

Capability of Workers of the Ant *Myrmica sabuleti* to Categorize Numbers of Elements into Even and Odd

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Abstract

Categorizing numbers into even and odd is an ability held by humans that has recently been found to be also held by honeybees. We examined whether ants could also make such parity discrimination. Working on the species *Myrmica sabuleti*, we learned the ants of two colonies to associate 2 black circles with a reward and 5 of these circles with the absence of a reward, as well as learned the ants of two other colonies to associate 3 of these same cues with a reward and 4 of these cues with the absence of a reward. By collectively testing foragers of each colony in a separate tray in front of these cues, it was first verified during three days if they dully learned the 'correct' cue. Thereafter, while the ants continued to be trained, foragers of each colony were collectively subjected to nine successive choice tests, each day in front of a pair of cues different from the one used during the learning process. The cues used during these tests differed from those used to train the ants by the number and size of the dots, the cumulative surface of the dots, the perimeter of their area (surfaces and perimeters being maintained equal between the cues) and their layout. A 'correct' cue had the same parity (even or odd) as the cue learned during training. The tested ants each time consistently responded to the number that had the same parity as that of the number they learned during conditioning. This sensitivity to the number parity occurred from the number 1 until the number 7. Discrimination between 7 and 8 dots was beyond the ant capability.

Keywords: Numerosity, operant conditioning, parity categorization, visual discrimination

1. Introduction

Humans can categorize what they perceive and, among their numerical abilities, they categorize by parity, distinguishing between odd and even numbers. There is a gradation in the acquisition of this categorization ability by children, who at age 8 show no pronounced recognition of number parity, at age 9 base their understanding of number parity on a skip-counting process (at least for even numbers) and at age 10 extract the parity information from semantic memory. Later on, they will be learned to extract the parity information by relating even numbers to division by 2 (Berch, Foley, Hill & Ryan, 1999). In number-parity judgments, parity was shown to have no influence until age 12 (Miller & Gelman, 1983). The understanding that the equivalence of evenness and divisibility by 2 is a particular case of divisibility by a prime number requires an appropriate pedagogic approach (Zazkis, 1998). Moreover, using the odd-even rule to verify the plausibility of a sum or product of two numbers by the parity of their terms also has to be learned (Krueger & Hallford, 1984; Krueger, 1986) and working with odd numbers is slower than working with even numbers (Hines, 1990). Number magnitude is more precociously acquired (at the age of 9 years instead of 12) than number parity (Miller & Gelman, 1983). In adults, a representation of number magnitude is automatically accessed when judging the parity of Arabic numbers as magnitude bears a correspondence with left-right spatial coordinates (Dehaene, Bossini & Giraux, 1993). The semantic number line has thus to be addressed to make a correct parity decision (Reynvoet & Brysbaert, 1999).

Honeybees have been shown to perform some categorization of perceived visual elements (Bernard, Stach & Giurfa, 2006). Among their numerical abilities, it has recently been demonstrated that they also can categorize numbers of visual elements into even and odd. Trained in front of 1 to 10 elements of up to four different shapes they can be learned to discriminate even and odds among 2 to 8 of these elements, and to extrapolate this parity discrimination to 11 and 12 elements (Howard, Greentree, Avarguès-Weber, Garcia, Greentree & Dyer, 2022).

In the present work we examine if the ability to categorize numbers of elements into even and odd ones could be detained by an ant. Workers of *Myrmica sabuleti* Meinert, 1861, although pertaining to a non-specialized ant species, detain many

numerosity abilities. Among others, they have a mental number line, can acquire the notion of zero and numerical symbolisms, can add visual as well as olfactory cues, can expect the following element of an increasing or decreasing arithmetic or geometric sequence (summaries of works on the subject can be found in Cammaerts & Cammaerts, 2020a, 2022a with more references therein). In addition, they can associate a quantity with the time period of its occurrence (Cammaerts & Cammaerts, 2022c) and take account of the characteristics (shape color, size) of the elements when associating numbers of elements with their time period of occurrence (Cammaerts, 2023a). Since the workers of this species have many numerical skills, it was not unlikely that they could be able to distinguish even from odd numbers of elements.

We thus trained workers of the ant *M. sabuleti* either to a cue bearing an even number of dots (2) to be learned *versus* an odd number (5) or to an odd number (3) to be learned *versus* an even number (4). After having checked if they acquired this conditioning, we tested them in front of other pairs of odd *vs* even or of even *vs* odd numbers of dots (from 1 to 8) differing from the learned numbers by at least one number, and by their size, total area and layout, to see if they would react to the parity of the number they learned. A secondary interest was in the effect of the numerical relation between the numbers of the two cues of a pair presented during a choice test and in knowing the limits of their perception of a difference in parity between two numbers.

2. Methods

2.1 Ants' Collection and Maintaining

The experiments were performed on four colonies of *Myrmica sabuleti* Meinert, 1861 collected in September 2022 from an abandoned quarry located in the Aise valley (Ardenne, Belgium). Each colony contained a queen, brood, and about 600 workers. Each of these colonies was maintained in a glass tube half-filled with water, a cotton-plug separating the ants from the water. For each colony, the nest tube was placed in a tray (34 cm x 23 cm x 4 cm) the sides of which having been slightly covered with talc. This tray served as a foraging area: food was placed inside of it, and ants were trained in it. The food consisted in sugared water (15% saccharose) permanently provided in a small glass tube plugged with cotton, and in pieces of mealworms delivered three times per week on a glass-slide. These two kinds of food were located near each other (for training purpose) and at a distance of about 12 cm from the nest entrance. The temperature of the room permanently equaled 20 ± 2 °C and the relative humidity about 80%. The luminosity was 330 lux during the experiments and the care of the ants and varied between 110 and 330 lux during the other time periods The electromagnetism had an intensity of $2 \mu\text{Wm}^2$. All these conditions were suitable for the species.

2.2 Visual Cues

Given numbers of circular black dots were drawn inside 2 cm x 2 cm white squares using Corel Draw® software. Each white square was cut and tied with extra transparent sticky paper on the front face of a stand two to seven days before the start of the experiments to avoid the remaining of any odor. Each stand was made of Steinbach® (Malmedy, Belgium) strong white paper (250g/m^2), had a vertical part (2 cm x 2 cm) and was maintained vertically thanks to a duly folded horizontal part [2 x (1 cm x 0.5 cm)].

The diameter of the black circles presented during the three first experimental days was 3.5 mm. From the fourth day onwards, the tested cues bear dots differing from those used during the learning process by their size, cumulative surface (always that of 5 circles of 3.5 mm in diameter, i.e., 48.1 mm^2), perimeter of the area in which they are contained (i.e., inside a virtual circle of 15 mm in diameter) and layout (Figure 1). To avoid as much as possible confusion variables, the cumulative surface of the dots and the area perimeter were then the same for all cues.

2.3 Experimental Design

Two series of experiments were performed, one on colonies A and B, and another one on colonies C and D. The ants in each of these two series were trained to distinguish two numbers of dots differing in parity, the number to be learned by colonies A and B being even and the number to be learned by colonies C and D being odd. This learning, done at a collective level and not at an individual level, was conducted in the foraging area and continued all along the whole experiment.

To train the ants, two identical cues of the kind they were expected to learn and memorize were deposited near places acting as rewards, one located at the nest entrance, the other near the food, and on the right of these places for one colony (e.g., colony A) and on the left for the other colony pertaining to the same series of experiments (e. g., colony B). At the same time, two identical cues that the ants were expected to not learn and memorize were deposited far from the rewarded places, on the left and on the right side of the foraging area. The 'correct' cues expected to be learned and the 'wrong' cues were simply left at their due places so that the foragers could associate the correct kind of cue with their rewards, i.e., the nest entrance and the food site (Figure 2). Several times per day, it was checked if ants duly foraged and they did.

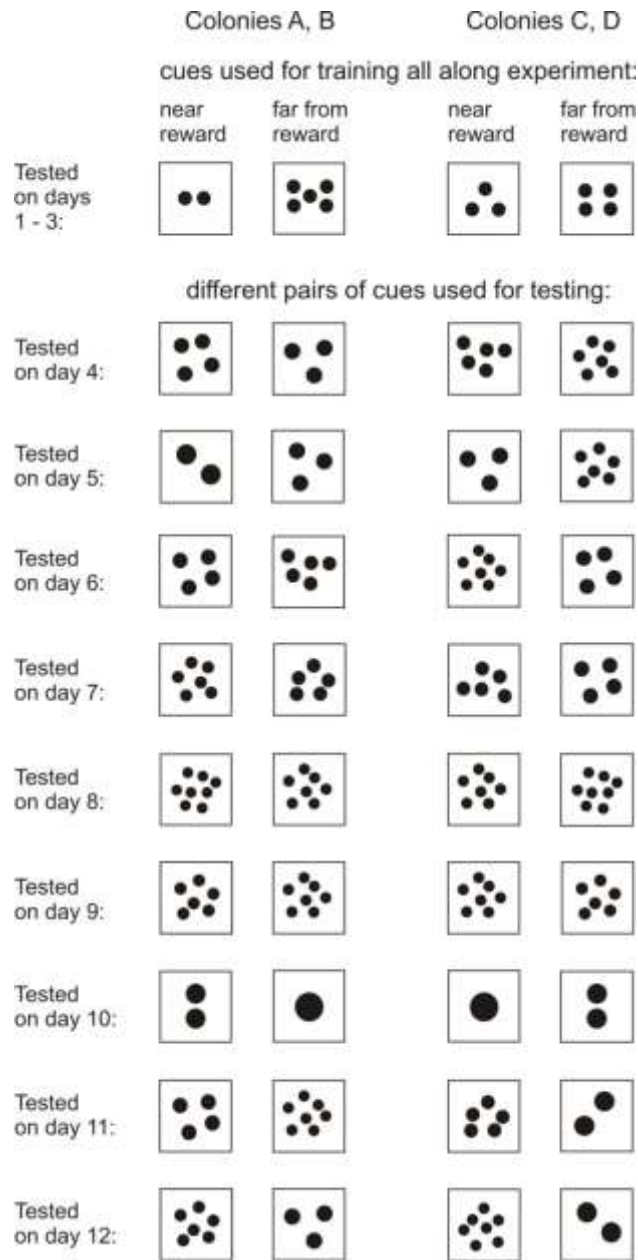


Figure 1. Pairs of cues presented, according to the daily experimental schedule, to 25 ants from each colony, while these colonies continued the same training as during the first three days

The cue corresponding to the correct response is here shown on the left side of each presented pair, although this parity may be presented to the ants on the left or the right-side during testing.

Testing was done in a separate tray (21 cm x 15 cm x 7 cm) in which a ‘correct’ and a ‘wrong’ cue were deposited, the correct one being set on the left for one colony of an experimental series and on the right for the other colony. Like learning, testing was done at a collective, not at an individual level, each colony having its own testing tray. For making a test on a colony, 25 ants of that colony were picked up, as randomly as possible, from their foraging area and transferred into the tray devoted to testing (Figure 2), The ants seen within 2 cm of each of the two cues were counted 20 times over 10 minutes. The sum of these counts made for each cue of a tested pair was established what allowed calculating the proportion of ants having given the correct response (Table 1).

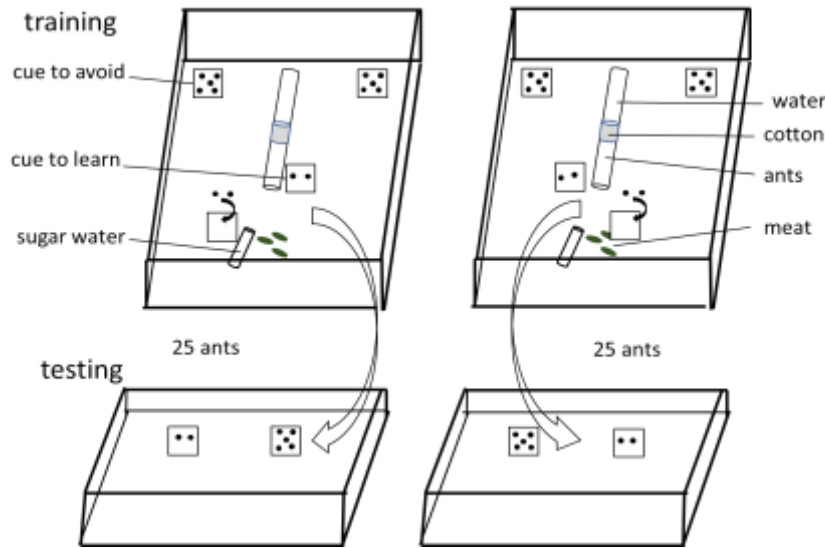


Figure 2. Experimental design to establish whether *M. sabuleti* ant workers can discriminate even and odd numbers. The ants were trained in their forging area, the rewards being the nest entrance and the food. They were tested in a separate tray, first in front of the cues presented during training to verify their learning (here shown for colonies A and B), thereafter in front of pairs of different even and odd numbers of dots (see Figure 1).

Table 1. Numbers of correct and wrong responses given by ants in the course of experiments made to know if they can discriminate even and odd numbers

Day	Time	Numbers of correct vs wrong responses in front of a cue having the same parity* or not as the one learned during training	
		Colony A and colony B	Colony C and colony D
Preliminary testing sessions examining the effectiveness of learning			
		in front of 2* vs 5 circles	in front of 3* vs 4 circles
1	12 h	26 (87%) vs 4 and 32 (65%) vs 17	17 (71%) vs 7 and 51 (94%) vs 3
	24 h	33 (83%) vs 7 and 39 (85%) vs 7	36 (97%) vs 1 and 42 (82%) vs 9
2	36 h	27 (82%) vs 6 and 33 (94%) vs 2	29 (97%) vs 1 and 49 (91%) vs 5
	48 h	29 (94%) vs 2 and 21 (88%) vs 3	52 (91%) vs 5 and 34 (94%) vs 2
3	60 h	31 (78%) vs 9 and 42 (88%) vs 6	40 (98%) vs 1 and 28 (80%) vs 7
	72 h	38 (95%) vs 2 and 27 (90%) vs 3	30 (97%) vs 1 and 57 (97%) vs 2
Testing in front of pairs of cues differing from those seen during learning			
		In front of 4* vs 3 circles	In front of 5* vs 6 circles
4	8 h	27 (82%) vs 6 and 28 (78%) vs 8	30 (88%) vs 4 and 45 (78%) vs 13
	16 h	21 (84%) vs 4 and 35 (75%) vs 12	22 (92%) vs 2 and 49 (89%) vs 6
	24 h	19 (76%) vs 6 and 23 (92%) vs 2	20 (91%) vs 2 and 58 (75%) vs 19
		In front of 2* vs 3 circles	In front of 3* vs 6 circles
5	8 h	32 (89%) vs 4 and 49 (100%) vs 0	33 (100%) vs 0 and 51 (94%) vs 3
	16 h	37 (93%) vs 3 and 38 (88%) vs 5	29 (100%) vs 0 and 46 (87%) vs 7
	24 h	27 (94%) vs 1 and 38 (91%) vs 4	28 (88%) vs 4 and 24 (73%) vs 9
		In front of 4* vs 5 circles	In front of 7* vs 4 circles
6	8 h	52 (87%) vs 8 and 51 (100%) vs 0	55 (97%) vs 2 and 32 (84%) vs 6
	16 h	28 (90%) vs 3 and 21 (84%) vs 4	42 (91%) vs 4 and 23 (79%) vs 6
	24 h	31 (91%) vs 3 and 66 (97%) vs 2	53 (100%) vs 0 and 32 (80%) vs 8

		In front of 6* vs 5 circles	In front of 5* vs 4 circles
7	8 h	28 (88%) vs 4 and 31 (78%) vs 9	37 (86%) vs 6 and 67 (91%) vs 7
	16 h	35 (85%) vs 6 and 27 (69%) vs 12	32 (76%) vs 10 and 50 (91%) vs 5
	24 h	35 (97%) vs 1 and 31 (82%) vs 7	42 (88%) vs 6 and 69 (97%) vs 2
		In front of 8* vs 7 circles	In front of 7* vs 8 circles
8	8 h	20 (46.5%) vs 23 and 18 (41.9%) vs 25	22 (59.5%) vs 15 and 20 (58.8%) vs 14
	16 h	17 (45.9%) vs 20 and 18 (43.9%) vs 23	17 (58.6%) vs 12 and 25 (59.5%) vs 17
	24 h	24 (44.4%) vs 30 and 21 (46.7%) vs 24	25 (55.6%) vs 20 and 15 (57.7%) vs 11
		In front of 6* vs 7 circles	In front of 7* vs 6 circles
9	8 h	35 (76%) vs 11 and 35 (81%) vs 8	35 (95%) vs 2 and 42 (82%) vs 9
	16 h	30 (88%) vs 4 and 26 (87%) vs 4	28 (76%) vs 9 and 23 (79%) vs 6
	24 h	27(68%) vs 13 and 54 (86%) vs 9	65 (87%) vs 10 and 32 (76%) vs 10
		In front of 2* vs 1 circle	In front of 1* vs 2 circles
10	8 h	48 (86%) vs 8 and 71 (92%) vs 6	27 (93%) vs 2 and 52 (91%) vs 5
	16 h	31 (89%) vs 4 and 33 (89%) vs 4	33 (92%) vs 3 and 29 (91%) vs 3
	24 h	61 (97%) vs 2 and 37 (80%) vs 9	41 (93%) vs 3 and 36 (95%) vs 2
		In front of 4* vs 7 circles	In front of 5* vs 2 circles
11	8 h	26 (100%) vs 0 and 51 (82%) vs 11	28 (82%) vs 6 and 47 (92%) vs 4
	16 h	42 (88%) vs 6 and 61 (88%) vs 8	41 (89%) vs 5 and 40 (95%) vs 2
	24 h	33(89%) vs 4 and 60 (88%) vs 8	20 (71%) vs 8 and 40 (80%) vs 10
		In front of 6* vs 3 circles	In front of 7* vs 2 circles
12	8 h	33 (87%) vs 5 and 48 (84%) vs 9	42 (88%) vs 6 and 73 (96%) vs 3
	16 h	25 (92%) vs 2 and 41 (85%) vs 7	58 (89%) vs 7 and 49 (92%) vs 4
	24 h	29 (83%) vs 6 and 22 (79%) vs 6	36 (77%) vs 11 and 33 (89%) vs 4

Colonies A and B were trained in their foraging area to 2 vs 5 black circles, colonies C and D to 3 vs 4 such dots. The effect of this training was collectively tested on 25 ants during 10 minutes in separate trays during the days 1 to 3. Thereafter, while being still trained to these cues, the ants were tested in the same way in front of pairs of cues differing by the number, size and layout of the dots, the total surface and perimeter of the sighted pattern remaining the same for all the cues. The ants reacted to the number of dots having the 'correct' parity, i.e., the one they learned. An * indicates the cue bearing the learned parity. During testing and depending on the colony, this parity was presented on the left or the right of the 'wrong' cue. The percentages (%) express the proportion of the 'correct' choice to the 'wrong' choice.

During the first three days of the experiment, the ants in each colony were trained to learn an even or an odd number of black circles placed near the reward (the nest entrance and food) against an odd or an even number of black circles (the wrong cue) placed far from any reward. During this period, they were regularly tested against the same pairs of cues to ensure that they correctly associated the right cue with the reward. This training continued with the same cues throughout the whole experiment, which ended on day 12.

After these first three days of training, and while remaining under the same training process, the ants were tested three times a day, each day in front of a new pair of cues of opposite parity and in which the number of circles of at least one of the cues differed from those of the pair used for training and of the pair previously tested. The 'correct' cue was the one with the same parity of values (even or odd) as the cue learned by the ants during training.

The pairs to be successively tested were not chosen at random because, starting with the learned number, there were very few possibilities of testing a different number of circles with the same parity as that of the learned number without testing the same number twice in a row and before reaching the limit of the ants' ability to discriminate between two numbers (former studies on visual discrimination in *M. sabuleti* estimated that this limit between lines was 4 vs 5 and that the one between dots approached 6 vs 7: Cammaerts, 2006, 2008; R. Cammaerts & M.-C. Cammaerts, 2020).

2.4 Experimental Planning

This is illustrated in Figure 1 and detailed in Table 1.

During three days, the ants of colonies A and B were trained to 2 black circles (the cue to learn and to memorize) set near a reward (the nest entrance and the food site) *versus* 5 such circles (the ‘wrong’ cue) set far from any reward. In order to check if the cues to which they were trained were dully learned, they were tested twice each day in front of these two kinds of cues, in a separate tray. Thereafter, the ants were tested each 8 hours. On the fourth day they were tested in front of 4 and 3 black circles presenting the same total surface as in the previous pair of numbers, but with a different layout. On the fifth day they were tested in the same way in front of 2 and 3 circles, on the sixth day, in front of 4 and 5 black circles, on the seventh day in front of 6 and 5 circles, on the eighth day in front of 8 and 7 circles, on the ninth day in front of 6 and 7 circles, on the tenth day in front of 2 and 1 circles, on the eleventh day in front of 4 and 7 circles and on the twelfth day in front of 6 and 3 circles.

In the same way, the ants of colonies C and D were trained during three days to 3 black circles (the cue to learn and memorize) set near a reward (the nest entrance and the food site) *versus* 4 such circles (the ‘wrong’ cue) set far from any reward. They were tested twice each day in front of these two kinds of cues. While being still trained to 3 *versus* 4 black dots till to the end of the experiment, they were tested during the successive following days in front of 5 *vs* 6 dots, of 3 *vs* 6 dots, of 7 *vs* 4 dots, of 5 *vs* 4 dots, of 7 *vs* 8 dots, of 7 *vs* 6 dots, of 1 *vs* 2 dots, of 5 *vs* 2 dots and finally in front of 7 *vs* 2 dots. To ensure the reliability of the results, these daily tests were replicated at intervals of 8 hours between them.

2.5 Statistical Analysis

Using Statistica[®] v10 software, a parametric ANOVA was performed to compare the proportions of correct responses observed during the 24 preliminary checking tests conducted during the training period of the first 3 days with those obtained in the definite tests that were conducted thereafter. The use of a parametric test is justified in the Results section by the conditions of the sample parameters.

Taking into account the pseudoreplications made in the presence of the same pairs of cues with ants of the same colony, a GLMM analysis was performed on a set of 78 testing sessions, i.e., those whose stands did not carry the number of dots the ants had learned or a pair of numbers beyond their discrimination ability. Therefore, the lme4 and MASS packages of v4.1.2 of the R statistical analysis environment (R Core Team, 2021) were used. The dependent variable was the weighted proportion of ants that choose either the even or odd number in response to the parity of the learned number. As for the independent variables, the fixed effects were the parity (even or odd) of the learned cue (‘learned parity’) and one of the numerical relations between the dots of each cue of a pair (‘relation’, i.e., one of four kinds of relations between the two presented cues, either the number of dots on each of the two presented cues, or the highest number of dots on one of the two cues, their ratio, mean and relative difference (the difference in number of dots between the two cues divided by their mean)). The random effect concerned the repetition of measurements made for each test (e.g., each of the three testing sessions performed in front of the pair 4 *vs* 3 dots bear the same test identifier (ID) ‘1’; each of the three sessions performed in front of 4 *vs* 5 dots bear the same ID ‘2’, etc.). A glmer function with a binomial distribution as error structure presented overdispersion values > 5, which forced to fall back on a model using a quasi-binomial error structure: `glmmPQL(cbind(score_even, score_odd) ~ learned_parity + relation, random=~1|ID, family=quasibinomial, data)`.

3. Results

A preliminary testing was performed during the days 1 to 3 to ensure that the ants in each colony have duly learned the cue with the parity they were expected to choose when the tests were conducted on the following days with cues bearing different number of dots. A glance to Table 1 shows that it was already the case after 12 hours of training and that a high score of correct responses was kept as long as training continued, i.e., until the end of the whole experiment. This table also shows that during the definite tests in the course of which the ants were exposed to pairs of cues different from those they were seeing in their foraging area, they chose the numbers having the same parity as that of the number they learned during training. The only exception holds for the pair of 7 *vs* 8 dots, which comparison of number of dots was found to have exceeded the capacity of the ants’ number or parity discrimination. The results concerning this outlying pair tested on day 8 were thus discarded from the analysis of the other cues and are detailed separately.

After consideration, the tests performed on day 5 as well as those made with colonies A and B on day 10 were also excluded from the statistical analysis because one of the presented cues bear the same number of dots (2 or 3) as the learned one. This is despite the fact that the relative position of these dots on the cue differed from that of the learned cue, and that it has been shown that *M. sabuleti* ants are sensitive to the dimension and orientation of a cue (Cammaerts, 2008) and also that a change in the layout of the presented elements affects their counting ability (Cammaerts & Cammaerts, 2020b). While not statistically used, the results relative to pairs with a number of dots similar to the learned number (2 or 3) were nevertheless kept for the record since their correct choice could possibly result from something else than a counting process.

A parametric ANOVA shows no significant difference between the four colonies which were, therefore, not analyzed as a distinct block in the GLMM analysis. There was also no difference between the percentages of the correct responses

observed during the 24 preliminary checking tests conducted during the first 3 days and those of the 78 definite tests conducted during the following 4-7 and 9-12 days ($P = 0.52$ for a total of 102 testing sessions, which excludes, for the reasons explained above, the tests made during days 5, 8 and, for colonies A and B, during day 10). By using the daily means of these testing sessions, thus without their pseudoreplications and with less analyzed variability, the same result held of course for a total of 38 percentages ($P = 0.58$). Thus, during testing, the ants choose, with the same performance as during the preliminary checking tests, the number of dots corresponding to the parity of the number learned during training. When only the definitive tests were taken into account the same kind of ANOVA analysis gave $P = 0.52$ for the totality of the 78 testing sessions and $P = 0.73$ for the 26 testing sessions without pseudoreplications. Note that the use of a parametric ANOVA is here validated by the homogeneity of the variances (Bartlett's test: $P = 0.93$ with the pseudoreplications and 0.28 without them) and the normality of the distribution of residuals (Henry's line). A Gaussian distribution is indeed expected when the responses are issued from a successful learning. Here, the 78 correct responses (percentages) containing pseudoreplications were characterized by a mean of 86.26, a median of 87.50 and a variance amounting to 54.81, and the 26 daily means of 'correct' percentages without pseudoreplications were characterized by a mean of 86.30, a median of 86.17 and a variance amounting to 33.56 (see also Cammaerts & Cammaerts, 2022d for a

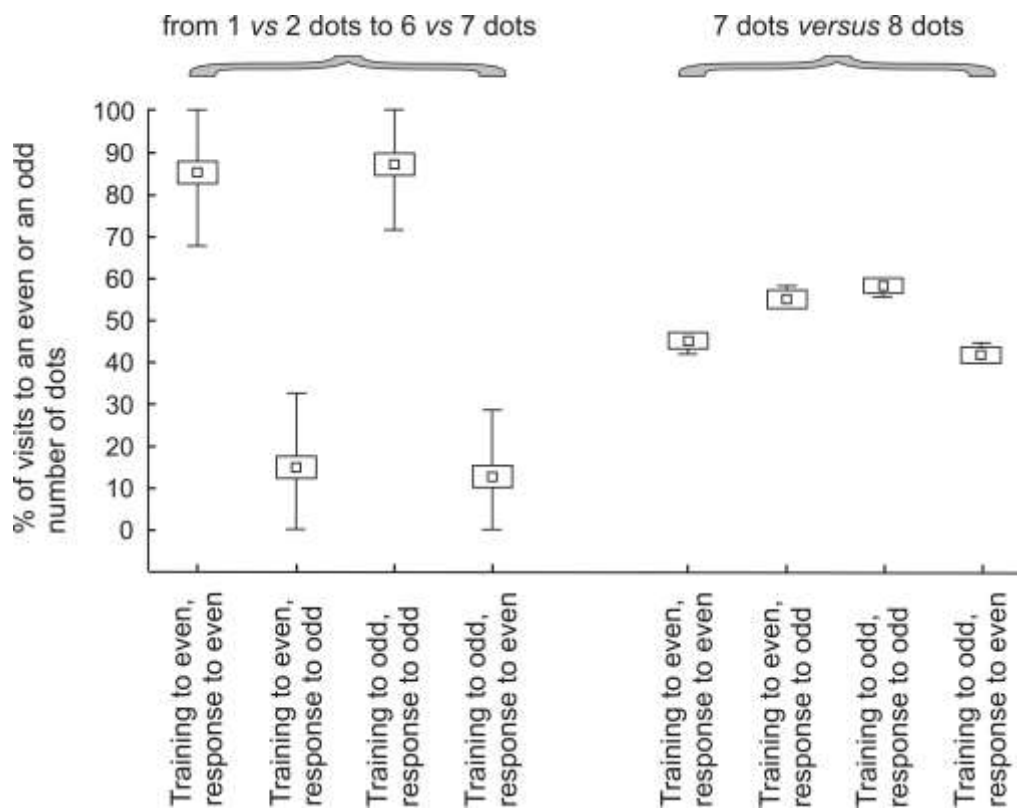


Figure 3. Graphical summary of the results of test sessions detailed in Figure 1 and Table 1, performed to determine if ants recognize the parity of numbers different from the learned one

The graphs represent, in relation to a learned even (2) or odd (3) number, the proportions of the pooled responses of 25 workers and 4 colonies in front of two cues that differed by the number of dots and their parity. Only the 78 testing sessions that presented cues bearing a number of dots different from the ones learned are taken into account (thus not the tests that were performed during day 5 and, for colonies A and B, during day 10) as well as, shown separately, the 12 testing sessions made at day 8 with cues bearing 7 and 8 dots. Mean, 95% confidence interval and extremes of the ants' responses.

further explanation on the relation between results of a learning process and Gaussian distribution).

In each of the 78 retained definite testing sessions, the total number of ants that were sighted near the cue pertaining to the learned parity (the 'correct' parity) was much greater than the number of ants sighted near the numbers having the parity not to be learned (the 'wrong' parity). The proportions of 'correct' choices amounted from 67.5 to 100% (Table 1), on average 86.26% with little variation in the responses (95% confidence limits: 84.59 and 87.93%) and those of 'wrong'

choices thus from 0 to 32.5% (Figure 3). Choosing the correct parity occurred thus in all of the 78 retained testing trials, whether the number of dots on the ‘correct’ cue was larger or smaller than that of the ‘wrong’ cue. After having noticed that fact, it may seem superfluous to conduct a Wilcoxon test on the percentages of ‘correct’ and ‘wrong’ responses to each pair ($P < 10E-6$ for $n = 78$ and $P = 8E-5$ for $n = 26$).

As for the pair 7 vs 8 dots, the percentage of ants in front of these cues showed that the ants could not readily discriminate between them, whenever the learned parity was even or odd (a binomial test on the mean number of responses gives $P = 0.15$ to 0.27 according to the colony). However, they were more numerous (meanly 58.22%, $n = 213$) in choosing the odd parity after having been trained to react to an odd number (i.e., 3) than in choosing the even parity (44.87%, $n = 263$) after having learned to react to an even number (i.e., 2), although this difference was not significant (Chi-square test on the mean daily numbers of ants near a cue: $\chi^2 = 2.70$, $df = 1$, $P = 0.10$). The reason of this difference may be that during the test under ‘even’ as the learned parity, the even cue presented 8 dots and this appeared to be beyond the ants’ visual acuity, while during the test with ‘odd’ as the learned parity, the odd cue presented 7 dots, what appeared to be at the limit but still in the range of the ants’ visual acuity.

Figure 3 summarizes the mean and variability of the responses of the ants to the ‘correct’ and ‘wrong’ presented cues after having been trained to learn a number with an even (2) or an odd (3) parity. It shows that for pairs of elements not exceeding 6 vs 7 dots, the responses were clearly distinct, with a positive reaction towards the parity that was learned and a negative reaction towards the parity that was not learned. On the contrary, for the pairs bearing 7 vs 8 dots, the correct and wrong responses tended to be equal, with nevertheless a higher score for the odd parity when the learned cue was odd and equaled 7 (for the possible reason given here above). This clearly showed the limit of the numbers’ parity discrimination of the workers of the ant *M. sabuleti*: comparing 7 against 8 elements is beyond their capability.

In a GLMM analysis the identity of the colonies (A, B, C or D) is redundant with the learned parity and thus of no use. The GLMM analysis on the 78 retained testing sessions with ‘treatment’ (i.e., learned parity) as the only fixed effect showed of course that this predictor was highly significant, the mean level of the proportions of ants sighted near the even number of dots of a pair having been drastically lower when the learned parity was odd ($P = 0$ with the odds of responding to an even number being only 0.023 times the odds of responding to an odd number). The complementary relation is of course true: when the learned cue was even, the proportions of ants near an odd number were negligible. This effect was also present when any relation between the presented cues of a pair was introduced as a supplementary predictor in the model. The interest of a GLMM analysis remains then in the effect of the relations between the numbers of elements of the two cues presented to the ants.

Performing different GLMM analysis, each including as predictors ‘treatment’ and one of the several numerical relations between the cues of the presented pairs, showed no significant effect due to any of these relations between cues. However, when the numerical relations between the cues of the presented pairs were calculated with the numbers of dots ordered as the learned parity (i.e. that to which the ants were expected to respond), the predictors ‘cue bearing a number with the learned parity vs cue bearing a number with the non-learned parity’, ‘ratio between the two numbers of dots of each pair of cues’ and ‘difference between the two numbers of dots of each pair of cues divided by their mean’ correlate with ‘treatment’ so that ‘treatment’ as a predictor could be (and had to be) removed and replaced by one of these predictors. The results from ‘ratio’ and ‘number difference between the cues on their mean’ were the ones that gave an insight on which pairs of cues had a significant effect on the ants’ response. These results are detailed in the Appendix.

Thus, performing a GLMM with ‘ratio’ as the only predictor, it appeared that when having been trained to an even (2) number of dots, and tested in front of the pairs 4 vs 3, 4 vs 5, 4 vs 7, 6 vs 3, 6 vs 5 and 6 vs 7, the mean level of the ants’ response to an even number was significantly ($P < 1E-4$) positively influenced by the sight of an even number. By raising the coefficient estimates of the outputs of these predictors (these logit values varied from 3.89 to 5.02) as a power of e, the odds of responding to an even number when having learned another even number were 49 to 151 times the odds of responding to an odd number.

Moreover, using ‘difference on mean’ as the only predictor showed that when having been trained to an odd (3) number of dots, and tested in presence of the pairs 1 vs 2, 5 vs 2, 5 vs 4, 5 vs 6, 7 vs 2, 7 vs 4 and 7 vs 6, the mean level of the ants’ response to an even number was significantly ($P < 1E-4$) negatively influenced by the sight of an odd number. Exponentiating the coefficient estimates of the outputs of these predictors (whose logit values varied from -3.01 to -3.93) shows that the odds of responding to an even number when having learned an odd number were only 0.02 to 0.05 times the odds of responding to an odd number.

Additionally, the Figure 3 tells us that when having been trained to an odd number (3), the mean difference between correct and wrong responses was higher than when having been trained to an even (2) number. Indeed, trained to odd, the mean score to odd was 87.22% while that to even was 12.78% and trained to even, the mean score to even was 85.15%

while that to odd was 14.85%. In other words, the difference (the distance) between correct and wrong mean score was higher (74.44%) when trained to an odd number than when trained to an even number (70.30%).

4. Conclusion and Discussion

Parity perception is an ability detained, not only by humans (maybe natively, then improved through mathematical education), but also by honeybees. We here examined if ants pertaining to an unspecialized species (*Myrmica sabuleti*) could also detain such ability.

By experimenting on ants collectively placed in front of a choice between two different numbers of dots, we found that they consistently responded to the number corresponding to the parity, even or odd, of the number they learned during operant conditioning, if we except the choices made when the numbers exceeded the discrimination capability of the species (i.e., 7 vs 8 dots). Indeed, the ant's responses to 13 different choice tests, each test in front of a pair of number of dots differing by their number, size and layout of the dots from the cue they learned during training, show that these insects appeared to be sensitive to the parity of numbers of elements. Their response to the parity of the sighted cues was not influenced by the quantity of dots (from 1 to 7), their size, cumulated area or layout, by the smallest or largest number of the two presented quantities, or their mean or difference in number (in most cases, it was 1) whatever was the parity (even or odd) of the learned number.

Compared to the very obvious effect of the learned parity on the choice between the two parities presented, that of a simple numerical relation between the two presented cues of a pair appeared not to be a determinant factor in the choice of the ants. However, when the numerical relations between the cues of the pairs presented to the ants were calculated with the numbers of dots ordered in function of the learned parity, the ratio between the two presented numbers of elements or their difference divided by their mean could replace treatment as an explanatory variable. A GLMM analysis showed that when the ants were trained to learn a given even number of dots, the odds of their responding to any even number were ca. 50 to 150 times higher than those of their responding to an odd number, and that when trained to an odd number, the odds of their responding to an even number were only 0.02 to 0.05 times the odds of responding to an odd number.

Although the workers of the ant *M. sabuleti* preferred numbers having the same parity than those to which they were conditioned, it do not necessarily means that they 'know' what is an even or an odd quantity. It can be as well that they simply rely on some parity-shared particularity of the visual aspect of the image of the presented quantities, a discriminating feature about which we did not intend to investigate in the present work.

Conceptual categorization of visual representations is a faculty present in humans but also in animals such as in pigeons who can be learned to recognize the presence or absence of humans on a photograph (Herrnstein & Loveland, 1964), and can even better discriminate the complex texture of a human face than its shape (Troje, Huber, Loidoldt, Aust & Fieder, 1999). These birds are able to recognize in very different artificial shapes the presence of a common topological feature such as a hole, although it was variable in its form, and to discriminate these shapes by this topological feature (Watanabe, Fujimoto, Hirai & Ushitani, 2019). Monkeys are able to categorize computer-generated synthetic but almost similar representations of cats or dogs (Freedman, Riesenhuber, Poggio & Miller, 2001). Baboons can categorize real objects as food or non-food and relate these items with their pictures (Bovet & Vauclair, 1998).

Symmetry perception is known in vertebrates but also in honeybees which can be learned to acquire a generalized preference for symmetrical or asymmetrical visual patterns (Giurfa, Eichmann & Menzel, 1996). Furthermore, honeybees can also learn to categorize the edge orientation of a pattern or its concentric organization as well as the layout of a visual pattern (Bernard et al., 2006). Howard et al. (2022) measured the correlation between the left and right as well as between the top and bottom halves of the cues bearing the elements among which honeybees were led to choose between an even or odd number, what showed that most of their displayed images were asymmetrical. We did not attempt to measure the degree of symmetry of the cues sighted by the *M. sabuleti* workers as they all appeared to display asymmetrical images (as shown in Figure 1) and moreover that some of them e.g., the obviously asymmetric cue with 4 dots tested on days 6 and 11 on colony A and on day 7 on colony D would be considered as symmetric when divided in four squares.

Anyway, the workers of *M. sabuleti* were not learned to distinguish a 'correct' and a 'wrong' parity, from one cue presentation to the next, by the addition or subtraction of one element or by their difference in magnitude (the difference was 1 to 3 less or more elements) or by distinguishing the parity by a multiple (suggested to be the mechanism of parity extraction in humans by Clark & Campbell, 1991 and disproved by Dehaene et al. (1993).

Former studies showed that the visual discrimination capabilities of *M. sabuleti* between lines 2 mm thick and distant 4 mm apart was limited to 4 vs 5, their choice between 5 vs 6 lines exceeding it (Cammaerts, 2006, 2008). More recently, we showed that *M. sabuleti* workers can distinguish up to 6 and 7 points of 4 mm in diameter (R. Cammaerts & M.-C. Cammaerts, 2020). Here we show that they obviously distinguished inside a virtual circle of 15 mm in diameter the parity of numbers up to 6 vs 7 (dots of 3.20 mm vs 2.96 mm in diameter), but not when they had to choose the right parity

between 7 and 8 presented dots (of 2.96 vs 2.77 mm in diameter), which appeared to be the limit of their discrimination faculty. This limit could correspond to the limited visual perception of the species. Indeed, this ant has small eyes, containing mainly only ca 105 ommatidia, with a subtended angle of vision of $5^{\circ}12'$ (Cammaerts, 2004; Rachidi, Cammaerts & Debeir, 2008). the species relying essentially on odors for navigating. It should be examined if another *Myrmica* species, *M. ruginodis*, which has larger eyes and a smaller subtended angle of vision ($3^{\circ}10'$) and thus a better visual perception (Rachidi et al., 2008) and relies on visual cues for navigating (Cammaerts & Cammaerts, 2014), could discriminate even and odd numbers beyond 7 elements. In comparison, honeybees can discriminate between up to 11 vs 12 elements (Howard et al., 2022), what is a bit more than *M. sabuleti*'s capacity, and can be explained by their high number of ommatidia (ca 5400 per eye: Jander & Jander, 2002) which gives them a higher visual acuity (up to 1.9° angular sensitivity (Rigosi, Wiederman, & O'Carroll, 2017).

The tests made on day 5 (2 vs 3 when under even training and 3 vs 6 when under odd training) and on day 10 (under even training), were done because although one of the cues of the presented pair had the same number of dots as the cue learned during training, their layout and size differed, which could make them look quite different from those of the learned cue. However, as *M. sabuleti* ants can distinguish 1 from 4 elements (Cammaerts & Cammaerts, 2020d), we cannot exclude that they have recognized a correspondence between the learned number and the one on the tested cue by counting the number of dots. Because of this, these particular tests were not included in the conducted GLMM analysis, but were nevertheless kept since they showed that whatever the number of dots and their kind of presentation, the parity corresponding to the learned one was always chosen. Moreover, the experiment made on day 10 showed that the right choice was even made at the lower discrimination limit of two numbers.

Young ants were present at the nest entrance, and could thus see the presented cues during training. It was observed that when they were tested among older ants, they perfectly reacted to the correct parity of the numbers of elements. This sensitivity to parity may be innate or early acquired, a presumption to be examined in a future work. Let us recall that having a number line is native in *M. sabuleti* ants (Cammaerts & Cammaerts, 2020b), but that they have to acquire the notion of zero through experiences (Cammaerts & Cammaerts, 2020c).

In the wild, *M. sabuleti* ants should be able to navigate by using visual (Cammaerts & Lambert, 2009) and olfactory cues (Cammaerts & Rachidi, 2009), possibly also benefiting from their capability to recognize the position of a given numerosity or odor in a sequence (references in Cammaerts & Cammaerts, 2022a; Cammaerts & Cammaerts, 2023b) and to associate a visual cue or an odor with the time of its perception (Cammaerts & Cammaerts, 2022b, c, 2023a). It remains an open question as to how useful it is for these ants to recognize the parity of a number of perceived visual elements. It may be that recognizing and remembering the parity of a numerosity inside a sequence of sighted cues could provide them an additional means for finding the way.

References

- Cammaerts, M.-C. (2004). Some characteristics of the visual perception of the ant *Myrmica sabuleti*. *Physiological Entomology*, 29, 472-482.
- Cammaerts, M.-C. (2006). Discrimination visuelle de formes, de contours, de nombres d'éléments et de l'orientation d'un élément par la fourmi *Myrmica sabuleti*. *Belgian Journal of Entomology*, 8, 43-54.
- 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(6), 1169-1180.
- Cammaerts, M.-C. (2023). When associating numbers of elements with their time period of occurrence, the ants take account of the characteristics of the elements. *International Journal of Biology*, 15(1), 1-12. <https://doi.org/10.5539/ijb.v15n1p1>
- Cammaerts, M.-C., & Cammaerts, D. (2014). Comparative outlook over physiological and ecological characteristics of three closely-related *Myrmica* species. *Biologia*, 69(8), 1051-1058.
- Cammaerts, M.-C., & Cammaerts, R. (2020a). Ants' numerosity ability defined in nine studies. *Journal of Biology and Life Sciences*, 11(1), 121-142.
- Cammaerts, M.-C., & Cammaerts, R. (2020b) Young ants already possess a mental number line. *International Journal of Biology*, 12(2), 1-12. <https://doi.org/10.5539/ijb.v12n2p1>
- Cammaerts, M.-C., & Cammaerts, R. (2020c) Ants acquire the notion of zero through experiences. *International Journal of Biology*, 12(2), 13-25.
- Cammaerts, M.-C., & Cammaerts, R. (2020d). Influence of shape, color, size and relative position of elements on their counting by an ant. *International Journal of Biology*, 12(2), 26-40. <https://doi.org/10.5539/ijb.v12n2p26>

- Cammaerts, M.-C., & Cammaerts, R. (2022a). A synthesis of six recent studies on numerosity abilities in an ant. *Journal of Biology and Life Sciences*, 13(1), 1-23. <https://doi.org/10.5296/jbls.v13i1.19346>
- Cammaerts, M.-C. & Cammaerts, R. (2022b). Association between visual cues and time of day in an ant. *Journal of Ethology*, 40, 223-232. <https://doi.10.1007/s10164-022-00751-4>
- Cammaerts, M.-C., & Cammaerts, R. (2022c). Association, in an ant, of a quantity with its time period of occurrence. *International Journal of Biology*, 14(1), 26-36.
- Cammaerts, M.-C., & Cammaerts, R. (2023a). Ants' capability of associating odors with time periods of the day. *Journal of Ethology*, 41, 79-89. <https://doi.org/10.1007/s10164-022-00770-1>
- Cammaerts, M.-C., & Cammaerts, R. (2023b). The workers of the ant *Myrmica sabuleti* can learn and use a sequence of four odors to navigate between nest and food site. *Journal of Ethology & Animal Science*, 5(1), 000127.
- 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). Olfactory conditioning and use of visual and odorous elements for movement in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). *Myrmecological News*, 12, 117-127.
- Cammaerts, R., & Cammaerts, M.-C. (2020). Ant's mental positioning of amounts on a number line. *International Journal of Biology*, 12(1), 30-45.
- Clark, J. M., & Campbell, J. I. D. (1991). Integrated versus modular theories of number skills and acalculia. *Brain and Cognition*, 17(2), 204-239. [https://doi.org/10.1016/0278-2626\(91\)90075-J](https://doi.org/10.1016/0278-2626(91)90075-J)
- Berch, D.B., Foley, E.J., Hill, R.J., & Ryan, P.M. (1999). Extracting parity and magnitude from Arabic numerals: developmental changes in number processing and mental representation. *Journal of Experimental Child Psychology*, 74(4), 286-308. Doi: 10.1006/jecp.1999.2518.
- Bernard, J., Stach, S., & Giurfa, M. (2006). Categorization of visual stimuli in the honeybee *Apis mellifera*. *Animal Cognition*, 9(4), 257-270. <https://doi.org/10.1007/s10071-006-0032-9>
- Bovet, D., & Vauclair, J. (1998). Functional categorization of objects and their pictures in baboons (*Papio Anubis*). *Learning and Motivation*, 29, 309-322.
- Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, 122(3), 371-396. <https://doi.org/10.1037/0096-3445.122.3.371>
- Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2001). Categorical Representation of visual stimuli in the primate prefrontal cortex. *Science*, 291, 312-316.
- Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science*, 146, 549-551.
- Hines, T. M. (1990). An odd effect: Lengthened reaction times for judgments about odd digits. *Memory & Cognition*, 18, 40-46. <https://doi.org/10.3758/BF03202644>
- Howard, S. R., Greentree, J., Avarguès-Weber, A., Garcia, J. E., Greentree, A. D., & Dyer, A. G. (2022). Numerosity categorization by parity in an insect and simple neural network. *Frontiers in Ecology and Evolution*, 10, 805385. <https://doi.org/10.3389/fevo.2022.805385>
- Giurfa, M., Eichmann, B., & Menzel, R. (1996). Symmetry perception in an insect. *Nature*, 382, 458-461.
- Jander, U., & Jander, R. (2002). Allometry and resolution of bee eyes (Apoidea). *Arthropod Structure & Development*, 10(3), 179-193. [https://doi.org/10.1016/S1467-8039\(01\)00035-4](https://doi.org/10.1016/S1467-8039(01)00035-4)
- Krueger, L. E., & Hallford, E. W. (1984). Why 2 + 2 looks so wrong: On the odd-even rule in sum verification. *Memory & Cognition*, 12(2), 171-180.
- Krueger, L. E. (1986). Why 2 x 2 = 5 looks so wrong: On the odd-even rule in product verification. *Memory & Cognition*, 14(2), 141-149.
- Miller, K., & Gelman, R. (1983). The child's representation of number: A multidimensional scaling analysis. *Child Development*, 54, 1470-1479.
- 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.
- Rigosi, E., Wiederman, S. D., & O'Carroll, D. (2017). Visual acuity of the honey bee retina and the limits for feature detection. *Scientific Reports*, 7, 45972.

R Core Team (2021). R: A language and environment for statistical computing. Vienna: The R Foundation for Statistical Computing.

Reynvoet, B., & Brysbaert, M. (1999). Single-digit and two-digit Arabic numerals address the same semantic number line. *Cognition*, 72(2), 191-201.

Troje, N. F., Huber, L., Loidoldt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: The role of texture and shape in complex static stimuli. *Vision Research*, 39, 353-366.

Zazkis, R. (1998). Odds and ends of odds and evens: An inquiry into students' understanding of even and odd numbers. *Educational Studies in Mathematics*, 36, 73–89. <https://doi.org/10.1023/A:1003149901409>

Watanabe, A., Fujimoto, M., Hirai, K., & Ushitani, T. (2019). Pigeons discriminate shapes based on topological features. *Vision Research*, 158, 120-125. <https://doi.org/10.1016/j.visres.2019.02.012>

Appendix

Results of GLMM analyses with as sole predictor the ratio of the two presented numbers or their difference on the mean, the calculation being done by prioritizing the number corresponding to the learned parity. The first column gives the numerical value of the predictor and the last column its correspondence with the pair of dots presented to the ants. An * marks the cue bearing the parity corresponding to the learned one. 78 testing sessions and 26 groups were taken into account. Significant probabilities and their corresponding pairs of dots are written in bold.

Function: `glmmPQL(cbind(score_even,score_odd)~cues_ratio, random=~1|ID, family=quasibinomial,data)`

	Value	Std.Error	DF	t-value	p-value	cue* vs cue
(Intercept)	-2.494971	0.3496353	52	-7.135925	0.0000	
cues_ratio 0.571	4.521752	0.4512631	13	10.020210	0.0000	4* vs 7
cues_ratio 0.8	5.015808	0.4853329	13	10.334780	0.0000	4* vs 5
cues_ratio 0.833	0.843260	0.4467440	13	1.887569	0.0816	5* vs 6
cues_ratio 0.857	3.932817	0.4396142	13	8.946066	0.0000	6* vs 7
cues_ratio 1.17	0.914387	0.4411721	13	2.072632	0.0586	7* vs 6
cues_ratio 1.2	4.084056	0.4499541	13	9.076606	0.0000	6* vs 5
cues_ratio 1.25	0.409977	0.4494953	13	0.912082	0.3783	5* vs 4
cues_ratio 1.33	3.889720	0.4524556	13	8.596910	0.0000	4* vs 3
cues_ratio 1.75	0.306236	0.4681960	13	0.654077	0.5245	7* vs 4
cues_ratio 2	4.236904	0.4540212	13	9.331953	0.0000	6* vs 3
cues_ratio 2.5	0.685966	0.4527507	13	1.515107	0.1537	5* vs 2
cues_ratio 3.5	0.367133	0.4511739	13	0.813727	0.4305	7* vs 2

Function: `glmmPQL(cbind(score_even,score_odd)~cues_diff_on_mean, random=~1|ID,family=quasibinomial,data)`

	Value	Std.Error	DF	t-value	p-value	cue* vs cue
(Intercept)	1.437846	0.2664878	52	5.395542	0.0000	
cues_diff_on_mean -0.182	-3.089558	0.3851637	13	-8.021415	0.0000	5* vs 6
cues_diff_on_mean -0.222	1.082991	0.4293237	13	2.522551	0.0255	4* vs 5
cues_diff_on_mean -0.545	0.588934	0.3903964	13	1.508555	0.1553	6* vs 7
cues_diff_on_mean -0.667	-3.932817	0.4396142	13	-8.946066	0.0000	1* vs 2
cues_diff_on_mean 0.154	-3.018430	0.3786868	13	-7.970781	0.0000	7* vs 6

cues_diff_on_mean	0.182	0.151239	0.3888825	13	0.388906	0.7036	6* vs 5
cues_diff_on_mean	0.222	-3.522841	0.3883516	13	-9.071266	0.0000	5* vs 4
cues_diff_on_mean	0.286	-0.043097	0.3917742	13	-0.110005	0.9141	4* vs 3
cues_diff_on_mean	0.545	-3.626581	0.4098517	13	-8.848521	0.0000	7* vs 4
cues_diff_on_mean	0.667	0.304087	0.3935811	13	0.772615	0.4536	6* vs 3
cues_diff_on_mean	0.857	-3.246852	0.3921149	13	-8.280357	0.0000	5* vs 2
cues_diff_on_mean	1.111	-3.565685	0.3902932	13	-9.135912	0.0000	7* vs 2

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