Published in final edited form as:

Anim Cogn. 2017 March ; 20(2): 215–220. doi:10.1007/s10071-016-1040-z.

A test of the reward-value hypothesis

Alexandra E. Smith¹, Stefan J. Dalecki¹, and Jonathon D. Crystal¹

¹ Department of Psychological and Brain Sciences, Indiana University, Bloomington, IN 47405-7007, USA

Abstract

Rats retain source memory (memory for the origin of information) over a retention interval of at least 1 week, whereas their spatial working memory (radial maze locations) decays within approximately 1 day. We have argued that different forgetting functions dissociate memory systems. However, the two tasks, in our previous work, used different reward values. The source memory task used multiple pellets of a preferred food flavor (chocolate), whereas the spatial working memory task provided access to a single pellet of standard chow-flavored food at each location. Thus, according to the reward-value hypothesis, enhanced performance in the source memory task stems from enhanced encoding/memory of a preferred reward. We tested the reward-value hypothesis by using a standard 8-arm radial maze task to compare spatial working memory accuracy of rats rewarded with either multiple chocolate or chow pellets at each location using a between-subjects design. The reward-value hypothesis predicts superior accuracy for high-valued rewards. We documented equivalent spatial memory accuracy for high- and low-value rewards. Importantly, a 24-h retention interval produced equivalent spatial working memory accuracy for both flavors. These data are inconsistent with the reward-value hypothesis and suggest that reward value does not explain our earlier findings that source memory survives unusually long retention intervals.

Keywords

Reward value; Source memory; Spatial memory; Episodic memory; Rats

Introduction

A fundamental characteristic of human cognition is the ability to remember an event that was personally experienced as an episode (Hasselmo and Eichenbaum 2005; Tulving 1983). The evolution of episodic memory emerged much earlier than previously supposed, and episodic memory is shared by a phylogenetically wide range of animals (e.g., scrub jays, rats, and primates) (Babb and Crystal 2005, 2006a, b; Clayton and Dickinson 1998;

Jonathon D. Crystal jcrystal@indiana.edu.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants performed by any of the authors.

Hoffman et al. 2009; Martin-Ordas et al. 2010; Zhou and Crystal 2009, 2011; Zhou et al. 2012). Episodic memory, as defined by Tulving (1983), is memory of a specific earlier event and of contextual features of the event (i.e., *what*, *where*, and *when* an event occurred). A prevalent view is that episodic memories can be examined through the study of source memory (Johnson 2005). Source memory is the recollection of the source, or origin, of information acquired in the past and allows for the recollection of conditions under which the information was acquired and the differentiation of similar events (Johnson et al. 1993). In humans, for example, source memory is why we can avoid telling our favorite joke to the person who originally told us the joke (Crystal 2016; Wright 2013). Failures in source memory result in incorrect attributions about one's mental experiences. Such impairments manifest in aging and clinical populations (e.g., Alzheimer's disease and schizophrenia) and can be debilitating (Johnson et al. 1993).

Source memory has long been studied in humans but is a recent venture in animal cognition. We have developed a model of source memory in rats (Crystal et al. 2013; Crystal and Alford 2014; Crystal and Smith 2014). In our approach, rats forage in a radial arm maze for chocolate-flavored food rewards that replenish (provide additional helpings at a later time) or fail to replenish (do not provide additional helpings at a later time). Replenishment of chocolate was dependent on a source-information rule. The source memory of eating chocolate at daily unique locations was manipulated by the experimenter by either allowing a rat to find the chocolate location by running down a runway (i.e., self-generated search) or placement by the experimenter at the chocolate location (i.e., experimenter-generated search). Rats successfully differentiate the two chocolate locations presumably based on the source feature; rats return to the replenishing chocolate location while avoiding the non-replenishing chocolate location (Crystal et al. 2013; Crystal and Alford 2014; Crystal and Smith 2014). Other locations provided standard chow-flavored food, which never replenished; the non-replenishing chow locations allowed us to measure spatial working memory concurrently in the same rats that provided an independent measure of source memory. This source memory task allows for the investigation of the characteristic bound quality of episodic memory. Success in the source memory task requires retrieval of the chocolate item (*what*), the location (*where*), and the type of search (*source*). We have previously demonstrated that rats bind together multiple features of an event (i.e., *what*, *where*, and *source*) using interleaved opportunities to forage for food in multiple contexts (Crystal and Smith 2014). Similar evidence was provided by (Clayton et al. 2001) in food-storing scrub jays. The primary function of feature binding is to disambiguate similar episodes from one another. Using a different approach, we recently demonstrated that rats remember many items and the contexts in which they occur (over 30) using episodic memory (Panoz-Brown et al. 2016).

Notably, we have previously demonstrated that the forgetting rates for source and spatial memory are different (Crystal et al. 2013; Crystal and Alford 2014; Crystal and Smith 2014). Spatial memory in rats is vulnerable to decay over retention intervals of 24 h, whereas source memory survives unusually long retention intervals (7–11 days). We have suggested that the different forgetting rates of source and spatial memory document a dissociation between two memory systems, namely source memory and spatial working memory. However, it is important to note that the source memory task used two different

food rewards; measures of source memory used locations that provide three of the preferred chocolate-flavored pellets, whereas measures of spatial memory used locations that provide one of the less-preferred chow-flavored pellets. It is notable that at long delays rats are unable to avoid the visited chow locations (based on spatial memory) while successfully discriminating the chocolate locations (based on source memory) within the same session as both tasks require memory of spatial information.

An alternative explanation for the long-lasting memory for source information is that a preferred reward may enhance encoding/memory, which we refer to as the *reward-value hypothesis* (Crystal 2016). The reward-value hypothesis proposes that higher encoding/memory, and therefore accuracy, occurs for the locations with high-valued chocolate-flavored pellets. In the source memory task, differentiation between accuracy for source information and spatial information was observed as a function of retention interval. After a retention interval of 24 h following encoding, spatial memory (chow rewarded) is degraded whereas source memory (chocolate rewarded) is preserved (Crystal et al. 2013; Crystal and Alford 2014; Crystal and Smith 2014). The reward-value hypothesis makes a striking prediction, namely that long-lasting memory would have been observed in a substantial body of earlier research (e.g., Beatty and Shavalia 1980; Crystal and Babb 2008) using the radial maze if only researchers had used sufficiently valuable food rewards. The focus of this hypothesis is on long retention intervals (e.g., 24 h). We believe that a direct test of the reward-value hypothesis can be addressed using a between-group design, in which the reward-value hypothesis predicts that high accuracy will occur even after a long delay for a group of rats tested with a high-value reward (e.g., multiple chocolate pellets at each location) relative to a group of rats that received a standard reward (e.g., an equivalent number of chow pellets). Thus, we assessed spatial working memory using retention intervals up to 24 h in a standard 8-arm radial maze (i.e., there were no replenishment contingencies and the rats never received experimenter placement at a food location). Given the widespread use of the radial maze (with the standard methods used here) in comparative cognition and neuroscience research, we believed that it was worth testing this hypothesis (because it has the potential to reveal a startling revision of our understanding of memory in rats). The impetus for considering this possibility was the surprising observation that we made in our other research focused on source memory, namely that briefly encoded, item-specific information is remembered for 7–11 days (Crystal et al. 2013; Crystal and Alford 2014; Crystal and Smith 2014), which is unprecedented in rodents and rivals abilities reported in primates and corvids (Clayton and Dickinson 1998; Martin-Ordas et al. 2013). Therefore, we used the following design in the current research. We used two independent groups of rats. One group of rats received three chocolate pellets at each location (referred to as the chocolate group); a second group of rats received three chow pellets at each location (chow group). Therefore, the reward-value hypothesis predicts that performance with high-value rewards (but not with low-value rewards) will survive a retention interval of 24 h. Alternatively, reward value may not contribute to accuracy of spatial memory; according to this view, we expect that spatial working memory will be degraded after 24 h for both chow- and chocolate-flavored groups. The latter view is consistent with the hypothesis that the long-lasting memory observed in previous experiments may be a distinct feature of source memory in rats.

Methods

Animals

Sixteen male Long–Evans rats (*Rattus norvegicus*; Harlan, Indianapolis, IN; 73 days old and 295 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. Two rats were excluded from testing with delays (one rat learned to escape the maze and another failed to visit pellet locations during initial stages of training); therefore, we report data from fourteen rats. The rats received 45-mg chow and chocolate pellets (F0165 and F0299, respectively; Bio-Serv, Frenchtown, NJ) during experimental sessions and 15 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 the maze. All procedures were approved by the Institutional Animal Care and Use Committee at Indiana University Bloomington (protocol 13-012) and followed national guidelines.

Apparatus

An 8-arm radial maze [described in Babb and Crystal (2005)] was used. The maze (positioned 81 cm above the floor) consisted of a central hub (29 cm in diameter, 11 cm high), eight runways (each 76 cm long, 9 cm wide, and 18 cm high), guillotine doors, and a food trough and pellet dispenser at the distal end of each arm. Experimental events, movement of guillotine doors, activation of food dispensers, and interruption of photobeams were controlled by a Nexlink 850 MHz Intel Celeron computer running Windows XP. Data were recorded (10-ms resolution) with MED-PC software (version 4.1). Chocolate- and chow-flavored pellets were placed outside each runway in order to keep food odors constant throughout all parts of the experiment. The maze was wiped down with 2 % chlorohexide prior to placing each rat in the maze.

Preliminary training

Pretraining consisted of two stages: maze familiarization and 8-arm training. Prior to maze familiarization sessions, rats were randomly assigned to either the chocolate- or chow-rewarded group. Chocolate- or chow-flavored pellets (consistent with group assignment) were placed along each arm in the food trough during four daily 10-min familiarization sessions. During daily sessions (i.e., once per day), each rat was placed individually in the central hub of the maze. After 30 s, all eight doors opened and the rats were allowed to explore and eat pellets for 10 min. Eight arm training occurred in ten daily sessions. Session initiation was as described above. Each location provided food once, contingent upon visiting the food trough; rats in the chocolate group received three chocolate-flavored pellets, whereas the rats in the chow group received three chow-flavored pellets. Locations did not replenish. Sessions terminated after food was dispensed from all eight locations, or 10 min had elapsed. Rats were always placed in a pseudorandom direction during maze hub placement prior to all preliminary training sessions.

Experimental procedure

Each session consisted of the following (Fig. 1): a study phase (encoding), a retention interval, and a test phase (memory assessment). A 1-day inter-session interval was used. To initiate the study phase, rats were placed in the hub; orientation of the rats was pseudorandom. Next, the rats were given access to four out of eight locations (randomly selected). The study phase ended when three pellets were dispensed at each of the four accessible locations when the rat first interrupted a photobeam in the food trough. The rat was removed from the maze and placed in the home cage for a retention interval of approximately 5 min, 30 min, or 24 h. The rat was returned to the central hub to begin the test phase (memory assessment). Memory assessment was prompted by the opening of all eight doors. In the test phase, three pellets were dispensed at each of the four previously unvisited arms when the rat first interrupted the food-trough photobeam. All rats received eleven sessions with a 5-min retention interval followed by eight pseudorandomly mixed sessions with longer retention intervals (five 30-min, three 24 h); although the 24-h retention interval sessions occurred after 5-min retention interval sessions, any new learning would have worked against the expected decline in accuracy due to long retention intervals. For a session using a 24-h retention interval, study and test phases occurred on sequential days; the next session began 1 day after the end of the test phase. Locations during the study and test phase did not replenish food. Each phase ended when the rat obtained all available pellets or 10 min elapsed.

Data analysis

Accuracy in spatial working memory (i.e., avoiding previously visited locations) was measured as the total number of correct (i.e., baited) arm visits during the first four choices of the test phase expressed as a proportion of four. An arm visit was defined as the rat breaking a photobeam at the distal end of the arm; a photobeam interruption at the entrance to an arm was required before the next trough entry was recorded as a visit. An arm visit was counted as an error if the arm had been visited earlier in the session. Spatial memory was analyzed by a mixed analysis of variance (ANOVA). Statistical analysis was performed using IBM SPSS Statistics version 22 (SPSS Inc., Chicago, IL, USA). Statistical tests were considered significant at alpha level of $p < 0.05$.

Results

Figure 2 plots accuracy as a function of retention intervals for the chocolate- and chow-rewarded groups. Accuracy declined as a function of retention interval. Notably, accuracy (mean $\pm$ SEM) in both chocolate (0 h: 0.75 ± 0.02 ; 0.5 h: 0.74 ± 0.06 ; 24 h: 0.55 ± 0.04) and chow (0 h: 0.78 ± 0.02 ; 0.5 h: 0.78 ± 0.04 ; 24 h: 0.56 ± 0.03) groups showed equivalent declines as retention interval increased. These observations are supported by a 2 (food type) $\times$ 3 (retention interval) mixed ANOVA. Spatial memory declined significantly as a function of retention interval, ($F(2, 24) = 15.63$, $p = 0.00005$). No effect of food type was found ($F(1, 12) = 0.80$, $p = 0.39$). No interaction was found between food type and retention interval ($F(2, 24) = 0.12$, $p = 0.89$). Post hoc pairwise comparisons (using Fisher's least significant difference) revealed that performance at 24 h was significantly lower than at each of 0 and 0.5 h, which did not differ from each other. If rats entered arms randomly, the dependent

measure expected by chance is 0.41 (Olton and Samuelson 1976). Performance was significantly above chance after the 24-h retention interval (chow: $t(5) = 5.24$, $p = 0.002$; chocolate: $t(7) = 3.20$, $p = 0.01$); although spatial memory declined, both groups of rats were locating the non-visited arms at above chance levels.

The reward-value hypothesis predicts that accuracy, after a long (i.e., 24-h) delay, will be higher in the chocolate group compared to the chow group. Our data do not support this hypothesis. We performed a planned comparison on accuracy at the 24-h delay; accuracy in chocolate and chow groups was not significantly different ($t(12) = -0.06$, $p = 0.95$) at the 24-h delay. Because rejecting the reward-value hypothesis involves a null-effect prediction (namely that equivalent accuracy will occur after a long delay in chocolate and chow groups), we used Bayesian statistics, which permits “proving the null” hypothesis (Gallistel 2009 p. 439; Rouder et al. 2009). The prior hypothesis used the effect size derived from our earlier work [Crystal et al. (2013); Figure 1C, 24-h source memory effect size = 1.97, using Equation 2.3.4 in Cohen (1988)]. The ZJS Bayes factor is 4.9; that is, the null hypothesis is almost five times more likely than the hypothesis that reward value impacts accuracy. A Bayes factor of this size is described as *substantial* evidence that the null hypothesis is correct (Gallistel 2009). Thus, these data provide substantial evidence that the reward value does not influence accuracy, which provides statistical evidence to reject the reward-value hypothesis.

Discussion

The reward-value hypothesis proposes that high-value rewards enhance encoding and/or retrieval of information. The reward-value hypothesis predicts that memory persists over long delays (e.g., 24 h) when a sufficiently high-valued reward is used. In the current study, there was no evidence for enhancement of performance in the chocolate-rewarded group; spatial memory performance did not differ between the chocolate- and chow-rewarded groups and both groups showed the typical decline in spatial memory following a 24-h retention interval. Moreover, we provided statistical evidence for equivalent accuracy after a long retention interval using a Bayesian analysis. These findings suggest that reward value does not explain our earlier findings that source memory survives unusually long retention intervals.

A recent study (Smith et al. 2016) sheds additional light on the reward-value hypothesis by using a pharmacological manipulation that differentially interfered with spatial and source memory. The reward-value hypothesis predicts that the strongly encoded information via high-value rewards would be less vulnerable to interference than information from low-value rewards. The opposite was found; source memory (rewarded with chocolate-flavored pellets) was selectively impaired by the nonselective NMDAR antagonist MK801 while sparing spatial memory (rewarded with chow-flavored pellets). Smith et al. (2016) findings lay in contrast with the predictions of the reward-value hypothesis.

In other experiments that used the radial maze, rats avoid visiting previously visited locations even if no explicit rewards are provided (Timberlake and White 1990; Gaffan and Davies 1981). This observation suggests that high accuracy occurs even when the reward

value is potentially zero, which is consistent with our view that reward value is not sufficient to impact accuracy in spatial working memory. This observation does not preclude the possibility that rats may learn about fixed reward values when experimental contingencies demand such learning. For example, Cohen et al. (2003) have shown that rats can learn about reward probabilities at fixed locations or locations predicted by non-spatial cues.

As previously mentioned, the rewards in the source memory task additionally differ in the quantity of food provided. It is possible that a reward of three pellets, instead of the standard one pellet, might drive high source memory performance in our previous work. This possibility was addressed in the current study; all locations provided three pellets per location, mimicking the reward magnitude used for measuring retention of source information in the source memory task. If a large reward magnitude is sufficient to produce long-lasting retention (as in previous work), then both groups in the current study would be expected to produce high accuracy after the 24-h retention interval. Notably, both groups in the current study show the typical decline in measures of spatial memory after a 24-h retention interval. Thus, the data in our earlier work are not likely to be explained by reward magnitude.

An alternative not addressed in the current experiment is the potential role of contrast in the source memory paradigm. Perhaps the contrast between high- and low-value rewards, in our previous work, contributed to survival of memory over a long retention interval. Our current experiment focused on testing a prediction of the reward-value hypothesis, namely that high-valued rewards may promote long-term retention of spatial information. Because the current experiment used a between-subjects design, we did not provide a test of the potential role of contrast. That being said, rats in the chocolate-reward group were presented with extra-context contrast in food flavors each day. The chow-flavored reward is similar to the daily food rations provided after daily testing. Therefore, rats in the chocolate-reward group experienced contrast between daily rations and the high-value reward of chocolate during testing. The effect of contrast between high- and low-value rewards, manifesting as decreased performance with low-value rewards, exists over long-interval interruptions of up to 70 h (Flaherty et al. 1979), well exceeding the intervals in the present study. Therefore, our findings suggest that contrast, at least spanning multiple contexts, is unlikely to support long-lasting memory. Moreover, contrast effects tend to produce changes in response that have a slow onset and cause small changes in measures such as running speed (Flaherty et al. 1973) and, thus, is perhaps unlikely to explain the increase in retention for source locations over 7–11-day retention intervals. However, further research using a within-subjects design to present two flavors per animal in a single experimental context would be needed to fully test the potential impact of contrast on long-term retention.

We propose that reward value is not sufficient to produce long-term retention of spatial information. These data suggest that our earlier observations of long-term retention of source information is not likely to be due to the high-reward value in those experiments. Further research should examine the role of within-context flavor contrast on spatial accuracy over long delays. We conclude that the dissociation between source and spatial memory systems in the rat in earlier work is unlikely to be explained by reward value, which

opens the door for the study of source memory in nonhumans and supports the translational use of models of cognition in rats.

Acknowledgments

This work was supported by National Institute of Mental Health R01MH098985 and National Institute on Aging R21AG044530 to JDC and the support of a Neuroscience Fellowship and the Harlan Scholars Program to AES.

References

- Babb SJ, Crystal JD. Discrimination of what, when, and where: implications for episodic-like memory in rats. *Learn Motiv.* 2005; 36:177–189.
- Babb SJ, Crystal JD. Discrimination of what, when, and where is not based on time of day. *Learn Behav.* 2006a; 34:124–130. [PubMed: 16933798]
- Babb SJ, Crystal JD. Episodic-like memory in the rat. *Curr Biol.* 2006b; 16:1317–1321. [PubMed: 16824919]
- Beatty WW, Shavalia DA. Spatial memory in rats: time course of working memory and effect of anesthetics. *Behav Neural Biol.* 1980; 28:454–462. [PubMed: 7406805]
- Clayton NS, Dickinson A. Episodic-like memory during cache recovery by scrub jays. *Nature.* 1998; 395(6699):272–274. [PubMed: 9751053]
- Clayton NS, Yu KS, Dickinson A. Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *J Exp Psychol Anim Behav Process.* 2001; 27(1):17–29. [PubMed: 11199511]
- Cohen, J. Statistical power analysis for the behavioral sciences. 2nd edn.. Lawrence Erlbaum Associates; Hillsdale: 1988.
- Cohen J, Pardy S, Solway H, Graham H. Chunking versus foraging search patterns by rats in the hierarchically baited radial maze. *Anim Cogn.* 2003; 6(2):93–104. [PubMed: 12720109]
- Crystal JD. Animal models of source memory. *J Exp Anal Behav.* 2016; 105(1):56–67. doi:10.1002/jeab.173. [PubMed: 26609644]
- Crystal JD, Alford WT. Validation of a rodent model of source memory. *Biol Lett.* 2014; 10(3): 20140064. doi:10.1098/rsbl.2014.0064. [PubMed: 24647728]
- Crystal JD, Babb SJ. Spatial memory in rats after 25 hours. *Learn Motiv.* 2008; 39(4):278–284. [PubMed: 19884952]
- Crystal JD, Smith AE. Binding of episodic memories in the rat. *Curr Biol.* 2014; 24(24):2957–2961. doi:10.1016/j.cub.2014.10.074. [PubMed: 25466681]
- Crystal JD, Alford WT, Zhou W, Hohmann AG. Source memory in the rat. *Curr Biol.* 2013; 23(5): 387–391. doi:10.1016/j.cub.2013.01.023. [PubMed: 23394830]
- Flaherty CF, Riley EP, Spear NE. Effects of sucrose concentration and goal units on runway behavior in the rat. *Learn Motiv.* 1973; 4(2):163–175.
- Flaherty CF, Ciszewski WA, Kaplan PS. Retention of taste quality following brief exposure to sucrose. *Chem Sens Flavor.* 1979; 4(1):73–78. doi:10.1093/chemse/4.1.73.
- Gaffan EA, Davies J. The role of exploration in win-shift and win-stay performance on a radial maze. *Learn Motiv.* 1981; 12(3):282–299. doi:10.1016/0023-9690(81)90010-2.
- Gallistel CR. The importance of proving the null. *Psychol Rev.* 2009; 116(2):439–453. doi:10.1037/a0015251. [PubMed: 19348549]
- Hasselmo ME, Eichenbaum H. Hippocampal mechanisms for the context-dependent retrieval of episodes. *Neural Netw.* 2005; 18(9):1172–1190. doi:10.1016/j.neunet.2005.08.007. [PubMed: 16263240]
- Hoffman ML, Beran MJ, Washburn DA. Memory for “what”, “where”, and “when” information in rhesus monkeys (*Macaca mulatta*). *J Exp Psychol Anim Behav Process.* 2009; 35(2):143–152. [PubMed: 19364223]

- Johnson MK. The relation between source memory and episodic memory: comment on Siedlecki et al. (2005). *Psychol Aging*. 2005; 20(3):529–531. doi:10.1037/0882-7974.20.3.529. [PubMed: 16248712]
- Johnson MK, Hashtroudi S, Lindsay DS. Source monitoring. *Psychol Bull*. 1993; 114(1):3–28. [PubMed: 8346328]
- Martin-Ordas G, Haun D, Colmenares F, Call J. Keeping track of time: evidence for episodic-like memory in great apes. *Anim Cogn*. 2010; 13(2):331–340. doi:10.1007/s10071-009-0282-4. [PubMed: 19784852]
- Martin-Ordas G, Berntsen D, Call J. Memory for distant past events in chimpanzees and orangutans. *Curr Biol*. 2013; 23(15):1438–1441. [PubMed: 23871242]
- Olton DS, Samuelson RJ. Remembrance of places passed—spatial memory in rats. *J Exp Psychol Anim B*. 1976; 2(2):97–116. doi:10.1037/0097-7403.2.2.97.
- Panoz-Brown DE, Corbin HE, Dalecki SJ, Gentry M, Brotheridge S, Sluka CM, Wu J-E, Crystal JD. Rats remember items in context using episodic memory. *Curr Biol*. 2016 doi:10.1016/j.cub.2016.08.023.
- Rouder J, Speckman P, Sun D, Morey R, Iverson G. Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonom Bull Rev*. 2009; 16(2):225–237. doi:10.3758/pbr.16.2.225.
- Smith AE, Xu Z, Lai YY, Kulkarni PM, Thakur GA, Hohmann AG, Crystal JD. Source memory in rats is impaired by an NMDA receptor antagonist but not by PSD95-nNOS protein-protein interaction inhibitors. *Behav Brain Res*. 2016; 305:23–29. doi:10.1016/j.bbr.2016.02.021. [PubMed: 26909849]
- Timberlake W, White W. Winning isn't everything: rats need only food deprivation and not food reward to efficiently traverse a radial arm maze. *Learn Motiv*. 1990; 21(2):153–163.
- Tulving, E. *Elements of episodic memory*. Oxford University Press; New York: 1983.
- Wright AA. Episodic memory: a rat model of source memory. *Curr Biol*. 2013; 23(5):R198–R200. doi:10.1016/j.cub.2013.01.055. [PubMed: 23473561]
- Zhou W, Crystal JD. Evidence for remembering when events occurred in a rodent model of episodic memory. *Proc Natl Acad Sci USA*. 2009; 106(23):9525–9529. doi:10.1073/pnas.0904360106. [PubMed: 19458264]
- Zhou W, Crystal JD. Validation of a rodent model of episodic memory. *Anim Cogn*. 2011; 14(3):325–340. doi:10.1007/s10071-010-0367-0. [PubMed: 21165663]
- Zhou W, Hohmann AG, Crystal JD. Rats answer an unexpected question after incidental encoding. *Curr Biol*. 2012; 22(12):1149–1153. doi:10.1016/j.cub.2012.04.040. [PubMed: 22633809]

Fig. 1.

A schematic of the maze for two independent experimental groups of rats (chocolate and chow). Each arm was baited with food (depicted by *gray shading*) once per day. When a rat visited an arm, it consumed the food, thereby depleting these arms of food. A revisit to a food-depleted location is considered an error. In the study phase (encoding), the rat chose from four randomly selected open doors, thereby depleting these arms of food, while closed doors prevented it from entering the remaining four arms. After a retention interval delay, all eight doors opened and the rat searched for the last four baited locations (test phase; memory assessment)

Fig. 2.

Rats visit previously baited locations while avoiding unbaited locations. No difference in probability of visiting baited locations during the first four arm choices in the test phase was observed between rats rewarded with chow- (*dashed line*) and chocolate-flavored pellets (*solid line*). Spatial memory declined as a function of retention interval for both groups. Notably, accuracy in chocolate and chow groups was equivalent after a 24-h retention interval delay, contrary to the reward-value hypothesis. The *horizontal dotted line* indicates chance. *Error bars* equal ± 1 SEM