

A temporal context repetition effect in rats during a novel object recognition memory task

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Abstract Recent research in humans has used formal models of temporal context, broadly defined as a lingering representation of recent experience, to explain a wide array of recall and recognition memory phenomena. One difficulty in extending this work to studies of experimental animals has been the challenge of developing a task to test temporal context effects on performance in rodents. The current study presents results from a novel object recognition memory paradigm that was adapted from a task used in humans and demonstrates a temporal context repetition effect in rats. Specifically, the findings indicate that repeating the first two objects from a once-encountered sequence of three objects incidentally cues memory for the third object, even in its absence. These results reveal that temporal context influences item memory in rats similar to the manner in which it influences memory in humans and also highlight a new task for future studies of temporal context in experimental animals.

Keywords Temporal context · Rat · Recognition memory

Introduction

Our surroundings shape our memories. The ambiance of a restaurant, for example, often frames one's memory of the dining experience to the extent that returning to the

restaurant later can cue a memory of the previous meal. In accordance with its importance, the influence of spatial context on memory has been a major area of research in humans and rodents, both in terms of behavior and neural activity (Godden and Baddeley 1975; O'Keefe and Nadel 1978; Burgess et al. 2001; Davachi 2006; Smith and Mizumori 2006; Rudy 2009). Indeed, several researchers have argued that a fundamental function of the mammalian hippocampal memory system is to support associations between items and their context (Hirsh 1974; Davachi 2006; Knierim et al. 2006; Manns and Eichenbaum 2006; Ranganath 2010).

Nevertheless, context involves more than one's immediate surroundings. A mental representation of the recent past lingers into the present and can become as much a part of a new memory as the current spatial context can. This running average of experience has sometimes been termed temporal context, yet the general idea that mental or physical "elements" change over time and influence everyday memory or conditioned responses has a long history (e.g., McGeoch 1932; Estes 1955; Bower 1972; Bouton 1993; Mensink and Raaijmakers 1988). A relatively recent formal model of temporal context is the temporal context model (TCM; Howard and Kahana 2002). TCM was originally focused on word recall but more generally detailed how a new item becomes associated with its temporal context, how a repeated or retrieved item can cue the temporal context with which it was associated, and how the retrieved temporal context can in turn cue memory for temporally adjacent items from the previous experience. As an everyday example, eating the same appetizer and entree at a restaurant—even if the establishment has changed locations—can cue memory of the previously enjoyed dessert.

TCM and related models have been successful in explaining a wide array of memory phenomena in humans

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(Howard et al. 2005; Sederberg et al. 2008; Howard et al. 2009; Polyn et al. 2009; Sederberg et al. 2011). These models often emphasize temporal contiguity effects emerging from item–context associations (Kahana 1996; Sederberg et al. 2010) and also intersect with a growing literature in both humans and experimental animals related to other temporal aspects of memory, including explicit memory for temporal order and the “when” of “what-where-when” definitions of episodic memory (Morris 2001; Clayton et al. 2003; Crystal 2010; Allen and Fortin 2013; Templer and Hampton 2013). Additionally, recent efforts have shown promise in connecting the proposed representational and mathematical mechanisms of temporal context and temporal order to brain function (Manns et al. 2007; Polyn and Kahana 2008; Aimone et al. 2009; Lehn et al. 2009; Kesner and Hunsaker 2010; Howard et al. 2012; Mankin et al. 2012; Turk-Browne et al. 2012; Eichenbaum 2013; Gershman et al. 2013; Kesner and Rolls 2015).

An important step in furthering this research will be to develop easily administered tasks for assessing temporal context in experimental animals in order to establish cross-species generality, to permit greater access to neural activity, and to open further opportunities for testing hypotheses regarding behavioral processes. Several tasks have been designed for experimental animals to test “episodic-like” memory or memory for temporal order (e.g., Clayton and Dickinson 1998; Fortin et al. 2002; Kesner et al. 2002; Dere et al. 2005; Zhou and Crystal 2009). These tasks and others have been—and will continue to be—key to a cross-species approach to understanding the behavioral characteristics of episodic-like memory and memory for temporal order. For example, a recent study (Allen et al. 2014) found that rats and humans showed memory for the temporal order of items that was similarly influenced by manipulations of item order (e.g., skipping an item). However, training experimental animals on these tasks tends to be labor intensive and/or to yield very few trials per test day. Thus, there is an opportunity for additional memory tasks to probe further the cognitive and neural mechanisms of temporal context, especially if those tasks can be easily administered and used similarly in both humans and experimental animals.

A recent study in humans reported robust effects of temporal context on memory using a relatively simple task that held promise for being adapted for use in experimental animals (Smith et al. 2013). In that task, participants viewed items (photographs or words) one at a time and made a simple judgment (e.g., indoor/outdoor) about each item. The stimuli were experimentally grouped in sets of three sequential items, and these items were either novel or repeated from one prior occurrence. In particular, triplets of items came from one of four conditions: (1) all three items

were novel, (2) all three items were repeated, (3) the first two items were repeated, and the third was novel, and (4) the first two items were novel, and the third was repeated. The motivation of the task design was to permit questions about the extent to which repeating the first two items in a triplet, which operationalized the temporal context for the third item, would cue memory for the original third item. Indeed, the results of the study indicated that when the temporal context of a third item (i.e., the first two items) was repeated without actually repeating the third item, participants later showed better memory for those third items as compared to third items for which the temporal context was not repeated, suggesting that repeating the first two items led participants to incidentally retrieve information about the third item.

The present study sought to adapt the human temporal context repetition task (Smith et al. 2013) for use in rats and to test whether rats would also show temporal context repetition effects. On each trial, rats were first presented with three novel objects that they encountered sequentially as they completed a lap on a circular track. On the next lap, rats again encountered three objects, the identity of which depended on the trial type: (1) all three items were novel (Novel Context Novel Item, NCNI), (2) all three items were repeated (Repeated Context Repeated Item, RCRI), (3) the first two items were repeated, and the third was novel (Repeated Context Novel Item, RCNI), and (4) the first two items were novel, and the third was repeated (Novel Context Repeated Item, NCRI). Recognition memory performance was measured as rats’ spontaneous preference for exploring novel objects more so than repeated objects. Similar to the goals of the study with humans (Smith et al. 2013), the key question was whether rats would show evidence that repeating the first two objects would incidentally cue memory for the third object, even if the third object was not repeated. That is, the present study asked whether rats would show temporal context repetition effects similar to those observed in humans using a task similar to one used previously in humans.

Methods

Subjects

Ten adult male Long-Evans rats, 10–11 months of age, were individually housed on a 12-h light/dark cycle (testing occurred during the light phase) with free access to water and were placed on a restricted diet such that they maintained at least 90 % of their free-feeding weight. All rats had participated more than 1 month previously in an experiment to test the acute effects of systemically administered muscarinic drugs on a standard novel object

recognition memory task (Galloway et al. 2014). All procedures were approved by the Institutional Animal Care and Use Committee at Emory University.

Novel object recognition memory task

Rats performed a recognition memory task that was based on their spontaneous preference for exploring novel objects more so than repeated objects (Ennacuer and Delacour 1988). In general, rats encountered new and repeated objects as they completed clockwise laps on a circular track (outside diameter = 91.5 cm; track width = 7 cm; track height = 82 cm). Four different types of trials (each consisting of three laps) were used to ask questions about rats’ memories for the order in which objects were encountered, and these trial types are detailed below. For all trial types, objects were attached to the outside edge of the track on small platforms at three fixed locations equally spaced around the track (at 3, 6, and 9 o’clock). The 108 objects (not counting duplicates) used in each session were selected from one of two sets of plastic, wood, metal, or ceramic junk objects that were typically larger than 10 cm³ but smaller than 2000 cm³. Figure 1a shows three example objects to illustrate typical size and material. Rats were rewarded with a small amount of chocolate (1–2 chocolate “sprinkles,” weighing approximately 20 g) for completing each lap, irrespective of object exploration. The chocolate was placed on a central runway (at 1 o’clock), where the

rats remained in between laps and trials. The task was self-paced, and the average time between laps was 39.2 s (range = 28.9–48.4 s), and the average time between trials was 83.4 s (range = 56.3–114.6 s). The testing for each rat was completed in a single session that typically lasted approximately 1.5 h. During testing, numerous stationary cues (e.g., shelves) in the testing room were visible to the rats.

Figure 1b shows a schematic of the four trial types used in the task design. Each trial consisted of a lap on an empty track (Lap 0), a lap in which the rat encountered three novel objects (Lap 1), and a lap in which the rat encountered three objects whose identity depended on the trial type (Lap 2). On each lap, the first, second, and third objects were positioned at the 3, 6, and 9 o’clock position, respectively, to keep the spatial position constant. In general, the first two objects on each lap were hypothesized to be a major component of the temporal context for the third object, which represented the object of interest on Lap 2 of each trial type. In RCRI trials, the same three objects were presented on Lap 1 and Lap 2 (e.g., A, B, C and A, B, C, on Lap1 and Lap 2, respectively). In NCRI trials, the first two objects were replaced with new objects on Lap 2 (e.g., A, B, C and X, Y, C). In RCNI trials, the third object was replaced with a new object on Lap 2 (e.g., A, B, C and A, B, Z). In NCNI trials, all three objects were replaced with new objects on Lap 2 (e.g., A, B, C and X, Y, Z). Rats completed 6 of each of the 4 trial types equally spaced

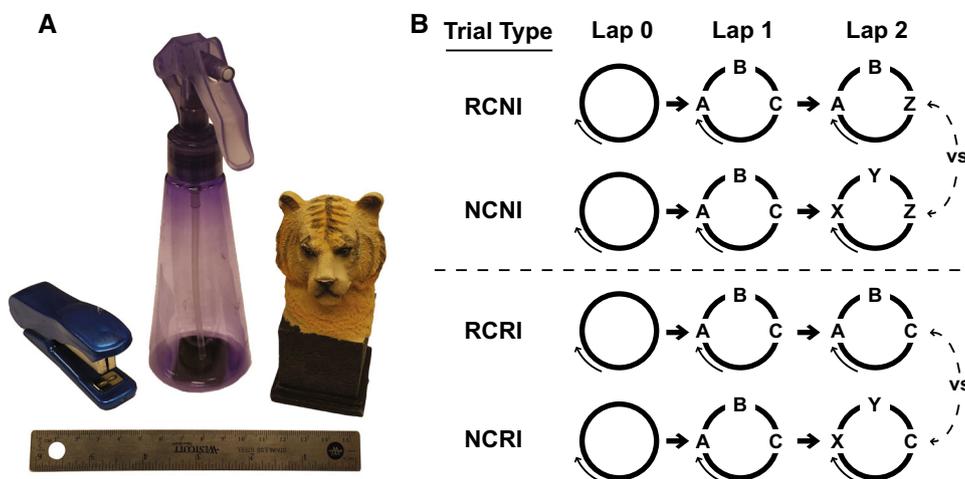


Fig. 1 a Three example objects. Most of the objects used in the present study were not smaller than the toy stapler (left) and not bigger than the spray bottle (middle). The ruler in the foreground is 16 cm long. **b** Schematic of the task design showing examples of each of the four trial types. Rats completed a total of 24 trials, and new objects were used on each trial. On each trial, rats completed three clockwise laps on a circular track. On Lap 0, the track was empty. On Lap 1, three novel objects (e.g., A, B, C) were placed at the 3, 6, and 9 o’clock positions (if 12 o’clock was the bottom of the circle). On Lap 2, three objects were placed in the same positions, but the identity of

the objects depended on the trial type: In Novel Context Novel Item (NCNI), all three objects were novel; in Repeated Context Repeated Item (RCRI) trials, all three objects were repeated; in Repeated Context Novel Item (RCNI) trials, the first two objects were repeated, and the third was novel; and in Novel Context Repeated Item (NCRI) trials, the first two objects were novel, and the third was repeated. The key comparisons were between the third objects on Lap 2 for the RCNI versus NCNI conditions and for the RCRI versus NCRI conditions

across the test session for a total of 24 trials. For each rat, objects were randomly assigned to trials and to object positions within trials. New object sets were used for each trial. For trials in which objects were repeated on Lap 2, identical duplicates of the objects were used to avoid the possibility of scent marking.

Data analysis

Frame-by-frame (30 frames/s) analysis of digital video was used to record times when a rat initiated or terminated exploration of an object. A rat was considered to be exploring an object only if the rat was within 1 cm of the object and was showing evidence of active investigation (e.g., sniffing and directed attention). Infrequent trials on which the rat displayed excessive chewing (>5 s) of any object were excluded from analyses (impacting only 2.9 % of all trials). All videos were rescored by a second blind rater after the videos were digitally respliced such that laps appeared in a random order to minimize inferring trial type. The inter-rater correlations of exploration times for each video were high (mean correlation = 0.916; range = 0.841–0.985). The data presented here are based on the original rater's scoring.

Exploration times were standardized by first calculating a rat's overall mean exploration time separately for the first, second, and third objects on Lap 1 and separately for the first, second, and third objects on Lap 2, collapsed across trial conditions. Standardized exploration times for each object were then calculated as a percent of the mean of the times for all items from that position and lap, giving rise to six total standardized means (e.g., the standardized exploration time would be 150 % for an object encountered and explored for 6 s in the third position on Lap 2 for a rat that on average explored objects in the third position of Lap 2 for 4 s). The standardization procedure was used to account for variability across rats in their general tendency to explore objects and to account for the general trend shown by rats to explore objects more at the beginning of a lap. Objects for which the exploration time was greater than four standard deviations from the mean for the lap position were excluded from the analysis (an average of 1.0 object encounters per rat were excluded). The key questions of interest centered on the third object in Lap 2, and paired-

samples *t* tests were conducted between the exploration times for these objects between the NCNI and RCNI conditions and between the RCRI and NCRI conditions. Additionally, a repeated-measures ANOVA was conducted for the data from Lap 2 to test the overall effects of trial types and for the data from Lap 1 to verify the lack of an effect of trial type for Lap 1. Unless stated otherwise, all statistical analyses used standardized exploration times.

Results

Table 1 shows mean exploration times and standard errors (across rats) for the four trial types. Exploration times were standardized (see “Methods”) to account for variability across rats in their general tendency to explore objects and to account for the general trend shown by rats to explore objects more at the beginning of a lap. Accordingly, Fig. 2 shows the standardized exploration times for the four trial types. Rats explored objects for similar amounts of time across trial types on Lap 1 (effect of trial type: $F(3,27) = 0.237$, $P = 0.87$, $\eta_p^2 = 0.03$; effect of object position: $F(2,18) = 1.651$, $P = 0.22$, $\eta_p^2 = 0.16$; trial type by object position interaction: $F(6,54) = 0.768$, $P = 0.60$, $\eta_p^2 = 0.08$), reflecting the fact that all objects were novel on Lap 1 for all trial types and were randomly assigned to conditions. For Lap 2, the amount of exploration depended on trial type and object position (trial type by object position interaction: $F(6,54) = 7.524$, $P < 0.01$, $\eta_p^2 = 0.46$; effect of trial type: $F(3,27) = 5.850$, $P < 0.01$, $\eta_p^2 = 0.39$; effect of object position: $F(2,18) = 1.686$, $P = 0.21$, $\eta_p^2 = 0.16$). In general, repeated objects were explored for less time than novel objects for objects in the first and second object positions (mean raw exploration time \pm SEM for all repeated and all novel objects in first and second positions = 1.36 ± 0.40 s and 2.34 ± 0.64 s, for repeated and novel, respectively; paired-samples *t* test: $t(9) = 3.455$, $P < 0.01$; 95 % Confidence Interval of the Novel—Repeat Difference = 1.63 to 0.34 s), replicating a well-established effect of repetition on spontaneous object exploration (Ennaceur and Delacour 1988).

The key comparisons centered on the exploration times of the third object on Lap 2. In particular, rats explored novel objects in the third position of Lap 2 more if those objects had been preceded by two repeated objects (RCNI trial type: mean

Table 1 Mean raw exploration times (and standard errors) across conditions for each lap and object type (O1, O2, and O3)

Condition	Lap 1			Lap 2		
	O1	O2	O3	O1	O2	O3
RCNI	2.59 (0.75)	1.34 (0.37)	1.63 (0.59)	2.23 (0.76)	0.76 (0.18)	1.49 (0.53)
NCNI	2.94 (0.89)	1.72 (0.44)	1.73 (0.79)	2.54 (0.58)	1.74 (0.50)	1.09 (0.60)
RCRI	3.21 (0.81)	1.16 (0.25)	1.52 (0.40)	1.84 (0.55)	0.62 (0.18)	0.67 (0.19)
NCRI	3.55 (1.05)	1.80 (0.42)	1.20 (0.26)	3.19 (1.23)	1.90 (0.41)	0.63 (0.22)

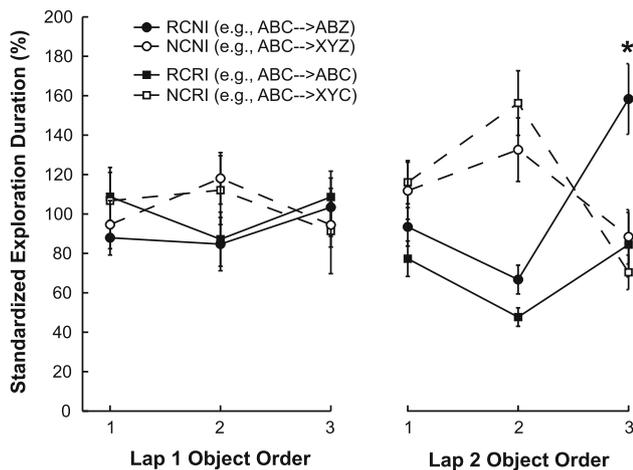


Fig. 2 Mean standardized object exploration times for each of the four trial types. The *lines* show mean standardized exploration times for objects encountered first, second, and third on Lap 1 and Lap 2. The *asterisk* indicates statistical significance ($P < 0.05$) for a key comparison between the third objects on Lap 2 for the RCNI versus NCNI conditions. *Error bars* show SEM

standardized exploration \pm SEM = 158.3 ± 17.9 %) when compared to novel objects in the third position that were preceded by two novel objects (NCNI trial type: 88.4 ± 13.8 %; $t(9) = 2.670$; $P = 0.03$; Cohen's $d = 1.15$; 95 % Confidence Interval of the Difference = 10.6 to 129.2 %). However, rats explored repeated objects in the third position of Lap 2 similarly regardless of whether those objects were preceded by repeated objects (RCRI trial type: 84.4 ± 16.4 %) or novel objects (NCRI trial type: 70.4 ± 8.8 %; $t(9) = 0.749$; $P = 0.47$; Cohen's $d = 0.34$; 95 % Confidence Interval of the Difference = -28.3 – 56.4 %).

Discussion

The main finding was that on Lap 2 rats explored novel objects preceded by two repeated objects (RCNI trials, e.g., object Z in A, B, C \rightarrow A, B, Z) significantly more so than novel objects preceded by two novel objects (NCNI trials, e.g., object Z in A, B, C \rightarrow X, Y, Z). These results suggest that, in RCNI trials, the repeated first two objects on Lap 2 (e.g., A, B) served as a repeated temporal context that cued memory not only for the original encounter with those two objects on Lap 1 (A, B), but also for the unrepeated third object (C). By this view, the memory of that unrepeated third object created a mismatch when the rat encountered a novel third object on Lap 2 (Z), a mismatch or unexpectedness that prompted additional exploration of the new object. In comparison, in NCNI trials, no objects were repeated on Lap 2, and thus, there was no repeated temporal context to cue a potentially conflicting memory or expectation of the third object encountered on Lap 1. This

finding parallels results from a similar task in humans (Smith et al. 2013) in which there was evidence that repeating the first two items in a once-presented triplet automatically cued memory for the third item despite a lack of explicit instructions (or training) to recall that item. In particular, the results provide clear evidence of temporal context repetition effects in rats and highlight the task developed for the present study as a promising route for future studies of temporal context to complement and extend work in humans.

One notable feature of the current task is that it requires relatively little training. Rats were trained only to complete laps on a circle track for a small piece of chocolate, and the reported behavioral effects emerged from rats' spontaneous preference for exploring novel objects. Another feature of the current task is that the temporal context effect occurred with only one repetition of the first two objects in a given trial without requiring a manipulation of the emotional salience of the stimuli (e.g., via fear conditioning). That is, a single exposure to a sequence of three objects was apparently sufficient for the rat to form a memory of the triplet, such that a repetition of the first two objects triggered memory for the third. Taken together, these features indicate that the task not only provides a feasible means for testing hypotheses about temporal context, but also does so in a way that highlights the robust and incidental nature of the temporal context effect in rats.

A second main hypothesis tested in the present study was that repeated objects encountered third on Lap 2 would be remembered better (i.e., explored less) if those objects were preceded by two repeated objects (RCRI trials, e.g., object C in A, B, C \rightarrow A, B, C) as compared to repeated objects preceded by two novel objects (NCRI trials, e.g., object C in A, B, C \rightarrow X, Y, C). However, rats explored the repeated third object similarly in both RCRI and NCRI trial types. It is unclear why a repeated temporal context did not alter performance for a repeated third object in this trial type when a repeated temporal context showed clear evidence of altering behavior for a novel third object in the RCNI trial type (vs. NCNI trials). One possibility for the lack of a behavioral effect is a floor effect on exploration times. Indeed, rats spent a relatively short amount of time exploring the third object in Lap 2 on the RCRI and NCRI trial types (mean \pm SEM = 0.670 ± 0.188 s and 0.626 ± 0.222 s, respectively). As a standardized percentage of all exploration times of third objects on Lap 2, these numbers were not particularly low, but the very short absolute times raised the possibility that a floor effect would have attenuated any potential differences between RCRI and NCRI trial types. Nevertheless, the clear effect in RCNI trial types (vs. NCNI trials) provides good evidence that repeating the first two objects in an triplet serves as a repeated temporal context that cues memory for the third object.

The present study contributes to the accumulating evidence that associative memory formation in humans and rats entails binding items to a temporal context in addition to a spatial context (Howard and Kahana 2002; Crystal 2010; Allen and Fortin 2013). In particular, the results indicate that in rats, as in humans, memory for an object is automatically associated with its temporal context and that repeating temporal context by itself can cue a memory of the object. The present study also establishes a relatively simple behavioral paradigm for testing further hypotheses about the specific cognitive and neural mechanisms of temporal context, potentially in parallel studies in humans and rodents.

One key question is whether the temporal context repetition effect reported here relates more to episodic-like memory as characterized by TCM (Howard and Kahana 2002) and related models of human declarative memory or to accounts of temporal context (e.g., Bouton 1993) and temporal coding (e.g., Arcediano and Miller 2002; Balsam and Gallistel 2009) based on data from classical conditioning experiments. A definitive answer may be beyond the current data. According to all of the above accounts, two stimuli encountered close in time (e.g., object 1 and object 2 or a conditioned stimulus and an unconditioned stimulus) will be associated with a “temporal context” (Bouton 1993; Howard and Kahana 2002) or “temporal map” (Arcediano and Miller 2002; Balsam and Gallistel 2009), and repetition of the first item can cue memory of the second item. The fact that objects in the present study were repeated only once and that exploration was spontaneous and not followed by external reinforcement would suggest that the context repetition effect related more to episodic-like memory. Nevertheless, further research will be needed to resolve the extent to which the proposed “expectation” of the third object on Lap 2 in the present experiment is best characterized as expectancy related to episodic-like recollection or as more simply an expected value in the statistical sense as it has been used to explain some conditioned responses (e.g., Balsam and Gallistel 2009). One useful manipulation for future studies would be to test whether rats would be sensitive to swapping the order of the first two objects on the second lap to determine the extent to which the repetition effects observed in the present study depend on temporal order per se.

Another key question centers on the neural correlates of temporal context and whether activity in particular brain regions shows a greater propensity for temporal integration of recent activity or for reinstatement of past temporal context. For example, the extent to which the temporal context repetition effect observed here depends on the integrity of the hippocampal memory system would help to understand the extent to which the effect reflects episodic-like memory. In particular, numerous studies in humans

and experimental animals point to key roles for subregions of the hippocampus in memory for temporal order (e.g., the potential role of region CA1 in temporal pattern separation; Kesner and Rolls 2015). The number of unanswered questions in part reflects previous challenges in testing hypotheses regarding temporal context effects in experimental animals, and the context repetition paradigm provides one route forward for acquiring answers.

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Conflict of interest None.

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