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The visual perception of the ant *Myrmica ruginodis* (Hymenoptera: Formicidae)

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Abstract: *Myrmica ruginodis* workers are able to distinguish black or white circles from black or white squares, black or white ellipses from black or white rectangles as well as hollow circles or ellipses from hollow squares or rectangles. They can also distinguish differently oriented elements as well as objects containing a various number of elements. These workers are also able to perceive and discriminate transparent cues on a black background and even small luminous spots on a black ceiling. Such visual abilities are in agreement with the species' eye morphology and system of navigation: the eyes are rather large with a well-developed posterio-dorsal part, and the foragers rely exclusively on cues located above them, neglecting odorous elements as long as visual perception is possible. Probably, they might use cues located in the canopy and the sky to travel in certain circumstances.

Key words: ant eyes; operant conditioning; orientation system; visual cues

Introduction

To forage, ants rely on their area marking pheromone and on their trail pheromone, as well as on perceived visual elements according to the 'snapshot' (use of memorized cues) or 'sketchmap' (use of a memorized map) models, as summarized in Passera & Aron (2005).

The ant species *Myrmica ruginodis* Nylander, 1846 nests at the edges of forests, in the surroundings of clearings, beneath branches where the sky is partly visible (personal observation). It can also inhabit rather open grasslands. During the day, these ants forage above vegetation, seldom under it; they also forage during the night when the moon and stars are visible and move only occasionally in darkness. *Myrmica ruginodis* workers have rather large eyes compared to *Myrmica rubra* L., 1758 and *Myrmica sabuleti* Meinert, 1861, and have a well-developed posterio-dorsal part (Rachidi et al. 2008). When foraging, they look essentially to what is above them (and not what is in front of them) and use visual cues as long as visual perception is possible, neglecting odorous elements which, however, are used when vision is no longer possible e.g. in darkness (Cammaerts et al. 2012). These ants so use their olfaction only in darkness what was confirmed by the finding that they could be olfactory conditioned only in darkness (Cammaerts & Némeghaire 2012). The visual subtended angle of *M. ruginodis* workers equals 3°10′ (Cammaerts 2011), while that of *M. rubra* equals 3°50′ (Cammaerts 2011) and that of M. sabuleti 5°12′ (Cammaerts 2004a). The latter species has thus smaller eyes than *M. ruginodis* and *M. rubra* and, together with *M. rubra*, lacks the enlarged posterio-dorsal part detained by *M. ruginodis* workers (Rachidi et al. 2008). These facts are in agreement with the orientation system of *M. sabuleti* and *M. rubra*: the first species uses odors as a priority and relies on visual cues only in the absence of odorous elements (Cammaerts & Lambert 2009; Cammaerts & Rachidi 2009); the second species uses, as best as possible, both olfactory and visual cues (Cammaerts 2012).

As a consequence, on the basis of their eye morphology and their navigation system, the visual perception of *M. ruginodis* may be of higher quality than that of *M. sabuleti* which has previously been well documented (Cammaerts 2004a, 2007a, b, 2008) and of somewhat higher quality than that of *M. rubra* already examined (Cammaerts, manuscript).

In the present paper, we intend to define the shapes which *M. ruginodis* workers are able to discriminate and the kinds of cues they can perceive among those which may be located above them, in their natural biotope. In the discussion section, we compare these visual perception abilities to those already known for *M. sabuleti* and recently found for *M. rubra*, as well as to those of other ants and insects.

Defining the visual perception of *M. ruginodis* will allow finishing our study of the biotope, eye morphology, recruitment strategy, visual perception, navigation system and olfactory as well as visual conditioning of three *Myrmica* species. On the other hand, a few ant species (e.g. desert ants) can see very well and use celestial cues to travel; *M. ruginodis* might be as exceptional as these famous ants.

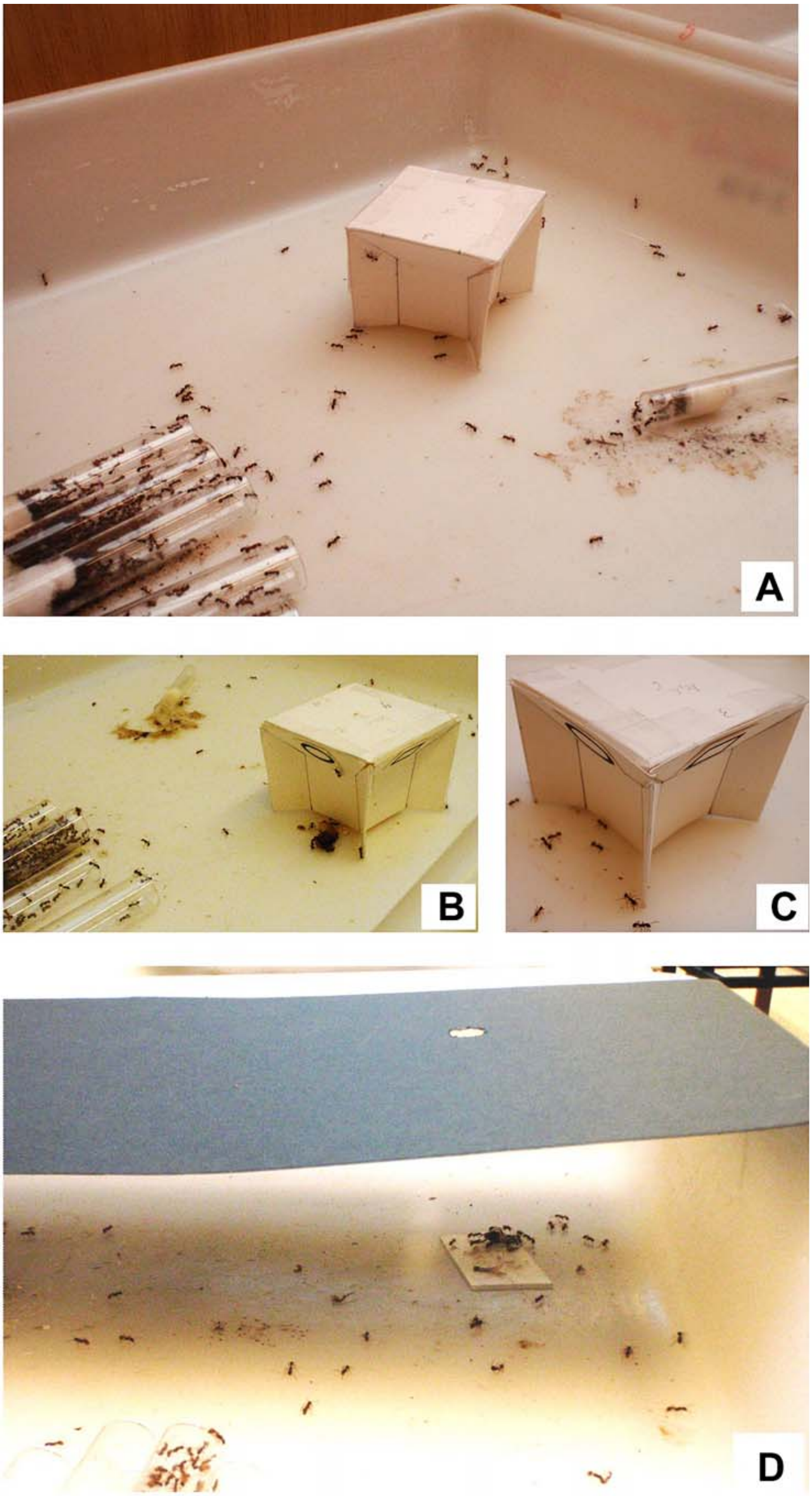

Fig. 1. Experimental design. A: An experimental colony during a control experiment. B: Training to a rewarded hollow black ellipse *vs.* a hollow black rectangle. C: Test in the presence of a previously rewarded hollow black ellipse and an unrewarded hollow black rectangle. D: Training to a luminous circle *vs.* no luminous elements in a black ceiling.

To perform our study, we used collective operant conditioning as a method (see the first paragraph of the 'Discussion'), whereby cues were presented to *M. ruginodis* workers from above and not in front of them, since when foraging they look essentially to what is above their heads.

Material and methods

Collection and maintenance of ants

The experiments were conducted on six colonies derived from large colonies collected in the Aise valley on the borders of a forest and around a clearing of a forest located at Petigny (Ardenne, Belgium). Each six experimental colony contained a queen, brood and about 500 workers. They were maintained in the laboratory in artificial nests made of a few (generally three) glass tubes half-filled with water and plugged with cotton. The ants nested in these tubes, near the cotton, where there was no water (Fig. 1A). The glass tubes were deposited in trays (52 cm × 37 cm × 8 cm), the sides of which were covered with talc. The trays served as foraging areas; food was placed in them, and the ants were trained, as well as tested, on the floor of the trays (Fig. 1).

Temperature was maintained at 20 ± 2 °C. Humidity was about 80% and remained constant over the course of the experimentation. The lighting had a constant intensity of 600 lux while caring for the ants (e.g., providing food, renewing nesting tubes), training them and testing them. At other times, the light intensity was dimmed to about 120 lux.

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. The meat food was withheld during experiments since it served as a reward during training (Figs 1B, D).

Experimental protocol

The ants were trained for six days to find meat food under a given cue in the presence of a second but unrewarded cue. The first test was performed on day seven. After that, the ants were again trained to the same cues during three more days and the second test was conducted the following day.

Training consisted of placing an experimental apparatus provided with two cues in or above the tray of each colony. The apparatus, described below, were either a tower structure with a corbelled construction on each side placed in the tray or a roof structure placed above the tray. Each colony had its own apparatus devoted to training. A piece of dead cockroach was set under one of the two cues located on the experimental apparatus (Figs 1B, D). Since the training lasted 6 + 3 = 9 days, the apparatus were relocated every day, once a day, during the training phases to avoid spatial learning by the ants (Cammaerts 2004b) and to prevent the establishment of a trail between the apparatus (provided with food) and the nest (Cammaerts & Cammaerts 1980). The meat food was renewed if necessary while relocating the apparatus. These relocations were never made every12 h or 24 h to preclude the ants from acquiring temporal learning (Cammaerts 2004b).

Testing consisted of removing the apparatus used to train the ants and presenting them with an identical but new apparatus without food (Fig. 1C). Each colony had its own apparatus devoted to testing. The ants located under each cue were counted fifteen times in the course of the test for each colony and the results were analyzed as explained below.

Experimental apparatus

Cues to which ants were trained were presented either on a square tower (Figs 1A–C) or on a ceiling which covered the foraging area (Fig. 1D).

Square towers. Each tower was constructed of either white or black strong paper, according to the shape and dimensions given in Fig. 2A. The towers had a corbelled surface above each side and a buttress on each corner (Figs 2B, C). The corbelled overhang was made at an angle of 45° to the corresponding side, and each corner buttress was angled at about 140° (i.e., a Wehner angle which divides 360° by Φ) to each of the two adjacent faces (Figs 2B, C). Cues were presented on the corbelled areas as follows. Four cues were located each one on a corbelled surface. Two identical cues were located on two opposing corbelled surfaces, and two other ones, also identical to one another, were placed on the two other opposing corbelled surfaces. During training, one kind of cue was associated with a reward, i.e., a piece of dead cockroach was placed on the foraging area under each of the two corbelled surfaces provided with this kind of cue. (Fig. 1B). Each colony had its own tower for training. New towers of the same shape and size, with the same cues, were used to test the ants. Each colony had its own tower for testing and, of course, during the tests no reward was provided (Fig. 1C).

Ceiling. For each of the six colonies, a piece of black strong paper (45 cm × 20 cm) was pierced at one or two given places, folded along two of its edges to form a roof that could be set over the colony's tray and which covered part of the ants' foraging area (Fig. 1D). The cues were located at 9 cm to the left or the right edge of the ceiling, as well as at 8 cm to the front or the back edge of the ceiling (Fig. 1D). This allowed locating the cues at four different places on the ceiling. A piece of dead cockroach was placed beneath a given cue – i.e. the cue associated with a reward (Fig. 1D) and was renewed if necessary when the ceiling was relocated during the training phases (see above). Each colony had its own ceiling for training purposes. New ceilings were used to test the ants. Each colony had its own ceiling for testing, and no reward (= meat food) was provided during the test.

Cues presented to the ants

The different kinds of cues used to study *M. ruginodis* workers' visual perception are schematically presented in Fig. 3. The gray colors of that figure refer to the grays appearing in Tables 1 and 2. The cues were either filled or hollow black elements on a white background (Fig. 3, upper left), filled white cues on a black background (Fig. 3 upper right), transparent elements on a black background (Fig. 3, lower left) or luminous elements on a black ceiling (Fig. 3, lower right). The first three kinds of cues were presented on the corbelled surfaces of the towers described above, the latter kind of cue on the black ceiling, also described above.

Quantification and statistical analysis of the ants' reaction

To assess the ants' response to the two kinds of cues (one previously associated with a reward, another not associated), the ants found beneath the cues were counted fifteen times at intervals, during the test, for each colony. The mean values of the counts were calculated for each colony and for all colonies together (Tables 1, 2). The mean number obtained for the cue associated with a reward was statistically compared to that obtained for the 'unrewarded' cue using the non-parametric 2 × 2 table contingency χ^2 test (Siegel & Castellan 1989).

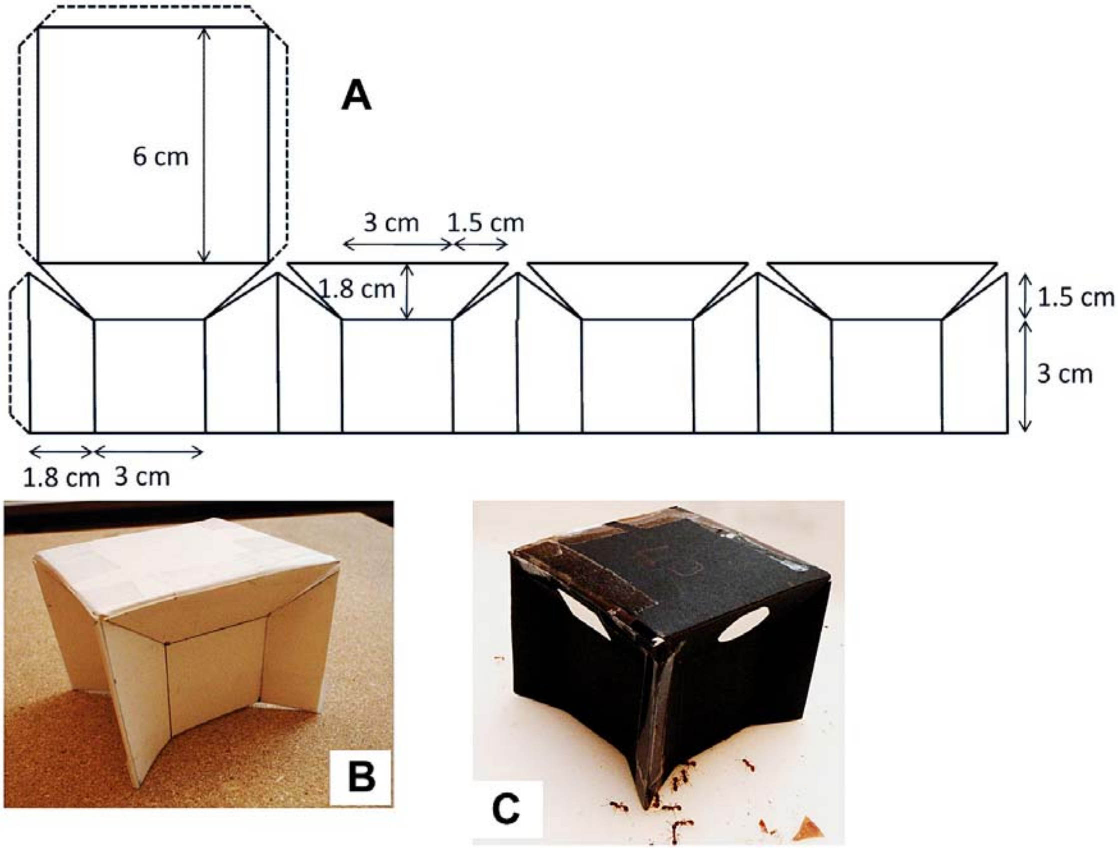

Fig. 2. Tower construction used to train and test the ants. A: Design of tower, made from white or black strong paper, with measurements for its dimensions and instruction on how to fold the paper. B: A tower made of white paper used in the control experiments. C: A tower made of black paper used to test the ants' discrimination between a white ellipse (previously rewarded) and a white rectangle on a black background.

Results

Controls

In the control experiments no cue was placed on the corbelled surface of the towers; a similar number of ants were present in front of each side of the towers (Table 1: 1).

In a second control experiment, the two opposing corbelled surfaces of a tower were entirely covered with black paper, while the other two sides remained uncovered. These towers were presented to the ants with a piece of meat under the black corbelled areas. In the tests following training, more ants were present beneath the black corbelled surfaces (Table 1: 2). This experiment provides evidence that the ants distinguished between the white and black areas located above them.

The two control experiments allowed us to validate the experimental method of using collective differential operant conditioning to two different cues prior to testing in the presence of the two cues.

Filled and hollow black cues on a white background; filled white cues on a black background (Fig. 3 upper, Table 1)

Workers of *M. ruginodis* could distinguish a filled black circle from a filled black square, as well as a filled black ellipse from a filled black rectangle (Table 1: 3, 4). They could also distinguish between a hollow black circle or a hollow black ellipse from a hollow black square or a hollow black rectangle, respectively (Table 1: 5, 6). This infers that they possess a visual perception system of rather high quality, as explained in the 'Discussion'.

A filled circle could also be distinguished from a filled square, and a filled ellipse from a filled rectangle, by *M. ruginodis* workers when these shapes were white on a black background (Table 1: 7, 8). This is in agreement with the results mentioned above (Table 1: 3, 4, 5, 6).

M. ruginodis workers could also distinguish between a right half circle and a left half circle (Table 1: 9). They are thus able to perceive the general orientation of a cue.

They could also detect the difference between one and two small circles, the circles being either vertically or horizontally presented (Fig. 3 upper right, lower half; Table 1: 10, 11). They thus were able to perceive the quantity of elements in a cue.

Transparent cues on a black background (Fig. 3 lower left, Table 2)

After completion of training to find food under a transparent circle located in the middle of a corbelled surface, *M. ruginodis* workers preferentially positioned themselves beneath the circle in the test experiments (Table 2: 1).

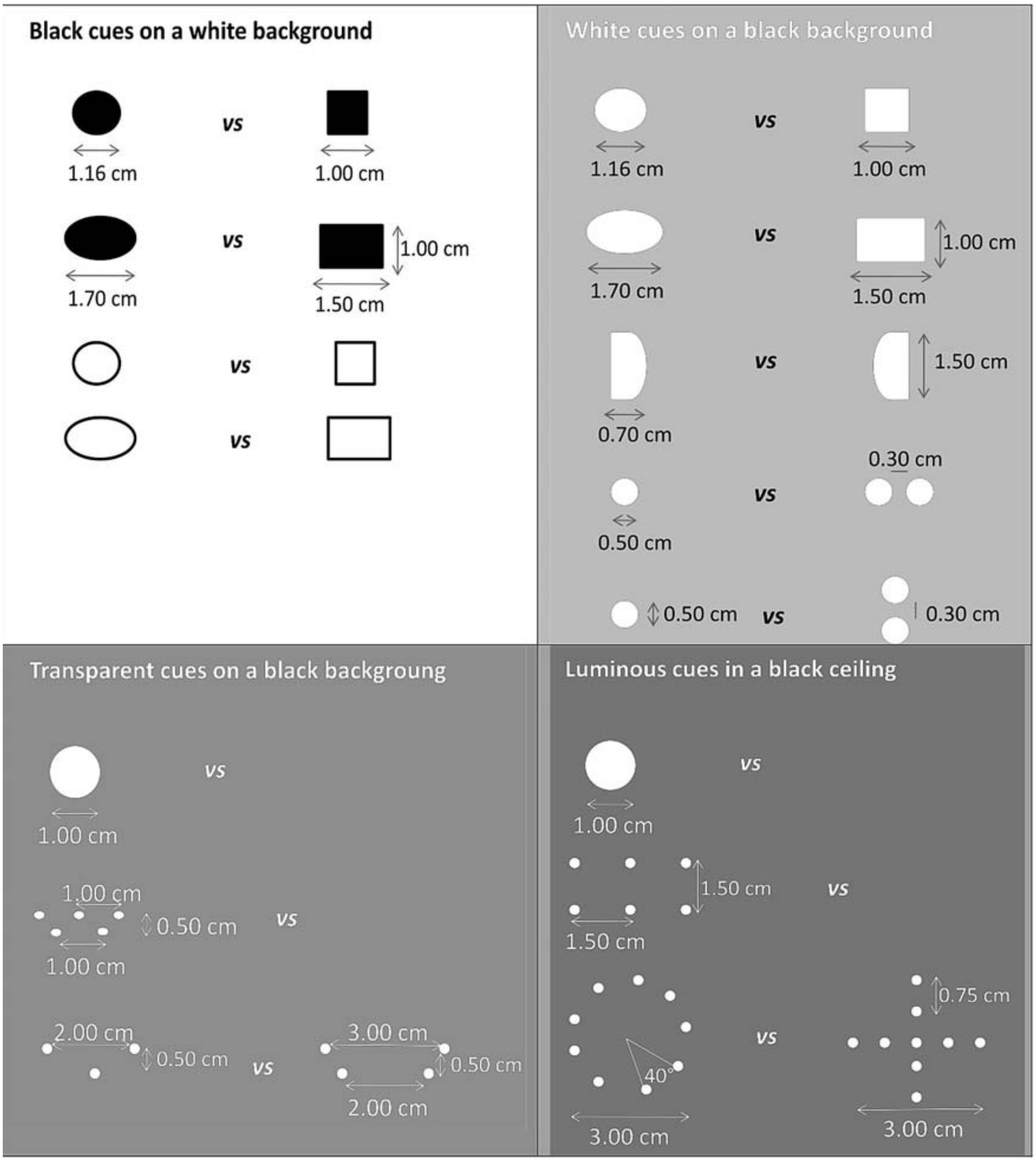

Fig. 3. Cues used to define *M. ruginodis* workers' visual perception. The four grays of the figure refer to the same grays of Tables 1 and 2. For each pair of cues, the left is the rewarded cue and the right the unrewarded cue. The black, white and transparent cues were presented on the corbelled surfaces of the towers (Figs 1A–C and Fig. 2). The luminous cues were presented on a black ceiling (Fig. 1D). When no cue is given to the right, it means that no unrewarded cue was presented and the ants had to respond to the given cue *vs.* no cue.

In the same way, they were conditioned to find food under five transparent small points (i.e., holes) (Table 2: 2). They were thus able to effectively perceive these small holes.

These ants were also able to distinguish a group of three small transparent points from a group of four transparent points that were differently arranged (Table 2: 3).

Luminous cues in a black ceiling (Fig. 3 lower right, Table 2)
When the ants' foraging area was covered with an intact ceiling, the ants foraged everywhere underneath that ceiling. During a control experiment, not reported in Table 2, we counted the ants foraging on the right and on the left under the ceiling and meanly obtained 0.99 and 1.16 respectively. These two mean values were statistically identical. However, for each colony, the ants were slightly more numerous in places where the meat had previously been given. This result underlined the importance of relocating the ceiling several times in the course of the training period.

M. ruginodis workers could be trained to find food under a hole (= a luminous cue) in a black ceiling (Table 2: 4). Likewise, they were able to perceive six small holes (= six small luminous cues) made in a black ceil-

Table 1. Mean numbers of ants of six colonies (second column) responding to previously rewarded (in bold) and unrewarded cues (first column), in a first and a second test (upper and lower numbers). In the third column, results of non-parametric χ^2 tests 2 × 2 contingency table between the two mean numbers obtained each time are given. Grays refers to grays in Fig. 3.

Rewarded and unrewarded cues	Test 1 Test 2	Mean numbers of ants beneath the **rewarded** and the unrewarded cue							Statistics
		for each colony						for all colonies	
1) no cue (control)		**0.4**	**0.1**	**2.9**	**0.0**	**0.3**	**0.0**	**0.61**	
		0.5	0.1	3.1	0.0	0.3	0.0	0.67	NS
2) **black** and white corbelled surfaces		**2.7**	**1.1**	**4.7**	**1.8**	**1.3**	**1.5**	**2.19**	
		1.0	0.0	1.3	1.0	0.0	0.7	0.66	< 0.001
		2.7	**0.9**	**9.6**	**1.7**	**1.3**	**0.9**	**2.86**	
		0.4	0.0	1.7	0.5	0.3	0.1	0.51	< 0.001
3) **filled black circle** and square		**0.3**	**0.3**	**2.0**	**1.5**	**0.9**	**0.9**	**0.99**	
		0.0	0.0	0.6	0.9	0.4	0.3	0.38	< 0.001
		1.0	**0.6**	**2.1**	**4.7**	**0.7**	**0.7**	**1.63**	
		0.4	0.1	0.6	1.3	0.3	0.1	0.47	< 0.001
4) **filled black ellipse** and rectangle		**1.1**	**1.1**	**2.5**	**2.5**	**0.6**	**0.7**	**1.42**	
		0.1	0.1	0.1	1.0	0.1	0.2	0.27	< 0.001
		1.1	**1.7**	**2.2**	**1.3**	**1.7**	**0.7**	**1.44**	
		0.1	0.1	0.0	0.1	0.1	0.0	0.05	< 0.001
5) **hollow black circle** and square		**1.3**	**1.0**	**7.6**	**3.5**	**0.7**	**0.9**	**2.51**	
		0.1	0.0	1.9	1.6	0.1	0.1	0.66	< 0.001
		1.3	**0.9**	**3.3**	**1.1**	**1.3**	**2.2**	**1.67**	
		0.1	0.0	0.7	0.0	0.0	0.0	0.13	< 0.001
6) **hollow black ellipse** and rectangle		**1.5**	**0.7**	**1.7**	**1.1**	**0.9**	**0.9**	**1.14**	
		0.0	0.0	0.8	0.1	0.1	0.0	0.17	< 0.001
		0.9	**1.0**	**3.1**	**1.5**	**1.0**	**3.1**	**1.78**	
		0.0	0.0	0.9	0.1	0.0	0.5	0.25	< 0.001
7) **filled white circle** and square		**2.8**	**1.6**	**5.4**	**1.1**	**7.5**	**4.4**	**3.89**	
		1.0	0.3	1.7	0.1	3.5	2.1	1.44	< 0.001
		1.1	**1.0**	**3.5**	**4.7**	**6.5**	**2.5**	**3.20**	
		0.4	0.1	0.8	1.3	3.4	0.4	1.07	< 0.001
8) **filled white ellipse** and rectangle		**1.5**	**3.3**	**5.3**	**1.9**	**5.6**	**4.0**	**3.59**	
		0.1	1.7	1.7	0.3	1.8	0.7	1.05	< 0.001
		0.9	**0.7**	**4.5**	**2.3**	**3.3**	**2.0**	**2.28**	
		0.1	0.1	1.2	0.4	0.1	0.1	0.32	< 0.001
9) **right half white circle** and left half circle		**1.0**	**1.9**	**8.1**	**3.0**	**1.7**	**0.8**	**2.76**	
		0.0	0.0	2.0	0.3	0.5	0.1	0.51	< 0.001
		1.2	**1.5**	**4.1**	**3.1**	**1.9**	**1.4**	**2.26**	
		0.0	0.0	1.1	0.1	0.5	0.2	0.31	< 0.001
10) **one white circle** and two horizontally set circles		**1.2**	**1.5**	**4.1**	**3.1**	**1.9**	**1.4**	**2.22**	
		0.0	0.0	1.1	0.1	0.5	0.2	0.31	< 0.001
		0.8	**1.7**	**3.7**	**2.2**	**1.4**	**1.4**	**1.94**	
		0.1	0.0	0.7	0.0	0.2	0.0	0.16	< 0.001
11) **one white circle** and two vertically set circles		**1.1**	**2.1**	**5.0**	**2.4**	**1.9**	**1.1**	**2.27**	
		0.0	0.4	1.1	0.1	0.2	0.0	0.30	< 0.001
		0.9	**1.5**	**2.3**	**4.8**	**1.5**	**1.3**	**2.04**	
		0.0	0.1	0.6	0.6	0.0	0.0	0.21	< 0.001

ing (Table 2: 5). They are thus able to detect large, as well as small, luminous elements.

Finally, the ants discriminated between two different arrangements of nine luminous points, one in the shape of a circle and one in the shape of a cross (Table 2: 6). They were thus fully able to perceive and distinguish different sets of luminous points located in the sky.

Discussion

We studied the visual perception of the ant *M. ruginodis* using a collective operant conditioning method because ants, when isolated and individually trained, scarcely take food – since they have no brood to care for – and may not be conditioned. Individual conditioning performed in other works is either collective condi-

Table 2. Mean numbers of ants of six colonies (second column) responding to previously rewarded (in bold) and unrewarded cues (first column), in a first and a second tests (upper and lower numbers). In the third column, results of non-parametric χ^2 tests 2 × 2 table contingency between the two mean numbers obtained each time are given. Grays refer to grays in Fig. 3.

Rewarded and unrewarded cues	Test 1 Test 2	Mean numbers of ants beneath the **rewarded** and the unrewarded cue							Statistics
		for each colony						for all colonies	
1) **a hole** and nothing on a black background		**2.0**	**2.3**	**1.9**	**1.9**	**1.3**	**1.7**	**1.86**	
		0.0	0.1	0.0	0.1	0.0	0.0	0.03	< 0.001
		2.0	**1.7**	**2.0**	**1.9**	**1.2**	**1.7**	**1.75**	
		0.0	0.0	0.1	0.8	0.3	0.0	0.06	< 0.001
2) **five small holes** and nothing on a black background		**2.0**	**1.3**	**3.1**	**2.1**	**1.4**	**2.9**	**2.12**	
		0.0	0.0	0.5	0.2	0.0	0.0	0.11	< 0.001
		1.4	**1.0**	**3.8**	**2.9**	**2.3**	**3.0**	**2.40**	
		0.0	0.0	0.4	0.7	0.2	0.0	0.21	< 0.001
3) **three small holes** and four ones otherwise set on a black background		**0.8**	**1.0**	**2.1**	**2.3**	**1.8**	**0.7**	**1.45**	
		0.0	0.0	0.3	0.2	0.0	0.0	0.09	< 0.001
		1.3	**1.5**	**2.1**	**2.1**	**1.5**	**1.7**	**1.67**	
		0.2	0.0	0.4	1.0	0.4	0.1	0.36	< 0.001
4) **a hole** and nothing in the black ceiling		**1.6**	**1.3**	**2.7**	**3.2**	**1.5**	**4.3**	**2.42**	
		0.0	0.0	0.5	0.7	0.8	0.5	0.42	< 0.001
		1.3	**2.2**	**1.4**	**1.8**	**1.5**	**1.7**	**1.66**	
		0.0	0.7	0.2	0.4	0.0	1.3	0.43	< 0.001
5) **six small holes** and nothing in a black ceiling		**0.8**	**1.3**	**4.9**	**3.7**	**1.0**	**1.7**	**2.23**	
		0.0	0.0	0.5	1.5	0.0	0.3	0.38	< 0.001
		1.3	**1.6**	**2.3**	**5.3**	**1.3**	**1.7**	**2.29**	
		0.1	0.0	0.7	0.9	0.1	0.5	0.38	< 0.001
6) **nine small holes in a circle** and nine in a cross, in a black ceiling		**1.3**	**1.0**	**3.2**	**5.2**	**1.7**	**5.1**	**2.93**	
		0.0	0.0	0.5	0.4	0.5	0.9	0.37	< 0.001
		1.0	**1.0**	**3.6**	**6.9**	**1.5**	**3.3**	**2.88**	
		0.0	0.0	0.3	1.1	0.3	0.7	0.39	< 0.001

tioning with individual assessment of acquired learning or true individual conditioning but of immobilized animals. The method here used is always operational, the animals are in conditions as natural as possible and the samples can be large. The ants tested were actually the trained ones: those responding during the test experiments were the foragers coming on the experimental apparatus during training.

On the basis of the results, it can be concluded that *M. ruginodis* workers perceive and distinguish, from one another, filled or hollow black shapes located on a white background. Foragers can thus detect and use cues located in the canopy. They also distinguish, from one another, different white shapes, differently oriented white shapes and different numbers of white elements located on a black background. They can thus detect and use different leaves or other elements as well as different clear spaces within the canopy. Foragers of *M. ruginodis* are also able to perceive and discriminate a transparent large circle, six small transparent points as well as, from one another, three small and four small otherwise positioned transparent points, on a black background. They can thus see and use areas, even if very small, of the sky, i.e. places free of canopy. Finally, *M. ruginodis* workers distinguish a large luminous circle, six small luminous points as well as, from one another, two groups of nine luminous points otherwise positioned, on a black ceiling. They may thus see and use celestial cues, such as the sun, moon and stars.

The results indicate an astoundingly good sense of vision for *M. ruginodis* foragers, a fact which agrees with the species' system of orientation. When travelling, *M. ruginodis* workers primarily use visual cues located above them; they use olfactory elements only when they no longer see (Cammaerts et al. 2012). The results are also in conformity with the species' eye morphology. The eye of *M. ruginodis* workers is large (meanly 149 ommatidia) compared to that of *M.* rubra (meanly 129 ommatidia) and of *M. sabuleti* (meanly 109 ommatidia). It has a well-developed posterio-dorsal part allowing the ants to detect what is above them (Rachidi et al. 2008). These findings agree with the previously assessed subtended angle of vision of *M. ruginodis* workers (3°12′), while that of *M. rubra* equals 3°50′ and that of *M. sabuleti* 5°12′ (Cammaerts 2004a, 2011). *Myrmica sabuleti* workers are not able to distinguish convex shapes (squares, circles, rectangles, ellipses, triangles, Cammaerts 2008), although they perceive the dimension, orientation and number of elements in a cue (Cammaerts 2004a, 2008). Their visual perception is thus of lower quality than that of *M. ruginodis* workers. Foragers of *M. sabuleti* primarily use olfactory elements to negotiate their way, although they can use visual cues located in front of them, when odorous elements are absent (Cammaerts & Lambert 2009; Cammaerts &

Rachidi 2009). The visual perception of *Myrmica rubra* is of better quality than that of *M. sabuleti* but of lower quality than that of *M. ruginodis* (Cammaerts, manuscript). The foragers of this species use, as best as they can, both visual and olfactory elements to travel (Cammaerts 2012). The visual and the olfactory conditioning of the three here above cited *Myrmica* species have been examined and appeared to agree with their vision and navigation system (Cammaerts et al. 2011; Cammaerts & Némeghaire 2012; Cammaerts, manuscript).

Note that the ants' eye morphology presents a large variability. For a species with variable possible biotopes and a large morphological variability, differences may appear, within the species, between the morphological characteristics of different populations inhabiting different biotopes. The ant *M. ruginodis*, with its variable eye morphology and biotopes, is a good model – a better one than species having a less broad habitat preference – for examining such a speculation.

Let us now insert our work in what is actually known, regarding the visual perception, for other ant species and insect families. In ants, a large variability exists in their visual perception abilities. Some species have eyes containing few ommatidia, while the eyes of several other species may contain hundreds of ommatidia (Passera & Aron 2005). As an example of an ant species with excellent vision, *Gigantiops destructor* (F., 1804) has 4,000 ommatidia per eye; this species relies on vision and memory to travel, it neglects odors and produces no marking pheromone (Macquart et al. 2008 and references therein).

Recently, the orientation system of ants has been rather well studied (Passera & Aron 2005 and references therein). Ants having a vision of intermediate quality find their way using their trail and area marking pheromone, as well as memorized visual cues according to a 'snapshot' (the ants learn to move on given distances, in given directions from memorized cues) or a 'sketchmap'(ants memorized relations between nest, cues, food sites e.g. a kind of schematic map) models. These models, however, are not mutually exclusive and both can be used by the same individual (Cammaerts & Lambert 2009).

Although the orientation system of ants has been well studied, their visual perception has not yet been adequately defined by experimentation. Can they detect and distinguish filled shapes, hollow forms (= lines), differently sloping backward cues, cues of different dimensions, cues made of a different number of elements or differently oriented cues? Attempts to answer these questions have generally been made for species with a pronounced sense of vision, such as *Formica rufa* L., 1761 (Jander 1957; Vowles 1965; Voss 1967) and desert ants (Kretz 1979; Collett et al. 2001 and references therein). In contrast, we previously investigated an ant, *M. sabuleti*, with weak visual abilities (Cammaerts 2004a, 2008). Furthermore, it is essential to know what an individual is capable of perceiving before correctly assessing the species' foraging system. Does the field of vision permit foragers to primarily detect objects located in front of them or above them? Can they distinguish colors, as well? Experimental research on this topic should pay attention, at the same time, to the species' foraging strategy, orientation system and visual perception abilities.

Of all hymenopteran species, the honeybees are of course the most thoroughly studied. Wehner (1981) determined that bees poorly differentiate among simple 'closed' shapes (such as squares, circles and triangles). Horridge (1999) also showed that not all patterns can be discriminated or remembered by trained bees, although in some cases, this was demonstrated (Hempel & Giurfa, 2003). Differences in the total perimeter of the presented shapes should be taken into account. Moreover, the location of the presented shapes within the insect's field of vision may influence this insect's visual perception of the shape. It is possible that certain parts of insects' field of vision cause the corners of shapes to appear faded and objects to appear convex. These tendencies can also be deduced from the works of Lehrer & Campan (2004, 2005) on bees and wasps. Although the fruit fly has large eyes, it fails to recognize certain shapes (Dill & Heisenberg 1995). Since the huge eyes of dragon flies (Odonata) possess a tremendous number of ommatidia, one might surmise that they must have excellent vision (Wehner 1981). Our preliminary conclusion is that the visual perception abilities of *M. ruginodis*, concerning filled and hollow shapes, is superior to that in many other insects.

M. ruginodis workers were able to distinguish cues made of one element from cues made of two elements. This result was expected since *M. sabuleti,* which has smaller eyes, can also distinguish between similar cues (Cammaerts 2008).

M. ruginodis workers distinguished among half circles that were variously oriented. *M. sabuleti* workers could perceive the orientation of an element (line or fragment of a circle) and were sensitive to a vertical difference of 20°, as well as a horizontal difference of 10° (Cammaerts 2008). We expect that *M. ruginodis* workers are similarly capable. Wehner (1969, 1972) showed that bees can differentiate among different 'orientations' (or more exactly positions) of a black-and-white disk. The visual abilities of bees and ants are similar regarding the perception of the orientation of a cue.

The fact that *M. ruginodis* workers detect, discriminate and use luminous cues located above them on a black ceiling is a new finding for a *Myrmica* ant, and allows us to put forth the hypothesis that the species can use celestial cues to travel.

Insect vision appears to be more complex than previously estimated (Horridge 2000, 2003a–d, 2005, 2006, 2009; Srinivassan et al. 1994; Giurfa et al. 2001; Stach et al. 2004). The only available method to gain insights into this complexity is through conditioning experiments which pool together two different complex physiological abilities (learning and visual perception) (Avergues-Weber et al. 2011).

As for our work, it can be concluded that the visual perception of *M. ruginodis* workers is well-developed, foragers being able to differentiate objects according to shape, line, orientation and number of elements, as well as elements that are transparent or luminous. To travel and forage they exclusively utilize visual cues located above them and quite possibly elements of the canopy, sky and celestial cues. The workers rely on odors only when they no longer see (Cammaerts et al. 2012). The visual capability of *M. ruginodis* is so in conformity with its system of orientation, and both abilities are well-adapted to its natural biotope. Indeed, the species inhabits in woodlands, on the borders of forests, under branches where the sky is partly visible, nesting in tree trunks, in rotting wood, under stones. It also inhabits moorlands, grasslands nesting in somewhat sheltered sites (Seifert 1996).

Three *Myrmica* species (*M. sabuleti, M. rubra, M. ruginodis*) have thus been investigated as for their eye morphology, visual perception, navigation system, visual and olfactory conditioning, recruitment strategy and usual biotope. All this will be summarized in a future short review.

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References

Avergues-Weber A., Deisig N. & Giurfa M. 2011. Visual Cognition in Social Insects. Ann. Rev. Entomol. **56:** 423–443. DOI: 10.1146/annurev-ento-120709-144855

Cammaerts M.-C. 2004a. Some characteristics of the visual perception of the ant *Myrmica sabuleti*. Physiol. Entomol. **29 (5):** 472–482. DOI: 10.1111/j.0307-6962.2004.00419.x

Cammaerts M.-C. 2004b. Classical conditioning, temporal learning and spatial learning in the ant *Myrmica sabuleti*. Biologia **59:** 243–256.

Cammaerts M.-C. 2007a. Perspective vision in workers of *Myrmica sabuleti* Meinert, 1861 (Hymenoptera: Formicidae). Myrmecol. News **10:** 21–26.

Cammaerts M.-C. 2007b. Colour vision in the ant *Myrmica sabuleti* Meinert, 1891 (Hymenoptera: Formicidae). Myrmecol. News **10:** 41–50.

Cammaerts M.-C. 2008. Visual discrimination of cues differing as for their number of elements, their shape or their orientation, by the ant *Myrmica sabuleti*. Biologia **63:** 1169–1180. DOI: 10.2478/s1175600801722

Cammaerts M.-C. 2011. Subtended angle of *Myrmica ruginodis* and *Myrmica rubra* (Formicidae, Hymenoptera). Bull. Ann. Soc. R. Belg. Entomol. **147:** 113–120.

Cammaerts M.-C. 2012. Navigation system of the ant *Myrmica rubra* (Hymenoptera, Formicidae). Myrmecol. News **16:** 111–121.

Cammaerts M.–C. & Cammaerts R. 1980. Food recruitment strategies of the ants *Myrmica sabuleti* and *Myrmica ruginodis*. Behav. Processes **5 (3):** 251–270. DOI: 10.1016/037663 57(80)900066

Cammaerts M.-C. & Lambert A. 2009. Maze negotiation by a Myrmicine ant (Hymenoptera: Formicidae). Myrmecol. News **12:** 41–49.

Cammaerts M.-C. & Nemeghaire S. 2012. Why do workers of *Myrmica ruginodis* (Hymenoptera, Formicidae) navigate by relying mainly on their vision? Bull. Ann. Soc. R. Belg. Entomol. **148:** 42–52.

Cammaerts M.-C. & Rachidi Z. 2009. Olfactive conditioning and use of visual and odorous cues for movement in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Myrmecol. News **12:** 117–127.

Cammaerts M.-C., Rachidi Z., Beke S. & Essaadi Y. 2012. Use of olfactory and visual cues for traveling by the ant *Myrmica ruginodis* (Hymenoptera, Formicidae). Myrmecol. News **16:** 45–55.

Cammaerts M.-C., Rachidi Z. & Cammaerts D. 2011. Collective operant conditioning and circadian rhythms in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Bull. Ann. Soc. R. Belg. Entomol. **147:** 142–154.

Collett T.S., Collett M. & Wehner R. 2001. The guidance of desert ants by extended landmarks. J. Exp. Biol. **204:** 1635–1639.

Dill M. & Heisenberg M. 1995. Visual pattern memory without shape recognition. Philos. Trans. R. Soc. Lond. B Biol. Sci. **349 (1328):** 143–152. PMID: 8668723

Giurfa M., Zhang S., Jenett A., Menzel R. & Srinivasan M.V. 2001. The concepts of 'sameness' and 'difference' in an insect. Nature **410 (6831):** 930–33. DOI: 10.1038/35073582

Hempel de I.N. & Giurfa M. 2003. Discrimination of closed coloured shapes by honeybees requires only contrast to the long wavelength receptor type. Anim. Behav. **66 (Part 5):** 903–910. DOI: 10.1006/anbe.2003.2269

Horridge G.A. 1999. Two-dimensional pattern discrimination by the honeybee. Physiol. Entomol. **24 (3):** 197–212. DOI: 10.1046/j.1365-3032.1999.00131.x

Horridge A. 2000. Pattern vision of the honeybee (*Apis mellifera*). What is an oriented edge? J. Comp. Physiol. A **186 (6):** 521–534. DOI: 10.1007/s003590000103

Horridge A. 2003a. Visual resolution of gratings by the compound eye of the bee *Apis mellifera*. J. Exp. Biol. **206 (13):** 2105–2110. DOI: 10.1242/jeb.00379

Horridge A. 2003b. Visual resolution of the orientation cue by the honeybee (*Apis mellifera*). J. Insect Physiol. **49 (12):** 1145–1152. DOI: 10.1016/j.jinphys.2003.08.008

Horridge A. 2003c. The effect of complexity on the discrimination of oriented bars by the honeybee (Apis mellifera). J. Comp. Physiol. A **189 (9):** 703–714. DOI: 10.1007/s00359-003-0446-7

Horridge A. 2003d. The visual system of the honeybee (*Apis mellifera*): the maximum length of the orientation detector. J. Insect Physiol. **49 (6):** 621–628. DOI: 10.1016/S0022-1910(03)00067-2

Horridge A. 2005. What the honeybee sees: a review of the recognition system of *Apis mellifera*. Physiol. Entomol. **30 (1):** 2–13. DOI: 10.1111/j.0307-6962.2005.00425.x

Horridge A. 2006. Visual discriminations of spokes, sectors, and circles by the honeybee (*Apis mellifera*). J. Insect Physiol. **52 (9):** 984–1003. DOI: 10.1016/j.jinphys.2006.06.007

Horridge A. 2009. Generalization in visual recognition by the honeybee (*Apis mellifera*): a review and explanation. J. Insect Physiol. **55 (6):** 499–511. DOI: 10.1016/j.jinsphys.2009.03.006

Jander R. 1957. Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa* L.). Z. Vergl. Physiol. **40:** 162–238.

Kretz R. 1979. A behavioural analysis of colour vision in the ant *Cataglyphis bicolor* (Formicidae, Hymenoptera). J. Comp. Physiol. **131 (3):** 217–233. DOI: 10.1007/BF00610430

Lehrer M. & Campan R. 2004. Shape discrimination by wasps (*Paravespula germanica*) at the food source: generalization among various types of contrast. J. Comp. Physiol. A **190 (8):** 651–663. DOI: 10.1007/s00359-004-0523-6

Lehrer M. & Campan R. 2005. Generalization of convex shapes by bees: What are shapes made of? J. Exp. Biol. **208 (17):** 3233–3247. DOI: 10.1242/jeb.01790

Macquart D., Latil G. & Beugnon G. 2008. Sensorimotor sequence learning in the ant *Gigantiops destructor*. Anim. Behav. **75 (5):** 1693–1701. DOI: 10.1016/j.anbehav.2007.10.023

Passera L. & Aron S. 2005. Les fourmis: comportement, organisation sociale et évolution. Les Presses Scientifiques du CNRC, Ottawa, Canada, 480 pp. ISBN: 066097021X, 9780660970219

Rachidi Z., Cammaerts M.-C. & Debeir O. 2008. Morphometric study of the eye of three species of Myrmica (Formicidae). Belg. J. Entomol. **10 (1–2):** 81–91.

Seifert B. 1996: Ameisen: beobachten, bestimmen. Naturbuch-Verlag, Augsburg, Germany, 352 pp. ISBN: 978-3-89440-170-2

Siegel S. & Castellan N.J. 1989. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill Book Company, Singapore, 396 pp. ISBN-10: 3894401702, ISBN-13: 978-3894401702

Srinivasan M.V., Zhang S.W. & Witney K. 1994. Visual discrimination of pattern orientation by honeybees. Phil. Trans. R. Soc. Lond. B **343 (1304):** 199–210. DOI: 10.1098/rstb.1994.0021

Stach S., Bernard J. & Giurfa M. 2004. Local-feature assembling in visual pattern recognition and generalization in honeybees. Nature **429 (6993):** 758–761. DOI: 10.1038/nature02594

Voss C. 1967. Über das Formensehen der roten Waldameise (*Formica rufa* – Gruppe). J. Comp. Physiol. A **55:** 225–254. DOI: 10.1007/BF00349601

Vowles D.M. 1965. Maze learning and visual discrimination in the wood ant (*Formica rufa*). Brit. J. Psychol. **56 (1):** 15–31. DOI: 10.1111/j.2044-8295.1965.tb00940.x

Wehner R. 1969. Die Mechanismus der optischen Winkelmessung bei der Biene (*Apis mellifera*). Zool. Anz. **33 (Suppl.):** 586–592.

Wehner R. 1972. Visual orientation performances of desert ants, *Cataglyphis bicolor*, towards astronemotactic directions and horizon landmarks, pp. 421–436. In: Galler S.R., Schmidt-Koenig K., Jacobs G.J. & Belleville R.E. (eds), Animal Orientation and Navigation, NASA SP-262, published by NASA, Washington, D.C., 606 pp. ISBN-10: 1410224015, ISBN-13: 978-1410224019

Wehner R. 1981. Spatial vision in Arthropods, pp. 288–616. In: Autrum H. (ed.), Comparative Physiology and Evolution of Vision in Invertebrates. C: Invertebrate Visual Centers and Behavior, II. Series, Handbook of Sensory Physiology, Vol. 7, 665 pp. ISBN: 978-3-642-67870-7

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