RACHIDI 2009). Noteworthy is that the species inhabits terrain which is typically covered with odorant plants, and the workers possess relatively small eyes (containing about 110 ommatidia) (RACHIDI & al. 2008).

In contrast, the workers of *Myrmica ruginodis* NYLANDER, 1846 have larger eyes with about 150 ommatidia, and the postero-dorsal zone of each compound eye is well-developed (RACHIDI & al. 2008). Nests of the species are often found along forest edges, around clearings and under low-lying branches. Authors have reported finding this species on woody lands however without specifically mentioning the presence of branches above the nests (GASPAR 1966, 1972, LENOIR 1971).

The present work aimed to investigate whether this ant species uses olfactory and visual cues, as *Myrmica sabuleti*, or whether it forages differently. To achieve this, foragers of *M. ruginodis* were conditioned with differential operant olfactory conditioning followed by differential operant visual conditioning (Fig. 1, upper part), afterward they were tested in maze experiments (Fig. 1, lower part). As shown in Figure 2, eight experiments in the first series were first conducted using mazes that differently utilized olfactory and / or visual cues to reveal if *M. ruginodis* foragers use these kinds of cues to orient and if one kind is predominant.

In the second series of experiments (six tests), the ants were tested in mazes to determine if:

- they effectively respond to the odor and not to the visual perception of olfactory cues,

– they are able to distinguish among the various odors,
– they are able to distinguish among the various colored cues,
– their main field of vision lies directly in front of and / or above themselves.

A third and final set of experiments involving three tests was designed to examine if, under low light intensity, *Myrmica ruginodis* workers:

– continue to use visual cues,
– partly or exclusively use odorous elements,
– persist in responding to obsolete olfactory cues.

In addition, a total of six control experiments were performed.

The overall goal of this work is to elucidate the foraging and orientation system of the ant *Myrmica ruginodis*.

Material and methods

Collection and maintenance of ants

The experiments were conducted on four large colonies collected in the Aise valley (Ardenne, Belgium). These colonies were demographically similar, each containing a queen, brood and about 500 workers. They were maintained in the laboratory in artificial nests made of one to three glass tubes half-filled with water. A cotton-plug separated the ants from the water. The glass tubes were deposited in trays (37 cm × 52 cm × 8 cm), the sides of which were covered with talc. The trays served as foraging areas for food which was placed in them, and the ants were trained, as well as tested, in the trays (Fig. 3 E, F).

Temperature was maintained at 20 ± 2°C. Humidity was about 80% and remained constant over the course of an experiment. The lighting consisted of five Osram concentra ® 60 W lamps that delivered a constant intensity of 600 lux. The lighting was used to care for the ants (e.g., providing food, renewing nesting tubes), to train them and to perform the first sixteen experiments. The last three experiments were conducted under conditions of low light intensity. Concerning the adjustment and measurement of lighting, see details below in the Experimental apparatus section.

Sugared water was permanently offered in a small glass tube plugged with cotton, and chopped cockroach was served twice a week on a glass slide. This feeding schedule was interrupted during experiments since these kinds of food served as reward during training (Fig. 3 A, C).

Experimental procedure

Ants were **collectively trained** using a training apparatus placed in the ants' tray. Each colony thus had its own apparatus. This form of collective permanent training corresponds to operant conditioning and is similar to that used in previous studies investigating the use of olfactory and visual cues for orientation during travel in *Myrmica sabuleti* foragers (Cammaerts & Lambert 2009, Cammaerts & Rachidi 2009). However, in the present study, the visual cues were shaped in the form of a square + trapezium, as described below. Foragers would visit the experimental apparatus provided with food several times per day. They were sufficiently conditioned when their olfactory and visual conditioning was assessed and, later on, they were fully conditioned when their use of cues was analyzed. This point is further developed in the Discussion section.

Ants were **individually tested** in mazes placed in their colony's tray. The mazes were constructed to have their own

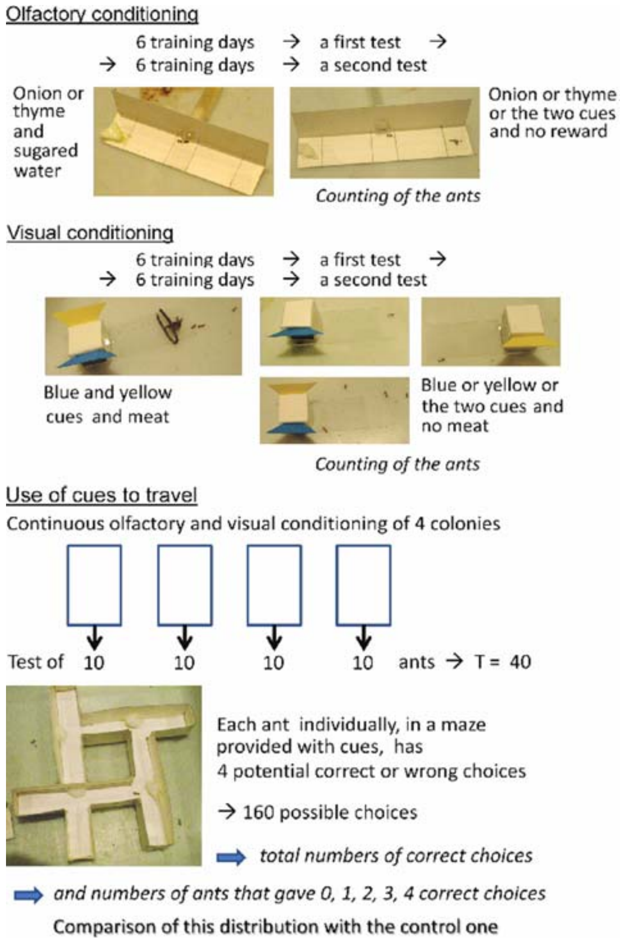

Fig. 1: Schematic representation of the experimental protocols employed for obtaining and quantifying ants' olfactory and visual conditioning and for analyzing the ants' use of cues to orient them.

bottom. The tests were similar to those performed to study *Myrmica sabuleti* foragers' use of olfactory and visual cues (Cammaerts & Lambert 2009, Cammaerts & Rachidi 2009), except the visual cues were shaped differently, as described below.

Experimental apparatus

To obtain and quantify olfactory differential operant conditioning, ants from each colony were trained with their own experimental apparatus (Fig. 3 A). Afterward they were tested using another, similar apparatus. Again, each colony had its own test apparatus (Fig. 3 B). The apparatus consisted of a piece of extra strong white paper (Steinbach ®, 12 cm × 6 cm) orthogonally folded lengthwise to present a horizontal and a vertical part. A small glass tube (length: 7 cm; diameter: 1 cm) was inserted into a hole (diameter: 1.2 cm) cut in the middle of the vertical part very close to the base. The glass tube was placed in the foraging area with the opening in the middle of the apparatus (Fig. 3 A, B). During training, the glass tube was filled with sugared water (the reward) and closed with a cotton plug, while a piece of onion or thyme were alternatively deposited on a glass slide cover slip (2.2 cm × 2.2 cm) located on the left and on the right horizontal ends of the experimental apparatus (Fig. 3 A). In this way, the

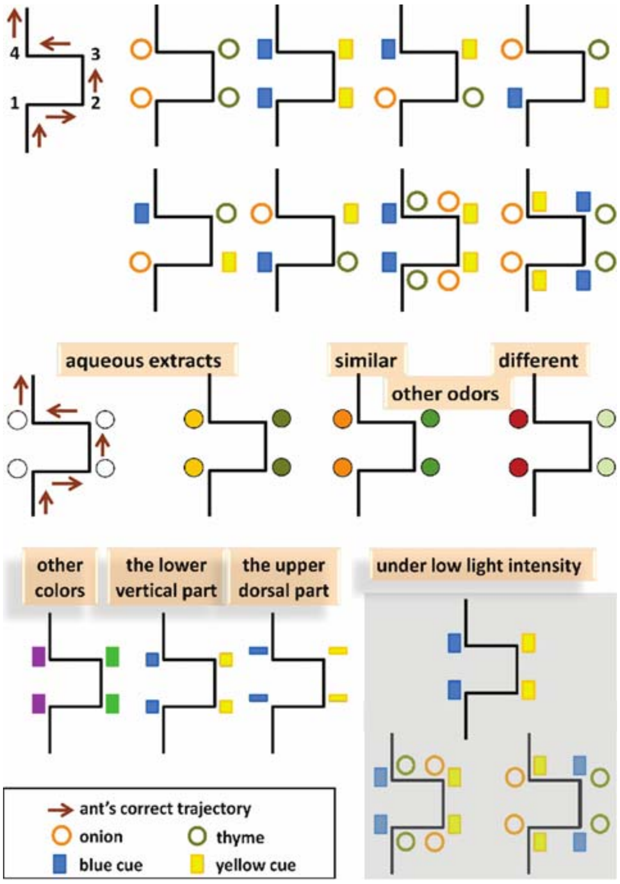

Fig. 2: Schematic representation of the experiments, using mazes (black lines) with four choice points (1 - 4), to study the use of olfactory and visual cues (colored elements) by *Myrmica ruginodis* when traveling. The arrows indicate the ants' correct trajectory. Details are given in the text.

reward (sugared water, renewed when necessary) was located 4 cm to the right of the onion and 4 cm to the left of the thyme. Another glass slide cover slip was located in the middle of the apparatus in front of the opening of the sugared water glass tube (Fig. 3 A).

The experimental apparatus used for testing was provided with onion or thyme or both cues depending on the experiments, and the glass tube was empty (i.e., no reward was given during tests), but closed with a cotton plug to prevent entry (Fig. 3 B).

To obtain and quantify visual differential operant conditioning, ants from each colony were trained with their own training apparatus (Fig. 3 C) and then tested using another similar outfit so that, again, each colony had its own test apparatus (Fig. 3 D). The apparatus consisted of a glass slide (2.6 cm × 7.6 cm) with a cube (2 cm × 2 cm × 2 cm) made of extra strong white paper (Steinbach ®) placed at each end. On one face of the cube was a square blue marking (visual cue) and on the opposite face a square yellow marking. The cube was positioned on the glass slide so that the blue cue appeared to the left and the yellow cue to the right of the glass slide. The square vertical markings (1.5 cm × 1.5 cm) and the trapezium (b = 1.5 cm; B = 3.5 cm), which was attached at a 45° angle to the upper edge of the cube, were cut from strong colored paper (Canson ®) (Fig. 3 C, D). During training, a piece of dead cockroach was tied to the end of the glass slide at 4 cm from the cube (Fig. 3 C). In this way, the reward was located 4 cm to the right of the blue visual cue, as well as 4 cm to the left of the yellow visual cue (Fig. 3 C). The piece of dead cockroach was renewed as necessary. During the tests, no meat was placed on the apparatus (Fig. 3 D).

To study the ants' use of olfactory and visual cues, workers were tested in mazes identical to those used to study the orientation system of *Myrmica sabuleti* (see CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009) (Fig. 3 E - H, Fig. 4), except the visual cues used to visually train *M. ruginodis* foragers were shaped in the form of a square + trapezium (Fig. 3 F), as described above. Each maze was made of white extra strong paper (Steinbach ®), the floor width and wall height being 2 cm and the distance between two turns (points of choice for the ants) being 4 cm. The maze had no ceiling and the walls were slightly covered with talc to prevent escape (Fig. 3 E, F, G, H). A sheet of white paper of appropriate shape and dimension was placed on the bottom of the maze and renewed after each experiment. The olfactory and / or visual cues were arranged inside the mazes before each point of choice, and they differed between the experiments (see below).

The light intensity could be adjusted by a dimmer and was measured using a Testoterm 0500 luxmeter (Testoterm GmbH & Co; D-7825, Lenzkirch). During the regular experiments, the light intensity was kept between 130 - 160 lux, however, for the low light intensity experiments the light intensity was < 5 lux.

In the low light intensity experiments, a red lamp was switched on to enable the experimenters to observe the ants and record their responses. The spectrum of the broadband emission of the lamp was measured using a 0.5 m triple grating monochromator / spectrograph, type 500i, Actor Research Corporation. The spectrum presented a maximum near 900 nm, which decreased rapidly toward the shorter wavelengths, finishing before 500 nm, and decreased slowly toward the longer wavelengths, finishing a little after 1,100 nm. Red light is only minimally perceived by the ants (CAMMAERTS 2007b).

Kinds of cues in mazes: Depending on the experiment, the cues placed in the mazes were either olfactory or visual or both kinds differently arranged or other judiciously chosen elements as detailed in Table 1 and schematically presented in Figure 1.

Aqueous extracts of onion and thyme were obtained by placing pieces of these two plants in glass tubes half filled with tap water and by warming the tubes to 100°C for 5 min in a double boiler.

Experimental protocol

To obtain and assess olfactory, as well as visual differential conditioning, ants were successively collectively trained (with two cues) during six days (including six onion and six thyme presentations for the olfactory conditioning), then individually submitted to a first test. Thereafter, they were trained again for six days before being finally submitted to the second test (Fig. 1 upper part).

Training. To train the ants, the appropriate experimental apparatus was placed in the foraging area of the colony and relocated every 5 - 25 h. We avoided intervals of 12 h and 24 h between relocation to inhibit spatial and temporal learning (CAMMAERTS 2004 b), as well as to prevent the establishment of chemical trails (CAMMAERTS-TRICOT 1974, CAMMAERTS & CAMMAERTS 1980). For each relocation, pieces of onion and thyme were respectively replaced by thyme and onion (olfactory conditioning), whereas the glass slide – on which the cube with the blue and the yellow cues were lying – was only rotated (visual conditioning). The reward (sugared water or piece of cockroach) was renewed when necessary.

Testing. To conduct a test or control experiment the feeding apparatus used to train the ants was removed and replaced with an apparatus designed for the test procedure and which lacked any reward for the ants. Ant reactions were quantified as follows.

Olfactory conditioning. Prior to olfactory conditioning, a control test was run in which the ants reaction was assessed. Two series of tests were then performed to assess the ants conditioning. During each control and test experiment, the ants were counted 15 times for each of the four colonies, successively (a) in the presence of onion, on the left-half area of the apparatus; (b) in the presence of thyme, on the right-half area; (c) in the presence of onion and thyme, on the entire area (Fig. 3 B). For each experiment, the four mean values were calculated and the mean of the four mean values established (Tab. 2, upper part). If the sum of the ants counted on the entire area is the sum of those counted on each of the two halves, then some ants were only conditioned to go to the right in the presence of onion and other ones to go to the left in the presence of thyme. Differential conditioning was successful when the number of ants counted on the whole area was less numerous than the sum of the two other counts.

Visual conditioning. Prior to visual conditioning, the ants were counted during a control experiment. Two series of tests were then performed to assess the ants conditioning. During each control and test experiment, the ants present on the glass slide were counted 15 times, for each of the four colonies, successively using: (a) a blue cue attached to a cube placed on the glass slide; (b) a yellow cue attached to a cube on the glass slide; (c) a blue cue and a yellow cue attached to the cube on the glass slide (Fig. 3 D). For each experiment, the mean value of the 15 counts was calculated and the mean of the four mean values established (Tab. 2, lower part). Differential visual conditioning was acquired when the number of ants responding to the cube provided with two colored cues was smaller than the sum of the numbers obtained for the cubes provided with only one visual cue (same reasoning as above).

To quantify the use of olfactory and visual cues by *Myrmica ruginodis* foragers (Fig. 1, lower part), control and test experiments were conducted for all four colonies with each colony using mazes differently provided with olfactory and / or visual cues.

In each test, a maze was provided with the respective cues and placed in the area of the four colonies. Ten ants from each colony were allowed, one by one, to enter the maze or were gently deposited inside near the entrance. After having moved all along the maze, each tested ant was allowed to exit the maze or was gently removed. It was then isolated for the duration of the experiment in a polyacetate glass covered with talc to avoid testing the same individual twice during the same experiment.

The quantification of the moves through the maze was identical to that used for studying the negotiation of a maze differently provided with cues by *Myrmica sabuleti* (see CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009). Briefly, for each point of choice traveled by each of the 10 tested ants during one experiment per colony, we recorded if the ants made an incorrect (= 0) or a correct (= 1) choice. The ants first response at each point of choice was taken into account, and not their possible second or later responses occurring when the ants retreated more than 4 cm. This quantification yielded for each colony a total

Tab. 1: Aim of the experiments performed and cues then set in the mazes where ants were tested.

Aim of the experiment	Cues set in the mazes
1 control	nothing
2 use of olfactory cues	onion and thyme
3 use of visual cues	blue and yellow cues
4 control	nothing
5 use of the two kinds of cues successively set	onion and thyme at choice points 1 and 2 respectively; a yellow and a blue cue at choice points 3 and 4 respectively
6 use of the two kinds of cues successively set	a blue and a yellow cue at choice points 1 and 2 respectively; thyme and onion at choice points 3 and 4 respectively
7 use of the two kinds of cues alternatively set	onion and thyme at choice points 1 and 3 respectively; a yellow and a blue cue at choice points 2 and 4 respectively
8 use of the two kinds of cues alternatively set	a blue and a yellow cue at choice points 1 and 3 respectively; thyme and onion at choice points 2 and 4 respectively
9 control	nothing
10 use of one kind of cue as a priority	a blue, a yellow, a yellow, a blue cue together with thyme, onion, onion, thyme at choice points 1, 2, 3, 4 respectively
11 use of one kind of cue as a priority	onion, thyme, thyme, onion together with a yellow, a blue, a blue, a yellow cue at choice points 1, 2, 3, 4 respectively
12 control	pure cotton
13 response to the odor of the olfactory cues	cotton imbibed with aqueous extracts of onion and thyme
14 discrimination of odors	pieces of leek and rosemary
15 discrimination of odors	pieces of fennel and sage
16 control	nothing
17 discrimination of differently colored cues	violet and green cues
18 using ahead or above head cues	only the lower vertical part of the visual cues
19 using ahead or above head cues	only the upper bent part of the visual cues
20 control	nothing
21 use of visual cues under low light intensity	blue and yellow cues, at < 5 lux
22 kind of cues used under low light intensity	cues as in experiment 8, but at < 5 lux
23 kind of cues used under low light intensity	cues as in experiment 9, but at < 5 lux

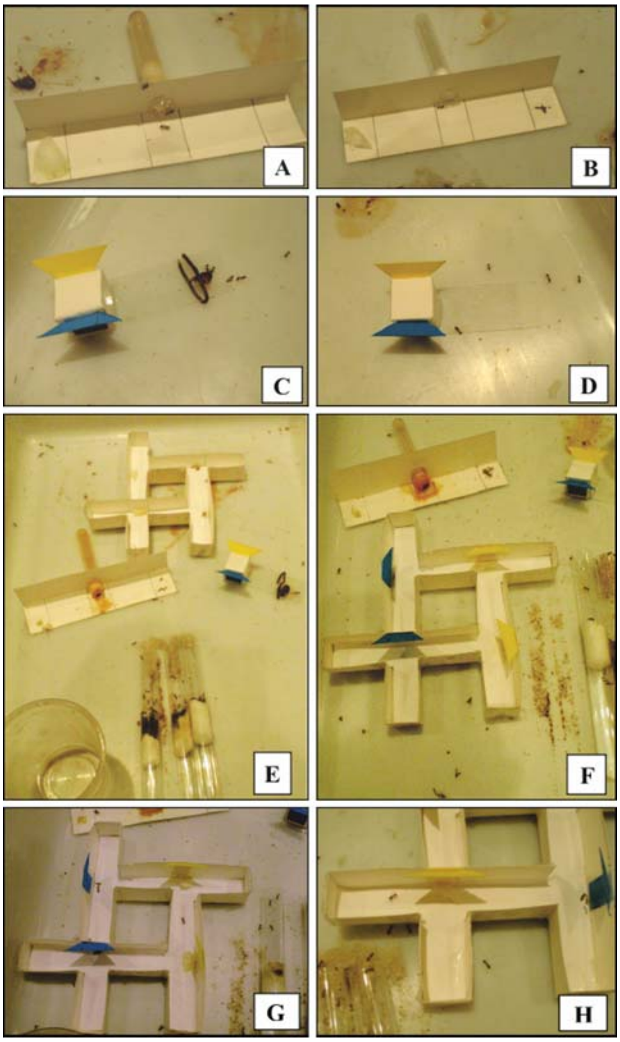

Fig. 3: Olfactory (A, B) and visual (C, D) differential conditioning of *Myrmica ruginodis* foragers and tests of these ants in mazes provided with these cues (E to H). (A) Olfactory conditioning to onion. (B) Assessment of the ants' differential conditioning to onion and thyme. (C) Differential conditioning to a blue and a yellow cue. (D) Assessment of the ants' differential conditioning to a blue and a yellow cue. (E) Experimental apparatus and design used to study the use of olfactory cues when traveling. (F) Experimental apparatus and design used to study the use of visual cues when traveling. (G) An ant tested in a maze provided with correct visual and wrong olfactory cues: the ant correctly negotiated the maze. (H) An ant tested in a maze provided with wrong visual and correct olfactory cues: the ant incorrectly moved through the maze.

number of correct choices out of 40 potential ones, and for the four colonies, out of a total of 160 potential correct choices (Tab. 3). The numbers of ants having given 0, 1, 2, 3, or 4 correct choices were also established for each colony, then for the four colonies on which the same experiment was performed (Tab. 3). For a few experiments, the total number of correct choices was also separately calculated either for the visual and the odorous cues (see Results) or for the first, the second, the third and the fourth point of choice in the maze (see Results).

Statistical analysis

For each of the two kinds of differential conditioning, the mean number obtained for each test was compared to the corresponding control mean value using the non-parametric 2 × 2 table contingency χ^2 test (Siegel & Castellan 1988). The difference was considered as not significant for $P > 0.05$.

For each test experiment made using mazes to determine how *Myrmica ruginodis* uses cues, the distribution of the numbers of ants that gave 0, 1, 2, 3, or 4 correct choices was compared to the corresponding control distribution using the non-parametric χ^2 test (Siegel & Castellan 1988). The choices observed for an experiment were considered as not statistically different from the choices obtained during the control experiment (unsuccessful negotiation because total number of correct choices = total control number) when P was higher than the level of probability 0.05 divided by the number of tests based on the same control. This level of probability adjustment is the Bonferroni correction. The adjusted level of probability is given, in Table 3, for each experiment. Values of P lower than the adjusted level of probability mean successful negotiation (total number of correct choices > total control number) or incorrect negotiation (total number of correct choices < total control number). This statistical analysis method was chosen for comparative purposes: it is identical to that used for studying *M. sabuleti*'s orientation system.

Results

Olfactory differential conditioning (Tab. 2, upper part, Fig. 3 A, B)

Although colonies 3 and 4 were slower in acquiring conditioning, *Myrmica ruginodis* foragers generally responded to onion, as well as to thyme, during the first test ($P < 0.01$) and more clearly, since more ants responded, during the second test ($P < 0.01$). In both tests, the ants responding to the simultaneous presence of onion and thyme were not as numerous as the sum of the ants responding to the presence of either onion or thyme. The ants were thus differentially conditioned to the two odors.

Visual differential conditioning (Tab. 2, lower part, Fig. 3 C, D)

In both tests performed, *Myrmica ruginodis* foragers were more numerous ($P < 0.01$) on the glass slide provided with either the blue or the yellow cue than on a similar glass slide in the control experiment. They were also more numerous ($P < 0.01$) on the glass slide provided with the two color cues than on a similar apparatus in the control experiment, and their numbers were lower than the sum of their numbers in the presence of either the two visual cues. They thus acquired differential conditioning for the two visual cues.

Olfactory and visual conditionings were conducted during the same elapsed time (six days, a first test, six more days, a second test). However, the numerical results of the second test were higher for the olfactory than for the visual conditioning.

Use of olfactory and visual cues to negotiate a maze, first step (Tab. 3, lines 1 - 11, Fig. 3 E, F, G, H)

In a maze provided with no visual or olfactory cue, ants turned randomly to the left or right at each point of choice.

Tab. 2: Ants' olfactory and visual differential conditioning. Ants of four colonies were differentially conditioned to onion and thyme, as well as to a blue and a yellow cue; afterward they were tested in the presence of these cues. Column 2: numbers of ants on areas where either onion, thyme or onion and thyme, as well as where either a blue, a yellow, or a blue and a yellow set of cues were presented. Column 3: sum and mean of numbers given in column 2.

Experiments	Colony: 1	2	3	4	Sum	Mean
Olfactory conditioning						
control						
onion	3	0	3	2	8	0.13
thyme	0	3	0	4	7	0.12
onion + thyme	1	0	4	2	7	0.12
test 1						
onion	14	7	0	0	21	0.35
thyme	5	14	0	0	19	0.32
onion + thyme	6	14	0	4	24	0.40
test 2						
onion	7	3	15	21	46	0.77
thyme	4	12	17	12	45	0.75
onion + thyme	5	15	3	21	44	0.73
Visual conditioning						
control						
blue	0	0	0	3	3	0.05
yellow	0	3	0	4	7	0.11
blue + yellow	0	2	0	4	6	0.10
test 1						
blue	7	4	13	4	28	0.47
yellow	7	7	4	5	23	0.38
blue + yellow	11	3	6	6	26	0.43
test 2						
blue	4	9	11	9	33	0.55
yellow	4	2	6	15	27	0.45
blue + yellow	9	1	4	11	25	0.42

Most of the ants made two correct choices and four ants made no correct choices (Tab. 3, lines 1, 4, 9).

In a maze provided with the learned olfactory cues, ants statistically made more correct choices (107) than in an empty maze (71) (P < 0.01). Most of them made three correct choices (Tab. 3, line 2).

Ants could negotiate a maze provided with the learned visual cues. They yielded a total of 114 correct choices, 18 ants having made three correct choices and ten of them, four. Such a score was highly significantly different from the control score (P < 0.001; Tab. 3, line 3).

Ants could also negotiate mazes provided with olfactory and visual cues successively set (Tab. 1, lines 5, 6) (P < 0.01, Tab. 3, lines 5, 6). They yielded 105 and 103 correct choices, respectively; most of them made three correct choices; eight and four ants made four correct choices, respectively. The numbers of correct choices observed in front of onion and thyme were 46 out of 80 choices (for each of the two successions), whereas the respective values were 59 and 57 in front of the blue and the yellow cues, for the experiments five and six, respectively.

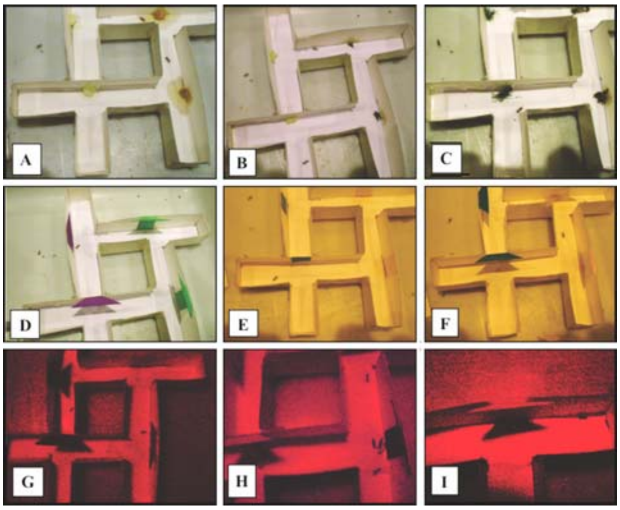

Fig. 4: Tests on *Myrmica ruginodis* foragers in mazes provided with cues listed below. (A) Aqueous extracts of onion and thyme; ants could negotiate the mazes (P < 0.01). (B) Pieces of leek and rosemary; ants could negotiate the mazes (P < 0.01). (C) Pieces of fennel and sage; ants could not find their way (NS). (D) Violet and green cues; ants could not find their way (NS). (E) Learned blue and yellow cues made of only their lower, vertical part; ants could not find their way (NS). (F) Learned blue and yellow cues made of only their upper, bent part; ants could negotiate the mazes (P < 0.001). (G) < 5 lux, learned blue and yellow cues; ants could not find their way (NS). (H) < 5 lux, visual cues incorrectly set and olfactory ones correctly set; ants could negotiate the mazes (P < 0.001, i.e., better than under higher light intensity). (I) < 5 lux, visual cues correctly set and olfactory ones incorrectly set; ants incorrectly moved through the mazes (P < 0.02) but progressively stopped doing so. Photos E, F are more yellow because they were taken with a differently adjusted apparatus. Photos G, H, I are red because they were taken in near darkness using a red lamp.

A maze provided with olfactory and visual cues alternatively set (Tab. 1, lines 7, 8) was also negotiated (P < 0.01; Tab. 3, line 7, 8). Most (17 or 16) of the ants yielded two correct choices, and 12 ants had three correct choices. In these two experiments, the number of correct choices in front of onion and thyme were 46 (onion and thyme at choice points 1 and 3) and 48 (onion and thyme at choice points 2 and 4), while those relying on the blue and the yellow cues were 56 (blue and yellow at choice points 2 and 4, as well as at points 1 and 3).

Myrmica ruginodis foragers correctly (P < 0.001; Tab. 3, line 10) negotiated a maze provided with a correct visual cue and a wrong olfactory one at each point of choice (i.e., blue and thyme at choice points 1 and 4, yellow and onion at points 2 and 3) (Fig. 3 G). The ants did not hesitate and made 29 and 30 correct choices at the first and the last choice points, respectively. Consequently, they used visual cues as a priority, neglecting the olfactory ones when the latter contradicted the correct visual ones. Indeed, in this experiment, the total number of correct choices (118) was similar to that when only correct visual cues (i.e., no wrong olfactory cue) were presented (114) (Tab. 3, lines 10 and 3).

In a maze provided with a correct olfactory cue and a wrong visual cue at each choice point (i.e., onion and yel-

Tab. 3: Use of olfactory and visual cues by *Myrmica ruginodis* foragers when traveling. Numbers of ants of four colonies with 0, 1, 2, 3, or 4 correct choices (column 2), as well as the total number of correct choices (column 3) when traveling through a maze provided with olfactory and / or visual cues as specified in the first column. Last column: results of non-parametric χ^2 tests between a control distribution (experiments 1, 4, 9, 12, 16 and 20) and that obtained while performing experiments 2 to 9, 5 to 8, 10 to 11, 13 to 15, 17 to 19 and 21 to 23 respectively. α = the adjusted level of probability according to the Bonferroni correction; P = the obtained level of probability; NS = not significant results at the adjusted level of probability. Circles: Note that these values are lower than the control ones.

Experiments	**No. of ants that had: 0**	**1**	**2**	**3**	**4 correct choices**	**No. of correct choices out of 160**	**Statistics**	
1. control (no cue)	4	11	15	10	0	71	–	
2. olfactory cues	0	5	12	14	9	107	α = 0.025	P < 0.01
3. visual cues	0	4	8	18	10	114	α = 0.025	P < 0.001
4. no cue	2	8	15	13	2	84	–	
5. olfactory and visual cues, successively	0	7	9	16	8	105	α = 0.0125	P < 0.01
6. visual and olfactory cues, successively	0	3	15	18	4	103	α = 0.0125	P < 0.01
7. olfactory and visual cues, alternatively	0	4	17	12	7	102	α = 0.0125	P < 0.01
8. visual and olfactory cues, alternatively	0	4	16	12	8	104	α = 0.0125	P < 0.01
9. no cue	4	8	14	11	3	81	–	
10. correct visual + wrong olfactory ones	0	2	10	16	12	118	α = 0.025	P < 0.001
11. correct olfactory + wrong visual cues	8	18	13	1	0	47	α = 0.025	P < 0.001
12. pure cotton	2	9	18	9	2	80	–	
13. aqueous extracts of onion and thyme	1	5	8	16	10	109	α = 0.017	P < 0.01
14. leek and rosemary	1	4	9	14	12	112	α = 0.017	P < 0.01
15. fennel and sage	1	15	12	11	1	76	α = 0.017	NS
16. no cue	3	9	15	11	2	80	–	
17. violet and green	2	8	19	9	2	81	α = 0.017	NS
18. lower vertical part	3	9	16	10	2	79	α = 0.017	NS
19. upper bent part	0	2	10	16	12	118	α = 0.017	P < 0.001
20. no cue	4	8	13	14	1	80	–	
21. < 5 lux, learned visual cues	1	10	18	9	2	81	α = 0.017	NS
22. < 5 lux, wrong visual + correct olfactory cues	0	5	6	17	12	116	α = 0.017	P < 0.001
23 < 5 lux, correct visual + wrong olfactory cues	6	17	13	4	0	55	α = 0.017	P < 0.01

low at points 1 and 4, as well as thyme and blue at points 2 and 4) (Fig. 3 H), *Myrmica ruginodis* foragers hesitated (stopped, turned their body toward the left and the right) and finally made more wrong choices than in an empty maze. This means they responded to the wrong visual cues in spite of the correct olfactory ones (Tab. 3, line 11). They continued to respond in this manner from the first until the last point of choice, their score at each of the four successive points being 12, 12, 10, and 13, respectively, out of 40 choices. The total number of correct choices was only 47 of 160. Eight ants made no correct choice; none had four correct choices and only three had three correct choices. Statistically, the distribution of the ants scores differed from the control (χ^2 = 16.46, df: 2, P < 0.001 with an adjusted level of probability of 0.025), indicating that the ants did not randomly travel through the mazes but effectively responded to the wrong visual cues. Moreover, they never stopped responding incorrectly despite their failure to find their way and despite the presence of correct olfactory cues at each point of choice.

Use of olfactory and visual cues to negotiate a maze, second step (Tab. 3, lines 12 - 23, Fig. 4)

Responses to olfactory cues. The ants randomly moved through a maze only provided with cotton. They yielded a total of 80 correct choices out of the 160 potential ones, and the numbers of ants having 0, 1, 2, 3, or 4 correct choices were normally distributed (Tab. 3, line 12).

The ants successfully negotiated mazes provided with cotton imbibed with aqueous extracts of onion and thyme (P < 0.01; Tab. 3, line 13, Fig. 4 A). Their responses were identical to those in mazes provided with pieces of onion and thyme (Tab. 3, line 2). The ants thus effectively respond to the odor and not to the visual perception of either presented odorous elements.

The ants also successfully found their way in mazes provided with pieces of leek and rosemary ($P < 0.01$; Tab. 3, line 14, Fig. 4 B). These two plants produce volatile substances similar to those emitted by onion and thyme, respectively. In contrast, the ants failed to negotiate mazes provided with fennel and sage (NS; Tab. 3, line 15, Fig. 4 C). The two latter plants have chemical volatiles very different from those of onion and thyme. Ants were thus able to discriminate learned odors from other odors.

Responses to visual cues. Ants did not correctly negotiate mazes provided with violet (instead of blue) and green (instead of yellow) visual cues. The total number of correct choices (81), as well as the distribution of their numbers with 0, 1, 2, 3, or 4 correct choices, was statistically similar to the control (NS; Tab. 3, line 17, Fig. 4 D). The ants could thus distinguish violet from blue and green from yellow, but not necessarily by actually discriminating the colors (see the Discussion section).

Ants failed to correctly travel through mazes provided with only the lower vertical part of the blue and the yellow visual cues. The total number of correct choices obtained (79) and the distribution of ants with 0, 1, 2, 3, or 4 correct choices were statistically similar to the controls (NS; Tab. 3, line 18, Fig. 4 E). Thus, traveling ants did not use the visual elements located directly in front of them.

In contrast, they perfectly negotiated mazes in which only the upper bent part of the blue and the yellow visual cues were present. Their responses were similar to those in the presence of entire visual cues (total number of correct choices = 118; $P < 0.001$ based on the numbers of ants having 0, 1, 2, 3, or 4 correct choices; Tab. 3, line 19, Fig. 4 F). Thus, traveling ants exclusively used the visual elements located above them.

Responses under conditions of low light intensity. At < 5 lux, ants could not find their way in mazes correctly provided with blue and yellow cues. The total number of correct choices was 81 / 160; the distribution of the numbers of ants with 0, 1, 2, 3, or 4 correct choices was statistically similar to the controls (NS; Tab. 3, line 21 *vs* line 20; Fig. 4 G). Under very low light intensity, the ants were thus no longer able to use the visual cues to negotiate their way.

The ants were tested at < 5 lux in mazes provided with incorrect blue and yellow cues but correct onion and thyme cues. They hesitated somewhat but ultimately found their way with a higher score (total number of correct choices = 116; Tab. 3, line 22; $P < 0.001$ based on the numbers of ants with 0, 1, 2, 3, or 4 correct choices, the control being at Tab. 3, line 20) than in mazes provided with only olfactory cues under higher light intensity (109 correct choices; $P < 0.01$) (Tab. 3, lines 22 *vs* 13; Fig. 4 H). The ants thus use olfaction to orient themselves during travel when they are unable to see sufficiently, and their decisions based olfaction are more efficient than under normal conditions when they can also use vision.

The ants were tested at < 5 lux in mazes provided with correctly set visual cues and incorrectly installed olfactory cues. In these instances, they failed to negotiate their trajectories. Their total number of correct choices (55) was lower than in the control experiment (80) (Tab. 3, line 23 *vs* line 20; Fig. 4 I). In fact, the ants responded to the incorrectly set olfactory cues at the beginning of their traveling but nearly no more at the end. Indeed, the number of correct choices obtained at the choice points 1, 2, 3, and 4 were 11 / 40, 13 / 40, 15 / 40, and 16 / 40, respectively. Thus, while moving through the mazes, the ants progressively stopped responding to the obsolete olfactory cues. It is the reason why the ants' score of 55 / 160 is not highly significant ($\chi^2 = 11.52$, df = 2, $P < 0.01$ with an adjusted level of probability of 0.017).

Discussion

Myrmica ruginodis foragers can acquire differential olfactory, as well as visual conditioning, and can use olfactory, as well as visual cues, to negotiate trajectories. They can also find their way using the two kinds of cues together, these two kinds of cues being either successively or alternatively presented to them along the way. In each case, *M. ruginodis* foragers respond more accurately to visual than to olfactory cues. Confronted with correct visual cues and wrong olfactory ones, these ants follow the correct visual cues without hesitation. In the presence of wrong visual cues and correct olfactory ones, they hesitate, then respond to the wrong visual cues and continue to do so all along their way, i.e., never neglecting the obsolete visual cues. The ants respond to the actual odor and not to the visual perception of olfactory cues and are able to discriminate odors from one another. They also discriminate differently colored elements. *Myrmica ruginodis* workers respond entirely to the upper, bent part of the learned visual cues and not to the lower, vertical part. They thus rely on cues which are above them to find their way, and neglect cues that are directly ahead of them. Anthropomorphically stated, the ants look up and not in front of them when traveling. At < 5 lux, *M. ruginodis* workers can no longer use visual cues to orient themselves during travel. They then respond to olfactory cues better than under higher light intensity, even in the presence of visual cues, and even if the olfactory cues were incorrectly set along the trajectory. When tested under low light intensity with olfactory cues incorrectly set along their path, *M. ruginodis* workers appeared to progressively stop responding to the obsolete olfactory cues, in the course of time.

In contrast to experiments using the classical T-maze to test ants, our specially designed mazes allow us (1) to use four points of choice for each tested ant, (2) to present the two learned cues at the same time, (3) to present successively or alternatively the learned olfactory and visual cues, and (4) to see if ants modify their use of cues while traveling through a maze provided with wrong olfactory or visual cues.

Theoretical and practical aspects of olfactory and visual conditionings are only briefly examined in the present paper, since our aim was to determine if the ants can be conditioned and if learned cues are used for traveling by *Myrmica ruginodis* workers.

Conditioning has already been obtained in several insects such as *Drosophila melanogaster* (see BREMBS & HEISENBERG 2001, SIWICKI & LADEWSKI 2003), bumblebees (LALOI & al. 1999), honeybees (ERBER & SCHILDBERGER 1980, KISCH & ERBER 1999, HUSSAINI & al. 2007, VERGOZ & al. 2007, CARCAUD & al. 2009) and ants (JOSENS & al. 2009, CAMLITEPE & AKSOY 2010, GUERRIERI &

D'ETTORRE 2010). Additional studies have shown that ants can be subjected to classical conditioning (CAMMAERTS 2004a, b) and operant conditioning (CAMMAERTS 2004c, 2007b, 2008).

We previously studied operant conditioning in *Myrmica sabuleti* (M.-C. Cammaerts, Z. Rachidi & D. Cammaerts, unpubl.) and are presently analyzing operant and classical conditionings in *M. ruginodis* using olfactory and visual stimuli on a collective and individual basis. We have already obtained, with an operant method, the kinetic of the ants' visual conditioning and discovered that ants can acquire conditioning only by seeing the cue and congeners eating near it, so without coming near the cue and being rewarded (M.-C. Cammaerts, unpubl.). Assessing ants coming to feed in the near vicinity of a cue has thus no fundamental significance since ants can also acquire conditioning without coming onto the food. On the other hand, an isolated ant, although it remains alive, will no longer eat and will scarcely drink sugared water. Isolated ants can hardly be conditioned. Regarding social insects, the best method for obtaining valuable conditioning is an operant and a collective one, such a method being the most natural one.

For many animals, learning, memory and conditioning are essential for traveling, foraging and returning to the nest. This has been amply demonstrated for ants, e.g., by BISCH-KNADEN & WEHNER (2003), FUKUSHI & WEHNER (2004) and KOHLER & WEHNER (2005). We also confirmed this dependence in our studies of the traveling systems in *Myrmica sabuleti* and *M. ruginodis* (see CAMMAERTS & LAMBERT 2009, CAMMAERTS & RACHIDI 2009 and present work).

The navigation system of *Myrmica ruginodis* differs from that of *M. sabuleti*, which primarily uses olfactory cues but ceases to do so when these cues become obsolete (CAMMAERTS & RACHIDI 2009). The system used by *M. ruginodis* corresponds with aspects of its biotope. We only found nests of this species under branches with nearly no odorous plants on the ground. In addition, we often observed this species relocating its nest according to the development of the surrounding vegetation (personal observations).

Myrmica ruginodis navigation system is likewise in agreement with the eye morphology of the workers, which differs considerably from that of *M. sabuleti*. The workers of the former species have larger eyes and the postero-dorsal part of the eye is more predominant (RACHIDI & al. 2008). *Myrmica ruginodis* workers might thus have more accurate vision than *M. sabuleti*. This calls for examining their visual perception in detail, as has been done for *M. sabuleti* workers (CAMMAERTS 2004a, 2005, 2007a, b, 2008, CAMMAERTS & CAMMAERTS 2009). Can *M. ruginodis* foragers distinguish shapes, lines and cue orientation? Do they perceive colors and perspectives and what are the light intensity thresholds for perceiving shapes and colors? *Myrmica ruginodis* workers were found in the present study to distinguish violet from blue and green from yellow. It is possible that they perceived only differences in luminosity or brightness and not actually the color itself. They should be trained and tested with colors and several shades of grays to demonstrate that these ants possess color vision, as has been done for *M. sabuleti* (see CAMMAERTS 2007b).

The discovery that *Myrmica ruginodis* workers use dorsally available information to orient themselves is surprising and was verified later on while studying the ants' visual perception. In summary, the cues must be presented dorsally to be perceived and memorized. It is, of course, possible that other fields of vision are used for other tasks (i.e., brood care).

Based on what *Myrmica ruginodis* foragers respond to while traveling, one can hypothesize that these ants can perceive and use canopy cues, polarized light and / or celestial cues to find their way. Such abilities have already been revealed in ants (canopy cues: HÖLLDOBLER 1980; polarized light and / or celestial cues in *Cataglyphis* spp. and in *Gigantiops destructor*: PASSERA & ARON 2005).

The ability of *Myrmica ruginodis* to use odors is weaker than that of *M. sabuleti* workers (CAMMAERTS & RACHIDI 2009). In the presence of olfactory and visual cues, whether successively or alternatively arranged, the response of *M. ruginodis* to visual cues was more accurate while in *M. sabuleti* the response to olfactory cues was more accurate. In the presence of correct visual cues and wrong olfactory cues or of wrong visual cues and correct olfactory cues, *M. ruginodis* workers responded only to the visual cues while *M. sabuleti* workers only to the olfactory cues (CAMMAERTS & RACHIDI 2009). Comparison between the two species is possible since the experimental and statistical methods are identical. In light of our results, it would be interesting to compare the antennae of the two species with regard to the number and types of sensillae.

Olfactory performance should be assessed under increasing light intensities to determine whether it decreases when vision becomes more efficient (or the inverse: under decreasing light intensities, does the olfaction performance increase when visual performance decreases?). The former assumption is plausible since *Myrmica sabuleti* workers exhibited better olfactory conditioning at early night and poorer conditioning during the day, as well as poorer visual conditioning at early night but better during the day (M.-C. Cammaerts, Z. Rachidi & D. Cammaerts, unpubl.).

Since *Myrmica ruginodis* foragers persisted in responding to obsolete visual cues, their visual memory may be long-term. Since they nearly immediately stopped responding to obsolete olfactory cues, their olfactory memory may be short-termed. These hypotheses should be experimentally tested, as has recently been done for *M. sabuleti* (M.-C. Cammaerts, Z. Rachidi & D. Cammaerts, unpubl.). This would be a major step toward establishing the dynamics of the acquisition and loss of visual and olfactory conditioning.

The related species, *Myrmica rubra* (LINNAEUS, 1758), differs in environment and eye morphology (RACHIDI & al. 2008) from *M. ruginodis* and *M. sabuleti* and should also be studied regarding the use of visual and olfactory cues when traveling. The present experimental setup would be optimal for this work.

Several ant species have been examined regarding their orientation systems. *Cataglyphis fortis* (FOREL, 1902) complementarily uses odors for orientation during travel (WOLF & WEHNER 2000). *Pachycondyla tarsata* (FABRICIUS, 1798) (see HÖLLDOBLER 1980) and *Formica polyctena* (FOERSTER, 1850) (see SALO 1998) use cues located in the canopy. *Formica* spp. memorize several bits of visual information inherent to their biotope (SALO & ROSENGREN 2001 and references therein). *Pachycondyla apicalis* (LATREILLE, 1802) (see FRESNEAU 1985) and *Dinoponera gigantea* (PERTY,

1833) (see FOURCASSIÉ & al. 1999) clearly memorize one or several trajectories and their surroundings. *Cataglyphis cursor* (FONSCOLOMBE, 1846) has been used as a model by CHAMERON (1999) to establish the snapshot and sketch-map systems which explain the use of memorized visual cues. *Cataglyphis* spp. use celestial cues (WEHNER 1997) and polarized light (WATERMAN 1989). Desert ants can also compensate for some uncertainty (WOLF & WEHNER 2005). *Gigantiops destructor* (FABRICIUS, 1804) is an example for advanced navigation: It can memorize locomotion reactions (MACQUART & al. 2006), sequences of visual cues (MACQUART & BEUGNON 2007), as well as the geometry of its environment (BEUGNON & al. 2005).

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