Trends in Entomology
Vol. 18, 2022

Original Article

Maximum time interval between two visual cues that still allows an ant to add them up

Marie-Claire Cammaerts[1,*] and Roger Cammaerts[2]

27, Square du Castel Fleuri, 1170 Bruxelles, Belgium.

ABSTRACT

Workers of the ant *Myrmica sabuleti* mentally add visual cues when they perceive them simultaneously. We previously showed that this requires a maximum horizontal distance of 5 cm and a vertical one of 4 cm between the sighted elements. A critical time limit allowing or not allowing these ants to add up two visual cues could also exist between their successive perceptions. The present experimental work aims to define this temporal limit. Working on four colonies and using two different kinds of graphical elements to be added, we conducted six experiments which showed that *M. sabuleti* workers still added up elements when the time interval between their successive perceptions equaled 7 minutes or less, but no longer did so when the interval was 8 minutes or more. The critical temporal limit for ants to add up perceived elements thus lies between 7 and 8 minutes.

KEYWORDS: adding capability, *Myrmica sabuleti*, operant conditioning, visual perception, temporal interval.

*Corresponding author: mccammaerts@gmail.com

The two authors are retired and the present work was done after their retirement.

[1]Assistant professor and researcher, retired from the Biology of Organisms Department, University of Brussels, Belgium.

[2]Senior researcher, retired from the Natural and Agricultural Environmental Studies Department (DEMNA) of the Walloon Region, Belgium.

INTRODUCTION

The workers of the ant *Myrmica sabuleti* Meinert 1861, can add (can sum) two numbers of elements when these numbers are seen simultaneously and not consecutively [1, 2]. We have demonstrated that, for seeing two cues simultaneously, these cues must be located at a maximum horizontal distance of 5 cm and a maximum vertical distance of 4 cm from each other [3, 4]. It remains to define the maximum time interval between the sights of two cues so that these workers perceive them as being seen simultaneously and, therefore, add them.

What could be the critical time interval? When we demonstrated that *M. sabuleti* ants did not add elements they saw consecutively, we presented two numbers of elements in such a way that the ants needed several minutes for going from one to the other [2]. The researched temporal gap could thus exceed a few minutes. When we studied whether the ants could associate a given cue with its time period of occurrence, we presented two different cues, each one during a different time period, with a gap of one hour between the two time periods [5]. When tested, the ants went to the cue corresponding to the time of the day of its presentation during training, with a score of about 85% and were not interested in a cue representing the sum of the two cues sighted during training [5]. The researched critical time interval should thus be smaller than one hour.

Before relating our experimental work, we recall below the characteristics of the summation ability of the workers of the ant *M. sabuleti*, as well as

their ability in estimating the running time, i.e. the time elapsed between two events. We also briefly give information about these topics in other animal species.

Myrmica sabuleti workers can 'count' (evaluate) the numbers of elements contained in a cue, and when doing so, they do not really take into account the shape, color and size of the elements, and poorly take account of their location [6]. These ants can also add or subtract numbers of elements (as well as odors) [7], but the elements must be identical [8] and perceived simultaneously [1, 2]. We have later on defined that, in order to be simultaneously perceived by these ants, visual elements must be located from each other at a maximum horizontal distance of 5 cm and a vertical distance of 4 cm [3, 4]. Here we researched the maximum temporal interval between the successive perception of two elements (numerosities) for these ants to still be able to add them up. As for the adding skill of other animals, much information can be found in the references cited above. Let us recall that honeybees can learn adding as well as subtracting one element (blue as well as yellow respectively) to or from 1 to 5 ones [9]. Adding or subtracting numbers of identical elements is a skill that can be observed in some birds, monkeys, rats and also in an elephant [10-17].

Myrmica sabuleti workers have a notion of the running time [18]. This is why they can acquire temporal learning, spatio-temporal conditioning, and can expect the time of the next food delivery on the basis of previous ones [19-21]. Several animals have been shown to have a notion of the running time [e.g., 22-25].

Concerning the experimental evaluation of the maximum temporal distance between visual cues for individuals of an animal species to still mentally add them up, no useful information could be found in the literature. Only indirect information on the importance of the intervals between cues could be found. For example, Fraisse explains that, in any communication system, information is transmitted by series of signals and relies on the number of these signals in a series (thus on the duration of the series), on the ordering of the series if they differ and on the duration of the intervals between them [26]. Experimental work on acoustic stimuli showed that frogs distinguish successive series of pulses, with short time intervals between the pulses and longer intervals between series. The number of pulses per series and the number of series over time form a sequence. These numbers and the duration of the different intervals are species-characteristic and convey information [27]. The duration of the intervals is even more important than the notes they separate in the species-specific song of a bird, the skylark (*Alauda arvensis*) [28].

Research about the maximum time interval between the successive perception of two cues for enabling an animal to still perceive these two cues as one single cue is thus scarce. The present experimental work on this subject using the ant *M. sabuleti* as a model helps to fill this gap.

MATERIALS AND METHODS

Collection and maintenance of ants

The experiments were performed on four colonies collected in 2021 in the Aise valley (Ardenne, Belgium). These colonies nested under stones, and contained about 600 ants, brood and a queen. In the laboratory, each colony was maintained in one to two glass tubes half-filled with water, a cotton plug separating the ants from the water and a red semi-transparent paper covering the space devoted to the ants. The nest tubes of each colony were deposited in a tray (34 cm × 23 cm × 4 cm) which served as foraging area. In this area, a cotton-plugged tube containing a sugar water solution was permanently provided and pieces of *Tenebrio molitor* larvae (Linnaeus, 1758) were delivered three times per week. The lighting of the laboratory was provided by a window (natural light) and annexed rooms (artificial light at a low intensity); it equaled 110 lux while not working on ants and 330 lux while caring for them or experimenting on them. The temperature equaled *ca.* 20 °C, the humidity *ca.* 80%, and the electromagnetic field *ca.* 2 μWm^2, these conditions being suitable for *M. sabuleti*. The ants are here often named 'workers' or 'nestmates' as commonly do researchers on social insects.

Experimental design, cues (numbers of elements) and planning

A glance at Figures 1 and 2 allows a better understanding of the following explanation.

The ants were trained in their foraging area, the cues they were expected to learn being placed close to their nest entrance, one cue being set at the left of the entrance during a given time period, another cue being set thereafter on the right of the entrance during another given time period. The places where the two successively presented cues were set were at a distance of 1.5 cm. Between these two successive presentations, a time interval of 't' minutes was provided, the value of 't' differing according to each of the six performed experiments. After having been trained to two cues successively presented (including the 't' time gap between their presentations), the ants were tested in a separate tray (21 cm × 15 cm × 7 cm) into which a cue or two cues identical to those used for training as well as a cue showing their addition had been placed.

The cues presented to the ants during testing were identical to those used for training, but were new, never used. These cues were black circles for colonies A and B and black stars for colonies C and D.

These cues were drawn on white paper using Microsoft Word® software, inside a square (2 cm × 2 cm). These squares were then printed and cut, and each one was tied on the front face of a stand made of Steinbach® (Malmedy, Belgium) strong white paper (250 g/m^2). These stands had a vertical part (2 cm × 2 cm) on which a cue was tied, and a horizontal part [2 × (1 cm × 0.5 cm)] duly folded in order to ensure their vertical maintenance. The cues were tied on the stands using extra transparent sticky paper, and this was done two days before starting the experiments for avoiding a possible residue of odor.

Three experiments (I, II, III) were done on colonies A and B using black circles as elements; three other experiments (IV, V, VI) were done on colonies C and D using black stars as elements. For training, 2 identical single elements were successively presented one after the other in experiments I and IV, 1 element followed by 2 elements were successively presented in experiments II and IV, and 2 elements followed by 2 identical elements were successively presented in experiments III and VI. The numbers of elements used for testing were respectively, 1 and 2; 1, 2 and 3; 2 and 4. During training, the first presented cue stayed at the left of the nest entrance for four hours; thereafter a time interval 't' equaling 5, 10, 6, 7, 8, and 9 minutes for experiments I to VI, respectively, was applied. A second cue was then presented to the ants on the right of the entrance for four hours. After that, the ants were tested. This experiment was repeated the following day, each experiment thus lasting two days (on days 1 and 2).

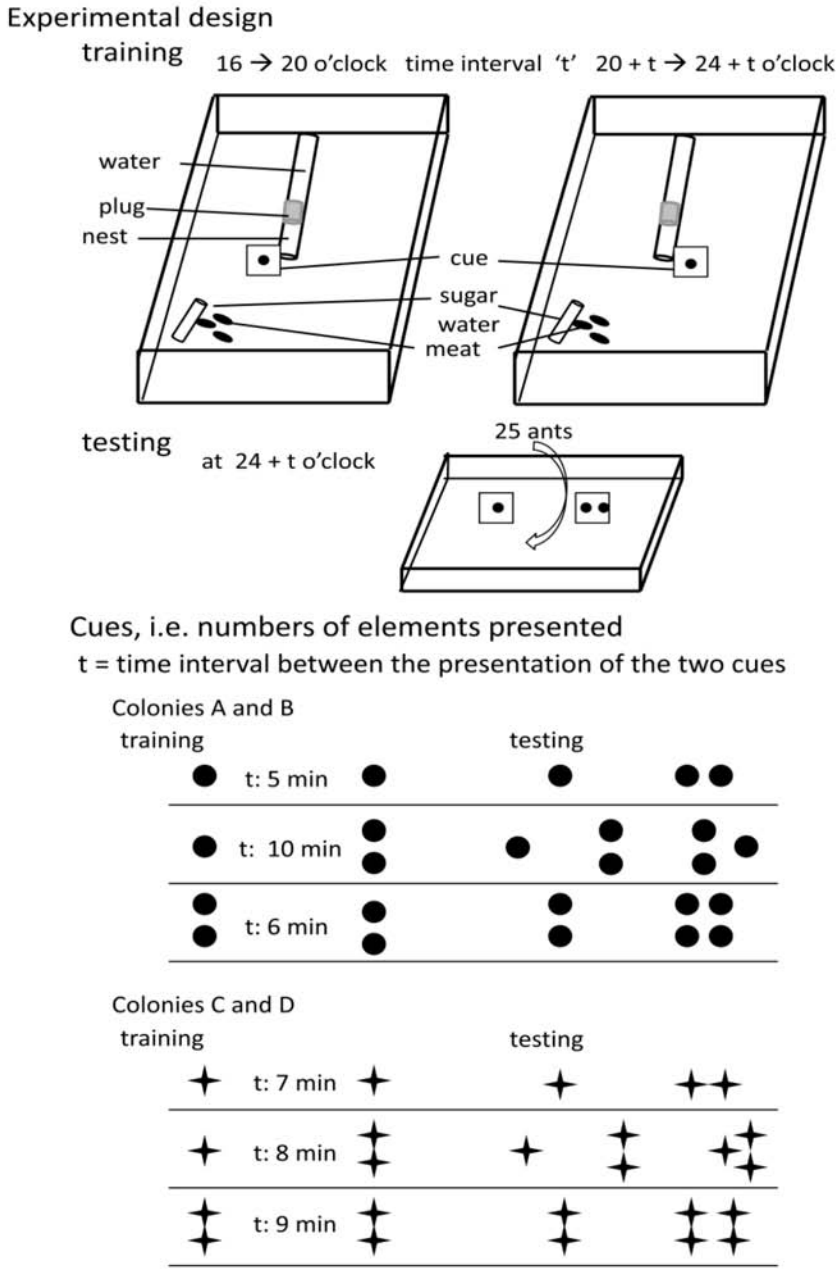
To perform a test on a colony, 25 ants were transferred into their tray devoted to testing, and half a minute later the ants approaching each of the two presented cues were counted 20 times over 10 minutes. The ants were then put back in their foraging area. For each test, each colony and each kind of cue, the sum of the 20 counts was established. These sums are given in Table 1. These sums of the 20 counts obtained for the two used colonies were correspondingly added, and the results allowed calculating the proportions of ants which reacted to each presented cue. These proportions are given in the text.

Statistical analysis

For each experiment, two tests were done (on day 1 and day 2).

The significance, on the workers' response (i.e. the total number of workers sighted near each cue), of an overall effect of the time interval between the successive sight of two cues and of the number of summed elements sighted during each test was analyzed by a GAM regression using 'mgcv' package in R software. The function is gam with the formula: (total number of workers near the added sum of elements) ~ (time interval) + (number of summed elements). The family error distribution was chosen by comparing the median, mean and variance of the workers' responses (N = 24). Mean and median values of the recorded data were almost identical and very different from the variance value and these two facts point to a Gaussian distribution.

Moreover, for each of the 12 tests, two statistical analyses were performed. The first one consisted of



Experimental planning

For each of the six experiments:

Day 1: training to a cue 16 → 20 o'clock / time interval / training to a cue 20+t → 24+t o'clock
and at 24+t o'clock: testing in front of the cue(s) and their addition

Day 2: repetition of the experiment

Day 3: nothing

Figure 1. Experimental materials and methods.

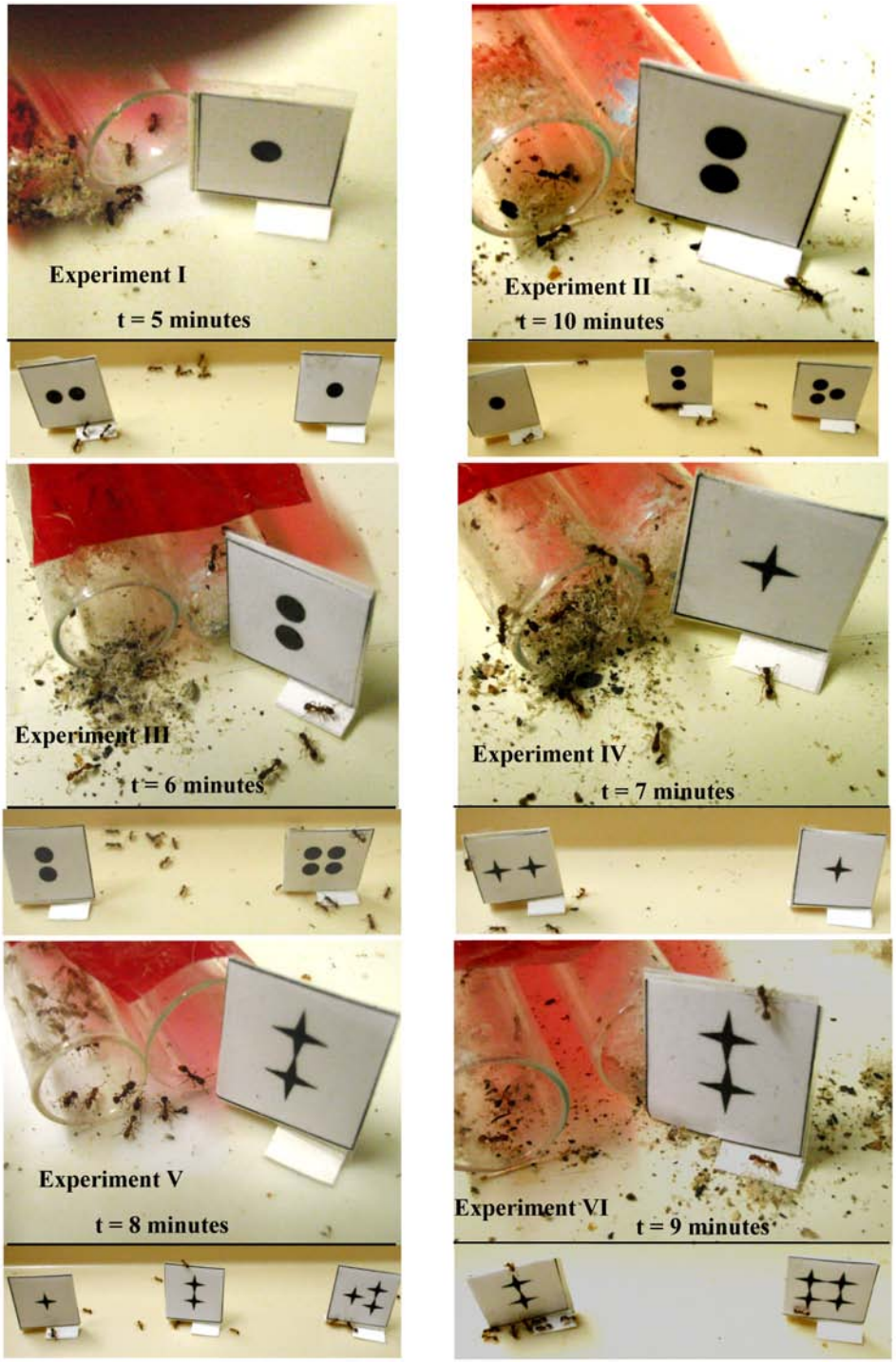


Figure 2. A few photos of the experiments. For each experiment (I to VI), the upper photo is an example of the ants' training, and the lower, of the ants' testing. It can be seen that when the time interval between the presentation of the two numbers equaled 5, 6, 7 minutes, the ants went mostly to the added numbers (respectively to two circles, four circles, two stars). It can also be seen that, when the time interval equaled 8 minutes, the ants went nearly equally to the single and the added cues (i.e. one, two and three stars), and that, when the time interval equaled 10 and 9 minutes, the ants seldom went to the added cues but essentially reacted to the single cue. The ants thus added the cues when the time interval between their perceptions was somewhat less than 8 minutes.

Table 1. Numerical data and statistical analysis of six experiments devoted to define the maximum time interval between the perceptions of two numbers of elements that still allows ants to add them up. The statistical tests compare the number of workers of colonies A+B or C+D counted in front of each cue during their testing. In brief, the ants duly added the two numbers perceived with a time lapse of 7 minutes between their presentations, did not add or very poorly added the numbers when the time lapse equaled 8 minutes, and obviously did not add numbers presented during training when the time interval between their presentations equaled 9 or 10 minutes.

Experiment (I to VI) time interval and cue(s)	**Testing: n° of ants of one and the other colony seen near the presented cues**			**χ^2 test**			**Wilcoxon test**		
				χ^2	**df**	**P**	**N**	**T**	**P**
I, 5 minutes, 1 circle	1 circle:	2 circles:							
day 1	8 and 8	62 and 44		67.20	2	< 0.001	5	15	0.031
day 2	13 and 6	64 and 41		64.17	2	< 0.001	5	15	0.031
II, 10 minutes, 1 and 2 circles	1 circle:	2 circles:	3 circles:	1*vs*3 47.27	2	< 0.001	5	15	0.031
day 1	28 and 45	48 and 26	11 and 4	2*vs*3 46.15	2	< 0.001	5	15	0.031
day 2	33 and 36	48 and 14	11 and 1	1*vs*3 54.15	2	< 0.001	5	15	0.031
				2*vs*3 31.43	2	< 0.001	5	15	0.031
III, 6 minutes, 2 and 2 circles	2 circles:	4 circles:							
day 1	11 and 10	62 and 40		57.87	2	< 0.001	5	15	0.031
day 2	16 and 10	63 and 60		76.09	2	< 0.001	5	15	0.031
IV, 7 minutes, 1 star	1 star:	2 stars:							
day 1	18 and 12	41 and 43		45.74	2	< 0.001	5	15	0.031
day 2	13 and 12	49 and 33		51.43	2	< 0.001	5	15	0.031
V, 8 minutes, 1 and 2 stars	1 star:	2 stars:	3 stars:	1*vs*3 1.28	2	> 0.50	5	10	0.500
day 1	18 and 22	27 and 20	22 and 23	2*vs*3 2.93	2	> 0.40	5	-8	0.500
day 2	30 and 23	39 and 29	32 and 21	1*vs*3 3.00	2	> 0.20	5	-8	0.500
				2*vs*3 8.23	2	~ 0.04	5	-13	0.188
VI, 9 minutes, 2 and 2 stars	2 stars:	4 stars:							
day 1	85 and 63	19 and 6		80.00	2	< 0.001	5	-15	0.031
day 2	58 and 47	15 and 10		76.10	2	< 0.001	5	-15	0.031

1) counting the numbers of times 1, 2, 3, etc… workers of the two colonies were sighted in front of each cue, then, on the basis of these counted numbers, 2) of establishing the distribution of the numbers of ants of colonies A+B or C+D that reacted to each cue, and finally, 3) of comparing to each other the distributions of numbers obtained for each cue by using the non-parametric χ^2 test [28]. For performing the second statistical analysis, the successive 20 counts made for the two colonies used for each test were correspondingly added for each cue, then, for each kind of cue, the 20 sums obtained were grouped chronologically by four and added up in each group so constituted. This provided five values (five sums of 4 × 2 counts) for each cue, which were compared to one another using the non-parametric Wilcoxon test [29]. The results of the two statistical analyses were adjusted for multiple comparisons by using the Benjamini-Hochberg procedure [30] with a false discovery rate of 0.05, and are given in Table 1.

RESULTS

The GAM analysis showed that, without going in detail, the time elapsed between the successive sight of two cues had a significant effect on the worker's response (P = 2.84E-09) while the number of the added elements had no influence (P = 0.41). Table 1 further analyzes the result of each of the 12 tests that were made. For each of these 6 different experiments, we recall below what the presented cues and the time interval between their presentations during training were. Then we report the percentages of ants that were sighted in front of the cues which were presented during testing at day 1 and at day 2, and conclude.

Experiment I

One black circle was presented for four hours, and then a time interval of 5 minutes was provided before presenting another black circle, also for four hours (no longer), its location being 1.5 cm away from where the previous cue was. The ants were tested twice in front of one and two circles. The proportions of their responses to each of these two cues were, at day 1, 13.11% and 86.89%, and at day 2, 15.32% and 84.68%. The data recorded during the two performed tests were in perfect agreement with each other and Table 1 shows that the ants significantly added the two numbers (1 and 1) which were presented during training, with a time interval of 5 minutes between their presentations. The mean response to the added cues equaled 85.78%.

Experiment II

One black circle was presented for four hours, then, after a time interval of 10 minutes, another cue consisting of two such circles was also presented for four hours at a distance of 1.5 cm from the location where the first cue was. Tested twice, on two consecutive days, in front of one, two and three circles, the ants reacted to these cues, respectively, with the scores of 46.91%, 45.68%, and 9.26% on day 1, and 48.25%, 43.36%, and 8.39% on day 2. The results of the two successive tests were in perfect agreement with each other, and each time, the ants mostly reacted to the two cues presented during training, i.e. one and two circles, and far less to three circles. Statistically, the difference between the ants' response to the added and the not added elements was significant (Table 1). They thus did not add the two numbers (1 and 2), successively presented during training with a time interval of 10 minutes between their presentations. Their mean response to the added cues equaled 8.82%. The temporal limit between the successive sights of two numbers enabling the ants to add them up is thus larger than 5 minutes (Experiment I) and smaller than 10 minutes (Experiment II). In order to precisely define this temporal limit, the four following experiments were carried out by establishing a time lapse of 6, 7, 8, or 9 minutes between the successive presentations of two numbers during training.

Experiment III

A cue with two black circles was presented for four hours, then, after 6 minutes, another such cue was presented also for four hours, but at a distance of 1.5 cm from where the previous cue had been presented. This was done twice, on two consecutive days, and each time, after these training sessions, the ants were tested in front of two and four circles. During these two tests, the ants went to two and to four circles with the respective scores of 17.07% and 82.93% at day 1,

and 17.45% and 82.55% at day 2. The results obtained at the two experimental days were in agreement with each other. The ants thus significantly added the two presented numbers when the time interval between their presentations equaled 6 minutes (Table 1). However, the score of their response to the added cues was slightly less than that presented when the time interval between the presentation of each two numbers during training equaled 5 minutes (mean score for 5 minutes = 85.79%, for 6 minutes, = 82.74%). The researched time interval is thus higher than 6 minutes and smaller than 10 minutes. The following experiments were consequently done with a time interval of 7, 8, 9 minutes between the presentations of the two numbers.

Experiment IV

One black star was presented for four hours. Then, a temporal interval of 7 minutes was provided, and thereafter, a similar star was presented, also for four hours, 1.5 cm away from where the previous star was. This procedure was carried out during two consecutive days, and during these two days, after their second training, the ants were tested in front of 1 and 2 stars. During these tests, the ants reacted to 1 and to 2 stars with a score of, respectively, 26.32% and 73.68% at day 1, and 23.36 % and 76.64% at day 2. The results of the two tests were in full accordance with each other. They showed that the ants significantly added the two numbers when they were presented during training with a time interval of 7 minutes between their presentations (Table 1). However, their response to the added numbers was lower than that given when single numbers were presented with a time interval of 6 minutes between their presentations (mean score for 6 minutes = 82.74%; for 7 minutes = 75.16%). The maximum time interval between the perceptions of two numbers for ants still adding them up is thus larger than 7 minutes, and lower than 10 minutes. The two following experiments were consequently performed using a time interval of 8 and 9 minutes between the presentations of the two numbers.

Experiment V

The ants were presented with one black star for four hours, then, after a temporal interval of 8 minutes, they were presented, again for four hours, with a cue consisting of two such stars set at a distance of 1.5 cm from where the previously presented star was. This was performed during two consecutive days, and each day, after having been trained to two stars (i.e. having been conditioned to two stars), the ants were tested in front of 1, 2 and 3 stars. During these tests, the ants reacted to 1, 2 and 3 stars with a score of, respectively, 30.31%, 35.61% and 34.09% at day 1, and 30.46%, 39.08% and 30.46% at day 2. The results of these two tests were in agreement with each other. This clearly demonstrates that the workers stopped adding the two numbers they saw during training when the time interval between their presentations equaled 8 minutes (Table 1). The maximum interval between the sights of two numbers for ants still adding them up was thus a little less than 8 minutes. The ants' mean response to 3 stars equaled 32.28%. A last experiment was conducted with a temporal interval of 9 minutes between the presentations of 2 and 2 stars (see below) to know if, indeed, the ants do not add them.

Experiment VI

The ants were presented with a cue consisting of two black stars for four hours, then after a temporal interval of 9 minutes, they were presented, also for four hours, with two such stars which were set at a distance of 1.5 cm away from where the previously presented two stars had been placed. This was done during two consecutive days, and each time, after the second presentation of two stars, the ants were tested in front of 2 and 4 stars. The ants then reacted to 2 and to 4 stars with a score of, respectively, 85.55% and 14.45% at day 1, and 80.77% and 19.23% at day 2. Thus, each time, they reacted more obviously to the 2 stars, and this was statistically significant. The results of the two tests agreed with each other and showed that the ants did not add two numbers presented with a time interval of nine minutes between their presentations (Table 1). As presumed at the end of Experiment V, the maximum temporal interval between the sights of two numbers, that still allowed the ants to add the numbers up is somewhat lower than 8 minutes, equaling probably 7¾ minutes. The ants' mean response to 4 stars equaled 16.84%. The six such

proportions obtained for the six successively performed experiments are graphically presented in Figure 3 which visually summarizes our findings.

Comparison of the six performed experiments

For each of the six experiments, a mean ants' response to the added cues was obtained. Plotting these six obtained mean scores with the time intervals elapsed between the presentations of the cues allowed obtaining the graph presented in Figure 3. This graph suggests that the critical time interval between the sight of two numbers that still allows the ants to add the cues equals about 7 minutes and 45 seconds. In addition, it appears that the ants' perception of the running time is not linear.

DISCUSSION

The workers of the ant *M. sabuleti*, collectively trained and tested, add numbers of elements when these elements are similar and seen simultaneously. We previously showed that, in order to be seen simultaneously, the elements must be located at a maximum horizontal distance of 5 cm and a maximum vertical distance of 4 cm from each other. Until the finalization of the present work, we were unaware of the maximum temporal gap between the successive sights of two elements, which would enable these ants to still add up the two elements. We here showed that this maximal time period lies between 7 and 8 minutes.

We used numbers of elements in order to find the maximum time interval between the sightings of two items allowing the ants to mentally 'see' them as a single item, but the concept of 'numbers' is optional here. The concept of 'cue' or 'picture' is sufficient for considering our assessment of the critical time interval, situated between 7 and 8 minutes, as valuable. Let us recall that, for being added by the workers of the ant *M. sabuleti*, the elements have to be identical [8], while they can be different when being simply counted [6]. In the present work, the elements must be added. We have thus cautiously used identical black circles and stars throughout the conducted experiments. Ants behaved in the same way faced with circles and stars. Thus, the shape of the cues did not affect the temporal distance here defined.

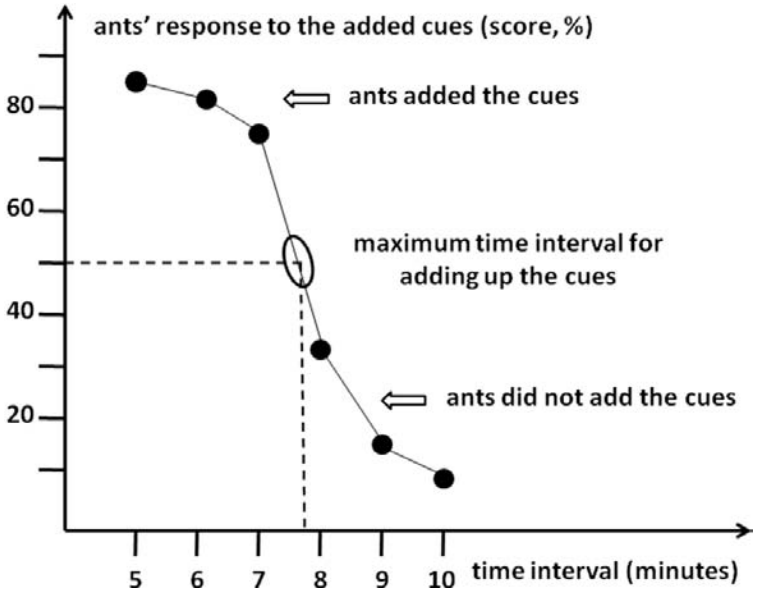


Figure 3. Graphical representation of the ants' response when tested in front of the added cues and of the 'single' cues they successively saw during training, with a time interval of 5 to 10 minutes between their presentations. Ants mentally summed the cues when the time interval between their successive presentations lasted up to 7 minutes, and did not do so when the interval was 8 minutes. The graph places the critical interval at 7¾ minutes. In addition, it shows that the perception of the running time is not linear.

Nevertheless, the critical time interval here brought to the fore may depend on some characteristics of the elements (some color or size may be better memorized) and the environment (cues may be more visible under a particular luminosity or in some landscapes), as well as on the ants' motivation (if located far from the nest or from any valuable reward, cues may be poorly memorized). The influence of, among others, the motivation of an individual on the memorization of ancient experienced events has been shown in pigeons [31]. It may be presumed that events or cues which are difficult to memorize should be experienced or perceived with a shorter time gap between them in order to be mentally added up while elements which are easily memorized could be more temporally distant for being still added up.

Regarding Figure 3, the graph suggests that, at least in ants, the perception of the running time is not linear, is irregular and depends, among others, on the temporal proximity of the experienced events.

Time intervals between the successive perceptions of acoustic stimuli have been considered in frogs. For being 'added', i.e. for being perceived as a single acoustic signal, sounds (pulses) must very closely follow each other, so that they constitute one series of pulses. Then, a time interval is needed to signify the beginning of a second series of pulses. The successive series of pulses and the intervals between them convey a specific message [27]. In the species-specific song of a bird, the skylark (*Alauda arvensis*), the information is only conveyed by a particular rhythm of successions of notes (series of pulses) and gaps (silences) between them, not by the contents of each note. In this case, the duration of the intervals is more important than the notes themselves [28]. In addition to these examples, we can cite human writing and Morse code, in which short intervals separate ordered letters that are mentally associated as parts of a word, while longer intervals separate letters that are no longer 'added together' as they would be in a word, but are the ends and beginnings of separate words in a sentence. Intervals (temporal gaps inside series of signals) and their duration are thus essential in any communication system.

CONCLUSION

The workers of the ant *M. sabuleti* add elements when they see them simultaneously. Here we defined the maximum time interval between the successive sights of two cues (black circles or stars set near the nest entrance during training) enabling these ants to still mentally add them up, as lying between 7 and 8 minutes (graphically 7¾ minutes). Our work also pointed out that the ants' perception of the running time is non-linear and non-uniform, and depends, among others, on the temporal proximity of the experienced events.

CONFLICT OF INTEREST STATEMENT

We affirm having no conflict of interest associated with the topic investigated here.

REFERENCES

1. Cammaerts, M.-C. and Cammaerts, R. 2019, Int. J. Biol., 11(3), 25-36.
2. Cammaerts M.-C. and Cammaerts R. 2019, Int. J. Biol., 11(3), 37-48.
3. Cammaerts, M.-C. and Cammaerts, R. 2021, Tren. Entomol., 17, 43-56.
4. Cammaerts, M.-C. and Cammaerts R. 2021, Tren. Entomol., 17, 77-90.
5. Cammaerts, M.-C. and Cammaerts, R. 2022, J. Ethol., https://doi.org/10.1007/s10164-022-00751-4
6. Cammaerts, M.-C. and Cammaerts, R. 2020, Int. J. Biol., 12(2), 26-40.
7. Cammaerts, M.-C. and Cammaerts, R. 2020, Int. J. Biol., 12(1), 1-13.
8. Cammaerts, M.-C. and Cammaerts, R. 2021, Tren. Entomol., 17, 21-34.
9. Howard, S. R., Avarguès-Weber, A., Garcia, J. E., Greentree, A. D. and Dyer, A. G. 2019, Sci. Adv., 5(2), eaav0961. doi: 10.1126/sciadv.aav0961
10. Garland, A. and Low, J. 2014, Behav. Process., 109, 103-110. http://dx.doi.org/10.1016/j.beproc.2014.08.022.
11. Pepperberg, I. M. 2006, Animal Cognition, 9(4), 377-391. psycnet.apa.org/record/2007-07451-012
12. Rugani, R., Fontanari, L., Simoni, E., Regolin, L. and Vallortigara, G. 2009, Proc. R. Soc. B, 276(1666), 2451-2460. doi: 10.1098/rspb.2009.0044.

13. Brannon, E., Herbert, M. and Terrace, S. 1988, Science, New Series, 282(5389), 746-749. doi:10.1126/science.282.5389.746. PMID 9784133.
14. Flombaum, J. I., Junge, J. A. and Hauser, M. D. 2005, Cognition, 97, 315-325. doi: 10.1016/j.cognition.2004.09.004.
15. Woodruff, G. and Premack, D. 1981, Nature, 293(5833), 568-570. doi:10.1038/293568a0.
16. Laing, D. G., Murray, K. E., King, M. G. and Cairneross, K. D. 1974, Chem. Senses, 1(2), 197-212. https://doi.org/10.1093/chemse/1.2.197
17. Irie, N., Hiraiwa-Hasegawa, M. and Kutsukake, N. 2019, J. Ethol., 37, 111-115. https://doi.org/10.1007/s10164-018-0563-y
18. Cammaerts, M.-C. 2010, Bull Soc. R. Ent. Belg., 146, 189-195.
19. Cammaers, M.-C. 2004, Biologia, 59, 243-256.
20. Cammaerts, M.-C. 2013, Bull Soc. R. Ent. Belg., 149, 131-138.
21. Cammaerts, M.-C. and Cammaerts, R. 2016, ISRN Entomology, Article ID 9473128, 9 p. doi:org/10.1155/2016/9473128.
22. Block, R. A. and Grondin, S. 2014, Front. Psychol., 29(5), article 648. https://doi.org/10.3389/fpsyg.2014.00648
23. Ng, L., Garcia, J. E., Dyer, A. G. and Stuart-Fox, D. 2021, Biological Reviews, 96(2), 526-540. https://doi.org/10.1111/brv.12665
24. Murphy, P. J. and Campbell, S. S. 1996, J. Clin. Neurophysiol., PMCID: PMC2713064, NIHMSID: NIHMS32244, PMID: 19623268.
25. Rivkees, S. A. 2007, Sleep Med. Clin., 2(3), 331-341 doi:10.1016/j.jsmc.2007.05.010.
26. Fraisse, P. 1978, Chapter 6: Time and Rhythm Perception, pp. 203-254. E. C. Carterette and M. P. Friedman, (Eds.), Handbook of Perception, vol. 6A, Academic Press, Elsevier. https://doi.org/10.1016/C2012-0-01462-7
27. Rose, G. J. 2017, Phil. Trans. R. Soc. B, 373, 1-8. http://dx.doi.org/10.1098/rstb.2016.0512
28. Aubin, T. and Bremond, J.-C. 1983, Z. Tierpsychol., 61, 141-152. https://doi.org/10.1111/j.1439-0310.1983.tb01334.x
29. Siegel, S. and Castellan, N. J. 1989, Nonparametric statistics for the behavioural sciences. Singapore, McGraw-Hill Book Company.
30. McDonald, J. H. 2014, Handbook for Biological Statistics. Baltimore, Sparky House Publishing.
31. Plowright, C. M. S., Church, D., Behnke, P. and Silverman, A. 2000, Behav. Process., 52(1), 43-48. https://doi.org/10.1016/S0376-6357(00)00110-8