Belg. J. Zool., 143(1) : 69-78 January 2013

Visual discrimination of shapes in the ant *Myrmica rubra* (Hymenoptera, Formicidae)

Marie-Claire Cammaerts

Université Libre de Bruxelles, Faculté des Sciences, DBO, CP 160/12, 50 Av. F. Roosevelt, 1050 Bruxelles, Belgique,
E-mail: mtricot@ulb.ac.be

ABSTRACT. Using collective differential operant conditioning, it could be shown that workers of the species *Myrmica rubra* distinguish different filled shapes of similar size (e.g. a black square from a black circle, a black triangle from a black circle, and a black triangle from a black square). They are unable to discriminate hollow shapes (e.g. a rectangle from an ellipse, or a lozenge from an ellipse) of similar size. When presented with hollow shapes, *M. rubra* workers rely more on the length of the perimeter than on the actual shape. A hollow lozenge and rectangle of identical height and width but with a different perimeter can be partly distinguished; hollow shapes of different height and width but identical perimeter are not at all discriminated. The visual perception ability in *M. rubra* is weaker than in *M. ruginodis* but superior to that in *M. sabuleti*; this assessment is consistent with the eye morphology and the navigation system of the three species.

KEY WORDS: differential conditioning, filled and hollow shapes, operant conditioning, visual cues.

INTRODUCTION

Ants are known to essentially use odors (principally pheromones) for communication, brood care, recruitment of congeners, food collection and nest relocation. However, they also use visual perception to perform tasks, such as foraging, returning to the nest after finding either a new food source or a new nest site and returning to the foraging area after having removed a dead nestmate. The fact that ants use their visual perception to forage has been shown for numerous species, e.g. *Gigantiops destructor* (Beugnon et al., 2005), *Cataglyphis bicolor* (Collett et al., 1992), *Leptothorax albipennis* (Pratt et al., 2001), *Formica rufa* (Nicholson et al., 1999), *Tapinoma sessile* and *Camponotus pennsylvanicus* (Klotz & Reid, 1992), *Myrmica sabuleti* (Cammaerts & Rachidi, 2009), *Myrmica ruginodis* (Cammaerts et al., 2011). In general, foraging ants orient themselves using visual cues according to the snapshot and sketch map models (Passera & Aron, 2005).

When examining an ant species' navigation system, it is essential to also analyze that species' ability to see and discriminate shapes, forms, dimension, orientation, coloration and other parameters.

Studies on the visual perception of ants have generally concerned species with large eyes and good vision, e.g. *Formica rufa* (Vowles, 1965; Voss, 1967).

Previously, we examined the visual perception (Cammaerts, 2004a, 2007a, b, 2008) and the orientation system (Cammaerts & Lambert, 2009; Cammaerts & Rachidi, 2009) of an ant with medium-sized eyes, *Myrmica sabuleti*, as well as the visual perception (Cammaerts, 2012a) and orientation system (Cammaerts et al., 2012) of an ant with somewhat larger eyes: *M. ruginodis*. The workers of *M. sabuleti* essentially use odors to find their way, while workers of *M. ruginodis* rely primarily on visual cues as long as vision is possible (references here above). For these two species, their visual perception and navigation system are in agreement with one another and are also in accordance with their usual habitat, eye morphology and subtended angle of vision (Rachidi et al., 2008;

Cammaerts, 2004a, 2011). Workers of *Myrmica rubra* have eyes of intermediate size compared with *M. sabuleti* and *M. ruginodis* (Rachidi et al., 2008) as well as a subtended angle of vision of intermediate value (Cammaerts, 2011).

In this study, we investigated how the visual perception of these ants could be characterized. Answering this question will provide further insight into the comparative study of the eye morphology, the subtended angle of vision and the visual perception of three closely related species, probably revealing accordance between these morphological and physiological studies. The travelling system of *M. rubra* has been elucidated (Cammaerts, 2012b): this species uses both its olfaction and its vision to explore the environment. Such a system differs from – and is, in fact, intermediate between – those of *M. sabuleti* (use of odors) and *M. ruginodis* (use of visual cues) (references here above). Is the navigation system of *M. rubra* in agreement with its visual perception and is its visual perception in accordance with its preferred habitat as is the case for the two other *Myrmica* species? Answering this question requires a detailed analysis of the visual perception of workers of *M. rubra* . Finally, such a study of this species' visual perception will consolidate a series of ecological, morphological, physiological and ethological studies on three closely related species, possibly helping to understand niche differentiation between these three related species.

MATERIAL AND METHODS

Collection and maintenance of ants

The experiments were performed on six experimental colonies derived from large colonies collected in the Aise valley (Ardenne, Belgium) on open grassland. These colonies were demographically identical: each contained a queen, about 500 workers and brood. They 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 (Fig. 1A). The glass tubes were deposited in trays (43 cm x 28 cm x 7 cm), the sides of which were covered with talc. The trays served as foraging areas wherein food was provided and the ants were trained, as well as tested on the floor of the trays (Fig. 1A, B).

Temperature was maintained at 20° ± 2° C. Humidity was approximately 80% and remained constant over the course of the experiment. Light intensity was held constant at 600 lux when maintaining the ants (e.g. providing food, renewing nesting tubes) and during the training and testing periods. Otherwise, the light intensity was adjusted to about 120 lux using a dimmer.

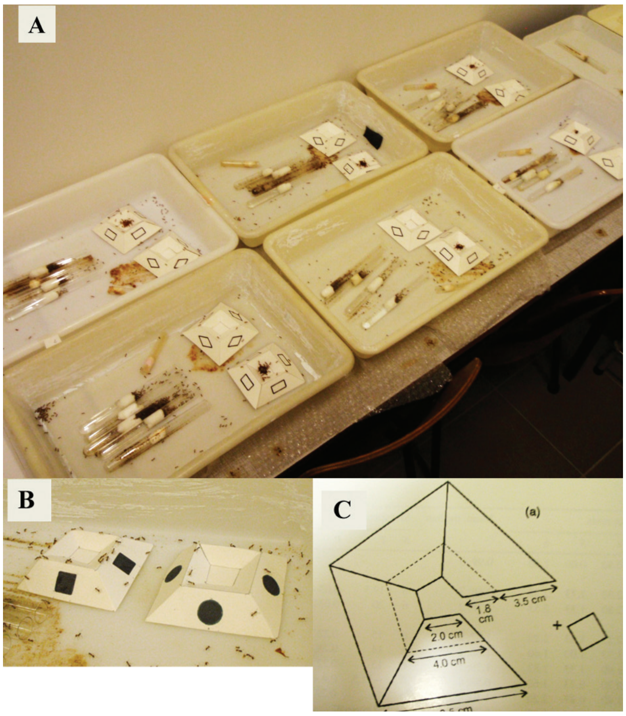

Fig. 1. – A: experimental design; training of six experimental colonies to a hollow black rectangle and lozenge of similar perimeter, the rectangle being the 'rewarded' cue. **B**: testing the ants in presence of a filled black square (previously 'rewarded') and circle of same area; the ants discriminated between the two shapes. **C**: experimental device: a kind of truncated pyramid with a reverse pyramid at its top, constructed from one piece of paper Steinbach ® ((a)), closed with a piece of same paper (+). The angle between the base and the edge of a face equaled 52° 5'. To study the ants' visual perception, cues were drawn on the center of each face of the device and two pyramidal devices, each one with a given kind of cue, were presented to the ants.

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. No meat food was given during experiments since it served as a reward during training (Fig. 1A).

Experimental device

The experimental device was made of very strong white paper (Steinbach®), which was cut to a precise form and dimension (Fig. 1C). Paper was folded to form a pyramid at the base and folded again inward at the top into an inverted pyramid. A strip of Sellotape paper® was attached on the interior to hold the device together. The inner inverted pyramid was closed by taping a square piece of the same kind of paper to its base. A cue was drawn with a black water proof marker in the center of each of the four outer surfaces of a device.

During an experiment, the six colonies were trained prior to testing (see below) with a pair of experimental devices each provided with one kind of cue (Fig. 1A, B). All colonies had their own devices for training and for testing. In other words, one complete experiment required 12 devices for training (= 6 devices with one kind of cue + 6 devices with another kind of cue), and another 12 devices for testing (= 6 with the first kind of cue + 6 with the second kind of cue).

Experimental protocol

For performing an entire experiment, the ants of the six colonies were trained for six days, then tested a first time, thereafter again trained during three days and finally tested a second time.

Ant training (Fig. 1A)

A pair of pyramidal devices was placed in each colony's tray, each device with a different cue drawn on the four sides. A piece of dead cockroach was placed in the inner square room of one of the two devices. The cue associated with food (= the "rewarded" cue) was considered as the correct cue, i.e. the one the ants should choose during the tests. In the course of each 6-day and 3-day training periods, the pair of pyramidal devices was turned and relocated 6 and 3 times, respectively, but never periodically, and the food was then renewed. This procedure prevented the ants from depositing a recruiting trail (CAMMAERTS, 1978) and from acquiring spatial and temporal learning (CAMMAERTS, 2004b). Moreover, due to the relocations, each cue was exposed to the ants in an identical way.

Ant testing (Fig. 1B)

All training devices were removed from the colonies and replaced with testing devices. During the tests, no food was provided. The ants present on each pyramidal device were counted fifteen times (during fifteen minutes) and the mean values of these counts were calculated for each of the two kinds of cues, first for each colony and second for all the colonies i.e. the total mean values (Table 1). The six mean values obtained for the six colonies for one kind of cue were compared to the corresponding six mean values obtained for the other kind of cue using the non parametric Wilcoxon signed rank test (SIEGEL & CASTELLAN, 1989) This statistical test was separately used for each experimental test, each providing the two series of values to be compared. As a checking statistical analysis, the total mean values were also compared using the non-parametric 2 x 2 table contingency χ^2 test (SIEGEL & CASTELLAN, 1989), two values of the table being the experimentally obtained ones, and two values being those expected if ants did not discriminate the two presented cues.

Each experiment used the foragers of six large colonies, included 48 cues, and lasted 6 + 1 + 3 + 1 = 11 days. Eventual bias and imperfection relative to the drawing of the cues and the presentation of the pyramidal devices to the ants probably cancel out each other.

Presented cues (Fig. 2)

To study the ants' discrimination of equally-sized filled shapes, a black square (c = 1.4 cm), a black circle (d = 1.58 cm) and a black triangle (b = 2.13 cm, h = 1.8 cm) were used.

TABLE 1

Mean numbers of ants responding, during two tests, to previously rewarded cues *versus* unrewarded. The cues (Fig. 2) were presented on the four faces of two pyramidal devices (Fig. 1) and the ants (of six colonies) that were present on these devices were counted fifteen times before establishing the mean values for each colony (column 2) and for all the colonies (column 2 on the right), for each kind of cue. The latter values are also schematically presented as black ('correct') and gray ('wrong') lines. Column 3: results of non-parametric Wilcoxon tests, with N, T and P according to the nomenclature of Siegel & Catellan, 1989.

rewarded and unrewarded cues (test 1 / test 2)	mean n^{ers} of ants in front of the **rewarded** and the unrewarded cue								statistics		
	for: each colony							all colonies	N	T	P
control experiment 1) two identical cues	**12.3**	**4.7**	**10.8**	**5.8**	**2.5**	**2.0**	▬	**6.37**	6	-15	
	12.1	4.2	11.2	9.7	2.8	2.3	▬	7.06			0.219
filled shapes **2) a filled black square** and circle	**17.1**	**7.8**	**8.4**	**10.9**	**2.9**	**4.7**	▬	**8.62**	6	21	
	11.8	4.1	2.8	4.3	1.8	2.4	▬	2.89			0.016
	17.1	**8.9**	**8.9**	**12.5**	**7.1**	**4.5**	▬	**9.82**	6	21	
	14.3	3.5	4.5	3.3	2.3	2.1	▬	5.01			0.016
3) a filled black triangle and circle	**29.2**	**15.1**	**26.9**	**18.7**	**8.9**	**3.5**	▬	**17.04**	6	21	
	11.0	3.5	15.1	3.3	0.5	0.4	▬	5.70			0.016
	15.5	**19.3**	**10.7**	**16.1**	**3.2**	**2.7**	▬	**11.27**	6	21	
	13.5	10.9	6.0	4.3	0.6	0.8	▬	6.01			0.016
4) a filled black triangle and square	**30.4**	**11.0**	**24.4**	**13.5**	**1.8**	**2.9**	▬	**14.00**	6	21	
	27.0	7.7	16.4	10.3	0.7	0.8	▬	10.47			0.016
	11.5	**12.5**	**10.2**	**8.4**	**7.0**	**5.6**	▬	**9.20**	6	21	
	6.1	4.7	4.8	1.1	1.7	1.5	▬	3.31			0.016
	28.9	**10.5**	**30.0**	**10.1**	**6.9**	**6.1**	▬	**15.42**	6	21	
	11.6	2.4	19.5	4.3	1.8	2.3	▬	6.98			0.016
hollow forms # perimeter **5) a hollow black rectangle** and ellipse *of same height and width*	**31.9**	**8.5**	**14.3**	**8.3**	**1.9**	**4.8**	▬	**9.95**	6	21	
	14.7	6.6	11.0	4.1	0.8	3.2	▬	7.73			0.016
	21.8	**4.7**	**8.9**	**9.3**	**0.1**	**1.9**	▬	**7.78**	6	12	
	17.4	6.6	10.3	5.4	1.1	1.1	▬	6.81			0.422
6) a hollow black lozenge and ellipse *of same height and width*	**23.3**	**12.9**	**14.1**	**8.4**	**0.0**	**3.1**	▬	**10.29**	5	-12	
	24.1	12.7	15.8	8.0	1.0	3.1	▬	10.79			0.156
	21.0	**23.1**	**15.1**	**6.1**	**1.9**	**4.5**	▬	**11.94**	6	-15	
	30.6	16.9	18.1	9.5	2.3	4.4	▬	13.63			0.219
7) a hollow black lozenge and rectangle *of same height and width*	**25.7**	**17.0**	**9.7**	**7.3**	**3.1**	**4.1**	▬	**11.16**	6	18	
	26.9	11.8	8.7	6.9	1.6	3.3	▬	9.86			0.078
	29.7	**19.5**	**22.4**	**10.0**	**3.9**	**11.5**	▬	**16.15**	6	21	
	28.9	18.3	7.9	9.9	1.9	2.5	▬	11.56			0.016
hollow forms ≈ perimeter **8)** before training, **a hollow black rectangle** and lozenge *of ≈ perimeter*	**10.6**	**28.8**	**12.2**	**5.6**	**0.9**	**6.8**	▬	**10.82**	6	18	
	11.0	28.0	8.8	5.4	0.8	6.0	▬	10.00			0.078
9) after training, **a hollow black rectangle** and lozenge *of same perimeter*	**5.5**	**18.0**	**11.7**	**0.9**	**1.3**	**0.7**	▬	**6.37**	5	9	
	5.7	15.3	8.6	1.7	2.0	0.7	▬	5.66			0.406
	7.5	**12.5**	**8.9**	**4.6**	**2.4**	**1.0**	▬	**6.16**	6	14	
	7.7	17.0	9.1	3.5	3.2	0.8	▬	6.90			0.281

To study the ants' discrimination of hollow shapes, three hollow shapes of the same height and width were used [a hollow rectangle (L = 3.2 cm, l = 1.6 cm), a hollow ellipse (D = 3.2 cm, d = 1.6 cm), a hollow lozenge (D = 3.2 cm, d = 1.6 cm)], in addition to two hollow shapes of the same perimeter [a hollow rectangle (L = 2.24 cm, l = 1.12 cm), a hollow lozenge (D = 3 cm, d = 1.5 cm)]. All hollow shapes were made of black lines 1 mm thick.

RESULTS

Control experiment

For checking our experimental method, two pyramidal devices provided with exactly the same cues [two filled black circles (d = 0.8 cm) horizontally set at 0.8 cm of distance from one another, in the center of each side of the device] were presented to the ants, a piece of dead cockroach being offered in one of the two devices. After training, during the subsequent control experiment, the ants visited similarly the two pyramidal devices. Statistical tests showed that ants were not differently numerous on the two devices (Table 1, line 1). The experimental method was thus unbiased.

Discrimination of filled shapes

After having been trained to a given filled shape in the presence of another different unrewarded filled shape, statistically more foragers came during the test experiments onto the device provided with the 'rewarded' cue (Table 1, lines 2, 3, 4). It can thus be concluded that workers of *M. rubra* could discriminate – e.g. a filled black square and a filled black circle even when these shapes had exactly the same area (Table 1, line 2; Fig. 1 B); - a filled black triangle and a filled black circle of equal area (Table 1, line 3); - a filled black triangle and a filled black square of equal area (Table 1, line 4; a supplementary test having been made previously to the two usual ones, after 4 training days).

Discrimination of hollow shapes of equal height and width but of different perimeter

After training to a hollow black rectangle (as the rewarded cue) and a hollow black ellipse (unrewarded), the number of ants at the rectangle in the test experiments was statistically slightly greater than those at the ellipse (Table 1, line 5). After training to a hollow black lozenge (rewarded cue) and a hollow black ellipse (unrewarded), the ants were found in statistically equal numbers at

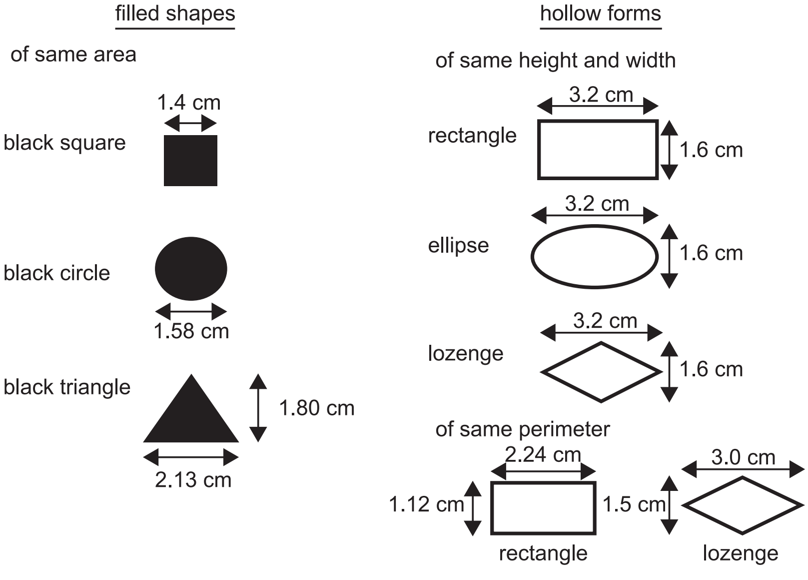

Fig. 2. – Cues presented to the ants: filled black shapes of equal area (square, circle, triangle), hollow black forms of equal height and width (rectangle, ellipse, lozenge) and hollow black forms of equal perimeter (rectangle, lozenge).

both shapes in the test experiments (Table 1, line 6). Workers of *Myrmica rubra* are thus poorly able to distinguish between hollow shapes, i.e. between hollow rectangle and ellipse, or between hollow lozenge and ellipse.

The three hollow shapes had the same height (1.6 cm) and width (3.2 cm) but somewhat different perimeters. The perimeter of the rectangle was 9.60 cm, that of the ellipse 7.54 cm, and that of the lozenge 7.16 cm. Ants were thus poorly able to discriminate between hollow shapes when the difference in the perimeter was small. In the next experiments, the ants were presented with hollow shapes having clear differences in perimeter, i.e. the lozenge and rectangle.

After training to a hollow lozenge (‘rewarded’; perimeter of 7.16 cm) and a hollow rectangle of same height and width but with a larger perimeter (unrewarded; perimeter of 9.60 cm), more ants were counted, in the test experiments, at the device provided with the hollow lozenge. This observation was statistically significant on the basis of the Wilcoxon test (ants of five colonies out of six for test 1 and ants of all colonies for test 2 successfully discriminating the shapes) though not significant on the basis of the χ^2 test (Table 1, line 7). Workers of *M. rubra* thus perceived a slight difference between the two presented hollow forms or required more time to better distinguish the difference. It can be hypothesized that although these workers have difficulties in discriminating the hollow shapes, they are able to achieve this by relying on the total length of the shape’s perimeter. This hypothesis was submitted to a further experiment.

Discrimination of hollow shapes of similar perimeter

Firstly, after a delay period of one month, the ants were tested prior to training in front of a hollow black rectangle and a hollow black lozenge of similar perimeter. The tested ants showed no preference for one or the other of these two forms (Table 1, line 8). They showed no natural preference for a given form and had lost their previous conditioning.

Secondly, after training to the following shapes (rewarded hollow black rectangle: L = 2.24 cm, l = 1.16 cm, perimeter = 6.80 cm; non-rewarded hollow black lozenge: D = 3 cm, d = 1.5 cm, perimeter = 4 x 1.677 cm = 6.71 cm) (note that in the previous tests, the lozenge shape was associated with the reward), workers came in equal numbers to the rectangle and the lozenge in the test experiments (Table 1, line 9). The Wilcoxon test and the χ^2 one are in agreement for such a verdict. The two presented hollow shapes were thus similarly perceived by the ants. Thus workers of *Myrmica rubra* rely more on the length of the perimeters of hollow forms than on their actual shapes to sufficiently distinguish these hollow forms.

DISCUSSION

Main findings and remarks

Using collective operant conditioning, it could be showed that workers of *M. rubra* distinguish filled shapes from one another but fail to do so for hollow shapes, then relying more on the total perimeter than on actual shape.

The difficulty in discriminating between hollow shapes exhibited by these workers may be due to the fact that several ant species may see with a slight convexity, therefore seeing rectangles and lozenges as similar to ellipses. These ants may utilize characteristics of cues other than the exact shape, such as dimension, area, perimeter, angularity, convexity, line-thickness, contrast, and brightness. This could account for the conflicting findings of certain authors regarding the visual perception ability of some insects, e.g. bees (Horridge, 1999, Hempel & Giurfa, 2003).

Comments on the methodology

In the course of the present work, the position of each cue – the ‘rewarded’ as well as the 'unrewarded' – was always on the same place of the experimental device, i.e. in the center of one side. Each experimental device was rotated and relocated several times during training while the ants' artificial nests were never moved or otherwise disturbed during the course of an experiment. The number of cues (48 each time), the number of tested ants (the foragers of six colonies), and number of times the ants were counted (15 x 6 *vs.* 15 x 6 each time) were held constant to ensure consistency in the results. Finally, as an added precaution, in experiment 9, the ants coming to the rectangle were rewarded, although previously in experiment 7 the lozenge was the 'rewarded' cue.

Integration of the present results with other findings on the same species and with those on two other species of *Myrmica*

The visual perception ability of workers of *M. rubra* is of higher quality than that of workers of *M. sabuleti*, which fails to discriminate filled shapes (CAMMAERTS, 2008), but of lower quality compared to individuals of *M. ruginodis*, which are able to discriminate between hollow shapes as well as other cues (CAMMAERTS, 2012a).

It may be presumed that workers of *M. rubra* can perceive the dimension, inclination, orientation and number of elements of a cue in a similar way to workers of *M. sabuleti* (CAMMAERTS 2004a, 2008). The fact that foragers of *M. rubra* poorly discriminate hollow shapes does not imperil their use of visual cues for travel. They simply use what they can see, even if imperfectly and also use any encountered odorous elements (CAMMAERTS, 2012b).

In summary, the perceptive abilities of the three species can be characterized as follows.

M. sabuleti has comparatively small eyes (with a mean of 109 ommatidia, RACHIDI et al., 2008), a subtended angle of vision equaling 5° 12' (CAMMAERTS, 2004a), a low-performance visual perception (CAMMAERTS, 2008), and the workers rely primarily on odors to travel (CAMMAERTS & RACHIDI, 2009). The species nests in open fields with small odorous plants (CAMMAERTS & CAMMAERTS, personal observations). *M. ruginodis* has comparatively large eyes (with a mean of 149 ommatidia, RACHIDI et al., 2008), a subtended angle of vision equaling 3° 10' (CAMMAERTS, 2011), a high-performance visual perception (CAMMAERTS, 2012a), and the workers essentially use visual cues located above them to travel (CAMMAERTS et al., 2012). This species nests near clearings under branches where the sky is partly visible (CAMMAERTS & CAMMAERTS, personal observations). *M. rubra* has eyes of intermediate size (with a mean of 129 ommatidia, RACHIDI et al., 2008), a subtended angle of vision equaling 3° 50' (CAMMAERTS, 2011) and a visual perception of middle quality (present work). This species nests in open grass lands (CAMMAERTS & CAMMAERTS, personal observations). The orientation system of foragers of *M. rubra* has been investigated: these ants use their vision and their olfaction as best as they can, according to the circumstances (CAMMAERTS, 2012b).

The three closely related *Myrmica* species have thus been examined at ecological, morphological, physiological and ethological points; the results of these different studies are in agreement with one another and in accordance with each species' usual habitat.

Comments about other works on the subject

The topic of insect vision has been broadly studied (WEHNER, 1981), and in particular for species of Odonata, Diptera and especially bees (Hymenoptera). Ants have not been commonly investigated in this respect. The species, which have been investigated so far, are ants having good vision and large eyes, *Formica* spp. (VOSS, 1967) and *Cataglyphis* spp. (PASTERGUE-RUIZ & BEUGNON, 1995). The present work examines the visual perception of an ant species having eyes of intermediate size.

While the visual perception system of ants has been neglected to an extent, their orientation system has received considerable attention. In general, ants memorize and use encountered visual cues according to a snapshot model (CARTWRIGHT & COLLETT, 1983; NARENDA et al., 2007) and a sketch map model (BEUGNON et al., 1996).

We argue that to efficiently investigate the orientation system of an ant species, one should know beforehand about their visual perception abilities. Do the ants concentrate on cues located in front of them or above them? Do they have color vision? Do they perceive their environment with perspective? Are they sensitive to dimension and orientation of a cue? We conducted such research on *M. sabuleti* before attempting to analyze the species' navigation system (CAMMAERTS, 2004a, 2007a, b, 2008; CAMMAERTS & RACHIDI, 2009). We also studied the visual perception and the travelling system of *M. ruginodis* (CAMMAERTS, 2012a; CAMMAERTS et al., 2012) and finally, we examined the traveling system of *M. rubra* (CAMMAERTS, 2012b) and, at last, this latter species' visual perception (present work which thus fills the last gap).

Visual perception is nearly always studied via visual conditioning or learning, which is in itself also a complex physiological ability (AVERGUÈS et al., 2011). The procedure of visual conditioning is time-consuming (CAMMAERTS et al., 2011) and difficult since it brings together two complex physiological abilities. However, it is the only practical method available. The results are generally surprising. Ants, as well as other insects, often appear to have a better sense of vision than previously expected - e.g. *M. ruginodis* (CAMMAERTS, 2012a). Ants can learn (i.e. can be conditioned to) a large number of cues (CAMMAERTS, 2004a, 2008). They have a rather long visual memory (e.g. *M. sabuleti,* CAMMAERTS et al., 2011) and sometimes a surprisingly long one (e.g. *M. ruginodis*, CAMMAERTS & NEMEGHAIRE, 2012). The visual memory of workers of *M. rubra* has also been assessed and is rather long lasting (CAMMAERTS, 2012c).

The ability of insects to discriminate shapes (such as squares, triangles, lozenges) has been disputed by some researchers (HORRIDGE, 2006 and references therein). It must be freely admitted that workers of *M. sabuleti* cannot discriminate filled or hollow shapes except when these shapes are presented with concavity (CAMMAERTS, 2008). However, foragers of *M. ruginodis* can perfectly discriminate filled (black or white) and hollow shapes (CAMMAERTS, 2012a) and foragers of *M. rubra* can distinguish filled black shapes from one another but not hollow shapes, especially when the perimeters of the shapes are very similar (present work). The ability to truly distinguish shapes from one another may depend on characteristics of the shapes, such as dimension (adapted to the animals' size), contrast (black, grey), filling (filled, hollow or transparent) and shape (triangle, square, hexagon, dodecagon or circle). Additional factors influencing insect visual performance are the animal's subtended angle of vision (3° 30' might be a limit for a good discrimination), the morphology and physiology of the eyes (i.e., the shape of the eye, the number of ommatidia, the performance of each ommatidium, the existence of several kinds of ommatidia), the performance of the neuronal structures that handle visual perception (i.e., the histological organization of the optic lobes, etc.). Since the three species we have studied (*M. sabuleti, M.ruginodis, M. rubra)* are closely related and since we conducted the experiments using cues of similar dimension, contrast and shape, we tentatively argue that the observed differences in their visual abilities are a consequence of differences in eye morphology, number of ommatidia (RACHIDI et al., 2008) and subtended angle of vision (CAMMAERTS, 2011).

A thorough study of an animal's visual perception should include ethological experiments, as well as a complementary physiological analysis at the neuronal level, as has been done for olfactory perception in bees (GIURFA, 2001; GUERRIERI et al., 2005; DEISIG et al., 2006).

In conclusion, our contribution to the ethological study of animal visual perception consists in establishing what three species of ants with middle-sized eyes can discriminate

(Cammaerts, 2004a, 2008, 2012a, present work), the proximate reasons for their ability or inability to discriminate (i.e., eye morphology: Rachidi et al., 2008; subtended angle of vision: Cammaerts, 2004a; Cammaerts, 2011), what their visual and olfactory learning characteristics are (Cammaerts et al., 2011; Cammaerts & Nemeghaire, 2012; Cammaerts, 2012c), how they negotiate their way (Cammaerts & Rachidi, 2009; Cammaerts et al., 2012; Cammaerts, 2012b) and why they nest in such usual natural biotopes (Cammaerts & Cammaerts, personal observation).

ACKNOWLEDGEMENTS

We are very grateful to T. Ellis who patiently copyedited our paper and to an anonymous referee whose comments allowed us improving our paper.

REFERENCES

Avergues-Weber A, Deisig N & Giurfa M (2011). Visual Cognition in Social Insects. Annual Review of Entomology, 56:423-443.

Beugnon G, Lachaud J-P & Chagne P (2005). Use of long-term stored vector information in the neotropical ant *Gigantiops destructor*. Journal of Insect Behavior, 18:415-432.

Beugnon G, Pastergue RI, Schatz B & Lachaud JP (1996). Cognitive approach of spatial and temporal information processing in insects. Behavioural Processes, 35:55-62.

Cammaerts M-C (1978). Recruitment to food in *Myrmica rubra*. Biology of Behaviour, 4:159-172.

Cammaerts M-C (2004a). Some characteristics of the visual perception of the ant *Myrmica sabuleti*. Physiological Entomology, 29:472-482.

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*). Myrmecological News, 10:21-26.

Cammaerts M-C (2007b). Colour vision in the ant *Myrmica sabuleti* Meinert, 1891 (*Hymenoptera : Formicidae*). Myrmecological 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 (Bratislava), 63:1169-1180.

Cammaerts M-C (2011). Visual vertical subtended angle of *Myrmica ruginodis* and *Myrmica rubra* (Hymenoptera, Formicidae). Bulletin de la Societe Royale Belge d'Entomologie, 147: 113-120.

Cammaerts M-C (2012a). The visual perception of the ant *Myrmica ruginodis* (Hymenoptera-Formicidae). Biologia, 67: 1165-1174.

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

Cammaerts M-C (2012c). Olfactory and visual operant conditioning in the ant *Myrmica rubra* (Hymenoptera, Formicidae). Bulletin de la Société Royale Belge d'Entomologie, 148:199-208.

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

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

Cammaerts M-C, Rachidi Z & Cammaerts D (2011). Collective operant conditioning and circadian rhythms in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Bulletin de la Société Royale Belge d'Entomologie, 147: 142-154.

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

Cammaerts M-C & Nemeghaire S (2012). Why do workers of *Myrmica ruginodis* (Hymenoptera, Formicidae) navigate by relying mainly on their vision? Bulletin de la Société Royale Belge d'Entomologie, 148: 42-52.

Cartwright BA & Collett TS (1983). Landmark learning in bees. Journal of Comparative Physiology, 151:521-542.

Collett TS, Dillman E, Giger A & Wehner R (1992). Visual landmarks and route following in desert ants. Journal of Comparative Physiology, 170:435-442.

Deisig N, Giurfa M, Lachnit H & Sandoz J-C (2006). Neural representation of olfactory mixtures in the honeybee antennal lobe. European Journal of neuroscience, 24:1161-1174.

Guerrieri F, Schubert M, Sandoz J-C & Giurfa M (2005). Perceptual and neural olfactory similarity in honeybees. PLOS biology, 3(4): e60,1-15.

Hempel de IN & Giurfa M (2003). Discrimination of closed coloured shapes by honeybees requires only contrast to the long wavelength receptor type. Animal Behaviour, 66:903–910. DOI 10.1006/anbe.2003.2269

Horridge GA (1999). Two-dimensional pattern discrimination by the honeybee. Physiological Entomology, 24:1-17.

Horridge GA (2006). Visual processing of pattern. In 'Invertebrate Vision' eds E Warrant & D.-E. Nilson, Cambridge University press.

Klotz JH & Reid B L (1992). The use of spatial cues for structural guideline orientation in *Tapinoma sessile* and *Camponotus pennsylvanicus* (Hymenoptera: Formicidae). Journal of Insect Behaviour, 5:71-82.

Menzel R & Giurfa M (2001). The cognitive architecture of a minibrain: the honeybee. Trends in Cognitive Sciences, 5:62-71.

Narenda A, Si A, Sulikowski D & Cheng K (2007). Learning, retention and coding of nest-associated visual cues by the Australian desert ant, *Melophorus bagoti*. Behavioural and Ecological Sociobiology, 61:1543-1553.

Nicholson DJ, Judd SP D, Cartwright BA & Collett TS (1999). Learning walks and landmark guidance in wood ants (*Formica rufa*). Journal of Experimental Biology, 202:1831-1838.

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

Pastergue-Ruiz I & Beugnon G (1995). La representation visuelle de l'espace chez un insecte: la fourmi *Cataglyphis cursor* (Hymenoptera, Formicidae). Thèse de doctorat, Université Paul Sabatier, Toulouse, pp 186. INIST – CNRS, cote INIST: T 105289.

Pratt SC, Brooks SE & Franks NR (2001). The use of edges in visual navigation by the ant *Leptothorax albipennis.* Ethology, 107:1125-1136.

Rachidi Z, Cammaerts M-C & Debeir O (2008). Morphometric study of the eye of three species of Myrmica (Formicidae). Belgian Journal of Entomology, 10:81-91.

Siegel S & Castellan NJ (1988). Nonparametric statistics for the behavioural sciences. McGraw-Hill Book Company, Singapore, 396 pp.

Voss C (1967). Über das Formensehen der roten Waldameise (*Formica rufa* – Gruppe). Zeitschrift für Vergleich Physiologische, 55:225-254.

Vowles D M (1965). Maze learning and visual discrimination in the wood ant (*Formica rufa*). British Journal of Psychology, 56:15-31.

Wehner R (1981). Spatial vision in Arthropods. Comparative Physiology and Evolution of Vision in Invertebrates (ed. H. Autrum): 288-616, Springer-Verlag, Germany.

Received: June 30th, 2011

Accepted: June 11th, 2013

Branch editor: Hendrickx Frederik