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Original Article

Memory loss and passing time perception in an ant

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ABSTRACT

Having previously showed that the workers of the ant *Myrmica sabuleti* have a sense of time, we here tried to define how they perceive the duration of time passing through the loss of their memory of a learned cue. Thanks to five experiments using olfactory and visual cues and performed on four colonies, we showed that a few hours after having learned a cue and having memorized it in a stable way, these ants lose their memory rather abruptly, according to a sigmoid curve. This shows that ants clearly distinguish events that they have recently learned and vividly remembered from those that took place more than a few tens of hours ago and, for the most part, have been forgotten since. The timing of this memory loss shows that the perception of the duration of time in these ants is affected by their degree of activity: they underestimated the duration of the time that passed when their activity was increased. Although the ants seemed to not react to events learned more than a few tens of hours ago, they nevertheless appeared to keep a weak residual trace of them though not locating them precisely in time. Keeping some faint memory of old events could allow the ants to use the information in the future.

KEYWORDS: activity, elapsed time perception, *Myrmica sabuleti*, memorization process, vivid memory, residual memory.

INTRODUCTION

Several experimental works demonstrate that the workers of the ant *Myrmica sabuleti* Meinert, 1861 have a notion of time. These workers can estimate the elapsed time [1]. They can acquire spatio-temporal learning [2]. They can expect the time o'clock of an event on the basis of previously experienced occurrences of such an event [3]. These workers can also expect the following quantity of an increasing or decreasing arithmetic or geometric sequence [4, 5]. In addition, they can associate a quantity, a cue, or an odor with the time of day during which they learned these items [6-8]. For adding two cues, *M. sabuleti* workers must see them simultaneously, which implies a maximum time lag not to be exceeded between the perceptions of these two cues [9]. This last finding once more points out that the workers of the ant *M. sabuleti* have a rather precise notion of the time, and in addition, on the basis of the recorded data, this last work showed that time perception in these ants does not fit a linear function, but another kind of function which still needed to be defined [9]. This incited us to extend this last work by trying to deepen the function or rule to which the perception of time obeys in *M. sabuleti* worker ants. Before relating our methods and results, we here below report information on time perception in animals.

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The two authors are retired from the below-mentioned institutions and the present work was done after their retirement.

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W. A. Roberts (2002) proposed the hypothesis that, contrary to humans, “animals are cognitively stuck in time, cannot anticipate long-range future events, cannot detect time of day, nor track short time intervals, cannot remember the order of a sequence of events nor anticipate future events” [10]. Our experimentation on *M. sabuleti* ants, related here above, however shows the contrary: the workers of this species detain, to a certain degree, all these abilities. We agree with the amount of information already reported in 1980 by Richelle and co-authors in their book about the animals’ time estimation which suggest that, indeed, several animal species, such as honeybees, fishes, birds and mammals, valuably perceive the elapsed time [11]. In his recent comprehensive review on Mental Time Travel (MTT) that particularly focuses on great apes, Martin-Ordas suggests that not only humans but also animal species may detain a basic way of understanding time [12]. In an opinion article on non-human mental time travel, Logan explains, on the basis of behavioral and neurological studies, that non-human species can remember past events and plan for the future, and that data are still lacking for knowing if, doing so, they reach equivalent complexity and imagination than those presented by humans [13]. Nevertheless, there is evidence that animals such as rats and pigeons are not stuck in time since they can ‘report’ about their recent past experience when they are asked to do so (presenting thus some kind of episodic memory), and since they can use the anticipation of a future event as the basis for a present task (presenting then some planning capability) [14].

By examining the perception of elapsed time in pigeons on the basis of conditioning and then testing, Zentall *et al.* observed that these birds underestimated the passage of time when they were active, i.e., when they had to peck [15]. It is notorious that humans overestimate the elapsed time when they do nothing. However, while in humans and other animals the time interval behavior obeys Weber’s law or its generalization, this is not the case in pigeons, in which, instead of a decreasing asymptote, Weber’s function has the shape of a U, rapidly decreasing to a low value, then increasing to a high value [16]. Although we have shown that, in the ant *M. sabuleti*, the visual perception of cues of different sizes obeys to Weber’s law [17], we here do not intend to verify if this law also applies to its time perception, but intend to define to which kind of function and rule its perception of the elapsed time obeys, by basing our research on the learning abilities of its workers and on their loss of memory over time after conditioning was stopped.

MATERIALS AND METHODS

Collection and maintenance of ants

The experiments were conducted on four colonies of *M. sabuleti* collected in May 2021 in an abandoned quarry located in the Aise valley (Belgium, Ardenne). Each colony contained about 500 workers, 1 queen, and brood. Each one was maintained in one to two glass tubes half-filled with water, a cotton plug separating the ants from the part filled of water. The nest tube of each colony was set in a tray (34 cm × 23 cm × 4 cm), the borders of which having been covered with talc to prevent ants from escaping. These trays served as foraging areas. Inside of them, pieces of *Tenebrio molitor* larvae (Linnaeus, 1758) were deposited three times per week, and a cotton-plugged tube filled of sugar water (~15% of sugar) was permanently set. The lighting of the laboratory varied between 110 and 330 lux. The ambient temperature permanently equaled 20-21 °C, the humidity about 80%, and the electromagnetic field 2 μWm^2. These environmental conditions are suitable for *M. sabuleti*.

Experimental design and protocol

Each experiment was performed on the same four colonies (labeled A, B, C, D) using olfactory and visual operant conditioning, first in their usual foraging environment, and then after introducing a physical change in this foraging environment in order to evaluate the effect of a physical effort made by the ants on their memory performance. Each time, the ants were conditioned in their foraging area, and tested in an own experimental design (Figures 1, 2, 3, 4). For conditioning the ants, either an olfactory or a visual cue was set on the left and the right of the nest entrance, the ants seeing thus inevitably these cues and being rewarded by the close proximity of the nest entrance.

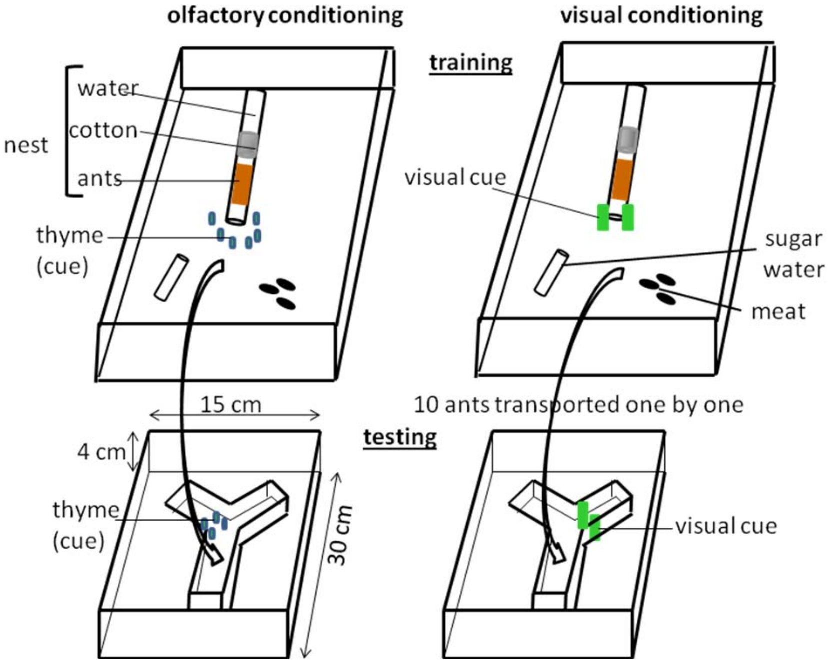

Figure 1. Experimental design used to examine the memorization of a cue by ants and, after its removal, the loss of its memory over time. Details are given in the text, and some photos are shown in Figure 3. The ants were conditioned in their foraging area, the olfactory or visual cue being set at the nest entrance (upper schemas), and they were tested in a Y-maze provided with the adequate cue in one of its branches (lower schemas).

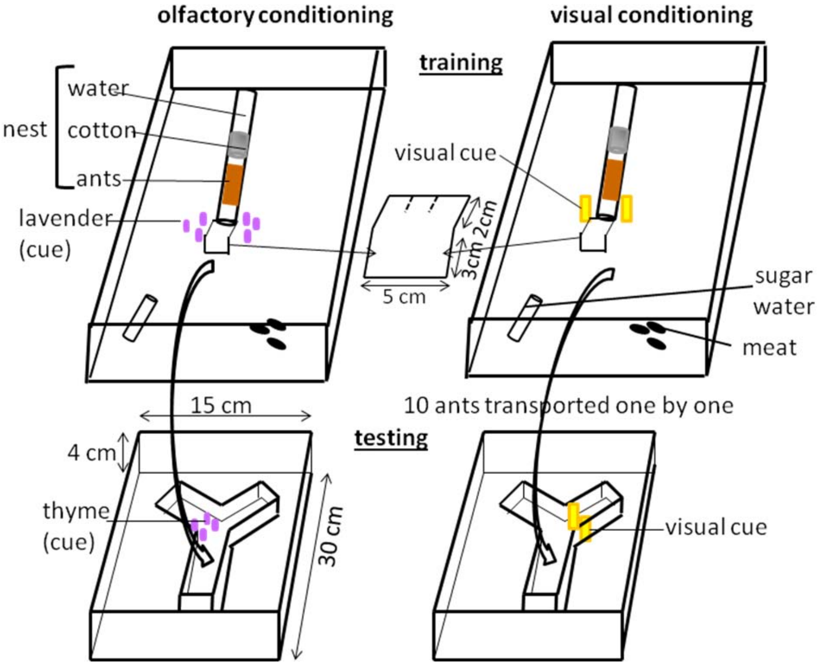

Figure 2. Experimental design used to examine through conditioning and under increased forager activity (by placing a ramp at the nest entrance and food farther away than usual) the acquisition of cue memory by ants and the loss of this memory after the conditional cue was removed.

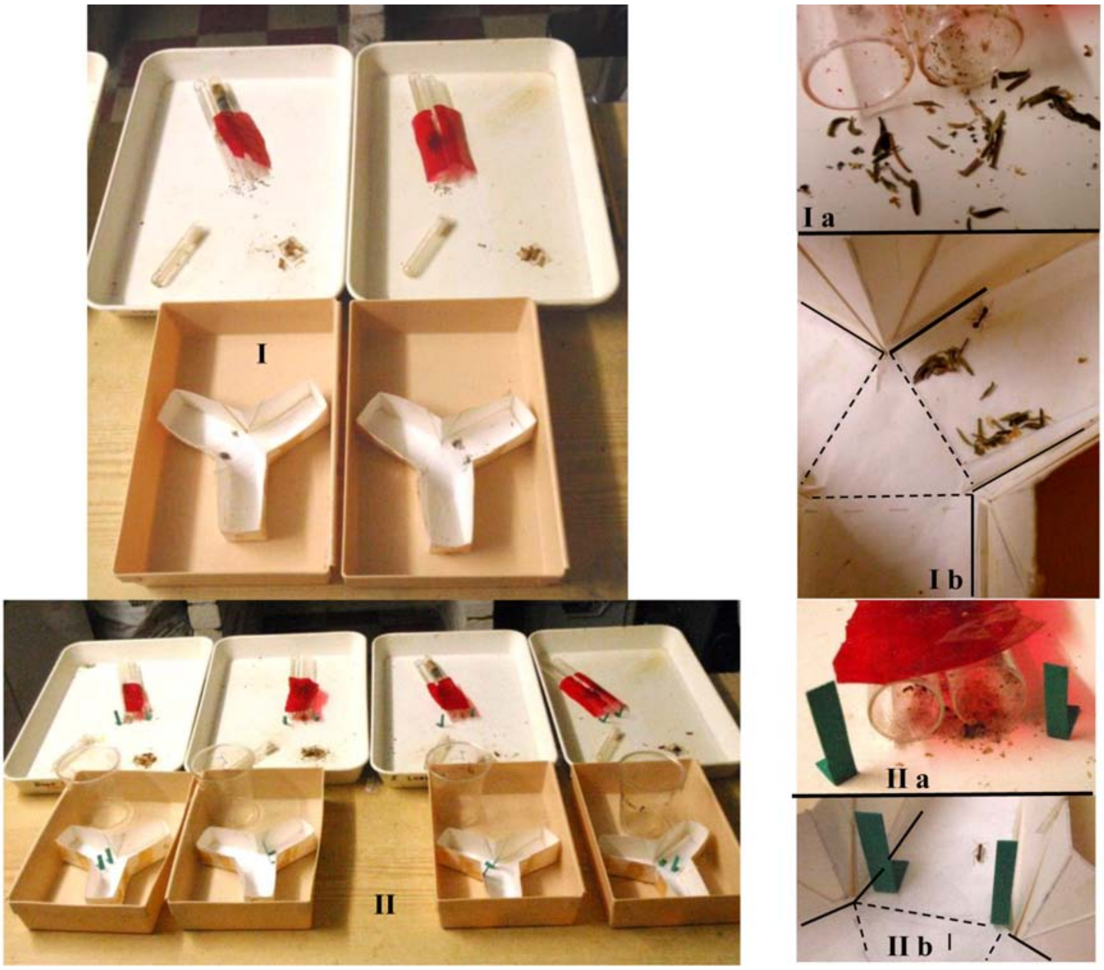

Figure 3. Some views of the experiments conducted to examine the loss of memory of a learned cue by ants. The study was made on the basis of the ants' recollection of a learned olfactory (thyme, I) or visual (green rectangles, II) cue. The ants were trained in their foraging area to these cues (Ia, IIa) until they reached a high conditioning score. Then, after the cue removal, their recollection of the cues over time was assessed by testing them in a Y-maze provided with the appropriate cue (Ib, IIb).

The olfactory cues were pieces (about 1 - 2 mm × 3 - 10 mm) of thyme or of lavender; the visual cues were green or yellow paper rectangles vertically maintained thanks to a horizontal base located behind them (Figures 1, 2, 3, 4). The vertical part of these visual cues measured 0.5 cm × 2.0 cm; the horizontal part measured 0.5 cm × 1 cm. The workers of the ant *M. sabuleti* are known to use essentially odors for navigating [18], and to well see the green as well as the yellow color, even under low light [19, 20]. Conditioning was conducted, and during it, ants randomly collected in their foraging area were tested over time, until their conditioning score no longer increased, i.e., until it reached 90% of correct responses or reached twice following the score of 85%. The cues were then permanently removed, and the ants were again tested over time either without a change in their foraging environment during experiments I and II, or by adding a ramp to the entrance of their nest and setting their food 6 cm farther from the nest entrance during experiments III and IV. The ants were tested in an own Y-apparatus built in strong white paper, the sides of which were slightly covered with talc to prevent escaping and the floor of which was covered by a piece of white paper removed at each testing. Each apparatus was placed in a distinct tray

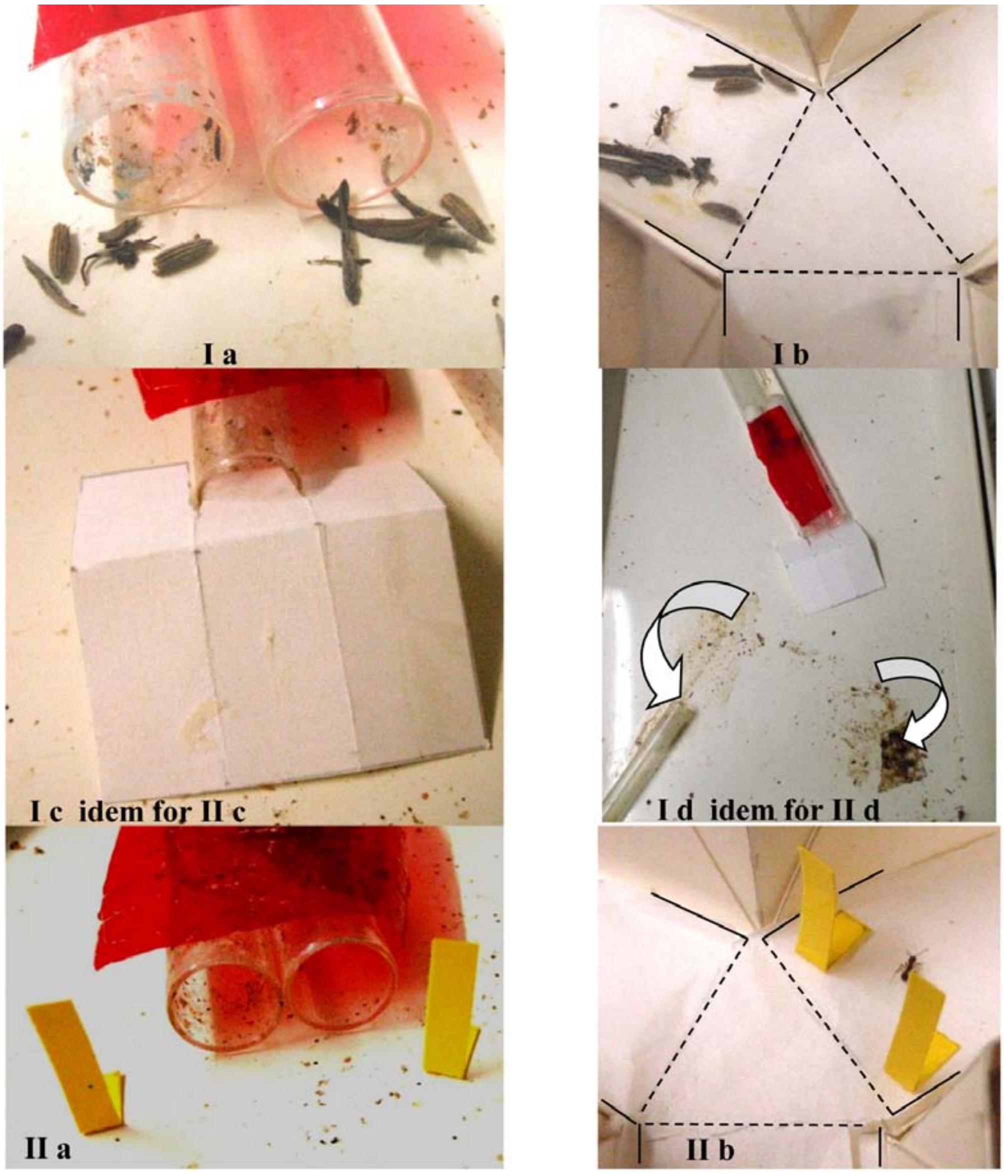

Figure 4. Same legend as for Figure 3 except that, during the ants’ recollection of the olfactory (lavender) or visual cues (yellow rectangles), the ants were induced to increase their activity (by placing a ramp at the nest entrance, and food farther than usually). I: olfactory cue; II: visual cue, a: training in the foraging area; b: testing; c: the ramp set at the nest entrance; d: food relocated farther from the nest.

(15 cm × 7 cm × 5 cm). Pieces of thyme or of lavender, or two green or two yellow paper rectangles were randomly deposited inside the entrance (so that the ants duly perceive them) of the left or the right branch of these Y-apparatus (Figures 1, 2, 3, 4). For conducting a test on a colony, 10 ants were transferred one at a time in the area lying in front of the Y-maze division into two branches, and for each ant, its first choice of one or the other branch of the Y-apparatus was recorded (Figures 3, 4). Moving into the branch containing the pieces of thyme or of lavender, or the green or yellow rectangle was considered as giving the correct response. After having been tested, each ant was kept in a cup, until 10 ants of its colony were tested, for avoiding testing twice the same ant of a colony. The 10 ants of the used colony were then transferred back into their

foraging area. For each time period and cue, the responses given by the 10 tested ants of each colony were added (Tables 1, 2, 3, 4, second column), and the overall proportions of correct responses (= the conditioning scores) of the four colonies, successively obtained during the ants' conditioning acquisition and during their loss of conditioning, were established (Tables 1, 2, 3, 4, third column).

After this experimental study was finished, we tested again the ants of the same four colonies in front of the cues to which they had been collectively conditioned, by using the same testing protocol as previously, in order to known if and how they remembered cues no longer perceived since different long time periods (Table 5).

Analysis of the results

The conditioning scores (% of correct responses established on the basis of the choices made by 10 tested workers of each of the 4 colonies) obtained after the removal of the conditional cue were plotted against the successive testing times. This relation between the decrease of the ants' scores and the time that elapsed since removal of the conditional cue did not correspond to a parametric regression model and was thus fitted using a scatter-plot smoother, the non-parametric local

Table 1. Ants' conditioning scores while acquiring olfactory conditioning, and then, after removal of the olfactory cue (pieces of thyme), while losing their conditioning.

Time	N^{os} of correct *vs* wrong responses given by ants of colonies A	B	C	D	Mean conditioning score	Cue memorization *vs* no memorization: binomial test, P value
Conditioning acquisition in						
7 hours	6 *vs* 4	6 *vs* 4	7 *vs* 3	5 *vs* 5	60.0%	0.1335
24 hours	6 *vs* 4	8 *vs* 2	6 *vs* 4	7 *vs* 3	67.5%	0.0197
31 hours	8 *vs* 2	8 *vs* 2	7 *vs* 3	8 *vs* 2	77.5%	0.0005
48 hours	9 *vs* 1	8 *vs* 2	8 *vs* 2	8 *vs* 2	82.5%	< 0.0001
55 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	8 *vs* 2	87.5%	< 0.0001
72 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
Cue removal						
Loss of conditioning after						
4 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
8 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
12 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
16 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
20 hours	9 *vs* 1	7 *vs* 3	8 *vs* 2	8 *vs* 2	80.0%	0.0001
24 hours	7 *vs* 3	7 *vs* 3	6 *vs* 4	8 *vs* 2	70.0%	0.0089
28 hours	6 *vs* 4	6 *vs* 4	6 *vs* 4	6 *vs* 4	60.0%	0.1335
32 hours	5 *vs* 5	6 *vs* 4	5 *vs* 5	6 *vs* 4	55.0%	0.3192
40 hours	5 *vs* 5	6 *vs* 4	5 *vs* 5	5 *vs* 5	52.5%	0.4364
50 hours	5 *vs* 5	6 *vs* 4	6 *vs* 4	5 *vs* 5	55.0%	0.3192
60 hours	5 *vs* 5	7 *vs* 3	6 *vs* 4	6 *vs* 4	60.0%	0.1335

Table 2. Ants' conditioning scores while acquiring visual conditioning, and then, after removal of the visual cue (a green rectangle), while losing their conditioning.

Time	**N^{os} of correct *vs* wrong responses given by ants of colonies**				**Mean conditioning score**	**Cue memorization *vs* no memorization: binomial test, P value**
	A	**B**	**C**	**D**		
Conditioning acquisition in						
7 hours	6 *vs* 4	6 *vs* 4	6 *vs* 4	5 *vs* 5	57.5%	0.2148
24 hours	6 *vs* 4	5 *vs* 5	7 *vs* 3	5 *vs* 5	57.5%	0.2148
31 hours	7 *vs* 3	7 *vs* 3	6 *vs* 4	7 *vs* 3	67.5%	0.0197
48 hours	7 *vs* 3	8 *vs* 2	8 *vs* 2	7 *vs* 3	75.0%	0.0013
55 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	7 *vs* 3	82.5%	< 0.0001
72 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
80 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
Cue removal						
Loss of conditioning after						
4 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
8 hours	8 *vs* 2	9 *vs* 1	8 *vs* 2	8 *vs* 2	82.5%	< 0.0001
12 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
16 hours	7 *vs* 3	7 *vs* 3	8 *vs* 2	9 *vs* 1	77.5%	0.0005
20 hours	6 *vs* 4	6 *vs* 4	7 *vs* 3	6 *vs* 4	62.5%	0.0778
24 hours	4 *vs* 6	6 *vs* 4	6 *vs* 4	7 *vs* 3	57.5%	0.2148
28 hours	4 *vs* 6	5 *vs* 5	5 *vs* 5	6 *vs* 4	50.0%	0.4364
32 hours	4 *vs* 6	5 *vs* 5	7 *vs* 3	6 *vs* 4	55.0%	0.3192
40 hours	5 *vs* 5	6 *vs* 4	5 *vs* 5	6 *vs* 4	55.0%	0.3192
50 hours	5 *vs* 5	5 *vs* 5	6 *vs* 4	5 *vs* 5	52.5%	0.4364
60 hours	5 *vs* 5	6 *vs* 4	6 *vs* 4	7 *vs* 3	60.0%	0.1357

polynomial LOESS function in R. The curve running the best between the data points turned out to require, by trials and errors, a smoothing span of 0.30 (for the olfactory lavender and the visual yellow cues), 0.50 (for the visual green cue) or 0.70 (for the olfactory thyme cue) with a polynomial degree 2. Additionally, 95% confidence bands were drawn. Plotting the residuals versus the fitted y values (not shown in a graph) showed a random distribution around a mean of zero, what fulfilled an assumption of the LOESS regression.

The four colonies being independent from each other, the numbers of tested ants corresponding to a given time were added, this sum amounting thus to 40 for each given time. For each given time, the binomial test was used to calculate the probability that the total number of observed correct and wrong choices of the ants is drawn from a population that would have gone equally towards the 'correct' and the 'wrong' branches of the Y-maze (i.e., with $p = q = 0.5$). As we were interested in knowing if a greater proportion of workers remembered the cue and therefore chose it, the statistical test was one-tailed. No correction for multiple comparisons was required since each statistical test was made on an independent set of data.

The kinetics of the memory loss observed in the experiments made with or without an induced increase of the ants' activity (i.e., Experiment I *vs* III and Experiment II *vs* IV) were compared by using the two-tailed non-parametric Wilcoxon test between the mean scores they presented at testing times ranging from 12 to 40 hours after the cue removal.

Table 3. Ants' conditioning scores while acquiring olfactory conditioning, and then, after the olfactory cue (pieces of lavender) removal and being induced to increase their activity (by having placed a ramp at the nest entrance and food farther), while losing their olfactory conditioning. This allowed to assess their loss of memorization of the cue and to know how they perceived the elapsed time when being more active than usual.

Time	**N^{os} of correct *vs* wrong responses given by ants of colonies**				**Mean conditioning score**	**Cue memorization *vs* no memorization: binomial test, P value**
	A	**B**	**C**	**D**		
Conditioning acquisition in						
7 hours	6 *vs* 4	7 *vs* 3	6 *vs* 4	5 *vs* 5	60.0%	0.1357
24 hours	7 *vs* 3	7 *vs* 3	7 *vs* 3	7 *vs* 3	70.0%	0.0089
31 hours	8 *vs* 2	8 *vs* 2	8 *vs* 2	7 *vs* 3	77.5%	0.0005
48 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	8 *vs* 2	87.5%	< 0.0001
55 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
72 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
Cue removal						
Loss of conditioning after						
4 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
8 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
12 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
16 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
20 hours	9 *vs* 1	9 *vs* 1	9 *vs* 1	9 *vs* 1	90.0%	< 0.0001
24 hours	8 *vs* 2	9 *vs* 1	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
28 hours	8 *vs* 2	9 *vs* 1	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
32 hours	8 *vs* 2	8 *vs* 2	8 *vs* 2	8 *vs* 2	80.0%	0.0001
40 hours	6 *vs* 4	6 *vs* 4	6 *vs* 4	6 *vs* 4	60.0%	0.1357
48 hours	5 *vs* 5	6 *vs* 4	5 *vs* 5	6 *vs* 4	55.0%	0.3192
56 hours	5 *vs* 5	5 *vs* 5	6 *vs* 4	5 *vs* 5	52.5%	0.4364
64 hours	6 *vs* 4	5 *vs* 5	6 *vs* 4	5 *vs* 5	55.0%	0.3192
72 hours	6 *vs* 4	7 *vs* 3	6 *vs* 4	5 *vs* 5	60.0%	0.1335
80 hours	6 *vs* 4	6 *vs* 4	6 *vs* 4	6 *vs* 4	60.0%	0.1335

RESULTS

Experiment I: memory loss of an olfactory cue (odor of thyme) after its removal

Numerical results are given in Table 1, photos can be seen in Figure 3, and Figure 5 presents a graph which visualizes the overtime memorization of the removed learned cue.

The ants rather quickly acquired olfactory conditioning, somewhere between 24 and 31 hours of learning, the very significant (P = 0.0005) mean conditioning score of 77.5% (80% for colony A, B, D and 70% for colony C) being attained at 31 elapsed training hours. They reached the score of 90% (P < 0.0001) after 72 training hours. After the removal of the cue, the ants kept intact the memory of the learned cue during some 8 hours and kept a high significant score during the 20 following hours (mean score = 80%; P = 0.0001). Thereafter, they quickly lost the memory of the learned cue: a mean score of 70% was observed 24 hours after the cue removal (P = 0.0089) and the score observed at 28 elapsed hours (60%) was no longer significant (P = 0.1335). The conditioning score fell from highly significant (80% at 20 hours after the cue removal) to non-significant (60% at 28 hours) in only 8 hours. The minimum score-value of 52.5%

Table 4. Ants' conditioning scores while acquiring visual conditioning, and then, after the visual cue (yellow rectangles) removal and being induced to increase their activity (by having placed a ramp at the nest entrance and food farther), while losing their visual conditioning. This allowed to assess their loss of memorization of the cue and to know how they perceived the elapsed time when being more active than usual.

Time	**N^{os} of correct *vs* wrong responses given by ants of colonies**				**Mean conditioning score**	**Cue memorization *vs* no memorization: binomial test, P value**
	A	**B**	**C**	**D**		
Conditioning acquisition in						
7 hours	6 *vs* 4	5 *vs* 5	5 *vs* 5	6 *vs* 4	55.0%	0.3192
24 hours	6 *vs* 4	7 *vs* 3	5 *vs* 5	6 *vs* 4	60.0%	0.1335
31 hours	6 *vs* 4	6 *vs* 4	7 *vs* 3	8 *vs* 2	67.5%	0.0197
48 hours	7 *vs* 3	8 *vs* 2	7 *vs* 3	8 *vs* 2	75.0%	0.0013
55 hours	7 *vs* 3	8 *vs* 2	8 *vs* 2	8 *vs* 2	77.5%	0.0005
72 hours	8 *vs* 2	8 *vs* 2	8 *vs* 2	9 *vs* 1	82.5%	< 0.0001
80 hours	9 *vs* 1	8 *vs* 2	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
88 hours	8 *vs* 2	9 *vs* 1	8 *vs* 2	9 *vs* 1	85.0%	< 0.0001
Cue removal						
Loss of conditioning after						
4 hours	8 *vs* 2	9 *vs* 1	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
8 hours	9 *vs* 1	8 *vs* 2	8 *vs* 2	9 *vs* 1	85.0%	< 0.0001
12 hours	9 *vs* 1	9 *vs* 1	8 *vs* 2	8 *vs* 2	85.0%	< 0.0001
16 hours	8 *vs* 2	9 *vs* 1	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
20 hours	8 *vs* 2	9 *vs* 1	9 *vs* 1	8 *vs* 2	85.0%	< 0.0001
24 hours	8 *vs* 2	9 *vs* 1	8 *vs* 2	8 *vs* 2	82.5%	< 0.0001
28 hours	7 *vs* 3	9 *vs* 1	8 *vs* 2	8 *vs* 2	80.0%	0.0001
32 hours	7 *vs* 3	7 *vs* 3	8 *vs* 2	7 *vs* 3	72.5%	0.0036
40 hours	6 *vs* 4	6 *vs* 4	6 *vs* 4	6 *vs* 4	60.0%	0.1335
48 hours	5 *vs* 5	4 *vs* 6	6 *vs* 4	5 *vs* 5	50.0%	0.4364
56 hours	6 *vs* 4	5 *vs* 5	5 *vs* 5	5 *vs* 5	52.5%	0.4364
64 hours	6 *vs* 4	5 *vs* 5	5 *vs* 5	6 *vs* 4	55.0%	0.3192
72 hours	7 *vs* 3	6 *vs* 4	6 *vs* 4	5 *vs* 5	60.0%	0.1335
80 hours	6 *vs* 4	6 *vs* 4	5 *vs* 5	7 *vs* 3	60.0%	0.1335

was reached 40 hours after the cue removal. A slight increase, though not significant, of the mean conditioning score appeared 60 hours after the removal of the cue.

The LOESS trend curve, established on the totality of the scores of the four colonies (48 observations), clearly shows an intact memorization of the cue during 8 hours, and thereafter a rapid loss of its memorization from 20 to 28 hours after its removal. This quick decrease was followed by non-significant overall scores till the end of the testing, 60 hours after the removal of the cue. However, these overall scores were all above 50%, with no score that was particular to a colony and testing time below 50%.

The 95% confidence bands were narrow.

Thus, the ants reacted well to a cue that they perceived 24 hours ago or less (i.e., recently), and then stopped reacting significantly after 28 hours, although they seem to have kept some trace in memory.

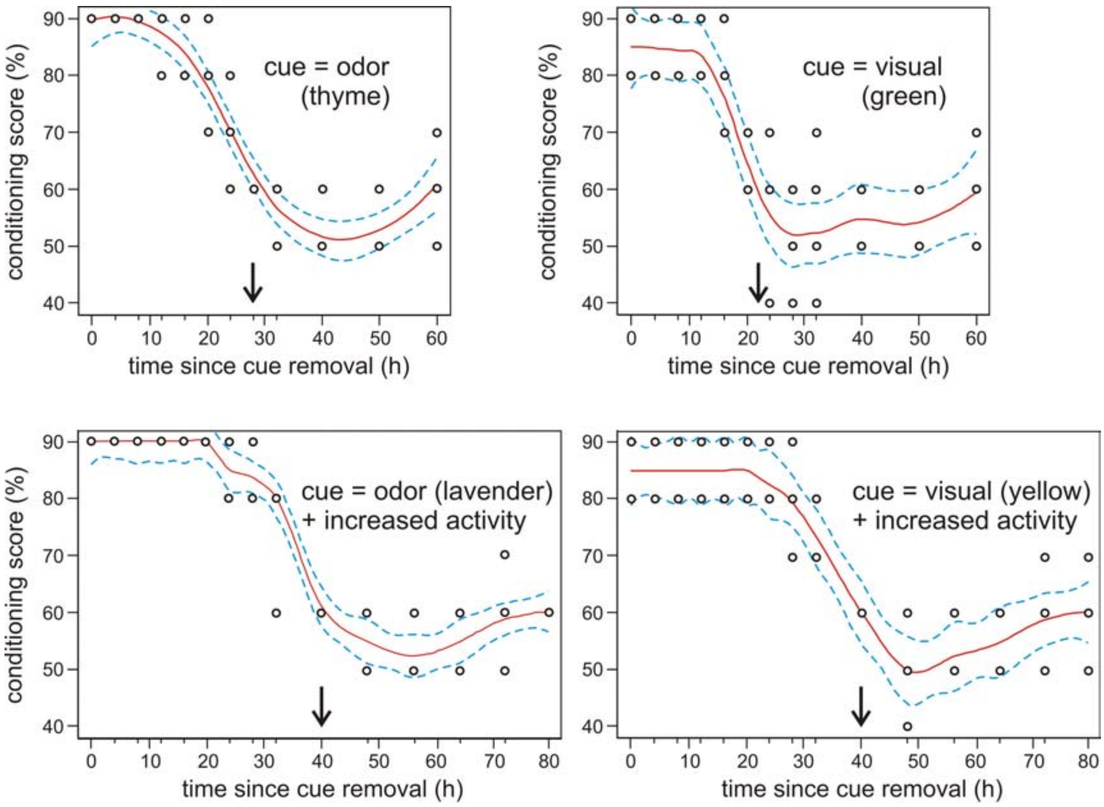

Figure 5. Scatterplot smoothing curves showing, through changes in the conditioning score of the four used colonies, the overtime loss of memorization of a learned cue after its removal. Local polynomial regression (LOESS) curve with 95% confidence intervals. The arrows show the time since when the ant colonies, as a whole, statistically no longer responded to the cue.

Experiment II: memory loss of a visual cue (green rectangle) after its removal

Numerical results are given in Table 2, photos can be seen in Figure 3, and Figure 5 presents a graph which visualizes the overtime loss of memory of the learned visual cue.

The ants rather quickly acquired visual conditioning, reaching a mean conditioning score of 75% (70% for colonies A and D, 80% for colonies B and C) in 48 training hours. The ants' mean score stabilized at 85% after 72 training hours ($P < 0.0001$). After the removal of the cue, the ants kept significantly intact the memory of the learned cue during some 16 hours ($P = 0.0005$). Thereafter, they quickly lost the memory of the learned cue: the mean score of 62.5% for the four colonies was at the edge of significance ($P = 0.0778$) 20 hours after the cue removal, the critical limit of 50% being even overstepped 24 hours after the removal of the cue in colony A and reached after 28 hours in colonies B and C. The conditioning score fell from highly significant (77.5% at 16 hours after the cue removal) to clearly non-significant values (57.5% at 20 hours) in only 8 hours. The minimum mean score-value of 50% was reached 28 hours after the cue removal. Later on, colonies C and D showed some slight increase of their conditioning score (e.g., 7 correct responses vs 3 wrong ones at respectively 32 and 60 hours after the cue removal), but the ants' mean score while climbing till 60% was still non-significant.

The LOESS trend curve, established on the totality of the scores of the four colonies (48 observations), clearly shows that the ants kept an intact memory of the cue during 12 or 16 hours and that they rapidly lost its memory from 16 to some 20 hours after its removal.

The lowest overall memorization score of 50% was observed 28 hours after the cue removal. This rapid loss with three particular score values (a particular score is the proportion of correct choices particular to a given colony and testing time) of 40% from 24 to 32 hours was followed by what could appear as a slow and weak memorization recovery of the visual cue with 5 particular scores of 60% and one of 70%, but the overall scores ranging from 52.5% to 60% were not significant till the end of the experiment, 60 hours after the withdrawal of the cue. Consequently, the ants remembered and reacted well to a recent event (an event that was present maximally 16 hours earlier), and no longer to an event perceived since a longer time, though they appeared to continue keeping some slight memory of them.

Experiment III: memory loss of an olfactory cue (odor of lavender) after its removal and while being under an experimentally induced increased activity

Numerical results are given in Table 3, a few photos are shown in Figure 4, and a graphical presentation of the results can be found in Figure 5.

As during Experiment I, the ants rather soon acquired olfactory conditioning. They reached a significant (P = 0.0089) mean conditioning score of 70% in 24 training hours and a 90% score after 55 hours. After having removed the olfactory cue, and having forced the ants to increase their activity (by placing a ramp at the nest entrance and setting their food farther from the nest), the ants kept intact their memory of the previously learned cue during a longer time than during Experiment I: they presented a high significant conditioning score of 90% and of 80% until 20 and 32 hours, respectively after the cue removal. After that, the ants' conditioning score quickly decreased, reaching in 8 hours a non-significant score of 60% 40 hours after the cue removal, and the smallest value of 52.5% in the course of the next sixteen hours. Thereafter, the ants' memory somewhat recovered, leading to a mean conditioning score of 60% at 72 as well as at 80 hours after the cue removal. Such a slight, however non-significant increase also occurred during Experiment I.

The LOESS trend curve, established on the 60 scores that were measured on the four colonies, clearly showed a rapid loss of memory from 32 to 40 hours after the removal of the cue, and the lowest value of memorization 56 hours after the cue removal. This quick decrease was followed from 64 h after the cue removal by what resembled to a slow, feeble memory recovery of the learned cue with no particular scores below 50%, but 8 of 60% and one of 70%. However, this led to still non-significant overall responses. As for the two previous experiments, the 95% confidence bands were narrow.

Thus, as in Experiment I, the ants appeared to remember and to significantly respond to recently perceived olfactory cues and, overall, to not respond to olfactory cues they have perceived since a longer period of time, although retaining some memory of them.

The difference between Experiments I and III did not concern the succession of events (intact memory, rapid loss and slight recovery), but the kinetics of the ants' reaction 12 to 40 hours after the cue removal (Wilcoxon test: N = 7, P = 0.018). In fact, what occurred from 20 to 60 hours after the cue removal during Experiment I (i.e., without an increase of the ants' activity) occurred from 32 to 72 hours during Experiment III (i.e. with an increase of the ants' activity). Consequently, when being induced to increase their activity they globally no longer reacted to an olfactory cue some 40 hours after its removal instead of after 28 hours without such an experimentally induced increase. Under increased activity, the ants thus underestimated the passing time, i.e., they lived it mentally some 1.4 times more slowly.

Experiment IV: memory loss of a visual cue (yellow rectangle) after its removal and while being under an experimentally induced increased activity

Table 4 gives the numerical results, Figure 4 presents some photos, and Figure 5 gives a graphical representation of the results.

As occurred for Experiment II, the ants rather rapidly acquired visual operant conditioning. They reached a mean conditioning score of 75% and 85% at respectively 48 and 80 training hours.

After the removal of the cue and having forced the ants to increase their activity (by placing a ramp at the nest entrance and locating the food farther than usually), the ants kept the conditioning score of 85.0% until 20 hours after the removal of the cue. Then, still being significant, their score decreased to 72.5% in twelve hours and after that, in eight hours it rapidly decreased to a non-significant value of 60% that was reached 40 hours after the removal of the cue. The lowest overall value of 50% with a particular score of 40% (colony B) was attained 48 hours after the removal of the cue. Thereafter, their memorization of the cue seemed to somewhat recover, even reaching a mean of 60% of correct responses, although this overall score was not significant.

The LOESS trend curve, established on the totality of the scores presented by the four colonies, clearly showed a rapid loss of memory from 28 to 40 hours after the removal of the cue, with the lowest value of memorization at 48 hours. This quick decrease was followed by some kind of slow, feeble memory recovery of the learned cue from 56 to 80 hours after the removal of the cue with 7 particular scores of 60% and two of 70%, although the overall scores were not significant. As for the three previous experiments, the 95% confidence bands were narrow. Consequently, as in Experiment II, the ants well remembered and reacted to recently perceived visual cues, but they no longer significantly reacted to those perceived since a long time, though keeping some memory of them, i.e., presenting a non null response in front of them.

The succession of events occurred as during Experiment II, but their kinetics differed from 12 to 40 hours after the cue removal (Wilcoxon test: N = 6, P = 0.028). What occurred from 16 to 60 hours after the cue removal in Experiment II occurred from 28 or 32 to 72 hours in Experiment IV, i.e., when the ants were more active. Under increased activity the ants no longer reacted to a cue 40 hours after its removal instead of about 20 hours without such an activity increase (Experiment II). They thus, as in Experiment III, underestimated the time spent, living it mentally approximately twice as slowly.

As for the slight recovery of the memory of the learned cue, it seemed to occur at equivalent speed during Experiments II and IV.

Experiment V: Ants' capability of remembering past events

As was described here above, during the period of non-significant conditional score values that followed the removal of the conditioning cue in the Experiments I-IV, the ants somewhat recovered its memory as is shown by the particular conditioning values scored by each colony, which amounted for the total of the 96 scores taken into account to: 4 scores of 40%, 34 of 50%, 50 of 60% and 8 of 70%, instead of a symmetrical distribution of the scores around the conditioning limit of 50%. This asymmetry clearly appears by comparing the number of 58 scores above and 4 scores under the limit of 50% with a theoretical distribution of equal proportions (binomial test: $P < 0.00003$).

Testing again the same colonies (Table 5) in front of a yellow rectangle 100 hours after the end of Experiment IV, in front of lavender 250 hours after the end of Experiment III, in front of thyme 380 hours (for colonies C and D) or 680 hours (for colonies A and B) after the end of Experiment I, and in front of a green rectangle 530 hours after the end of Experiment II, showed that by using binomial tests, the colonies equally (mean score: 57.5% to 60%) and not significantly responded to the long ago learned cues. However, the number of particular scores amounted to none under 50%, 4 scores of 50%, 9 of 60% and 3 of 70%. A statistical comparison of the 12 scores found above 50% and none below this limit with a theoretical equal distribution of proportions shows this asymmetry (binomial test: $P < 0.003$).

Thus, the ants took no account of temporal differences between events that occurred more than 100 hours ago. In other words, they clearly distinguished recent and old events, i.e., events that occurred less than about 20-40 hours ago and those that occurred since any longer times, not distinguishing the exact time of occurrence of the latter. However, although the overall score towards long ago learned cues was not significant, the score per colony was significantly higher than by chance, showing that the ants nevertheless somewhat remembered the cues although they had lost the greatest part of their memory.

Table 5. Ants' reaction to cues no longer perceived since differently long time periods, in order to examine how the ants estimate different past time periods. The results show that they poorly although significantly remembered these cues, and that the time that passed since the last sight they had of the cue had no influence on their memorization performance.

Time elapsed since preceding test :	Cues	N^{os} of correct *vs* wrong responses given by ants of colonies A	B	C	D	Mean conditioning score	Binomial test, P value
100 hours	yellow rectangles	6 *vs* 4	6 *vs* 4	5 *vs* 5	7 *vs* 3	60.0%	0.1335
250 hours	lavender	6 *vs* 4	6 *vs* 4	5 *vs* 5	6 *vs* 4	57.5%	0.2148
380 hours	thyme			5 *vs* 5	7 *vs* 3	60.0%	0.2514
530 hours	green rectangles	6 *vs* 4	6 *vs* 4	7 *vs* 3	5 *vs* 5	60.0%	0.1335
680 hours	thyme	6 *vs* 4	6 *vs* 4			60.0%	0.2514

DISCUSSION

From our work on the maximum time interval admitted between the perceptions of two visual cues allowing *M. sabuleti* ant workers to still be able to mentally add them up [9], it was obvious that this insect has a non-linear perception of the running time. We here investigated on this presumption. We worked on forager ants of four colonies of this species and used operant conditioning. The obtained conditioning scores during learning were rather high because the cues were placed at the nest entrance and not near the food: the ants saw thus the cues very often, and in addition, the nest entrance in itself represents for them a very valuable reward. After having removed the learned cues, we quantified over time their memorization by the ants, and this showed that they very well remembered the cues during a few tens of hours, and then quickly, in less than ten hours, ceased to remember them. In the present work as well as in the previous one [9], the loss of memorization appeared to obey to a decreasing sigmoid, showing that the ants obviously discriminated recent and older events, with a clear temporal threshold between them. We also showed that they did not differentiate long past events as for the time period of their occurrence, but nevertheless appeared to keep a faint reminder of them after having lost their main memory. Indeed, some 60 and more hours after the cue removal, lightly better scores were observed than those obtained after some 30 to 50 hours. This is discussed below.

In the present work, we wanted to know if the ants' general activity influenced their perception of the elapsed time, as was demonstrated to be the case in pigeons [15]. To examine this factor, we took care to implement the experimentally induced activity of the forager ants after having withdrawn the learned cue and not during its learning, because it has been shown that an increase of the ants' activity reduces the conditioning score they can acquire [21]. Moreover, such an experimental work had to be done either using the same cues on different colonies, or using different cues on the same colonies. Indeed, when an individual has acquired conditioning to a cue, it is no longer 'naïve' for that cue; it acquires again conditioning to that cue more quickly than usually. In the present work, we used the same colonies, but different cues. The result of the experiments was that, when the ants were more active than usual (they were induced to walk on a ramp at the nest entrance and to walk farther for getting food), they delayed in losing their memory of the previously learned cues, thus underestimating the elapsed time when they were more active. In other words, they acted at 40 elapsed hours as if they had lived only some 20 hours, underestimating by a factor of about two the time spent while being active.

The kind of curve that describes the ants' loss of conditioning over time is suitable for any kind of learned events, but it should be kept in mind that the progression of the curve along time may differ according to the nature of the events remembered by the ants (pleasant or uncomfortable odors, differently shaped or colored visual cues) and to the environmental circumstances of the experiments (e.g., location of the cues, rearing of brood or callows). Other physiological or ethological traits as well as some environmental factors may also affect the individuals' time perception. For instance, parasitoid wasps have their time perception affected by the ambient temperature [22], and in a wide range of vertebrate species, from fishes to man, including amphibians, reptiles and birds, the perception of temporal change is linked to metabolic rate and body size [23]. These kinds of factors were however kept stable during the present experiments.

Humans can have a precise notion of the 'running' time due to their skill of acquiring a mental representation of it; they conceptualize mental travel in time nearly as they travel in space [24]. It is still debated if non-humans detain or lack such a time conceptualizing [24, 25]. Humans remember the order of events in time [10] and thus have what we could call an 'oriented time line' as they have an 'oriented number line' [26]. Ants have a left to right orientated number line [27]. Do they acquire in the course of their life a 'time line', at least at a rudimentary level? To answer this question, experiments on the subject should use several different conditioning acquisitions and losses performed at different times, and then assess the ants' recollection of the cues presented during each of these conditionings. It is what we made in 'Experiment V', by using the four previous conditionings. This investigation was not a non-sense since pigeons appear to represent time on a line, and moreover on a logarithmic scale, as they do for numbers [28]. Our result was that the ants do not detain this skill: they did not locate in the elapsed time events experienced since differently long time periods (Experiment V). They may thus have an only rudimentary time representation in which the recently passed events are rather well located, and the events passed since a long time are located 'behind' or 'farther', with no further distinction about more precise time periods of occurrence. However, even if the conditioning scores that were measured 60 hours and more after the removal of the learned cues were on average not significantly different from chance, the amount of the score values that were particular to a colony and a given testing time were statistically above the 50% limit. This suggests that the ants do not entirely forget past information and learning (as they continuously kept about 60% of their memorization) and could keep in mind this information for acting in the future (see below).

It may be argued, on one hand, that if *M. sabuleti* workers chose more frequently than expected the cue they had learned long ago instead of choosing the empty branch of the Y-maze it could be because they were more attracted by something present in a branch instead of nothing. However, they could have chosen it as well by having remembered something of the cue they had learned long ago. On the other hand, the here reported ants' late slight memory increase could not have been obtained if a complete extinction had been performed (extinction occurs by presenting the conditional stimulus without the unconditional stimulus [29 and references therein]. After the fall of the ants' conditioning score, we no longer tested the ants every 4 hours, but spaced the testing sessions 8 to 10 hours apart in order to reduce the extinction effect because performing any test implies that the conditional stimulus is presented without the unconditional stimulus. Having been less often tested should have helped the ants to retain some residual memory of the previously learned cues. This may explain the increase in their responses from 60 hours after the removal of the cues. Furthermore, as long as 22 and 28 days after removing the cues, and without having tested the ants in the meantime, they still presented scores of 60%. Thus, they retained the memory of the previously learned cues in the long term.

The faculty for an animal to remember the content (the 'what'), the spatial location (the 'where') and the occurrence in time (the 'when') of previous experienced events is called the episodic-like memory ('-like' because it is not possible to know if animals consciously recall what they experienced) [30]. In the present work on *M. sabuleti* workers, we did not investigate about their mental recollection ability to discriminate different kinds of formerly experienced events (as learned cues), but only about their ability to memorize the occurrence of a passed event. Moreover, the workers were not tested as for their memorization of the locations where events occurred. As for the time elapsed since the learning of a cue, the experimented ants lost their vivid memory in a few tens of hours, keeping only some residual recollection for events that occurred since longer times (up to about one month), without reacting discriminatively to cues last perceived for different lengths of time. Thus, the way in which the present experiments were conceived does not enable to conclude that *M. sabuleti* workers have an episodic-like memory. However, a previous experiment [31] in which *M. sabuleti* workers had to choose between two learned cues, one of them having been associated to a food item they no longer received since one day, they chose this cue, expecting to receive the food item that was no longer provided since one day. This kind of flexibility is one characteristic of an episodic-like memory, allowing the ants to make future choices according to the circumstances. It is possible, but not demonstrated, that the vivid memory of *M. sabuleti* workers corresponds to an episodic-like memory of short duration (a few hours). Alternatively, the recall of residual memory over long durations could be attributed to semantic memory, which relies on a sense of familiarity based on knowledge alone [32, 33].

Having memorized somewhat of an event learned in the past should be sufficient for *M. sabuleti* workers to, later on, use this recollection in order to adequately react when this situation occurs again, without having memorized, and thus taken into account, the precise time of learning occurrence. Two previous experimental works, one on the ant *Myrmica rubra* and one on the ant *M. ruginodis*, showed that these ants kept over the long term some slight memory of the learned cues since, if conditioned again to the same cues, they acquired far more quickly than during their first conditioning session a high level of conditioning [34, 35].

Researchers estimate that detaining a 'running' time notion is a part of conscious experience, and thus a self-projection over time-scales [36]. Ants might approach some kind of consciousness since it was shown that *M. rubra, M. ruginodis* and *M. sabuleti* workers were able to recognize themselves in a mirror [37]. Concerning the perception of elapsed time, which consists in perceiving the succession and the duration of events, this skill can be detained by individuals only if they are able to distinguish between succession and simultaneity [38]. The workers of the ant *M. sabuleti* have such a skill: they mentally add up elements if they perceive them simultaneously and not if they perceive them consecutively [39, 40]. Furthermore, as workers 2 to 3 years old, but not young ants [2, 41] can acquire spatio-temporal learning, it might be presumed that the latter acquire the notion of time through a maturation process.

Let us note that we worked at a colonial level, not at an individual level and that differences could exist between individual ants (idiosyncrasy) and between colonies [42] as for their learning, memorization, and elapsed time perception, like for most tasks and skills.

CONCLUSION

Myrmica sabuleti worker ants are not 'stuck' in time as they remember past events, have a notion of the time spent, and detain some kind of episodic memory. After having shown that they can expect future events on the basis of previously experienced ones [3-5], and can associate learned items with their time period of occurrence [6-8], we here show that these insects remember cues learned during a few tens of hours before, then quickly (but not entirely) and non-linearly lost their memory according to a kind of sigmoid curve, what makes them to clearly distinguish between past and recent experienced events. Their time perception is influenced by their level of activity: while being more active, they underestimate the duration of the elapsed time (e.g., they loss the memory of a cue after 40 hours under an increase of activity while after 20 hours under normal activity). After having lost the main part of the memorization of an event, they nevertheless appear to keep a faint reminder of it as was shown when testing again the ants in front of the different cues to which they had been trained since differently long time periods (up to some 28 days). During these tests, the ants appeared to not precisely locate in time the old experienced events, but to simply retain some residual memory of them, what may help them acting in the future as adequately as possible when in presence of similar events.

CONFLICT OF INTEREST STATEMENT

We affirm having no conflict of interest as for the here related work.

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