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Report

Binding of Episodic Memories in the Rat

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Summary

People remember an event as a coherent scene [1–4]. Memory of such an episode is thought to reflect binding of a fully integrated representation, rather than memory of unconnected features [4–7]. However, it is not known whether rodents form bound representations. Here we show that rats remember episodes as bound representations. Rats were presented with multiple features of unique episodes at memory encoding: *what* (food flavor), *where* (maze location), *source* (self-generated food seeking—running to the food site—or experimenter-generated food seeking—placement by the experimenter at the food site), and *context* (spatial cues in the room where the event occurred). After a delay, the trial continued with a memory assessment in which one flavor replenished at the self-generated—but not at experimenter-generated—locations. We presented rats with multiple overlapping features, in rapid succession, to ensure that successful memory retrieval required them to disambiguate multiple study episodes (using two rooms). We found that binding is resistant to interference from highly similar episodes and survives long retention intervals (~1 week). Our results suggest that multiple episodic memories are each structured as bound representations, which suggests that nonhumans represent episodic memories using a structure similar to that of people. This finding enhances the translational potential for utilizing animal models of episodic memory to explore the biological mechanisms of memory and validate therapeutic approaches for treating disorders of memory.

Results and Discussion

The ability to remember specific earlier episodes that happened to you in the past is a fundamental attribute of human cognition [3]. People remember earlier events as a coherent episode or scene [1–4]. Such an episode is thought to be structured as a bound representation [8], rather than as unconnected features [4–7]. The origin (i.e., source) of information and other aspects of the context in which the event occurred are critical pieces of information that disambiguate similar events that may share several common features [9]. For example, you might remember reading some important news in your kitchen and hearing a later development on the radio while in your car. Certainly, many aspects of the source or context of the information are frequently forgotten (e.g., was it a female voice on the radio or text above the fold in a newspaper?). However, if the information is retained, it is the binding of the multiple pieces of information that is critical for the recollection of an earlier scene, event, or episode [3].

In previous work on animal models of episodic memory using item-specific information [10–24], the episode presumably consists of multiple elements (e.g., what-where-when [12–22] or what-where-source [10, 11]). A primary function of binding is to disambiguate similar episodes from one another (i.e., episodes that share some, but not all, features). Importantly, discrimination of what-where-when or what-where-source could be based on the use of multiple independent features, which we refer to as the unbound feature hypothesis. For example, a three-way conditional discrimination (using a series of conditional rules [25]) represents a viable alternative to the proposal that animals represent a bound episodic memory [26–28]. Clayton and colleagues used multiple, interleaved caching opportunities to show that what-where-when information is integrated [29] in food-storing scrub jays; this approach has also been used to investigate binding in young children [7]. We adopted this strategy here using rats, which are the most widely used biomedical model for translation to human diseases. Retrieving information about two relatively similar events is expected to produce confusion between episodes according to the unbound-feature hypothesis if at least some of the features overlap; to produce such confusion, we used two identical radial mazes, with each arm pointing in the same orientation in two rooms that had similar geometric cues and a range of visual cues (some identical and some different). The precise mechanism by which rats may confuse events from two rooms is not known; however, a number of factors may contribute to making the two events similar, namely (1) orientation [22, 30–35] given the corresponding orientation of the mazes, (2) global geometry of the rooms [36, 37], (3) overlap of a subset of global landmarks in the room [38–41], and (4) baiting configurations of the mazes ([42]; but see [43]). Moreover, in earlier work (experiments 2b and 2c in [22]), we found that presentation of a retrieval cue prompted the rats to continue a trial from one room to a second room based on the shared orientation of the mazes.

We used a source-memory preparation [10, 11] to test whether bound or unbound representations are coded by rodents (see the Supplemental Experimental Procedures for a description of preliminary training stages). In this approach, rats were presented with multiple aspects of an event at memory encoding (study phase). The details of the event include multiple features: *what* (flavor of food, namely chocolate or standard chow), *where* (location in a radial maze), *source* (self-generated food seeking—running to the food site—or experimenter-generated food seeking—placement by the experimenter at the food site), and *context* (the spatial cues in the room where the event occurred). After a delay, the trial continued with a memory assessment (test phase) in which one flavor (chocolate) replenished at its previously encountered, self-generated location, whereas that flavor did not replenish at the experimenter-generated location (see Figure 1 for an example of a trial); chow locations are encountered in study-test sequences but do not replenish. Thus, solving this task requires knowledge about what and where events occurred in addition to source information about how the chocolate was obtained at daily unique locations.

According to the unbound-feature hypothesis, the rats may retrieve a set of unconnected features [26–28] to successfully return to the replenishing chocolate location while simultaneously avoiding revisits to nonreplenishing chocolate and depleted chow locations. To arrange conditions in which the unbounded-feature hypothesis predicts failure (rate of revisiting replenishing and nonreplenishing chocolate locations are

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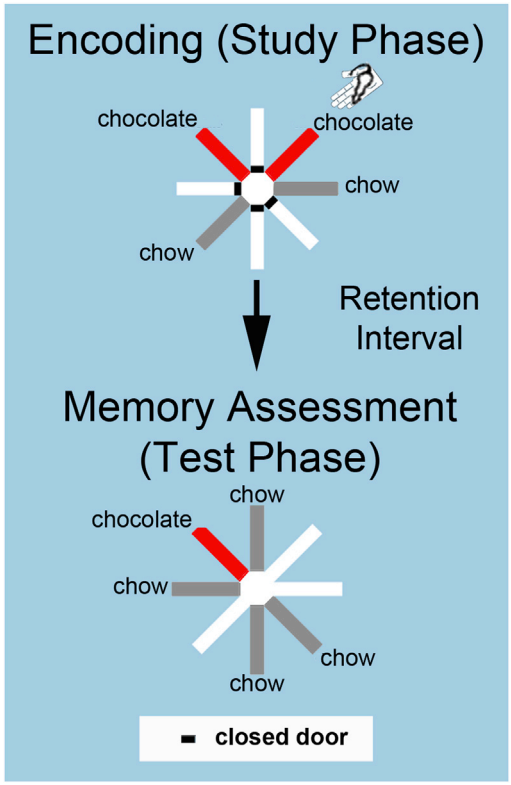


Figure 1. Schematic of the Maze Illustrating Experimental Design

Two locations (randomly selected on each trial; shown in red) provide chocolate in the study phase—one is encountered when the rat navigates the maze (self-generated chocolate feeding), whereas the other is presented to the rat when the experimenter places the rat in front of the food source (experimenter-generated feeding; depicted by the hand icon). After a retention interval, the self-generated chocolate location replenishes (provides additional chocolate), whereas the experimenter-generated location does not replenish. Chow locations (shown in gray) are encountered in study and test phases but do not replenish.

equal), we increased the memory load from one episode (in one context; study and test in room A) to two episodes (study in room A, study in room B, followed by tests in rooms A and B). On many trials, the independent features will overlap across the two episodes (see Figure 2 for an example configuration of trials, proposed representation of unbound features, and predicted memory failure); the features in the two rooms include similar geometric cues and the same orientation cues, in addition to some identical and some different global landmarks. When the memory load is minimal (i.e., study in room A, test in room A), successful memory performance (higher revisit rate to the replenishing than nonreplenishing chocolate location) can be supported by unbound features. Accordingly, the rats may match currently experienced features with a list of unbound features stored in memory. By increasing the memory load, we presented the rats with multiple overlapping features that can only be fully disambiguated by remembering that one study episode occurred in one particular context, whereas the other episode occurred in a different context. Notably, retrieving information about two relatively similar study events is expected to produce confusion between the episodes if at least some of the features overlap according to the unbound hypothesis. Thus, according to the unbound-feature hypothesis, it is not possible to fully disambiguate multiple, interleaved episodes, and the probability of revisits would be predicted to be equal at replenishing and nonreplenishing chocolate locations. By contrast, bound representations of separate episodes predict successful performance with both memory loads (higher revisit rate to the replenishing than nonreplenishing chocolate location). To determine whether rats rely on unbound features or use bound episodic memories, we varied memory load (experiment 1). When replenishment in the test phases was predicted by self-generated, but not experimenter-generated, events in two different rooms, the rats revisited the chocolate location in the memory assessment phase at a higher rate than the nonreplenishing chocolate location; as expected, the same pattern of data was documented when only one episode was studied in a single room (Figure 3A; replenishment $F(1,5) = 81.23$, $p = 0.0003$; memory load $F(1,5) = 0.07$, $p = 0.8$; interaction $F(1,5) = 0.97$, $p = 0.4$); these results are consistent with bound episodic memories and rule out the unbound-features hypothesis. As expected, the rats also successfully avoided revisits to chow locations, which never replenished (see Table S1).

Distinguishing multiple episodes with similar features is a central function of bound memory representations. If episodes are remembered as unbound features, then presentation of the same or conflicting features across multiple events should produce patterns of facilitation or interference, respectively. By contrast, if episodes are remembered as distinct bound representations, then rats should be resistant to facilitation and interference. Thus, we varied the similarity of two study configurations (using the same, different, or random baiting configurations with a memory load of two; experiment 2). Facilitation would increase source memory performance, whereas interference would decrease it. Hence, the unbound-features hypothesis predicts the following rank ordering of source-memory performance (replenish-nonreplenish): same > random > different. By contrast, the bound-representation hypothesis would be documented by excellent source memory performance in each condition (same = random = different). Despite the presentation of same or conflicting features in multiple study events, rats showed excellent source memory performance (revisiting the chocolate location in the memory assessment phase at a higher rate than for the nonreplenishing chocolate location) when baiting configurations were the same, different, and randomly patterned across two study episodes (Figure 3B; replenishment $F(1,6) = 155.65$, $p = 0.00002$; baiting condition $F(2,12) = 1.19$, $p = 0.2$; interaction $F(2,12) = 0.89$, $p = 0.1$); these results suggest that binding of each episode functions to disambiguate highly similar events from the past. As expected, the rats also successfully avoided revisits to chow locations, which never replenished (see Table S1).

We have previously shown that source memory survives unusually long retention intervals (7–14 days) [10, 11]. Thus, we sought to determine whether source memory binding also survives such long retention intervals. We exploited the different empirical retention functions for two components of our task [10, 11]: memory for global cues in the room (using a less preferred chow flavor) decays rapidly (1–2 days), whereas memory that supports differential revisits to replenishing and nonreplenishing chocolate locations decays more slowly (7–14 days). Hence, we calibrated the retention interval so that memory for location ([38–41]; as indexed by chow accuracy) was below threshold for accurate performance, whereas memory for source information (as indexed by differential

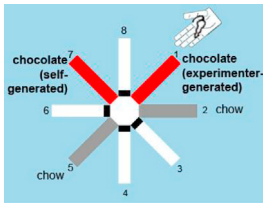
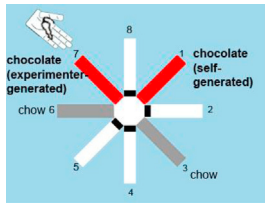
Encoding in Room A	Encoding in Room B	Proposed Memory Representation (Unbound Features)	Tests in Rooms A and B
		Room A Room B Chocolate-1 Chocolate-7 Self-generated-1 Self-generated-7 Experimenter-generated-1 Experimenter-generated-7 Chow-2 Chow-3 Chow-5 Chow-6	Very poor performance: p(revisit replenish) = p(revisit nonreplenish)

Figure 2. An Example Configuration of Trials, Proposed Representation of Unbound Features, and Predicted Memory Failure

Very poor performance is predicted because an unbound-feature representation does not segregate the relevant features according to the rooms in which the events occurred. Hence, revisits to replenishing and nonreplenishing chocolate locations are predicted to be equal according to the unbound-feature hypothesis.

revisits to replenishing and nonreplenishing chocolate locations) was retained above threshold (experiment 3). If binding survives long retention intervals, then we expect to observe differential revisits to the replenishing chocolate location with a memory load of two despite the use of a retention interval that is long enough to eliminate accurate avoidance of revisits to depleted chow locations. Alternatively, if binding does not survive such a long retention interval, then differential revisits to chocolate locations will be eliminated with a memory load of two.

We used a memory load of one episode to select a retention interval for each rat with little evidence for memory of chow locations (accuracy = 0.567 ± 0.028, mean ± SEM, which was not significantly different from that expected by chance; chance = 0.518; $t(4) = 1.72$, $p = 0.2$) and verified intact source memory performance (higher revisit rates to replenishing than nonreplenishing chocolate locations); see the Supplemental Experimental Procedures. At a retention interval delay selected to lower memory for chow locations, the rats revisited the replenishing chocolate location in the memory assessment phase at a higher rate than the nonreplenishing location at both memory loads (Figure 3C; replenishment $F(1,4) = 64.67$, $p = 0.001$; memory load $F(1,4) = 0.87$, $p = 0.4$; interaction $F(1,4) = 0.68$ $p = 0.5$); these results are consistent with the hypothesis that binding survives long retention intervals.

Rats are able to complete the chocolate discrimination at long delays, at a time when they are no longer able to complete the chow discrimination ([10, 11] and experiment 3). This empirical dissociation is puzzling because both discriminations presumably require memory of spatial information. It is likely that our use of a highly preferred flavor (chocolate) for the source memory task contributes to this empirical dissociation. Yet, it is potentially intriguing that binding of multiple cues (e.g., flavor, location, source, and context) may increase the durability of memory for a unique episode beyond that which would occur for one feature alone (chow accuracy). We note that the specific stimuli that constitute context are not known and that it is possible that rats encode events within specific spatial contexts with a high degree of spatial precision [44].

Our findings suggest that binding of episodic memory is evolutionarily quite old. Moreover, strong demonstrations of episodic memory in species as widely separated as rats and scrub jays [29] suggest that binding is an evolutionary primitive. Importantly, our findings support the view that rats may be used to model fundamental aspects of human memory. This view will enable combining a comprehensive understanding of biological mechanisms with animal models of human cognition. Such a combination will advance translational research that may ultimately foster the development of therapeutic approaches to disorders of human memory [45] (e.g., age-related cognitive impairments and Alzheimer's disease).

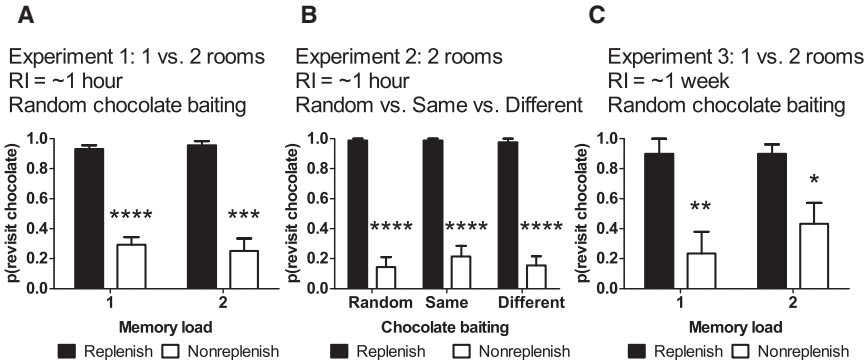


Figure 3. Bound Episodic Memories Function to Disambiguate Multiple, Interleaved Study Episodes

Successful memory performance is shown by a higher revisit rate to replenishing than to nonreplenishing chocolate locations. Rats visited two chocolate locations per study phase, one self-generated and one experimenter-generated. Rats preferentially revisited the chocolate location when it was about to replenish; chow locations never replenished.

(A) The memory load was one (study and test in the same room) or two (study in one room, followed by study in a second room, followed by a test in each room) in experiment 1 with a short (~1 hr) retention interval between corresponding study and test phases; chocolate baiting in each room was randomly selected.

(B) The memory load was two, the retention interval was short, and the chocolate baiting was varied across three conditions in experiment 2: the *random* condition used random baiting in each room (as in experiment 1), the *same* condition used the same orientation for replenishing and nonreplenishing chocolate arms in both rooms, and the *different* condition reversed the orientation of replenishing and nonreplenishing chocolate arms across the two rooms.

(C) The memory load was one or two (as described in experiment 1) with a long (~1 week) retention interval.

n = 6 (A), n = 7 (B), and n = 5 (C). *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001. Data are shown as means with 1 SEM. The probability of a revisit to the chocolate location was calculated from the first five choices in test phases. RI, retention interval.

Experimental Procedures

General Methods

Male Long-Evans rats obtained chocolate at daily unique locations (study phase; first helpings of food), which sometimes replenished later (test phase; second helpings of food); other locations provided chow but never replenished. The replenishment of chocolate depended on the source by which the rats had initially obtained the chocolate. Rats were placed by an experimenter in the study phase at one of two randomly selected chocolate locations. After self-generated, but not experimenter-generated, encounters with chocolate during the study phase, replenishment occurred at the self-generated chocolate location in the test phase. Chow-flavored locations from the study phase never replenished at the test phase. Thus, solving this task requires knowledge about what and where events occurred in addition to source information about how the chocolate was obtained at daily unique locations. Memory load was varied as follows. For a memory load of one episode, study and test occurred in the same room (either all in room A or all in room B). For a memory load of two episodes, study occurred in two rooms (either Room A followed by room B, or the reverse), followed by a retention interval, followed by a test (either room A followed by room B or the reverse).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.10.074.

Acknowledgments

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Supplemental Information

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Supplemental Information

Table S1. Accuracy in avoiding revisits to depleted chow-flavored locations

Experiment	Condition	mean ± SEM
1	ML = 1	0.755 ± 0.027
1	ML = 2	0.814 ± 0.022
2	Random	0.833 ± 0.023
2	Same	0.824 ± 0.031
2	Different	0.839 ± 0.032
3	ML = 1	0.567 ± 0.028
3	ML = 2	0.646 ± 0.031

Accuracy was measured as the proportion correct in the first four choices excluding the chocolate locations in a test phase. This analysis of chow accuracy was restricted to the six non-chocolate arms. ML: memory load.

Supplemental Experimental Procedures

Subjects

Eight male Long-Evans rats (*Rattus norvegicus*; Harlan, Indianapolis, IN; 82 days old and 289 g, on average, at the start of the experiment) were individually housed with light onset and offset in the colony at 7 a.m. and 7 p.m. EST, respectively. Because one rat did not consistently revisit the replenishment location at initial stages of training, it was excluded from all experiments. The rats received 45-mg chow and chocolate pellets (F0165 and F0299, respectively; Bio-Serv, Frenchtown, NJ) during experimental sessions and 15-20 g/day of 5012-Rat-Diet (PMI Nutrition International, St. Louis, MO) after completing each session. Water was available ad lib, except when the rat was in a maze. All procedures were approved by the Bloomington institutional animal care and use committee at Indiana University and followed national guidelines.

Apparatus

Two identical 8-arm radial mazes (described in [S1, S2]) were used; each had a central hub and 8 arms and guillotine doors. A food trough and a 45-mg pellet dispenser were located at the distal end of each arm. These are the same mazes and are located in the same rooms used in [S1]; we previously demonstrated (see Experiment 2 Supplemental Information in [S1]) that Rooms A and B are discriminable by conducting a study phase in Room A and a test phase in Room B, with the trial continuing with corresponding arms between the rooms: Performance was severely disrupted (chow accuracy = 0.54 ± 0.05, mean ± SEM), documenting that the rooms are discriminable. A photobeam in the trough detected head entries. Other photobeams were 3.8 and 5.1 cm from guillotine doors. White noise masked outside noise. Experimental events (guillotine doors and food) were controlled by computers. Data were recorded (10-ms resolution) with MED-PC software (version 4.1). Maze arms were cleaned with chlorhexidine after each rat was removed from the maze. Chow and chocolate pellets were placed beside the filled pellet dispensers (i.e., food odors were constant throughout all parts of the experiment).

Preliminary Training

Rats were allowed to explore the maze individually in 6, 10-min daily sessions (chow or chocolate pellets were placed in 6 and 2 randomly selected arms and corresponding troughs, respectively).

Eight-arm Training

Each rat was trained individually; a rat was placed in the central hub (pseudorandom orientation) and 30-s later doors to all 8 arms of the maze were opened for the rat to visit. A visit was defined by the interruption of a food-trough photobeam as described in [S1]. Interrupting the photobeam dispensed food. Six arms dispensed 1 chow pellet/visit/daily session. Two arms (randomly selected daily) dispensed 3 chocolate pellets/visit and the rat could revisit each of these two chocolate arms an additional 4 times for a total 5 visits, each time obtaining 3 chocolate pellets. There were 12 sessions; each daily session consisted of one trial which ended when food was obtained at each location or 10 min had elapsed.

Initial Study-Test Training

The next 28 daily sessions also consisted of one trial, but they were divided across study and test phases as follows: a study phase (first helpings of food), a retention interval, and a test phase (second helpings of food). In the study phase (first helpings), doors to 4 out of 8 arms (randomly chosen for each rat each day) were opened; visits to 2 of these arms were reinforced with 3 chocolate pellets and visits to the other 2 arms were reinforced with 1 chow pellet. As before, pellet(s) were delivered to accessible troughs with the interruption of the trough photobeam. The study phase ended when food had been dispensed at each accessible location and then the rat was removed. After a delay of ~4 min, the animal was replaced in the hub and all 8 arms opened for a test phase (second helpings). In the test phase, 1 chow pellet was available in each arm that was not accessible during the study phase (first helpings); in addition, the two

study-phase chocolate locations provided three chocolate pellets per visit (second helpings) up to 5 visits per chocolate location. These 28 preliminary-training sessions used self-generated encounters of chocolate to avoid potential disruption by the experimenter placing rats at a selected chocolate location–a procedure to be used next, and used replenishment of chocolate to promote revisits that may have been difficult to establish after occasional non-replenishments with a discrimination procedure also to be used next. On any given day, one study and one test was conducted in one room. The use of rooms alternated across daily sessions.

Study-Test with Controlled Access to Study Locations and Placement Feedings

In all subsequent sessions, access to the 4 study arms were controlled each day by the experimenter opening and closing doors individually so the rat would enter a predetermined (randomly selected) sequence of arms. As previously, 2 arms (randomly selected) delivered chocolate and the other 2 delivered chow. Controlled access also allowed the experimenter to place the rat in one of the designated chocolate arms (randomly selected); the rat was placed at the distal end of the arm near the food trough and facing the trough and dispenser. Following the study phase the rat was removed from the maze; after a delay of ~4 min, the rat was replaced in the hub for a test phase. On any given day, one study and one test was conducted in one room. The use of rooms was randomly selected across 40 daily sessions, p(room A)=p(room B). At the beginning of this stage of training (initial 2 sessions), the rats did not initially revisit the replenishing chocolate location more than the nonreplenishing chocolate location

($t(5)<1$, $p=0.7$), but they did so by the end of this stage of training ($t(5)=6.71$, $p=0.001$; last 2 sessions); the improvement from training was significant ($t(5)=3.16$, $p=0.03$).

Experiment 1

One rat did not complete the initial training described in the sections above until the other rats had completed Experiment 1; therefore, this rat progressed to Experiment 2 without participating in Experiment 1. The procedure in Experiment 1 was as described in the preceding section, except as follows. Memory load of 1 and 2 episodes were interspersed across days. Thus, on 12 sessions, the memory load was 1, and only a single room was used; on the remaining 5 days, the memory load was 2, and 2 rooms were used for two study episodes: Study in two rooms (A followed by B; or B followed by A; randomly selected), followed by a retention interval, followed by tests in each room (A followed by B; or B followed by A; randomly selected). The retention interval from the end of the study episode to the corresponding test phase was ~1 hr. Two chocolate and two chow locations were randomly and independently selected in each study phase.

Experiment 2

The objective of Experiment 2 was to select the baited configuration during two study phases (conducted on the same day) so that the replenishment of chocolate in the corresponding test phases would be the same or in conflict across the two rooms. All sessions in Experiment 2 used a memory load of 2 episodes (details as described in Experiment 1). As in Experiment 1, each study phase consisted of two chocolate and

two chow locations in each study phase. However, the configuration of baited locations in the two consecutive study phases in the same day was manipulated across 3 conditions. The locations of chocolate (2 of arms 1-8) were always randomly selected for the first study phase; similarly, one of these arms provided a self-generated chocolate feeding and the other provided an experimenter-generated chocolate feeding, and this selection was also randomly determined for the first study phase. The chocolate locations were selected in the second study phase of the same day as follows: In the Random condition, the locations of self-generated and experimenter-generated chocolate were randomly selected in the second study phase, independent of the locations that were selected in the first study phase. In the Same condition, the values selected for the first study phase were also used in the second study phase (e.g., self-generated chocolate at arm 3 and experimenter-generated chocolate at arm 7 in the study phase in both rooms); thus, the same pattern of replenishment occurred in both corresponding test phases. In the Different condition, the values selected for the first study phase (e.g., self-generated chocolate at arm 3 and experimenter-generated chocolate at arm 7 in one room) were reversed for the second study phase (e.g., self-generated chocolate at arm 7 and experimenter-generated chocolate at arm 3 in the other room). Thus, in the Different condition, the same two arms were used in the two study phases, but self-generated and experimenter-generated feeding in study were swapped between rooms; accordingly, one chocolate location replenished in the test in one room and the other replenished at test at the opposite location in the other room. Chow baited locations were independently and randomly selected in all study conditions. In summary, in the two test phases, also conducted on the same day,

chocolate would replenish at the same arm in both rooms in the Same condition; in the Different condition, one chocolate location would replenish in one room, and the other chocolate location would replenish in the other room. In the Random condition, the chocolate arms occasionally overlapped but the extent of overlap or conflicting cues could not be predicted. The three conditions (Random, Same, and Different) were each presented twice in randomized blocks of 6 days, with the constraint that identical conditions were not repeated in more than three consecutive days.

Experiment 3

In Experiment 3, we examined a range of long retention intervals using a memory load of 1 episode, to identify a retention interval challenge for each rat in which accuracy in avoiding revisits to the chow locations was lowered while the rat continued to preferentially revisit the replenishing chocolate location. In all other respects, the procedure was as described in Experiment 1. For one rat, it was not possible to identify such a retention interval, and a second rat stopped differentially revisiting the chocolate location; hence, we did not test these rats in Experiment 3. Because of an experimenter error, the retention interval was longer for two rats in the memory load of 2 than in the memory load of 1. The retention intervals were as follows across individual rats: 3, 4, 6, 7, and 7 days (mean = 5.4 days) for memory load of 1; for the corresponding rats, the retention intervals were 3, 4, 6, 11 and 11 days (mean = 7 days) for memory load of 2. Because our hypothesis sought successful source memory performance when the memory load was increased, the slightly longer delay with a memory load of 2 relative to that used with the memory load of 1, is conservative with respect to our hypothesis.

Data analysis and statistics

The probability of revisiting chocolate (data in Figure 3) was calculated as follows: The probability of at least one revisit to the chocolate location was calculated for the first five choices in the test phase (1 if at least one revisit occurred; 0 otherwise); the probability expected by chance (i.e., random arm entries) is 0.487 (calculated with a geometric distribution). For estimates of accuracy in avoiding chow-flavored locations (data in Table S1), a correct visit was defined as visiting an arm that was baited with chow in the test phase, and the analysis of the first four choices was restricted to the six non-chocolate arms; accuracy expected by chance (i.e., random arm entries) is 0.518 (the Bayesian expected value was calculated by enumerating all possible sequences of arm entries). Statistical tests were considered significant at an alpha level of 0.05.

Supplemental References

S1. Crystal, J.D., Alford, W.T., Zhou, W., and Hohmann, A.G. (2013). Source memory in the rat. Curr. Biol. *23*, 387-391.

S2. Babb, S.J., and Crystal, J.D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. Learn. Motiv. *36*, 177-189.