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Episodic-like memory: New perspectives from a behavioral test in rats

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In order to have a tool to empirically test the ideas derived from a theoretical model, we extended a protocol for evaluation of episodic-like memory in rats, based on the triad "what, where, context" for definition of memories. As with the computational model, our intention was for the animal being tested to store a specific number of object-place-context configurations as different memories, which would then be retrievable from cues. The aim of this work was to evaluate the influence of the number of configurations to be memorized on the performance of the task. Sixty-five Wistar male rats were evaluated. In accordance with previous work, for two configurations, the recognition index was indicative of recognition of the element mismatching the original memory (mean = 0.28; SEM = 0.12). The recognition index for three configurations was lower (mean = 0.15; SEM = 0.10), evidencing less recall with increasing requirements. The results also showed a trend toward recognition of novelty for the first and the last memory when evaluating three configurations (a "U" shape in the exploratory preference's curve), showing the primacy and recency effects typical of memory both in humans and animals. Nonetheless, the data presented a high inter-subject variability which makes the test non-robust for small groups. However, if used before and after a treatment for a same subject, we suggest that the protocol presented in this work can be a useful behavioral test for the evaluation of episodic-like memory in rats in terms of a variable task demand.

Keywords: Episodic-like memory; hippocampus; rats.

1. Introduction

In a previous theoretical study about the functioning of the hippocampus in memory, we found some important though not striking facts: the more we learn, the less we recall, i.e., an increase in the number of patterns to be memorized is accompanied by a poorer performance in recalling the patterns (Weisz & Argibay, 2009). In terms of episodic memory, these results, though intuitive, have not been shown in animals.

In fact, showing evidence of episodic memory in animals has not been easy, mainly because this kind of memory was first defined for humans — as a neuro-cognitive system that enables human beings to remember past experiences —, making use of purely human qualities (self, autonoetic awareness and subjectively

sensed time) (Tulving, 2002). The introduction of the term "episodic-like" to refer to episodic memory in animals turned the issue into a less controversial topic for debate; according to it, episodic recall is identified as the retrieval of information about "where" a unique event or episode took place, "what" occurred during that episode, and "when" it happened (Clayton *et al.*, 2007). Above and beyond reaching a consensus in the strict world of definitions, the evaluation of this cognitive function has been even more difficult.

The need of such a test is not trivial. Episodic memory is an important cognitive ability needed to be used over and over for a normal development of our daily life. A lot of processes impact on this function, ranging from normal to pathological and from natural to artificially driven. The testing of episodic memory becomes crucial when seeking to understand the mechanisms that could interfere with, improve or affect this kind of memory in an experimental context. Being one of the several types of hippocampal-dependent learning, it is desirable to be able to differentiate its evaluation from other hippocampal-dependent tasks (e.g., spatial navigation and contextual fear conditioning) in view of the differential effects some processes could have on them. Such a test would increase basic research on cognitive sciences in fields such as psychiatry, psychology and neuropsychopharmacology.

1.1. *The study of episodic-like memory*

Beginning little more than a decade ago with a work in scrub jays (Clayton & Dickinson, 1998), researchers have developed several tests in different species to show evidence that animals can recall a specific past experience. Some of these tests are based on more traditional behavioral tasks, such as object recognition tasks, fear conditioning learning or tasks using radial or E-mazes (Babb & Crystal, 2005; Dere *et al.*, 2005; Eacott & Norman, 2004; Eacott *et al.*, 2005; Kart-Teke *et al.*, 2006; Crystal, 2009; Barbosa *et al.*, 2010). Also, as it is known that the temporal lobe is essential for episodic memory function (Squire *et al.*, 2004), a series of works have studied the impact of several lesions made to this lobe or to the hippocampus itself on the performance in tests involving objects, places, and context in order to elucidate their specific contributions to memory (Mumby *et al.*, 2002; Eacott *et al.*, 2005; Eacott & Gaffan, 2005; O'Brien *et al.*, 2006; Piterkin *et al.*, 2008; Sauvage *et al.*, 2008; Easton *et al.*, 2009; Li *et al.*, 2011).

Besides the traditional view that an episodic-like memory is defined by its "what-where-when" components, different approaches have also been taken (Fortin *et al.*, 2004; Eacott *et al.*, 2005). In the present study, we started from the work of Eacott & Norman (2004) and their alternative view by which the "when" component can be defined by the context in which the episode takes place. This protocol was later extended and redefined so that the animals being studied could store different object-place-context configurations as different memories that were then retrievable from cues, in order to test the predictions from a neurocomputational model (Weisz & Argibay, 2009).

Episodic-like memories simultaneously answer to the what, where and when problem and although the former two are easy to address in one paradigm, inclusion of the latter — the issue of time — has proved difficult. Here, the focus is put on the *occasion* in which an event takes place, which can be crucial for episodic memory. This occasion can be specified by some characteristic of the event that can include its temporal context, but it can also be specified by the visuo-spatial cues in which the event took place (Eacott & Norman, 2004; Eacott & Easton, 2007, 2010).

As in Eacott & Norman (2004), in the current work, a single exposure phase is followed by a test phase where the rats are presented with two copies of the same familiar object, only one of which has not been encountered previously in the current location and context, although both location and context are themselves familiar. Thus, the *configuration* of the object, location and context is novel, although no other aspect or combination of aspects is new. If rats possess integrated memory for the "what, where, context" triad, they will preferentially explore the object that appears in a novel configuration of place and context over the object that appears in a familiar configuration.

In each experiment and during the study phase, each object appears both on the left and on the right of the arena, but in different contexts. Later, in the test phase, it is this context (indicative of the occasion or the time when the scene was learned) which points out the relative position of objects (that enables the recall of the specific what-where-which combination).

The episodic nature of the memory used in the task was further supported by studies of the same authors, who found that when sectioning the fornix, rats greatly decreased their performance in the test[a] (Eacott & Norman, 2004). Other studies, using similar tasks involving objects, places and contexts, have found that damage to the hippocampal formation, believed to support episodic memory functions, would not cause an inability to encode or store a representation of the context in which the objects are encountered. Instead, it would impair the ability to remember specific locations of familiar objects within a particular context (O'Brien *et al.*, 2006; Piterkin *et al.*, 2008), basis of episodic encoding, as we propose.

1.2. *Objectives*

In our experiments, more than two configurations were presented to further evaluate if they were recognized as different memories, thus extending the work of Eacott & Norman (2004). Under the working hypothesis that performance of rats in an episodic-like task will decrease as the number of configurations to be memorized is increased, the aim of this paper was to assess the influence of the number of configurations to be learned on the performance of the task, as a way to evaluate how the system works with an increasing task demand.

[a]The memory impairments following fornix lesions are typically equivalent to those caused by complete hippocampal lesions (Squire *et al.*, 2004).

2. Materials and Methods

2.1. *Subjects*

Sixty-five male Wistar rats were used as subjects, which were $12-16$ weeks old at the beginning of the experiments. They were housed individually during the test, having free access to food and water. All experiments were conducted during the light phase (12-hour light/dark cycle). All procedures were approved by the Institutional Ethical Committee for Experimental Protocols. All efforts were made to minimize animal suffering or discomfort.

2.2. *Arena and experimental conditions*

The experimental arena was mounted in an open field made of acrylic (base dimensions: $1\,m^2$; height: $48\,cm$) with white walls and exchangeable flooring (creating different contexts) (Fig. 1). In the testing room, external landmarks helped the spatial orientation of animals in the open field. Room temperature was maintained within a range of $20 \pm 2°C$.

Two perforations equidistant from walls were made to the open field, allowing the fixations of objects at two different locations (right and left). In all the experiments, three different configurations were created (A, B and C) using three different contexts, three different objects and the right and left positions (Fig. 2).

The objects were made of wood, of similar size (around $12\,cm$ height, $10\,cm$ width and $10\,cm$ depth), varying in shapes and colors. Multiple copies of them helped prevent odor marking. An exhaustive selection of objects was made before the beginning of the experiments. The choice was made on the basis of their levels of exploration by rats. The purpose was that there were no significant differences in the salience of objects in order to avoid any bias in the test. Several objects producing too much or too little exploration were discarded.

2.3. *Habituation*

In this work, habituation had two objectives: first, to accustom animals to handling and to experimental conditions (testing room, open field), and second, to familiarize

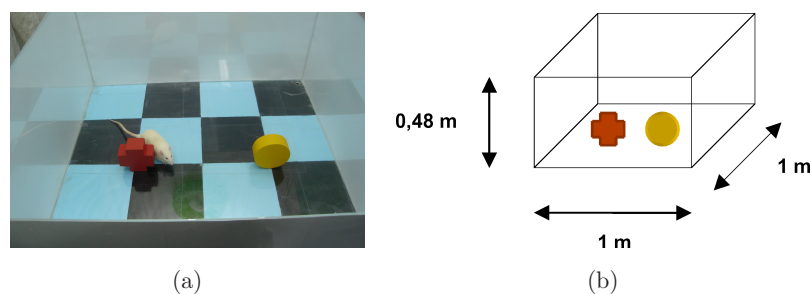(a)   (b)

Fig. 1.   Experimental arena. (a) Open field with white walls and exchangeable flooring. Two perforations equidistant from walls allowed the fixations of objects at two different locations (right and left). The objects, made of wood and with similar size, varied in shapes and colors. (b) Dimensions of the arena.
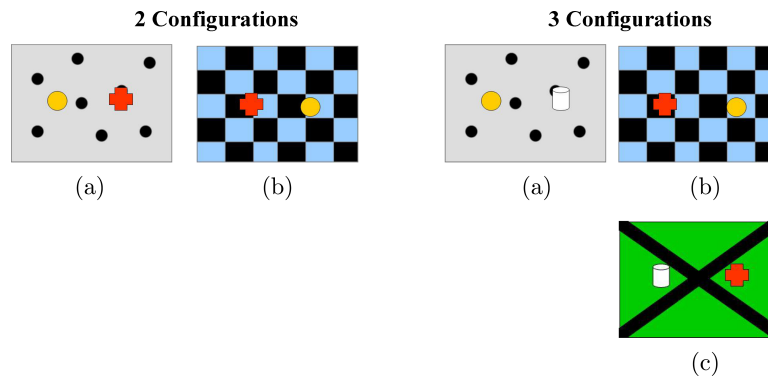
Fig. 2.   Configurations. Throughout the experiments, three different configurations were used (a, b and c) by means of three different contexts, three different objects and the right and left positions. For both two and three configurations, each object appeared both on the left and on the right of the arena. Thus, it was the context which pointed out the relative position of objects (providing a specific what-where-which combination).

them with the different contexts and objects to be used in the protocol. Thus, once evaluated, neither the contexts nor the objects were new for rats.

Habituation took place in 2 or 3 consecutive days (depending on whether two or three configurations were being tested), in two daily sessions per rat (at 8:00 a.m. and 2:00 p.m.). Each day, a different context was used with two different objects (one object per session). A simple session consisted in allowing the rat to freely explore the open field for 10 min, with the object to be familiarized with placed at its center.

2.4. Behavioral testing

Behavioral testing took place the day following the habituation. All rats were evaluated in a single testing session.

The protocol was as follows: throughout the exposure phase, the rat was placed in the open field and was allowed to freely explore the arena, setting each of the configurations A, B and C (only A and B when testing two configurations) for 5 min. Between configurations, the rat was removed from the open field and kept individually in a holding cage, in the same testing room, for periods of 5 min. Having completed the exposure phase, a retention interval (5 min or 24 h) separated this phase from the test session, lasting for another 3 min (Fig. 3).

In this last phase, the arena was set as a modified Configuration A, B or C (one group was tested with Configuration A, another group with Configuration B and a third group with Configuration C). Now, the testing configuration had two copies of the same object where only one of them did not match the original configuration. The novelty, counterbalanced between animals to be placed either to the right or to the left in the open field, consisted then in a new *combination* of context-object-place, since no simple context, object or place was by itself novel (Fig. 4).
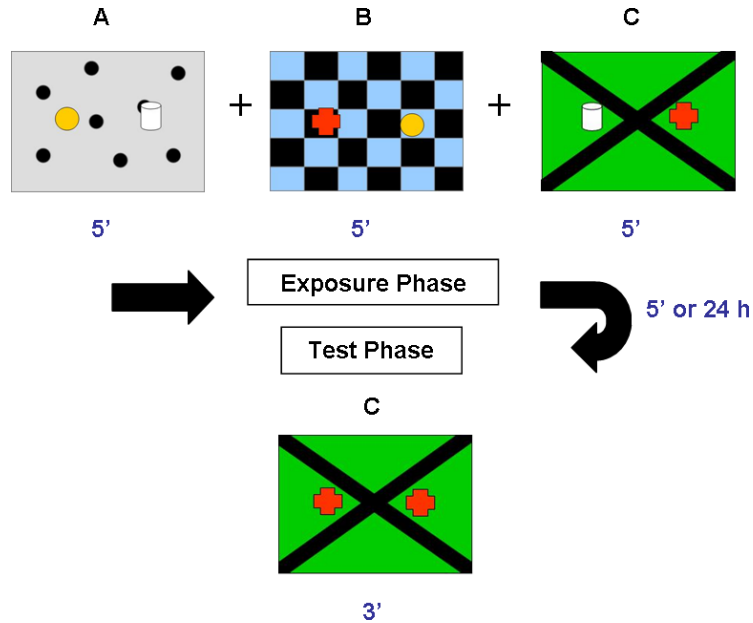
Fig. 3.   Behavioral protocol. Throughout the exposure phase, the rat was placed in the open field and was allowed to freely explore the arena, set as each of the configurations A, B and C (only A and B when testing two configurations) for 5 min. Between configurations, the animal was removed from the open field and kept individually in a holding cage (in the same testing room) for periods of 5 min. Finally, after a retention interval (5 min or 24 h), the rat was evaluated with configuration A, B or C slightly modified, for another 3 min.

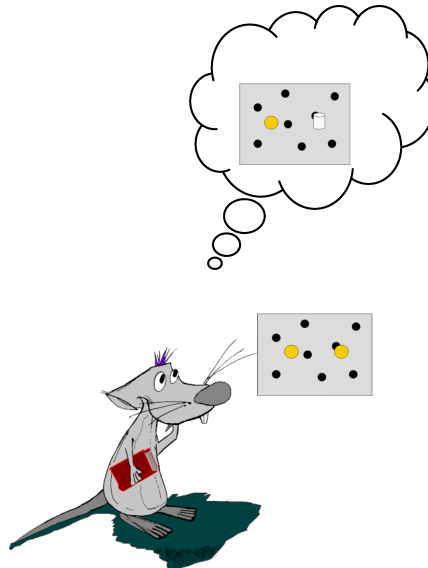Fig. 4.   Episodic retrieval. The testing configuration has two copies of the same object, where only one of them does not match the original configuration. The novelty consists then in a new *combination* of context-object-place, since no simple context, object or place is by itself novel. To successfully solve the task, the rat has to remember the specific settings learned at the time of the study phase.

2.5. *Data handling and analysis*

For each rat, recognition of novelty during the test phase was assessed by an index of exploratory preference. Exploration of an object was defined as the rat's nose being within 1 cm from and orientated toward the object, sniffing at or otherwise closely attending to the object. The exploratory preference index (EPI) was computed as the difference between time spent exploring the objects in the novel and in the familiar object-place-context combinations, calculated as a proportion of the total time spent exploring both objects:

$$EPI = \frac{t_{\text{nov}} - t_{\text{fam}}}{t_{\text{nov}} + t_{\text{fam}}} \tag{2.1}$$

Thus, individual differences in the overall level of exploration were taken into account (Ennaceur & Delacour, 1988). On this index, ranging from -1 to 1, a value higher than zero reveals an exploratory preference for the novel combination.

The animals were divided into sex groups (Table 1) depending on the number of configurations they were exposed to (two or three), the particular configuration being tested (A or B for two configurations and A, B or C for three configurations), and the retention interval between the exposure phase and the test phase (5 min or 24 h); this last option was done in order to study the short or long-term nature of the memory under test. An inclusion criterion was established for data, and it was based on an adequate exploration of the objects. To be included in the analysis, rats had to spend a minimum of 15 s exploring both objects in the exposure phase or a minimum of 10 s exploring both objects in the test phase (taken from Barker *et al.* (2007)).

Finally, previous studies on the kind of tasks that can be thought as components of the present test (i.e., testing memory for objects, memory for place, memory for object in place and memory for context) have demonstrated that the level of discrimination varies along 3 min of the test phase (Dix & Aggleton, 1999; Mumby *et al.*, 2002). We then started analyzing only the first minute of the test phase, as this time bin was found to be a better choice in previous works with tasks involving memory of places (Dix & Aggleton, 1999; Mumby *et al.*, 2002; Barbosa *et al.*, 2010). We will later compare and analyze the results for the first minute, the first 2 min, and the complete 3 min of the test in those cases presenting a tendency to recall.

Table 1.   Sample groups.

	Group 1 ($n = 10$)	Group 2 ($n = 9$)	Group 3 ($n = 7$)	Group 4 ($n = 12$)	Group 5 ($n = 13$)	Group 6 ($n = 14$)
Number of configurations	2	2	3	3	3	2
Test	A	B	A	B	C	B
Retention interval	5 min	5 min	5 min	5 min	5 min	24 h

3. Results

3.1. *Retrieval of two and three configurations*

Sixty-five rats were incorporated to the analysis, having passed the inclusion criterion. The exploratory preference indexes for groups 1 to 5 (see Table 1) are shown in Fig. 5(a). Though without statistical significance in all the cases due to the high variability of the responses, the data shows a clear tendency towards positive values, indicating a preference for novelty, when rats are tested with the first and the last configurations (two configurations, test A: $t = 0.86$, df $= 9$, $p > 0.05$; two configurations, test B: $t = 3$, df $= 8$, $p < 0.05$; three configurations, test A: $t = 1.26$, df $= 6$, $p > 0.05$; three configurations, test B: $t = 0.08$, df $= 11$, $p > 0.05$; three configurations, test C: $t = 2.04$, df $= 12$, $p > 0.05$; one-sample t-test comparing the
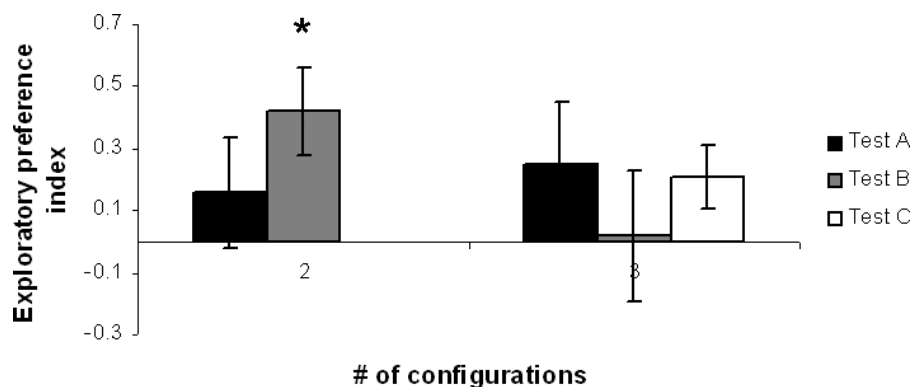
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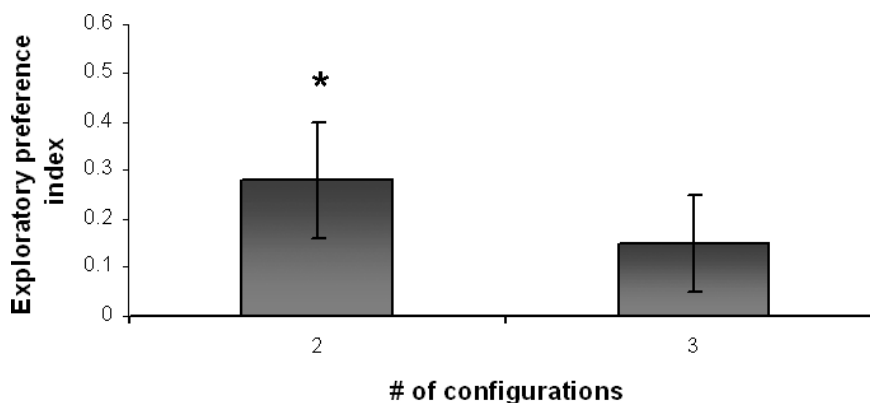
(b)

Fig. 5.   Performance on the episodic-like memory task. (a) The exploratory preference indexes for groups 1 to 5 when computing the first minute of the test phase, with their mean $\pm$ SEM values. The data shows a trend toward successful recognition of novelty when rats are tested with the first and the last configurations, either for two or three configurations. (b) Grouping for two and three configurations (two configurations $=$ group $1 +$ group 2; three configurations $=$ group $3 +$ group $4 +$ group 5) with their mean $\pm$ SEM values. The data shows recognition of novelty for two configurations. $^*p < 0.05$; one-sample t-test.

exploratory preference index with 0, the null preference value). However, an analysis across groups did not show statistical differences (two configuration: $t = -1.16$, df $= 17$, $p > 0.05$, t-test; three configurations: $F_{(2,29)} = 0.54$, $p > 0.05$, One-way ANOVA).

As we can see from Fig. 5(a), grouping the results for two or three configurations would not be representative of the recall of two or three memories, as the recall index depends on which configuration is being tested (A or B for two configurations and A, B or C for three configurations). However, we believe this grouping would be illustrative of a general recall level for a specific number of memories, just for comparative purposes (Fig. 5(b)). Though both indexes show a tendency to success in recognizing novelty, only the case for two configurations was statistically significant (two configurations: $t = 2.41$, df $= 18$, $p < 0.05$; three configurations: $t = 1.51$, df $= 31$, $p > 0.05$ for one-sample t-test). Again, an analysis across groups did not show statistical differences ($t = 0.89$, df $= 49$, $p > 0.05$, t-test).

3.2. Analysis of the level of discrimination along the 3 min of the test phase

As already introduced in Sec. 2.5, previous studies on the kind of tasks that can be thought as components of the present test (i.e., testing memory for objects, memory for place, memory for object in place and memory for context) have demonstrated that the level of discrimination varies along the 3 min of the test phase (Dix & Aggleton, 1999; Mumby et $al.$, 2002). In view of that, in Fig. 6, the exploratory
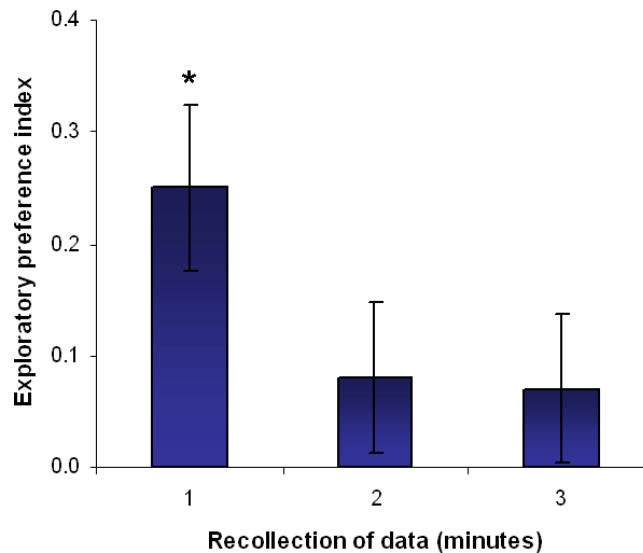

Fig. 6. Variation of the level of discrimination within the 3 min of the test phase. The bars (mean-$\pm$ SEM) represent the exploratory preference index when evaluating the first, the first 2 or 3 min of the test phase for the cases with a tendency to recall (group 1 + group 2 + group 3 + group 5) (n = 39). Data taken from the first minute was the most indicative of recognition. $^{*}p = 0.01$; one-sample t-test, test value $= 0$.

preference index for the cases presenting a tendency to recall (group $1 +$ group $2 +$ group $3 +$ group 5) (n $= 39$) is shown when analyzing the first minute, the first 2 min, and the complete 3 min of the test to see which measure was more sensitive to recognition of novelty. In accordance with previous works with tasks that involve memory of places (Dix & Aggleton, 1999; Mumby *et al.*, 2002; Barbosa *et al.*, 2010), we found that data taken from the first minute was the most indicative of recognition (1 min: $t = 3.43$, df $= 38$, $p = 0.01$; 2 min: $t = 1.25$, df $= 37$; $p > 0.05$; 3 min: $t = 1.07$, df $= 37$, $p > 0.05$; one-sample t-test, test value $= 0$). However, an analysis across groups did not show statistical differences ($F_{(2,112)} = 2.11$, $p > 0.05$, One-way ANOVA).

3.3. *Long-term evaluation of the episodic-like memory*

The episodic-like memory evaluated in this study has been evidenced in the short term (5-min retention interval). Its potential long-term presence was studied in a different group (group 6, Table 1) with a 24-h retention interval and two configurations (test B), for being the case with the largest probability to be retained. As previously reported by Eacott & Norman (2004), who did not find memory maintenance beyond the first 2 h, we found no retention of the tested configuration 24 h after its presentation (group 6: $t = 0.31$, df $= 13$, $p > 0.05$; one-sample t-test) (Fig. 7). Altogether, these results are indicative of the short-term nature of the memory formed during the task. Again, a comparison of means did not show statistical differences ($t = 1.49$, df $= 21$, $p > 0.05$, t-test).

3.4. *Study of laterality*

While during the test the relative position of novelty (right or left) was counterbalanced among animals in order to avoid misinterpretations due to side preferences, a last analysis was done for studying laterality. To do this, we discriminated the
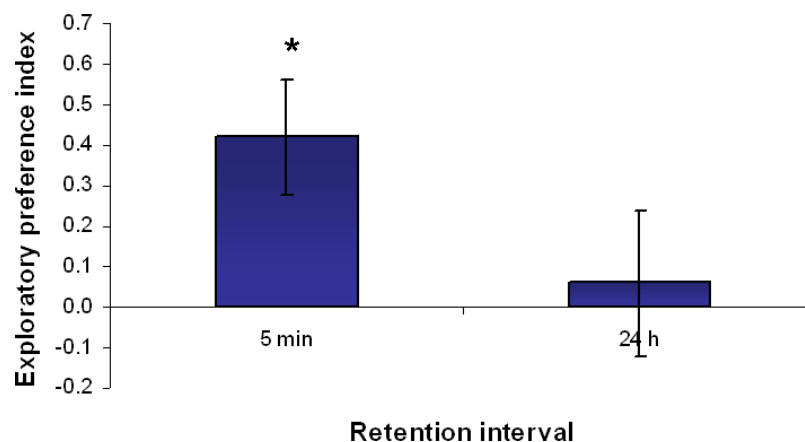
Fig. 7.   Long-term evaluation of the episodic-like memory. The bars (mean $\pm$ SEM) represent the performance on the task for a short (group 2) and a long retention interval (group 6). The bar for 5 min is reproduced from Fig. 5(a). The close-to-zero value for 24 h (indicating no retention) signals the short-term nature of the memory. $^{*}p < 0.05$; one-sample t-test, test value $= 0$.
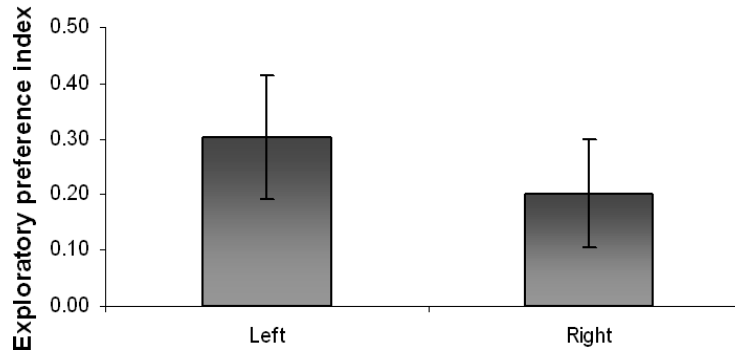
Fig. 8. Study of laterality. The recognition index for the cases with a tendency to recall (group 1 + group 2 + group 3 + group 5) was discriminated depending of the position left/right of the novelty. A comparison of means showed no differences between them ($p > 0.05$, t-test).

recognition index for the cases with a tendency to recall (group 1 + group 2 + group 3 + group 5), depending on the position left/right of the novelty (Fig. 8). A comparison of means showed no differences between those indexes ($t = 0.67$, df $= 37$, $p > 0.05$; t-test)) while both are indicative of recognition (Left: $t = 2.68$, df $= 19$, $p < 0.05$; Right: $t = 2.09$, df $= 18$, $p = 0.05$; one-sample t-test, test value $= 0$), showing that the resolution of the task was no guided by side preferences.

4. Discussion

In this study, we have attempted to develop a behavioral test that assesses episodic-like memory in rats by redefining and extending a test previously published (Eacott & Norman, 2004). Episodic-like memories simultaneously answer to the "what, where and when" problem and although the former two are easier to address in one paradigm, inclusion of the latter — the issue of time — has proved difficult. Nevertheless, progress has recently been made on this issue and here we used the way provided by Eacott & Norman (2004) to address this topic. We reduced episodic-like memory to being specified by a number of object-place-context configurations which can be acquired and form representations; this, during probe trial, can be recalled and differentiated in terms of place, item and time (here, provided by context). Then, we implemented a series of two or three configurations and tested animals for each of the memories (A and B for two configurations; A, B and C for three configurations). We found a better performance after short intervals (5 min) compared to longer ones (24 h) and after two rather than three configurations.

4.1. *The testing of episodic memory*

With the aim of capturing the central aspects of episodic encoding, we believe the task used in this study has several advantages, which can be summarized as follows:

- Trial-unique learning: Only one session is sufficient for rats to learn and then discriminate the configurations, avoiding extensive training.

- Incidental learning: Subjects do not have any kind of instruction about which aspects they have to learn in the learning session. Incidental learning depends entirely on individual subjects' motivation.
- Lack of primary reinforcers: As pointed out by Dere *et al.* (2006), the use of stimuli which are assumed to have no natural significance for the animal and which have never been paired with a reinforcer is important in the study of episodic-like memory.
- No food and water deprivation: Animals do not have to be manipulated to solve the task.

4.2. *Primacy and recency effects*

An important feature of the exploratory preference's curve shown in Fig. 5 for three configurations signals an interesting fact: the recognition curve adopts a "U" shape, indicating that when learning series of configurations occurs, rats have a better recall of the first and the last configurations; this phenomenon is known as *primacy* and *recency* effects. The potential presence of a recency phenomenon was already suggested in a recent work based on the same test but only derived from pilot studies (Le Cozannet *et al.*, 2010). The U-shaped serial position curve (this curve shows the relation between position within the series and likelihood of recall) is typical of short-term memory in humans but has also been observed in long-term memory, yielding the view that the phenomenon is multiply-determined (Reisberg, 2007). This feature of memory has been early evidenced in rats using spatial tasks (Kesner & Novak, 1982; Bolhuis & van Kampen, 1988), as well as with nonspatial items (Reed *et al.*, 1991). In this study, we acknowledge that three time points may be unconvincing to show ostensible primacy and recency effects while not showing statistically significant differences across groups. This fact, mainly due to the high variability of the results, is discussed in Sec. 4.3. However, we found the results very interesting as they are novel in the context of episodic-like memory. We take these findings as preliminary and leave the issue open for future studies.

4.3. *Variability of the test. Remarks about its use*

As seen in Fig. 5 (and also reflected in the other figures), the data obtained in this study is characterized by a high variability, a fact that in some cases makes showing a statistical significance of results difficult. This high variability in the rats' responses is not surprising since we are evaluating an exploratory behavior which is depicted as being *per se* highly variable, easy to interrupt and highly sensible to changes in stimuli (Veá, 1990). Many variables would interact here, a fact that is easy to realize: we are looking for a spontaneous, self-motivated and not reinforced behavior which would yield very different responses, ranging from not paying attention to the environment at all to memorizing all the surrounding information

and later being able to detect any changes in it. A proactive exploratory behavior is needed to solve the task; nevertheless, this was not always the case, since this behavior depends entirely on the specific individual characteristics. Another source of variability is added by how, having detected the novelty, the rat responds to it: some of them would subtly signal the non-matching object while others would spend a lot of time on it. In spite of what was stated above, what we saw in the present study was a replicative behavior and a clear tendency to respond to novelty, which would suggest that the test is useful for evaluation of this kind of memory. Moreover, the indexes are in agreement with similar indexes previously reported for the only comparable case of two configurations (Eacott & Norman, 2004; Barker *et al.*, 2007; Le Cozannet *et al.*, 2010). In view of that, and in order to be less affected by the inter-subject variability, we propose the use of this test as a paired test; that is, we suggest it should be delivered both before and after a treatment for a same subject.

4.4. *Conclusions*

In summary, we have presented a novel test for episodic-like memory evaluation in rats, which shows important features of memory in humans and animals. Interestingly, we obtained the same results as those predicted by our previous neuro-computational work (Weisz & Argibay, 2009): we saw with the present test that an increasing demand of the task decreases the quality of retrieval. Also, we think that the variable task demand of the test represents a novel and useful feature to take into account when looking for a test for episodic evaluation.

   More studies are needed to support some of the results. Although they are very replicable, we would need to amplify the sample size to achieve the statistical significance (more than animals would be necessary, which exceeds our objectives) due to the high variability of the responses. However, for its use with small groups, we suggest that part of this problem can be avoided if the test is delivered both before and after a treatment or intervention that we are interested in studying in relation to episodic memory.

   In light of what has been exposed above, we believe that the clear tendency and the relevance of the results, in addition to the support and contribution to previous methodologies in the field of the behavioral studies, justify the present work.

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