Mental time travel in the rat

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Abstract

I outline the perspective that searching the contents of memory is a form of mental time travel in nonhumans that is relatively tractable because it focuses on the contents of memory. I propose that an animal model of mental time travel requires three elements: (1) the animal remembers multiple events using episodic memory, (2) the order of events in time is included in the representation, and (3) the sequence of events can be searched to find a target that occurred at a particular time. I review experiments suggesting that rats represent multiple items in episodic memory (Element 1) in order of occurrence (Element 2) and engage in memory replay to search representations in episodic memory in sequential order to find information at particular points in the sequence (Element 3). The cognitive building blocks needed for mental time travel may be quite old in the evolutionary timescale.

Introduction

Mental time travel (MTT) is the human capacity to reexperience the past and imagine the future (1-3). Episodic memory involves recalling the past and in humans is described as the phenomenological conscious experience of projecting oneself (autonoesis) in time (chronesthesia) (4, 5). Because there are no agreed upon empirical approaches to investigate subjective experiences in nonhumans, efforts to develop animal models of episodic memory have focused on the contents of episodic memory (6). Although theoretical perspectives about MTT in people focus on autonoetic consciousness (4) and chronesthesia (5), these types of subjective experiences may not be assessed in nonhumans. Therefore, comparative studies of mental time travel take a behavioral perspective, asking what an animal capable of MTT can do via its behavior (6).

According to the central hypothesis of animal models of episodic memory, at the moment of a memory assessment, the animal remembers back in time to a specific earlier event (7-13). We have conducted a number of tests of this hypothesis and described evidence for what-where-when memory (14), source memory (15), binding of episodic memories (16), memory of multiple items in context (17), replay of episodic memories (18, 19), and answering unexpected questions after incidental encoding (19, 20). These lines of evidence suggest that rats are a suitable model of episodic memory (10).

Here, I outline the perspective that rats are capable of MTT. I review research that demonstrates that rats can search representations in episodic memory to find specific event memories, rules out the use of memory trace strength and working memory in this approach, shows that this ability is hippocampal dependent, and shows that rats replay incidentally encoded episodic memories.

Animal models of episodic memory: Overview

Whether animals can remember back in time to an earlier event or episode is a fundamental question in comparative cognition (21, 22). Thus, the suitability of nonhumans as a model of episodic memory has been investigated and debated for over two decades. Tulving (23) initially defined episodic memory as memory for the spatial and temporal characteristics of an event. Subsequently, Tulving focused on the conscious experience of episodic memory (3-5). The initial definition of episodic memory is suitable for studies in animals because it focuses on the content of episodic memory (e.g., what, where, when), and avoids the human subjective experiences that cannot be evaluated in animals. Clayton and Dickinson (24) were the first to show that animals retrieve episodic memories. Cases of episodic memory have subsequently been shown in other species, e.g., (25-34).

To validate an animal model of episodic memory, it is necessary to rule out non-episodic hypotheses (29). To establish that an animal remembers a a unique episode, it must be shown that it is not using judgments of familiarity of the event. Episodic memory involves memory of an event and the contextual details surrounding the episode. Familiarity is the impression that an item is known without remembering the contextual details associated with the event (4).

When developing animal models of episodic memory, we do not expect all aspects of human episodic memory to be included in any one model. I favor this terminology because the focus is on developing a model of selected aspects of human cognition. In the sections that follow, I describe our efforts to develop an animal model to document that rats replay a stream of episodic memories. I outline the perspective that this research may be used to develop an animal model of MTT.

An animal model of mental time travel

I outline the development of an animal model of MTT and weigh the constraints, strengths, and weaknesses of such an approach. At the end of this review, I offer suggestions for future research.

A major shift in thinking about mental time travel proposed here is the focus on searching the content of multiple representations in episodic memory. MTT cannot exist in a framework without multiple representations. For example, early work in the development of animal models of episodic memory focused on the question – does a particular animal have a representation of a single earlier event. It is natural to begin the development of such a model by focusing on a *single* event (35). However, episodic memory in people is characterized by a multitude of episodic memories, and MTT in people necessarily involves remembering a target event amid many temporally nearby event memories. In the early stages of development, it was unknown if the documentation of episodic memory of a single event represented a major limitation of animal models of episodic memory. Clayton and colleagues (25) were the first to document that a nonhuman represented multiple events using episodic memory. Crystal and colleagues (16) initially showed that rats can remember two events with several overlapping features using episodic memory. Subsequently, we showed (17) that rats remember at least 30 events by documenting that rats remember odors and the contexts in which these odors occurred. For a review of the methods used in these studies with rats see (10).

An animal may represent multiple events in episodic memory, but the representations may not preserve the temporal flow of the events. Moreover, an animal may have rudimentary information about the order of events but may be unable to search these representations to find a target that occurred at a specific time. I outline the perspective that an animal model of MTT requires three elements. Element 1: the animal remembers multiple events using episodic memory; Element 2; the order of events in time is included in the representation; and Element 3: the sequence of events can be searched to find a target that occurred at a particular time. I propose that rats represent multiple items in episodic memory (Element 1) in order of occurrence

(Element 2), and they replay their memory by searching their episodic memory to find items at targetted locations in the sequence (Element 3) (10, 18, 19). In the sections that follow, I review experiments that show that rats meet the three criteria outlined above. The theme of the experiments that follow involves ruling out non-episodic solutions to the memory problem.

It is worth emphasizing that the proposed animal model of MTT represents a shift in thinking about MTT. The focus here is on the contents of memory. Namely, do animals use episodic memory to represent multiple events, their order, and are they capable of searching these representations to find a target that occurred at a particular time. The model captures the content of MTT (the events, their order, and searching in time), but the focus on content imposes constraints on inferences about non-content-based processes. Notably, the model does not include subjective experiences. Thus, the model is silent on the role of the self being situated in the flow of events and the feeling of knowing that the events occurred in one's personal experience. Nevertheless, a strength of this approach includes the potential to model the decline in the contents of episodic memory that occurs in human diseases of memory (e.g., Alzheimer's disease) (36). A limitation of this approach includes the absence of information about subjective changes in experiences that may accompany declines in memory content in human diseases of memory.

Replay of episodic memories

People can replay of the flow of past events in sequential order (37-39). In our experiments (18), rats received a list of odors (Figure 1a). Household spices and oils were infused on plastic lids, which covered cups with food at random locations in distinctive arenas. In list encoding, the length of the list was unpredictable (5-12 items/list); the large number of items in the list satisfies Element 1. When a list ended, the rat was placed in one of two distinctive memory-assessment contexts, where two items from the list were presented (referred to as list memory assessments). In one context, the correct (rewarded) choice was the second to the last item from the earlier list. The correct choice was the fourth from the last item in the other context . The incorrect choice (referred to as a foil) was randomly selected from a different position in the list. Because the list length changed randomly during list encoding, the rat could not know at the time of presentation which items would be the correct or incorrect choices in the subsequent memory assessment. If the rat replayed the sequence of episodic memories (Elements 2 and 3), it would choose the correct item in second- and fourth-last contexts. The rats passed an initial test of episodic memory replay; accuracy was above chance in second- and fourth-last memory assessments (Figure 1d).

Ruling out memory trace strength

An animal model of MTT requires that the animal uses episodic memory to solve the memory problem. Our approach to strengthening the claim that rats rely on episodic memory focuses on showing that other aspects of memory are not sufficient to explain choices in the memory task. When an odor is presented, it produces a memory trace, but the retrievability of that memory decreases as a function of time; this type of account is referred to as *familiarity*. The age of the memory provides a cue that may be used to solve the task without episodic memory (29, 40). For example, items that occur earlier in the list will typically have smaller memory trace strengths at the time of a memory assessment. Because the likelihood of memory retrieval depends on the similarity between encoding and retrieval contexts (41), small changes in the retrieval context are assumed to occur over time. Accordingly, the probability of retrieving the memory declines as a function of time due to moment-to-moment changes in context (42-44).

If the animal remembers multiple events using episodic memory (Element 2), we should be able to dissociated episodic memory replay and non-episodic memory hypotheses (Element 1, Figure 1b). Rats represent multiple items in episodic memory (Element 1) in order of occurrence (Element 2) and engage in memory replay (Element 3) according to the episodic memory replay hypothesis. Accordingly, it is proposed that the rat searches episodic memory to find a target that occurred at a specific time (Element 3). Alternatively, according to a non-episodic memory hypothesis, when an event occurs, it produces a memory trace whose probability of retrieval declines as a function of time. Accordingly, the rat may learn to select the choice item that matches the typical memory trace strength of a second- or fourth-last item in each memory-assessment context. By using memory trace strength, it could identify the second-last (large trace) and the fourth-last (smaller trace) items in the corresponding context; depending on their positions in the list, the incorrect choice would have memory trace strength that is too high or too low relative to that of the second- or fourth-last items. According to this non-episodic memory hypothesis, the rat would choose an item that matches the typical memory strength for the current context while avoiding values above and below the expected level, without replaying episodic memories. Because episodic memory and familiarity are confounded, we developed an approach to dissociate familiarity and episodic memory. The time between list items was doubled (Figure 1b), which impacts the profile of memory trace strengths of items but obviously does not impact the sequential order of items. To dissociate processes, the incorrect choice (i.e., foil) in the memory assessment had the typical memory strength of a correct item. Consequently, the incorrect choice was attractive because its delay matched that of a second (or fourth) last item; therefore, a rat using memory trace strength would choose the foil (leading to below-chance performance). In contrast, an animal using episodic memory replay would choose the second (or fourth) last item correctly (leading to above-chance performance). We observed above chance accuracy (Figure 1d) in both second- and fourth-last dissociation tests, which rules out memory trace strength; similarly, these data rule out the use of judgments of familiarly, the age of memories, and timed intervals between the event and the memory assessment. These data are consistent with the hypothesis that rats replay episodic memories.

Ruling out working memory

An animal model of MTT requires that the animal uses episodic memory to solve the memory problem. Working memory is defined as the active maintenance of information despite ongoing information processing or distraction (45). Working memory resources would be required to retain and rapidly update the last items in memory when each new item is presented. It is unlikely that rats relied on working memory in the absence of episodic memory to solve the list task for four reasons (18). First, because episodic memory, but not working memory, is considered long-term memory (46-48), we examined list memory after a 60-minute delay. List memory survived a 60-minute retention-interval challenge (Figure 1d), consistent with episodic memory but not with working memory.

Second, episodic memory is resistant to interference from new information whereas working memory is displaced by new information. We evaluated resistance to interference by presenting odors in a new-old memory task in a distinctive context after encoding a list; rats were trained to select a new odor (not previously presented) while avoiding old odors (recently presented), which documents that they smelled and remembered odors after presentation of the earlier list task. Thus, we showed that list memory withstands interference from memory of other odors (Figure 1c-d). Third, working memory is susceptible to manipulations of memory load (49, 50). We evaluated acquisition and terminal performance when rats searched for second- and fourth-last odors. Although we manipulated memory load, performance did not decline as memory load increased (Figure 1d-e), which is inconsistent with the use of working memory. Fourth, because episodic memory depends on the hippocampus, we showed that replay of episodic memories is hippocampal dependent as described in the next section.

Reliance on hippocampus

Because the hippocampus is critical for episodic memory (51-53), we inhibited neurons in the dorsal hippocampus using DREADDs (Designer Receptor Exclusively Activated by Designer Drug). The selective and reversible impairment of list-memory performance following temporary suppression of hippocampal neurons did not impact other aspects of memory; hippocampal-independent assessments of memory included new-old recognition memory for odors and a simple odor discrimination. These data support the hypothesis that list-memory performance requires episodic memory (Figure 1c,f).

Incidental encoding and an unexpected question

Overview

People remember events even though they were apparently unimportant when they occurred. Although events are not always known to be important when they occur, people may remember details about such incidentally encoded information using episodic memory. In most experiments using animals, information may be explicitly encoded in anticipation of an expected test of memory. Accordingly, an animal may use explicitly encoded information to generate a *planned action* (10, 20, 26). Hence, when the test occurs, the planned action can occur *without remembering back in time to the earlier episode*.

Notably, a powerful solution to this problem is provided by the combination of *incidental encoding* and an *unexpected question* (10, 20, 26, 30-33). To describe information as encoded incidentally is to highlight that it is not yet known that the information is needed for a future test. To describe the test of memory as unexpected is to highlight that predicting the later test is not possible when the information was originally encountered. Consequently, one cannot generate a planned action when an unexpected test occurs after incidental encoding. Thus, the only solution in this situation is to retrieve an episodic memory of the incidentally encoded event. Answering an unexpected question after incidental encoding of a single event has been demonstrated in pigeons (26), rats (20), dogs (30-32), dolphins (33), and Eurasian jays (54). In earlier work, we showed that rats can answer an unexpected question after incidental encoding of a single event (20); for review, see (10).

Replay of incidentally encoded episodic memories

We tested the hypothesis that rats encode multiple pieces of seemingly unimportant information (Element 1) in order of occurrence (Element 2) and later they replayed a series of episodic memories (Element 3) when information was needed to solve an unexpected memory assessment. Rats were initially trained in two tasks (Figure 2a-b). In the list encoding task, rats were trained to select odors that were the third to last item in a list (Figure 2a). Lists consisted of 4-11 odors presented one at a time in a distinctive encoding context; the large number of items in the list satisfies Element 1. Next, in the list memory assessment, the rat was presented with two odors from the list in a distinctive memory-assessment context. The rats were rewarded for choosing the odor that was the third-last item in the list; the rats were not rewarded for choosing the other odor, which was randomly selected from a different ordinal position in the list. Explicit encoding of information for the purpose of taking an expected test of memory cannot be ruled out because the rats were trained in this task.

In the second task, rats foraged for food in a radial maze with eight runways (Figure 2b). Food was covered by *unscented* plastic lids at the end of each arm. Food was initially available in four arms (study phase) followed by food in not-yet visited locations with access to all 8 arms (test phase). When foraging in a study phase, the rat likely anticipates foraging in the subsequent test phase. The contents of memory from foraging are maze locations (55-58).

Our approach in a critical test allowed rats to forage in the radial maze with incidental exposure to scented lids unexpectedly covering food cups. Next, the rats received a memory assessment for odors that were encountered in the maze. However, it is possible that the rats treated odors in the new condition as they had in the earlier training condition (i.e., stimulus generalization), which provides a non-episodic memory solution. To address this issue, we designed a control condition to determine if rats generalize or fail to generalize in a novel situation. The rationale for the control condition is that it is unlikely that rats generalized in the novel situation in the critical test If they fail to generalize in the control condition. In the control condition (Figure 2c), the rats received a list of odors in the previously trained list encoding context (List 1), a list of odors in a novel context (List 2; yet another arena with distinct features), and a memory assessment where the choice was the third-last odors from Lists 1 and 2. According to stimulus generalization, rats automatically encode odors for the purpose of taking an anticipated memory test and would choose the odor from List 2 (because the third-last odor is literally in List 2). By contrast, a failure of stimulus generalization would occur if rats do not automatically encode odors for the purpose of taking an upcoming memory test. In this situation, the rats may choose the List-1 odor because it occurred in the arena that was used during training of the original list encoding task. This latter option is not possible if rats automatically encode odors for the purpose of taking a test using stimulus generalization because the actual third-last item occurred in List 2. As shown in Figure 2e, all of the rats chose the odor from List 1 and none chose the odor from List 2. These data document a failure of stimulus generalization. Because rats did not automatically encode odors for the purpose of an upcoming test in the control condition, it is unlikely that they automatically encode odors in the critical test.

In a critical test, an opportunity for incidental encoding was provided on a single occasion when rats foraged in the radial maze with *scented lids* covering the food cups (Figure 2d). Next, the rats were immediately and unexpectedly provided with a single list memory assessment with a choice between the third-last odor from the radial maze and another odor from the maze. Prior to the critical test, rats did not encounter scented lids while foraging in the radial maze and did not receive a list memory assessment after foraging in the radial maze. Notably, based on earlier training, the rats could not predict that the odors in the radial maze were important or that they would later be asked about the maze odors. To answer the unexpected question after incidental encoding, the rat would need to use episodic memory to replay the sequence of odors encountered in the maze. In contrast, rats without this ability would choose randomly.

When rats unexpectedly found odors during radial-maze foraging and their memory for the order of these odors was assessed immediately, the rats correctly answered the unexpected question (Figure 2f. Radial maze test). The critical test was conducted once per rat to ensure that the data were obtained before any new learning could occur. These results are consistent with the hypothesis that rats can replay a stream of multiple sequential events (Elements 1 and 2) that were not known to be important when the events occurred and report this information when unexpectedly asked to search episodic memories (Element 3). In a complimentary experiment, when rats found odors during radial-maze foraging and their memory for the order of these odors was assessed after a 15-minute delay, they also correctly answered the unexpected question (Elements 1-3, Figure 2g). These data are consistent with the hypothesis that rats replayed long-term episodic memories after incidental encoding.

Future research on an animal model of mental time travel

As noted above, a theme of the experiments reviewed here involves using experimental techniques to rule out non-episodic memory solutions to the memory problems. Remembering the order of stimulus presentations alone does not imply that episodic memories are formed and that these memories are replayed. The conclusion that rats search representations in episodic memory to find specific event memories is bolstered by experiments that rule out the use of memory trace strength, working memory, and expectations of a memory test in this approach, and by experiments that show that this ability is hippocampal dependent. Moreover, the focus on the content of memory is devoid of subjective experiences such as re-living the experience, being situated in the flow of events, and other aspects of the full recollective experience.

This review highlights evidence that multiple events are represented using episodic memory (Element 1), the order of events are represented (Element 2), and representations are searched to find a target at a particular time (Element 3). However, episodic memory involves memory for items and the contexts in which they occurred (17, 52, 53). People can use MTT to remember events that occurred in different contexts (e.g., I can remember breakfast at home, a conversation in my office, a lecture at the end of the day). Thus, a case for a richer model of MTT would show that the flow of events includes not just the events but the context in which these events occurred in future research. Future research may explore the abilities (or limitations) of replaying a sequence of events that were interleaved across multiple contexts. Another avenue for future research involves parametric exploration of the abilities (or limits) of the replay of episodic memory. For example, although we have used lists of up to 12 items and shown that rats can search for targets 2, 3, or 4 items from the end of the list (18, 19), it is unknown if substantially larger lists and targets may be replayed. Some earlier work suggests we have not reached the limits of memory in our approach. For example, rats remember at least 30 items-in-context using episodic memory (17). Moreover, memory for odors in rats is remarkably robust. For example, we have shown that rats remember at least 100 odors (59) (see also (60)), although these studies did not evaluate the contributions of episodic memory). A further future direction involves exploring the longevity of episodic replay; we have used relatively long delays (e.g., 15-60 minutes) without substantial declines in performance (17-19). Similarly, we have used relatively modest interference (4 odors) without evidence of performance declines (18, 19). These observations may suggest that the temporal limits may be quite extended in time, which may be explored in future research. Establishing the limits of MTT in animals may provide insights about similarities or differences to MTT in people.

Conclusions

I propose that searching the contents of memory is an animal model of MTT. Rats incidentally encode multiple pieces of seemingly unimportant information, and later they replayed a stream of episodic memories when that information was needed to solve an unexpected problem. Our findings suggest that the cognitive building blocks needed for MTT (i.e., replaying a stream of episodic memories) is relatively old from an evolutionary perspective. It is widely assumed that fundamental elements of human memory do not occur in non-primates (e.g., (61-63)). Testing this hypothesis requires exploring cognitive processes in non-primates. We have modeled a number of critical aspects of human cognition in rats, such as: what-where-when memory (14), source memory (15), binding of episodic memories (16), memory of many items and the contexts in which they occurred (17), retrieval practice (64), prospective memory (65), and replay of incidentally encoded episodic memories (18, 19). Overall, our research supports the hypothesis that rats may be used to model key elements of human memory. All of these approaches focus on the contents of memory. In conditions in which non-episodic memory solutions are ruled out, searching the contents of memory is an animal model of MTT that is relatively tractable because it too focuses on the contents of memory.

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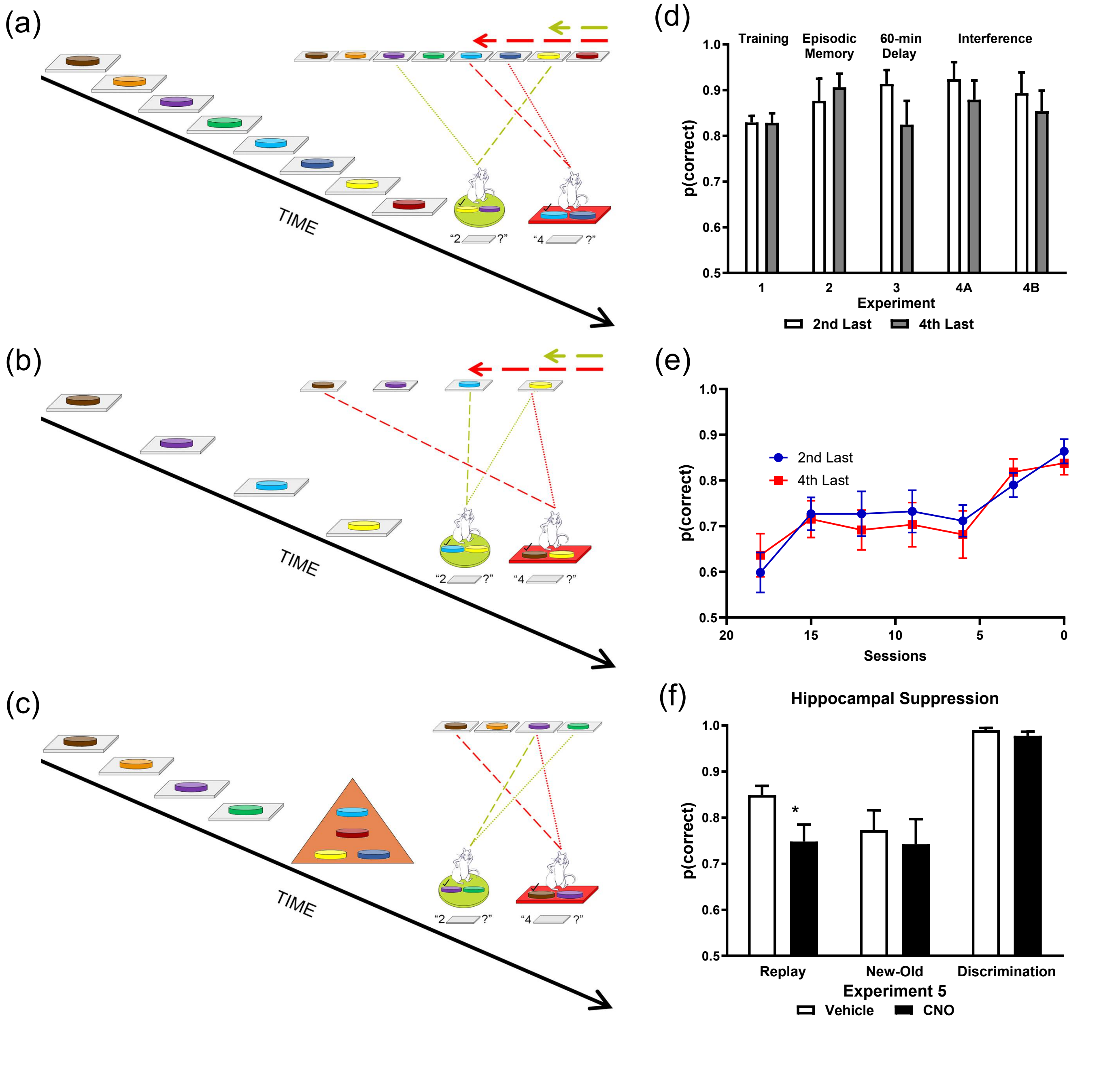
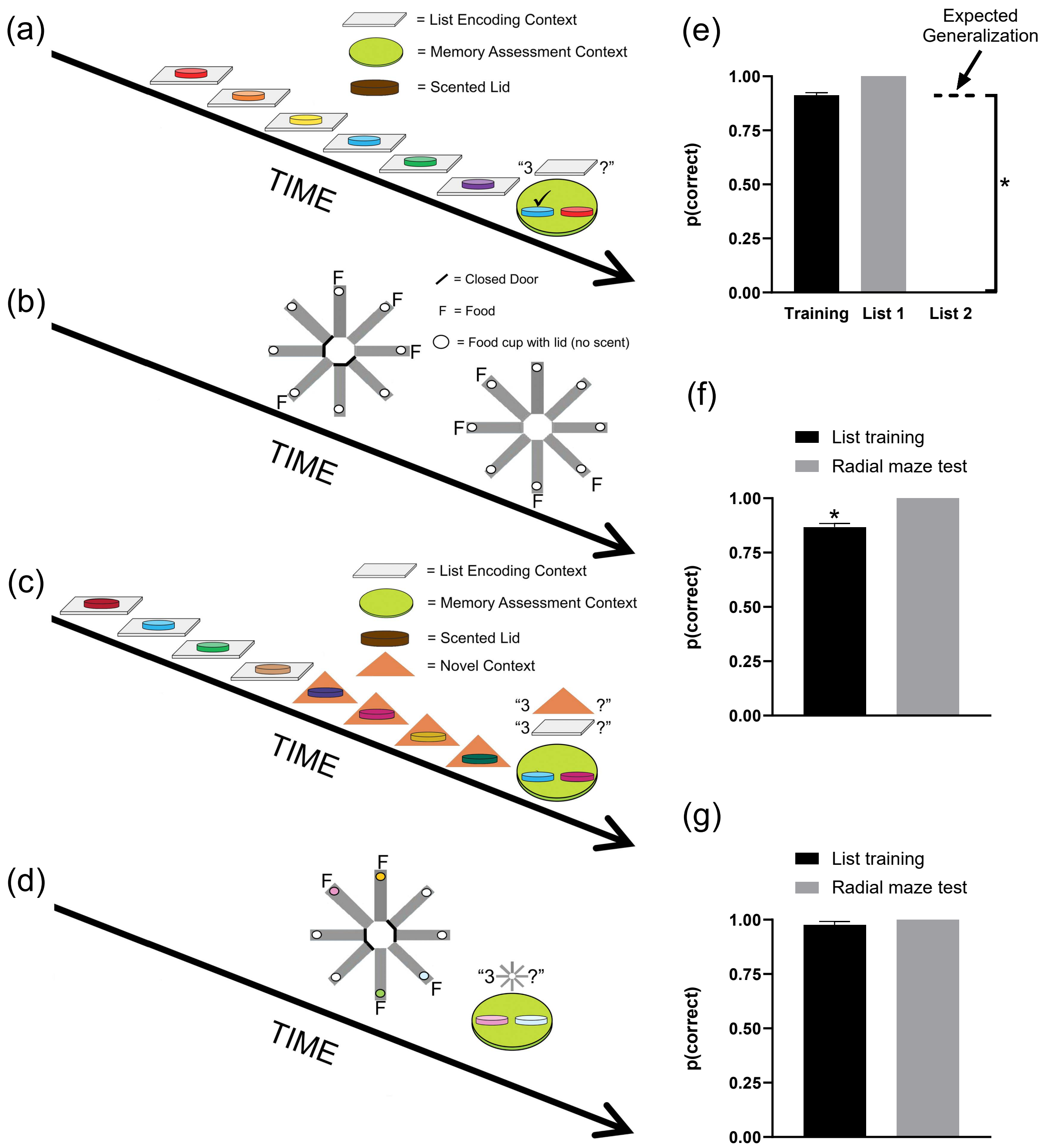
Figure captions

Figure 1. Rats replay a stream of multiple episodic memories. Schematic depiction of (a) list encoding and memory assessments, (b) dissociation of episodic-memory and memory-trace-strength accounts of list-memory performance, and (c) an interference test. Because the same time scale is used in (a) and (b), it may be noted that the second-last item in (b) occurred at the time of the fourth-last item in (a), and the fourth-last item in (b) occurred at the time of the eighth-last item in (a). Data from (18) showing (d) reliance on episodic memory rather than memory trace strength and overall high accuracy in list memory task, including after a 60-min delay and interference, (e) equivalent performance in acquisition under varying memory loads, and (f) list-memory performance is impaired by inhibition of hippocampal neurons while sparing other aspects of memory. (d-f) Error bars represent 1 SEM. Adapted and reproduced with permission from Panoz-Brown, D., Iyer, V., Carey, L.M., Sluka, C.M., Rajic, G., Kestenman, J., Gentry, M., Brotheridge, S., Somekh, I., Corbin, H.E., Tucker, K.G., Almeida, B., Hex, S.B., Garcia, K.D., Hohmann, A.G., & Crystal, J.D. (2018). Replay of episodic memories in the rat. Current Biology, 28(10), 1628-1634.e1627. ©2018

Figure 2. Replay of episodic memories after incidental encoding of multiple events in an unexpected assessment of memory. Schematic depiction of (a) list encoding and memory assessment, (b) foraging for food (encountered below unscented lids on a radial maze), (c) a control condition that pits explicit encoding of an initial list in the trained list-encoding context (List 1) against stimulus generalization in a novel context

(List 2), and (d) a critical test in which rats forage on the radial maze but encounter food below scented lids followed by a memory assessment to prompt replay of episodic memories. Data from (19) showing (e) failure of stimulus generalization (i.e., failure to automatically encode odors for the purpose of an upcoming test in a novel context), and (f-g) high accuracy when rats encountered odors while foraging in the radial maze and their memory for the order of encountered odors was unexpectedly assessed (f) immediately or (g) after a 15-min delay. (e-g) Error bars represent 1 SEM. Adapted and reproduced with permission from Sheridan, C. L., Lang, S., Knappenberger, M., Albers, C., Loper, R., Tillett, B., Sanchez, J., Wilcox, A., Harrison, T., Panoz-Brown, D., & Crystal, J. D. (2024). Replay of incidentally encoded episodic memories in the rat. Current Biology. ©2024


(a)
TIME
"2 ?"
"4 ?"
(b)
TIME
"2 ?"
"4 ?"
(c)
TIME
"2 ?"
"4 ?"
(d)
Training
Episodic Memory
60-min Delay
Interference
p(correct)
1.0
0.9
0.8
0.7
0.6
0.5
1
2
3
4A
4B
Experiment
2nd Last
4th Last
(e)
p(correct)
1.0
0.9
0.8
0.7
0.6
0.5
20
15
10
5
0
Sessions
2nd Last
4th Last
(f)
Hippocampal Suppression
p(correct)
1.0
0.9
0.8
0.7
0.6
0.5
*
Replay
New-Old
Discrimination
Experiment 5
Vehicle
CNO



(a)
= List Encoding Context
= Memory Assessment Context
= Scented Lid
TIME
"3 ?"
(b)
= Closed Door
F = Food
= Food cup with lid (no scent)
F
TIME
(c)
= List Encoding Context
= Memory Assessment Context
= Scented Lid
= Novel Context
TIME
"3 ?"
"3 ?"
(d)
TIME
"3 ?"
F
(e)
Expected Generalization
p(correct)
1.00
0.75
0.50
0.25
0.00
Training
List 1
List 2
*
(f)
List training
Radial maze test
p(correct)
1.00
0.75
0.50
0.25
0.00
*
(g)
List training
Radial maze test
p(correct)
1.00
0.75
0.50
0.25
0.00