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Ants' Numerosity Ability Defined in Nine Studies

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Abstract

The ants *Myrmica sabuleti* Meinert 1861 can add numbers (as non-symbolic displayed elements) or odors when having perceived them simultaneously. Otherwise, (i.e. having perceived them consecutively), they cannot do so. They can subtract one visual element or an odor when perceiving the result of the subtraction. These ants present a concrete notion of zero when faced to visual or olfactory cues. They locate the zero at the end of a decreasing and at the start of an increasing series of elements, i.e. at its due location. Experimented with smaller and larger numbers, the ants locate the smaller numbers on their left and the larger ones on their right, having thus a mental number line. The ants' accuracy in discriminating two successive numbers obeys to a logarithmic function of the relative difference between these numbers. Their arrangement of amounts on the number line is thus non-linear but compressed with increasing number magnitude.

Keywords: adding, *Myrmica sabuleti* Meinert 1861, number line, numerical cognition, subtracting, zero

1. Introduction

Among cognitive abilities, that of numerosity, which is the ability to draw information from a number of displayed items (Verguts & Fias, 2004) rather than from symbols representing numbers, is less frequently investigated in invertebrates than in vertebrates. We examined the numerosity ability of the ant *M. sabuleti* Meinert 1861 in a series of nine successive works. Before synthesizing the results of this investigation, we briefly skim what is known about the ability of organisms other than ants in counting, adding and subtracting, in having the notion of zero and locating it at its due place, and in having a ‘number representation’, a ‘number line’.

A first step in numerosity ability consists in distinguishing amounts of elements, at least numerically small ones, without counting them, but only ranking them on an ordinal scale. Such ability is commonly detained by animals and has been reported, among others, in fishes (Agrillo et al., 2008; Gómez-Laplaza & Gerlai, 2011; Stancher et al., 2013; Agrillo et al., 2017), including a blind cavefish (Bisazza et al., 2014), in frogs (Stancher et al., 2015), salamanders (Uller et al., 2003; Krusche et al., 2010), domestic rats (Cox & Montrose, 2016) and cats (Bánszegi et al., 2016), in dogs and coyotes (Baker at al., 2012; Range et al., 2014), in rhesus (Brannon & Terrace, 1998; Brannon & Terrace, 2000; Hauser et al., 2000) and capuchin monkeys (Addessi et al., 2008), in Indian and African elephants (Perdue et al., 2012; Irie et al., 2019), in birds (Al Aïn et al., 2009; Garland et al., 2012; Tornick et al., 2015), but also in a spider (Rodriguez et al., 2015) and in an ant living in very small colonies (Cronin, 2014), as well as, based on odor amount, in *Tenebrio* beetles (Carazo et al., 2009).

A second step in numerosity ability is the counting of perceived elements for obtaining a precise notion of their amount. Such ability has been observed for instance in male frogs (Rose, 2018), birds (Hunt et al., 2008; Pepperberg, 2006; Pepperberg, 2012); and in rhesus and capuchin monkeys (Beran, 2008). Honeybees can count up to four landmarks for navigating to a food source (Dacke et al., 2008) as well as a number of dots up to four (Gross et al., 2009). Furthermore, they could be learned to add 1 to a number of elements when the elements were blue and to subtract 1 from a number of elements when the elements were yellow, not making an arithmetic operation, but acting according to conditioning (Howard et al., 2018).

A third step of numerosity ability is the capability to add or to subtract numbers of identical elements. Such ability has been demonstrated in some birds and monkeys. Proto-arithmetic ability was shown in a wild bird (Garland & Low (2014). Even newly hatched chicks can spontaneously make simple additions and subtractions (Rugani et al., 2009). Pigeons could subtract by comparing a constant number with what remained after a subtraction (Brannon et al., 2001). Concerning rhesus monkeys, Sulkowski & Hauser (2001) showed their ability in subtracting one object from a number up to three, and Flombaum et al. (2005) showed they can make additions.

A fourth step in number ability is making a correspondence between numbers and symbols. Up to now, the ability to use number symbolism has been shown in parrots (who can phonetically represent the numbers 1 to 9) (Pepperberg, 2006), pigeons (Xia et al., 2000) and chimpanzees (who can visually recognize the numbers 1 to 3 and add them: Boysen & Berntson, 1989). The latter species could also be trained to use symbols for numbers 1 to 9, but without attaining the humans’ level of abstraction (Biro & Matsuzawa, 2001). Matsuzawa (2009) also showed that chimpanzees could outperform human adults in memorizing small numerals and could represent the cardinal and ordinal aspects of symbolic number, but without being as proficient as humans for many cognitive tasks asking abstraction. Beran et al. (2015) explain that “monkeys can count though having this ability at a limited extent, can estimate magnitudes, and can learn to associate symbols with numbers though larger numbers are represented less and less precisely”.

A remarkable and most useful notion, lately acquired by humans in the course of their individual life as well as in the course of their history (Ifrah, 1981), is that of the *zero*. At the most basic level, the notion of *zero* consists in understanding the absence of an element. A following step consists in considering the ‘*zero*’ as a particular number, locating it at the start of the number series, and thereafter representing it by a symbol, and ultimately in using such a ‘*zero*’ into mathematical concepts (Nieder, 2016). Very few information exist about the detention of the notion of *zero* by animals. It seems to be detained only by evolved species. The chimpanzee (*Pan troglodytes*) approaches the zero concept: it considers the zero as being the lower number, but not as an abstract notion (Biro & Matsuzawa, 2001). The Grey parrot (*Psittacus erithacus)* comprehends the numbers 2 to 6, as well as the absence of an element, approaching thus the notion of *zero* (Pepperberg & Gordon, 2005). Nieder (2005) presumes that the parrots’ comprehension of *zero* is higher than that of monkeys. Honeybees have been trained to discriminate non-symbolic numbers 1 to 6, then to discriminate an empty set from these numbers (Howard et al., 2018). They could distinguish non-symbolic amounts, having the notion of ‘what is lower’, and could also distinguish ‘no element’ from ‘one element’, perceiving thus ‘no element’ as being at the lower end of a numerical continuum. Setting the zero at its due mathematical place constitutes effectively a numerosity ability, detained by honeybees and by the vertebrates examined until now as for this topic (grey parrot: Pepperberg & Gordon, 2005; chimpanzee: Biro & Matsuzawa, 2001; rhesus monkey: Merritt et al., 2009; as well as young children: Merritt & Brannon, 2013).

A last notion of numerosity to be considered is the individuals’ representation of the numbers, on a ‘number line’ setting the lower values on the left and the larger ones on the right. Humans possess this cerebral property (Dehaene et al., 1998; Dehaene, 2011). In animals, this property was reported up to now only in some vertebrates. Guppy fishes present some number representation (Agrillo et al., 2012). Rugani et al. (2015) showed that newborn chicks locate the smaller amounts on the left and the larger ones on the right. While studying the pigeons’ ability in subtracting, Brannon et al. (2001) accidentally found that these birds may also natively locate the numbers on a scale. Accordingly, monkeys natively mentally arrange amounts on a scale (Hauser et al., 2000; Brannon & Terrace, 1998).

In humans, the arrangement of the numbers on the number line is initially logarithmic, but mathematical education transforms it linearly (Dehaene, 2011). In their study of the pigeons’ subtracting ability, Brannon et al. (2001) concluded that the numbers arrangement of these birds may be linear rather than logarithmic (i.e. they have a subjective linear number representation), but Dehaene (2001) demonstrated that their results could be obtained under a logarithmic scaling with constant log variability as well as under linear scaling with scalar variability. Non-symbolic number discrimination in robin birds declines linearly with number magnitude (Hunt et al., 2008).

To finish, let us add that when brain electrophysiological experiments were made on humans and on non-human vertebrates (primates and birds) during counting or serial order judgments, each time, a similar particular part of the brain was activated (Nieder, 2005).

2. Material and Methods

2.1 Collection and maintenance of Ants

The experiments were conducted on colonies of *Myrmica sabuleti* Meinert 1861 maintained in the laboratory, in glass tubes half filled with water and deposited in trays serving as foraging area. The ants received mealworm larvae three times per week and had permanently a tube filled with sugar water at their disposal. The temperature was *ca* 20°C, the humidity 80%, and the lighting 330 lux while working on the ants and caring of them.

2.2 Cues, Design and Protocol

Visual cues (black or colored circles, squares or rectangles) were drawn on white paper. They were cut and tied to a stand made of strong white paper (2.5 cm x 2.5 cm) and maintained vertically thanks to an added orthogonally folded base. They were presented to ants during training and testing. During training, the cue to be learned was set near the food and the other cue far from it. The ants were tested in a separate tray, faced with cues identical to those used for training, but new, never used ones. The numbers of ants approaching each kind of cue were counted 20 times over 10 minutes; the proportion of correct responses was calculated, and the recorded data was statistically analyzed using the non-parametric Wilcoxon test (Siegel & Castellan, 1989). Details can be found in Cammaerts and Cammaerts (2019a, b, c, d, e, f, g, 2020a, b). Photos of ants' training can be seen in Figures 1, 2, and photos of ants' testing in Figures 1, 2, 3. The tables and photos here provided are other ones than those already published (same references as above).

3. Results

3.1 Addition and Subtraction of Visual Cues (Table 1, Figure 1)

Ants were trained to two displayed amounts of blue squares set side by side near the food. The two numbers were thus sighted simultaneously. When tested, the ants essentially responded to the sum of the two amounts of squares. In a next experiment, the ants were trained to the same two numbers of blue circles, this time not presented side by side but making an angle of 270° between them. The ants could thus see them only consecutively. When tested, the ants went preferentially to each of the two presented numbers of blue circles, and not to their sum. They thus did not add two numbers of elements when they did not see them all together. These two kinds of experiments showed that the ants responded in fact to what resembled the best to what they saw during training.

Later on, ants were trained to a number of blue circles, one of them being crossed. When tested, the ants went essentially to the remaining number of uncrossed circles, having thus made the subtraction. In fact, they responded to what resembled the best to what they saw during training, i.e. the result. After that, they were trained to a number of blue circles and, set aside, to the same number of circles, one of them crossed and the others empty. When tested, the ants reacted essentially to the number of blue circles sighted during training, i.e.

once more to what resembled the best to what they saw during training. They did not subtract the crossed circle presented among the number of empty circles since they did not concretely sight the result of the subtraction during training.

Table 1. Ants' adding and subtracting abilities

Kind of cue	Operation	Training presentation	*	Mean % of correct responses to the operation, among possible responses
visual	addition	simultaneously	8	1+1: 56.4 2+1: 56.4 3+1: 54.2 3+2: 49.8
		consecutively	8	1+1: 15.9 2+1: 14.5 3+1: 10.1 3+2: 11.3
visual	subtraction	result presented	8	2-1: 92.5 3-1: 89.0 4-1: 85.4 5-1: 83.3
		not presented	8	2-1: 16.2 3-1: 18.9 4-1: 16.1 5-1: 18.0
olfactory	addition	result presented	2	lavender + thyme mixed odor: 73.4
		not presented	2	orange + basilica mixed odor: 14.1
olfactory	subtraction	result presented	2	orange + basilica: 21.0 orange: 75.6
		not presented	2	lavender + thyme: 71.2 thyme: 8.6

The ants responded to what resembled the most to what they sighted or perceived during training, i.e. to visual cues seen simultaneously or to the presented result. *: number of colonies used. More information (on the cues, the methods, the samples, and statistics) can be found in Cammaerts and Cammaerts (2019c, d, f, 2020a).

3.2 Addition and Subtraction of Olfactory Cues (Table 1, Figure 1)

Ants of two colonies were trained to the odor of lavender and to that of thyme, presented in two diffuses set side by side near the food. When tested faced with each of these two odors and with the mixed lavender + thyme odor, the ants went preferentially to the mixed odor. The ants have thus added two odors simultaneously perceived.

Ants were also trained to the odor of orange and to that of basilica, presented in two diffuses set near the food but at a distance of 5 cm from one another. When tested in front of the odor of orange, of basilica, and of the mixed orange + basilica odor, the ants went preferentially to the odor of orange and to that of basilica. They far less approached the mixed orange + basilica odor. Thus, the ants did not add two odors when they consecutively perceived them.

Ants of two other colonies were trained to a mixed orange + basilica odor set far from the food and to the odor of orange set near the food. When tested in front of the orange odor, of the basilica odor and of the mixed orange + basilica odor, the ants went preferentially to the orange odor and far less to the mixed orange + basilica one. They thus mentally subtracted the basilica odor from the mixture orange + basilica, having perceived the result of the subtraction (= the orange odor) during training.

Ants were also trained to the odor of lavender and to that of thyme set closely side by side near the food (being simultaneously perceived, these two odors were mentally added by the ants), and, at the same time, to the odor of thyme set far from the food. They were tested in front of the odor of lavender, of thyme, and of the mixed lavender + thyme odor. The ants essentially approached the mixed lavender + thyme odor. They thus did not subtract the odor of thyme from the mixture, having not perceived the result of the subtraction during training. A complementary experiment showed that the ants did not subtract the odor of thyme for the reason that they might have preferred the odor of lavender.

Consequently, the tested ants preferentially approached the olfactory cue resembling the most to that perceived near the food during training. They behaved just like when experimented with visual cues. They seemed to add and to subtract, but in fact, they simply responded to the result of the operation shown and perceived during training.

Such a behavior is that which could optimally help the ants foraging in the wild.

3.3 Notion of Zero on the Basis of Visual Cues (Table 2, Figure 2)

For knowing if ants have a visual notion of *zero*, operative conditioning experiments were performed on at least two colonies. In one experiment, for comparative purpose, the ants were trained to two different cues, one of them being associated with food. In a second experiment, the ants were trained to a visual cue associated or not with food and to a white (= empty) paper not associated or associated with food. In two other experiments, made on different colonies, the ants were trained to a visual cue associated with food or not and to 'nothing' not associated or associated with food. Whatever the kind of association made during training, the ants could correctly respond to the white paper or to 'nothing' when these elements were associated with food, though somewhat less well than when responding to a true visual cue associated with food. The ants appeared thus to have a notion of *zero*, of nothing, on the basis of their visual perception. Their notion of 'nothing' was not as obvious as that of the existence of a true visual cue. The ants' notion of zero is concrete, perceptual and not abstract.

3.4 Notion of Zero on the Basis of Olfactory Cues (Table 2, Figure 2)

To know if ants have also a notion of zero on the basis of their olfactory perception, operative conditioning experiments were performed on two colonies using a given odor and 'no odor', each of these items being associated with food or not. In other words, during each experiment, the ants could acquire conditioning to 'no odor' *vs* an odor or to an odor *vs* no odor. Contrary to what occurred with visual cues, the kind of association used had an effect on the result. At all events, the ants learned that 'no odor' exists; they presented the notion of 'nothing', of '*zero*' on the basis of their olfactory perception. These experiments also revealed that the ants better learned the presence of a pleasant odor than the absence of that odor (rosemary, vanilla), and better learned an absence of an unpleasant odor than the presence of that odor (onion).

Consequently, the ants possess the notion of 'no odor', of *zero odor*, since they could be learned to react to such an absence as well as to the presence of an odor. This is possibly the first time an animal has been conditioned to the absence of a conditional stimulus.

Table 2. Investigation on the ants' notion of zero by using operative conditioning.

[1]Visual notion of zero

Cues presented during training and testing			Mean % of correct responses
two black circles	-	one black circle	82.5%
one black circle	-	a white paper	74.2%
one black circle	-	nothing	78.5%
one black circle	-	nothing (2^{nd} time)	77.0%

[2]Olfactory notion of zero

Cues presented during training	Cues for testing	% of correct responses
lavender near food *vs* no odor	lavender ; no odor	73.5%
no odor near food *vs* lavender	no odor ; lavender	69.1%
no odor near food *vs* rosemary	no odor ; rosemary	70.6%
rosemary near food *vs* no odor	rosemary ; no odor	80.0%
onion near food *vs* no odor	onion ; no odor	72.2%
no odor near food *vs* onion	no odor ; onion	87.5%
no odor near food *vs* vanilla	no odor ; vanilla	70.6%
vanilla near food *vs* no odor	vanilla ; no odor	87.8%

[3]Location of zero at its due place

kind of series colonies	Mean n^{os} of ants responding to two numbers of black rectangles, the second written number having been set near the food during training					
decreasing series	5 and 4	4 and 3	3 and 2	*2 and 1*	2 and 1	*1 and 0*
colonies A, B, C	0.7 3.1	0.6 2.8	0.9 4.1	*0.5 2.7*	0.8 4.0	*0.9 3.1*
increasing series	4 and 5	3 and 4	2 and 3	*1 and 2*	1 and 2	*0 and 1*
colonies D, E, F	0.6 3.4	0.7 3.8	0.5 2.7	*0.8 3.3*	0.8 3.8	*0.7 3.4*

[1]The ants could be conditioned to a visual cue *vs* a white paper or no cue. They thus well perceived the 'no visual cue' as a zero cue. [2]They could also be conditioned to an odor *vs* an absence of odor. They thus well perceived the absence of odor, i.e. zero odor. The latter experiment also showed that the ants responded better when a pleasant odor (lavender, rosemary, vanilla) and not its absence was associated with food, as well as when the absence of an unpleasant odor (onion) and not its presence was associated with food. [3]*The results written in italics* were obtained without training the ants, which thus duly considered the zero as '1 minus 1' at the end of a decreasing numerical series (colonies A, B, C), and 1 as 'larger than zero', the 'zero' being at the start of an increasing numerical series (colonies D, E, F). More information in Cammaerts & Cammaerts (2019 a, b, e).

3.5 Location of Zero at Its Due Mathematical Place (Table 2, Figure 2)

The ants of three colonies could be conditioned step by step to a decreasing series of elements, the elements associated with food being always those not associated with food minus one element. It was checked if the ants could expect the following number of elements associated with food (i.e. the previous one less one). At the end, they were tested, without conditioning, faced with 0 and 1 elements: they correctly responded to 0 element. They thus considered the *zero* as being 1 minus 1, i.e. at the end of the decreasing series of elements.

The ants of three other colonies could be conditioned step by step to an increasing series of elements, presented in an inverse order, the elements associated with food being always those not associated with food plus one. It was checked that the ants could expect the following number of elements associated with food (i.e. the previous one plus one). They were then tested, without conditioning, faced with 1 and 0 elements: they correctly responded to 1 element. They thus considered 1 as being '*zero*' plus 1, locating the zero at the start of the increasing series of elements.

3.6 Numbers Representation on a Left to Right Oriented Line (Table 3, Figure 3)

A total of six colonies were each trained to a given number of visual elements (green, yellow or violet rectangles according to the experiment) set near the food *vs* a larger or a smaller number of same elements, including zero element, set far from the food. They were then tested faced with two identical sets of the number of elements associated with food during training (the 'correct' number), one placed on the left, the other on the right of a set of the number of elements not associated with food during training (the 'wrong' number). The ants went mostly to the set with the correct number located on the left of the wrong number when this correct number was smaller than the wrong one, and went mostly to the correct number located on the right of the wrong number when this correct number was larger than the wrong one. It was verified that such an ants' left or right choice only occurred in the presence of a larger or smaller number placed between the two correct numbers. The ants located thus the smaller amounts on their left and the larger ones on their right, on an oriented number line. Such an arrangement of the numbers (amounts) on a line could be linear (the difference between two successive numbers being exactly estimated over the line, i.e. whatever the value of the numbers) or non-linear (the difference between two successive numbers being less and less well estimated as the numbers become larger). The next experimental work tempted to define the kind of numbers arrangement

3.7 Numbers Arrangement on the Number Line (Table 3, Figure 3)

We tried to define the number arrangement on the number line by assessing the ants' accuracy of discrimination between two successive displayed amounts. The ants were trained to a given number of green circles set near the food *vs* this number plus one set far from the food. Their response was assessed six times, i.e. after 7, 24, 31, 48, 55 and 72 training hours. The values obtained after 7 hours as well as the average of the six successively obtained values were consistent and used preferentially to those obtained after 31, 48, 55 and 72 training hours, at which times the ants' responses largely fluctuated as in any conditioning. The mathematical and statistical analysis of these responses revealed that the ants' discrimination accuracy between two successive numbers varied with the kind of variables assessing the numbers magnitude and difference, and somewhat with the ants' training time. We have tried as possibilities, the mean, the ratio and the relative difference between the two successive numbers sighted by the ants as the x variable, as well as linear, power (with exponents 0.50 and 0.33), logarithmic, and second-order fractional polynomial (exponents 0.33 and 2) functions for describing the relation of the ants' discrimination between two successive numbers to these numbers. In fact, mean and ratio appear to not express the difference between two successive numbers as perceived by the ants. The relative difference between the two numbers was probably the variable to which the ants reacted. The relation between the ants' discrimination and this relative difference was best described by a logarithmic function. This is detailed in Cammaerts and Cammaerts (2020b).

The relation between the ants' ability in discriminating two numbers and these numbers reflects the ants' positioning of the numbers on their number line. Their number representation appears thus largely compressed.

Table 3. Ants' left to right oriented number line, and numbers arrangement on that line.

[1] Results revealing the ants' left to right oriented number line

Numbers of elements presented	Mean numbers of tested ants in front of		
	the smaller n° on the left	the larger n°	the smaller n° on the right
(1 + food) *vs* 3	2.1	0.5	0.8
(2 + food) *vs* 4	3.7	0.6	0.9
(3 + food) *vs* 4	3.5	0.5	0.9
	the larger n° on the left	the smaller n°	the larger n° on the right
(4 + food) *vs* 2	0.6	0.5	2.3
(5 + food) *vs* 3	0.6	0.7	4.1
(3 + food) *vs* 1	0.6	0.4	2.9
	the correct n° on the left	the wrong n°	the correct n° on the right
(0 + food) *vs* 2	2.9	0.6	0.4
(2 + food) *vs* 0	0.7	0.9	4.7

[2] Results allowing studying the ants' numbers arrangement on the number line

Presented numbers, used colonies	Proportions (%) of correct responses after						Average score (%)
	7h	24h	31h	48h	55h	72h	
1 *vs* 2, A	78.7	80.3	86.4	88.2	84.7	84.2	83.1
2 *vs* 3, B	73.7	74.7	78.3	82.3	85.9	78.1	79.1
3 *vs* 4, C	67.2	71.2	76.1	84.6	75.5	82.5	76.0
4 *vs* 5, D	63.8	69.1	70.7	77.7	81.1	71.9	73.0
5 *vs* 6, E	61.1	64.1	67.5	73.0	69.0	72.6	68.5
6 *vs* 7, F	60.6	63.4	66.7	72.4	68.5	69.4	66.9

[1] Trained to a number of elements associated with food *vs* another larger or smaller number not associated with food, the ants went essentially to the number associated with food located on the left of a larger number as well as located on the right of a smaller number, including the zero. They thus mentally located the small amounts on the left and the larger amounts on the right on a number line. Details in Cammaerts & Cammaerts (2019g). [2]Trained to two successive numbers, the smaller being associated with food, the ants of course reacted essentially to the smaller number, and the accuracy of their response decreased with increasing number size. This decrease appeared to vary with the relative difference between two successive numbers according to a logarithmic function. Details in Cammaerts & Cammaerts (2020b).

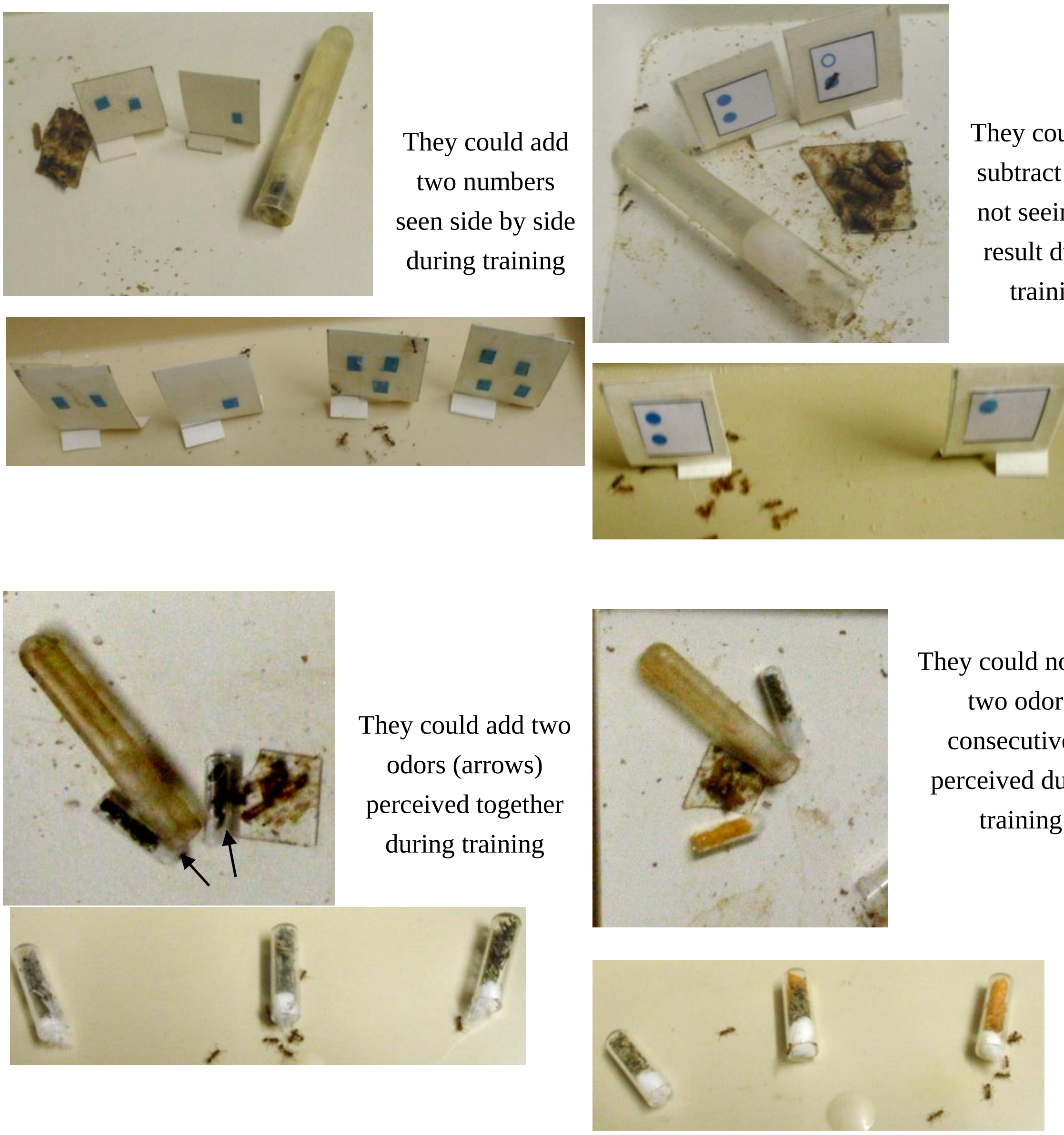

Figure 1. Views of some experiments relative to the ants' adding and subtracting abilities

The ants could make the addition when they clearly perceived its result during training. Otherwise, they responded to the number of visual elements or to the odor perceived during training near the food. Such a behavior may be useful for correctly navigating. Numerical results are given in Table 1, and details can be found in Cammaerts & Cammaerts (2019c, d, f, 2020a).

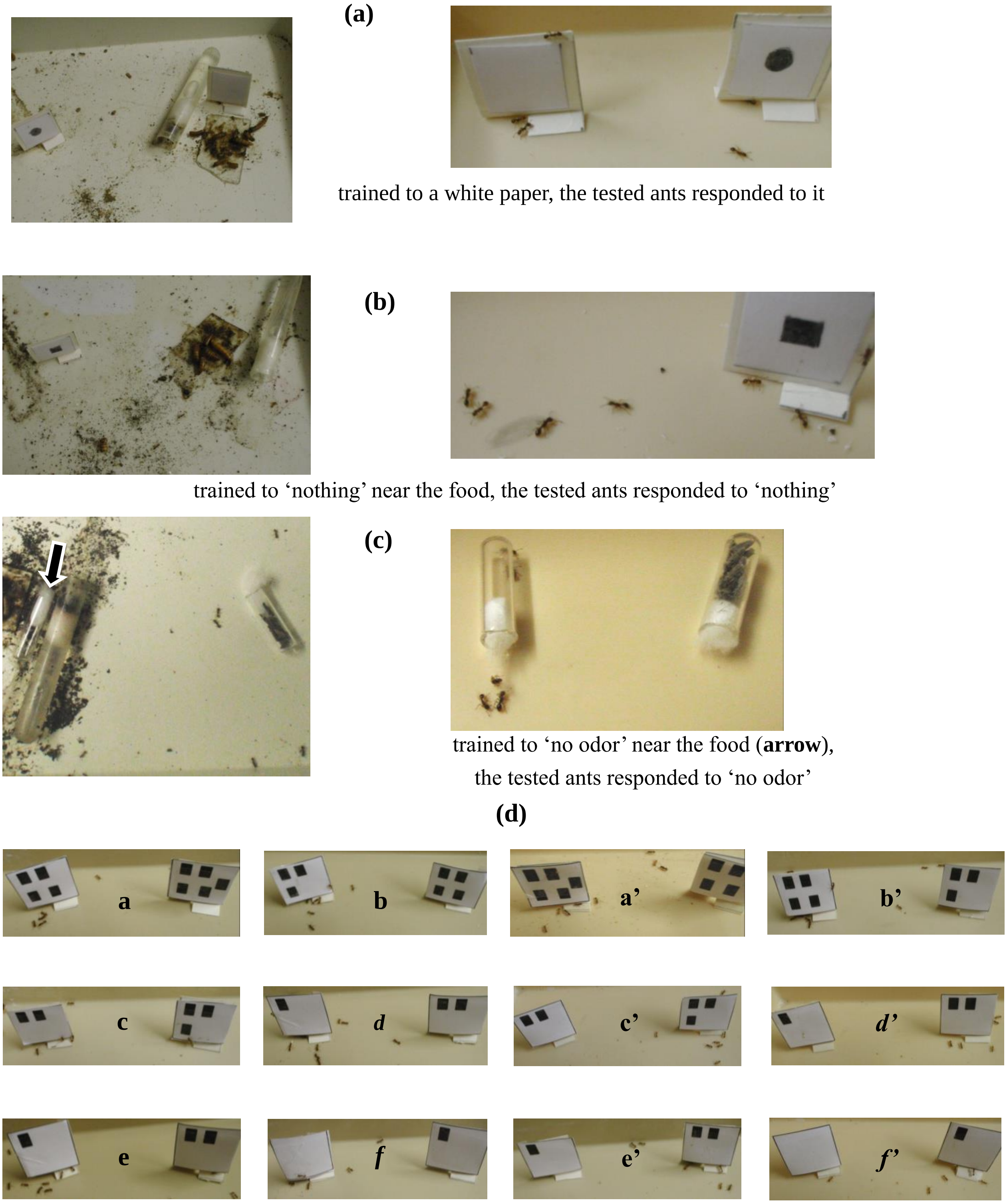

Figure 2. Views of some experiments made to know if ants have the notion of zero, on basis of visual and olfactory cues, and if they locate the zero at its due place

The ants could acquire conditioning to 'no cue' (a) (b) or 'no odor' (c). They have thus some basic notion of zero. (d) The ants were trained to a decreasing series of numbers (a-*f*), the smaller number having being associated with food, or to an increasing series of numbers

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(a'-*f'*), the larger number having being associated with food. *d, f, d'* and *f'* were tests made without training the ants. The ants could expect the following number associated with food (*d*, *d'*) including the zero (*f*) and the number one (*f'*), locating thus the zero at the end of a decreasing series, as well as at the start of an increasing series. Numerical results are given in Table 2, and details can be found in Cammaerts & Cammaerts (2019 a, b, e).

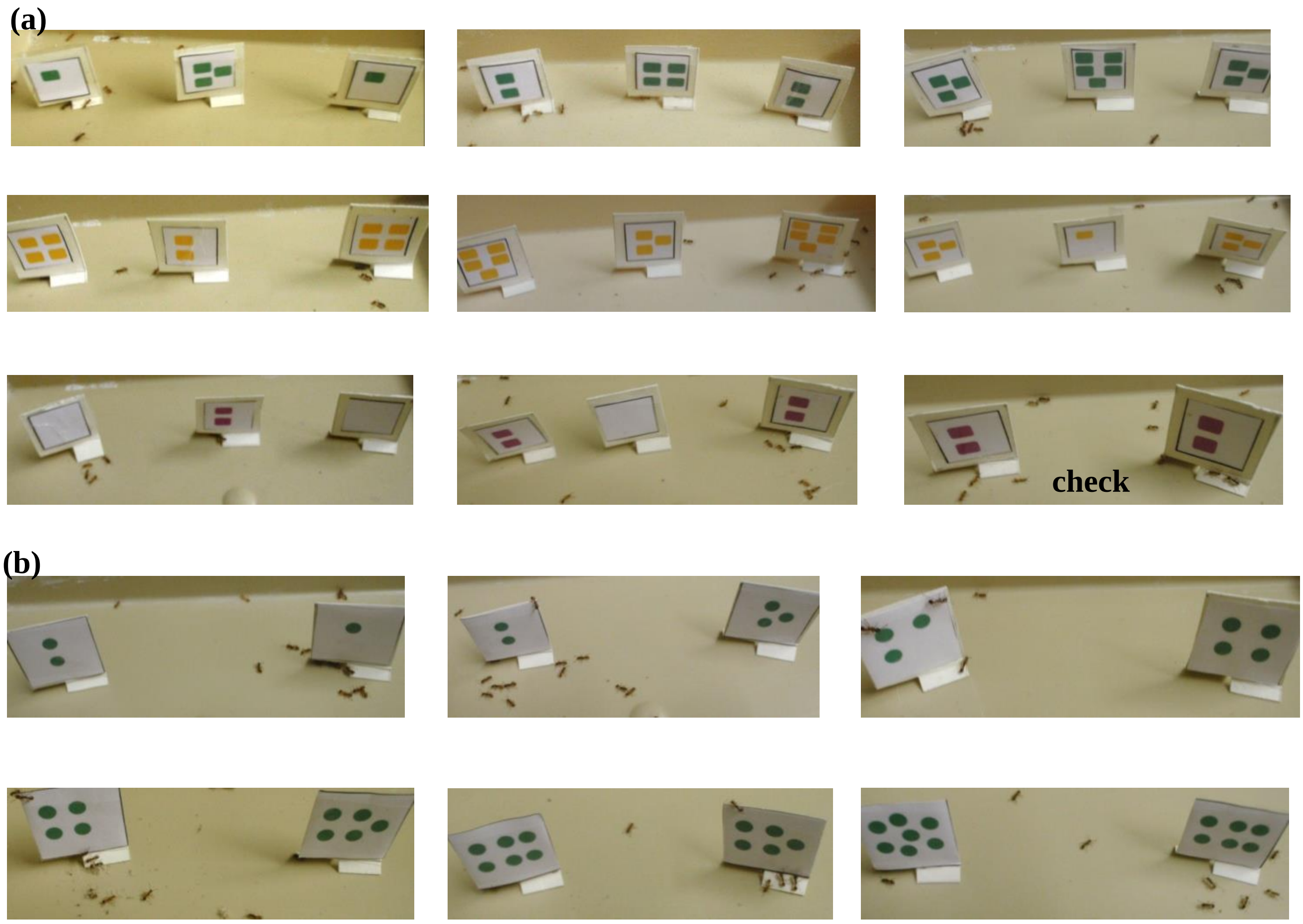

Figure 3. Some views of the experiments made to study the ants' representation of numbers

(a) Trained to a number of elements set near the food *vs* another larger or smaller number, the tested ants went mostly to the number associated with food (of course), and located on the left of a larger number or on the right of a smaller number, including the zero. **Check**: in the absence of a larger or smaller number in the middle, the ants went equally to the left and the right number previously associated with food. They thus represent the numbers on a left to right oriented 'number line'. **(b)** Ants were trained to distinguish two successive numbers of elements. The accuracy of their response decreased with increasing numbers. This decrease depends on, i.e. varies with, the relative difference between the numbers and obeys the best to a logarithmic function. Numerical results are in Table 3 and details are given in Cammaerts & Cammaerts (2019g, 2020b).

4. Discussion and Conclusion

In the course of nine works on the numerosity ability of the ant *M. sabuleti*, we showed that conditioned workers of this species can add and subtract a visual as well as an olfactory element to a number of these elements but only when the result of the operation was clearly perceptible during training sessions. They thus reacted to the display being the most similar to the one they perceived during training, having simply been conditioned to the result of these operations. This differs from what has been found in robin birds and monkeys (Garland & Low, 2014; Beran et al., 2015). In fact, when vertebrates are presented with a given number of elements, and thereafter with another number of identical elements, they can later on react to the correct number of added elements. They thus make the operations without having seen the result. On the contrary, our findings on the ants' adding and subtracting abilities were similar to the up to now brought to the fore honeybees' abilities: these insects added and subtracted one element only after having been conditioned to do so (Howard et al., 2019).

The workers of the ant *M. sabuleti* are very sensitive to odors. Most ants are so. As an example, the ant *Formica fusca* very rapidly learn an odor, do not forget it for three days, and is very resistant to extinction (Piqueret et al., 2019). Coming back to the present subject, when experimented with olfactory cues, their responses were rather affected by the kind of odor used (pleasant or unpleasant) and its localization (near the food or far from it) what did not occur when experimented with visual cues. However, in both cases they responded to what they obviously perceived during training. Such a reaction could help them navigating.

Myrmica sabuleti ants have a basic, concrete, notion of zero which they locate at its due mathematical place, on basis of visual as well as olfactory elements. They also possess a left to right oriented number line. As shown by the decline of their discrimination accuracy between numbers of increasing magnitude and separated by a fixed distance, the ants mentally arrange the amounts on a non-linear number scale, more probably according to a logarithmic function of the relative difference between the amounts.

The *M. sabuleti* representation of numerosity on the number line is basic, not evolved, and resembles to what exists in some animal species as well as in children having not yet been linguistically and mathematically learned. Indeed, young children have a mental compressed, logarithmic representation of numerosity, but later in their life they progressively acquire, thanks to mathematical education, a linear number representation (Laski & Siegler, 2007; Siegler et al., 2009). Rhesus monkeys and crows were shown to have a logarithmic mental number representation on a number line (Nieder & Miller, 2003; Ditz & Nieder, 2016). However, pigeons were found to have subjective linear number representation on the number line instead of a logarithmic one (Brannon et al., 2001). Dehaene (2001) gives another interpretation of Brannon et al.'s results as he showed that similar performance can be achieved under a logarithmic number coding, in which the numbers are mentally perceived as being distributed with a fixed width on the number map (the variability of their perception is constant) with their central location on the map being a logarithmic function of the input, as well as under a linear number coding, in which the location of the numbers and their width (the scalar variability of the perception) on the number map are proportional to the input (but see also the reply of Gallistel et al., 2001 to Dehaene's reasoning). Indeed, Beran et al. (2008) showed that quantity representation in children and rhesus monkeys can correspond to either these two scales. The debate about linear or logarithmic number encoding is not closed. In a more recent experiment on pigeons, Roberts (2005) obtained a better qualitative fit to the data with numbers represented on a log scale than on a linear scale. On the contrary, in robin birds, a subjective linear number representation was found (Hunt et al., 2008).

Our experiments on the *M. sabuleti* numerosity abilities were made using simple visual cues (e.g. a number of identical shaped black or colored circles or rectangles) which enabled the ants to distinguish between amounts of items without counting their numbers. To bring to the fore the latter ability should necessitate separating the physical size and the shape of the cues from their number. This has been performed e.g. in works on rhesus monkeys (Jordan & Brannon, 2008; Cantlon & Brannon, 2006; Merten & Nieder, 2008), crows (Ditz & Nieder, 2016), and honeybees (Howard et al., 2019).

We have thus shown that *M. sabuleti* ants have only a concrete notion of numbers, a concrete notion of *zero*, can 'add' small amounts according to a concrete manner, and have a compressed representation of numerosity. Concerning their numerosity abilities (counting, adding, subtracting, having the notion of zero etc…), ants appear to be at the first step of numerosity ability, the ordinal stage, at a level somewhat similar to that of some fishes, frogs, salamanders, some mammals and monkeys, some birds (see references in the introduction section) and to that of young children being e.g. at the 'one to four-knower' level of understanding cardinality (= the 'subset-knowers') when they start comprehending the notion of numbers (Pixner et al., 2018). The frontier or limit of the ants' cognitive abilities may thus be true counting (i.e. based on number, not on characteristics of the cues - configuration, surface, density, etc. - displayed with their number) and the transition to abstraction.

Myrmica sabuleti workers rely essentially on odors for navigating. We showed that they can add and subtract an odor when the result is obvious and should be chosen for efficiently navigating. Having numerosity abilities is advantageous for an ant in the wild. For example, foragers of the red wood ant *Formica polyctena* can evaluate the walked distance by counting the number (the quantity) of steps traveled before reaching food. They are also able to add or subtract numbers of walked steps and doing so, to shorten the time of transmission of the information to recruit congeners (Reznikova & Ryabko, 2011). Odometry has also been found in *M. sabuleti* (Cammaerts, 2005) and in the desert ant *Cataglyphis fortis* (Wittlinger et al., 2006, 2007). It may be rather common in ants. Possessing numerosity abilities may thus help ants to at least navigate, and perhaps, as for bees, to perform several social tasks.

Humans must be educated for acquiring mathematical abilities of high level (Meyer, 2015). Some children may suffer of developmental dyscalculia (i.e. difficulties in acquiring mathematical skills) because they are lacking the number line. They are treated thanks to particular medical program and make progress in mathematical learning in the course of their acquisition of the number line (Kucian et al., 2011). This leads to wonder if the number line possession is native or is acquired. The ontogenesis of the number line possession and the ontogenesis of the notion of zero in an ant are two next challenges, the experiments having to be made on newly emerged individuals.

Specific zones of the brain were found to be concerned with number knowledge and use in humans (Dehaene et al., 1998), and with numerosity or number coding in non-human primates (e.g. Nieder & Miller, 2002; 2003; Sawamura et al., 2002) and birds (Ditz & Nieder, 2015, 2016). Since brain functioning under stimulation by odors has already been examined in ants and bees (e.g. by Akers & Getz, 1993; Lachnit et al., 2004; Sandoz, 2011; Lopez-Riquelme et al., 2009), a research on their brain functioning under numerosity use should be attempted.

In conclusion, ants have basic cognitive numerosity abilities, being at a stage similar to that presented by some vertebrate species and young children having not yet been initiated to mathematics. Such abilities should help the ants in navigating and performing social tasks. What we found allows defining the ants' cognitive frontiers: they stay at a concrete level, for any cognitive topic, and do not go into abstraction. Investigation on the onto-genesis of ants' numerosity abilities and on their brain functioning under numerosity use should enlarge our knowledge on this broad and interesting subject.

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