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A test of the reward-contrast hypothesis

Stefan J. Dalecki^a, Danielle E. Panoz-Brown^a, and Jonathon D. Crystal^{a,*}

^aDepartment of Psychological and Brain Sciences, Indiana University, IN 47405

Abstract

Source memory, a facet of episodic memory, is the memory of the origin of information. Whereas source memory in rats is sustained for at least a week, spatial memory degraded after approximately a day. Different forgetting functions may suggest that two memory systems (source memory and spatial memory) are dissociated. However, in previous work, the two tasks used baiting conditions consisting of chocolate and chow flavors; notably, the source memory task used the relatively better flavor. Thus, according to the reward-contrast hypothesis, when chocolate and chow were presented within the same context (i.e., within a single radial maze trial), the chocolate location was more memorable than the chow location because of contrast. We tested the reward-contrast hypothesis using baiting configurations designed to produce reward-contrast. The reward-contrast hypothesis predicts that under these conditions, spatial memory will survive a 24-hour retention interval. We documented elimination of spatial memory performance after a 24-hour retention interval using a reward-contrast baiting pattern. These data suggest that reward contrast does not explain our earlier findings that source memory survives unusually long retention intervals.

Keywords

reward-contrast; source memory; spatial memory; episodic memory; rat

1. Introduction

Dissociating memory systems can be achieved by comparing quantitative features of performances. For example, comparing forgetting functions may suggest different characteristics of memory systems. Crystal and colleagues (2013) recently argued that distinctive aspects of forgetting functions suggest a dissociation of memory systems. In one system – source memory (i.e., a representation of the origin of information) – no forgetting occurred with retention intervals up to two days, and source memory was intact, although reduced, after seven days. By contrast, in the other system (spatial memory), all forgetting occurred after one to two days, with no further forgetting after longer retention intervals. The long-lasting nature of source memory was replicated under varying conditions (Crystal

*Corresponding author: Jonathon D. Crystal, jcrystal@indiana.edu.

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& Alford, 2014; Crystal & Smith, 2014). However, because performance in the two tasks was rewarded by different food types (chocolate and chow), different levels of motivation may complicate the interpretation of forgetting functions. Two alternative, nonmemory-system explanations focus on the intrinsic values of the different rewards and the comparative value of two nearby rewards, which we refer to as the reward-value hypothesis and reward-contrast hypothesis, respectively.

As described above, source memory is the memory of the origin of information. For example, people sometimes remember that a recent news story was heard on the TV or the radio, which represent instances of source memory. Crystal and colleagues (2013) developed an animal model of source memory using an 8-arm radial maze. To manipulate the source of information in the radial maze, rats could forage for distinctive flavors of food that replenished or failed to replenish at its recently encountered location according to a source-information rule. To this end, an experimenter placed the rat at the food trough of an arm which then dispensed chocolate (i.e., an experimenter-generated event), whereas the rat encountered chocolate on its own at a different food trough at another arm in the maze (i.e., a self-generated event). The rat also discovered chow-flavored pellets at yet two additional arms; the assignment of self-generated chocolate, experimenter-generated chocolate, and chow locations were randomly selected for each encoding phase of the trial. Next, the trial continued after a retention interval, at which point the rats discovered chow-flavored pellets at the other four arms that had not been visited in the trial. At this stage, source memory was assessed: The arm at which self-generated chocolate was previously available, now provided additional chocolate at the test (replenishment), whereas the arm at which experimenter-generated chocolate was previously available, now did not provide additional chocolate (nonreplenishment) in some experiments. In other experiments, the replenishment contingency was reversed. Notably, to successfully revisit the replenishment location, the rat needed to remember the source of information, namely self-generated vs. experimenter-generated information. Evidence for source memory comes from the observation that rats revisited the replenishment location at a higher rate than the nonreplenishment location while avoiding revisits to chow locations.

As one can see, remembering source information yielded a high value reward (i.e., chocolate) and remembering spatial information yielded a low value reward (i.e., chow). Therefore, the dissociation of forgetting functions may be explained by alternative hypotheses. According to the reward-value hypothesis (Crystal, 2016; Smith et al, 2017), chocolate (a high-value reward) supports longer-lasting retention than chow (a low-value reward). Thus, according to the reward-value hypothesis, the source-memory measure survived long retention intervals merely because a high-value reward was used, which would leave no reason to propose a dissociation of two memory systems based on earlier work (Crystal, 2016; Smith et al., 2017).

To test the reward-value hypothesis, Smith and colleagues (2017) characterized spatial memory using all-chocolate or all-chow baiting patterns in a between-subjects experiment. To this end, one group of rats received chocolate as a reward at all eight arms, whereas an independent group of rats received chow at all eight arms. The reward-value hypothesis predicts that spatial memory will survive a long retention-interval challenge when the reward

is chocolate, whereas spatial memory will not survive a long retention interval when the reward is chow. No difference in performance was found between the group of rats: Notably, both groups showed the typical forgetting of spatial information after a 24-hour retention interval.

Here, we test the reward-contrast hypothesis. According to this hypothesis, when chocolate and chow are presented in the same context (i.e., within a single radial maze trial), the chocolate location is more memorable than the chow location due to simultaneous positive contrast (Flaherty, 1996). Notably, the reward-contrast hypothesis predicts that, when chocolate and chow are presented in the same context, spatial memory will survive a long-retention interval challenge.

To test the reward-contrast hypothesis, rats received a baiting pattern that recapitulated the potential contrast that may have been generated in earlier source memory experiments (Figure 1). To this end, foraging on the radial maze was divided into a study phase, retention interval, and test phase. In the study phase (with four doors open), two randomly selected locations provided chocolate, and two other randomly selected locations provided chow. In the test phase, food was available at locations previously blocked by closed doors in the study phase, and all eight doors were open; one randomly selected baited location provided chocolate and the other three provided chow. The reward-contrast hypothesis predicts that spatial memory under these baiting conditions will survive a long retention interval; we characterized spatial memory after 5-min, 30-min, and 24-hour retention intervals. A decline in spatial memory after a 24-hour retention interval would rule out the reward-contrast hypothesis.

2. Methods

2.1 Subjects

Six male Long-Evans rats (*Rattus norvegicus*; Envigo, Indianapolis, IN; 49 days old and 225 g on average, at the start of the experiment) were individually housed with light onset and offset in the colony at 7:30 and 19:30 EST, respectively. Rewards consisted of 45-mg chow and chocolate pellets (F0165 and F0299, respectively; BioServ, French town, NJ). Rats received daily rations of 5012-Rat-Diet (PMI Nutrition International, St. Louis, MO) after the completion of each session conducted five days per week. 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 15-019) and followed national guidelines.

2.2 Apparatus

An 8-arm radial maze (positioned 81 cm above the floor) consisted of a central hub (29 cm in diameter, 11 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 Intel Centron 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 perforated bags in order to keep food odors constant throughout all parts of the experiment. The maze was cleaned with 2% chlorohexide prior to placing each rat in the maze.

2.3 Preliminary Training

Pretraining consisted of two stages: maze familiarization and 8-arm training. Three maze arms were baited with 15 chocolate pellets (5 pellets per arm) and five maze arms were baited with 25 chow pellets (5 pellets per arm) such that each arm contained one flavor. A typical daily session (i.e., once per day) involved each rat being placed individually in the center hub of the maze. After 30 seconds, all eight guillotine doors opened and the rats were permitted to explore and eat pellets for 10 minutes. Next, all guillotine doors closed and the rat was removed from the maze. Uneaten pellets were removed, the maze was cleaned, and the next rat was placed in the central hub. Maze familiarization consisted of five sessions with one exception; one rat received an additional three sessions before transitioning to eight arm training. Eight arm training involved session initiation as described above. Each location provided food, contingent upon the first visit to the food trough; rats received three chocolate pellets from each of the three chocolate locations and one chow pellet from each of the five chow locations. Chocolate and chow locations were randomly selected at the start of each testing day. Sessions terminated after food was dispensed from all eight locations or 10 minutes had elapsed. Eight-arm training lasted 12 sessions. Rats were placed in a pseudorandom direction during the hub placement.

2.4 Study-Test Procedure

Daily sessions consisted of two phases: a study (encoding) phase and a test (assessment) phase (Figure 1). The study phase began with a rat placed in the central hub. After the experimenter left the room and thirty seconds after the program was initiated, four of the eight guillotine doors (randomly selected) were opened. Two of the available arms provided the rat with three chocolate pellets each, and the remaining two arms provided one chow pellet each. The study phase terminated when all four accessible food troughs had been visited. Once the rat was removed from the maze and following an approximately 5 minute, 30 minute, or 24 hour retention interval, the test phase began. In the test phase, rats were placed in the central hub and all eight guillotine doors opened, allowing rewarded visits to one chocolate trough and three chow troughs at locations not previously accessible in the study phase. Locations that were accessible in the study phase did not provide food in the test phase. Rats completed 14 sessions with a retention interval of approximately 5 minutes followed by three session at a retention interval of approximately 30 minutes. Next, three randomly generated blocks of 5 minute, 30 minute, and 24 hour retention intervals took place, resulting in 17, 6, and 3 overall sessions of each retention interval, respectively. In all cases, the study or test phase ended when all baited locations had been visited or after ten minutes had elapsed.

3. Results

Accuracy was calculated as the number of correct visits made within the first four choices divided by four. Figure 2 shows the probability of a rat making a correct choice (mean $\pm$

SEM) as a function of retention interval. As can be seen in the figure, accuracy remained high after relatively short retention intervals but declined precipitously after approximately a day. There was a significant effect of retention interval, based on a one-way analysis of variance ($F(2,10) = 11.66$, $p = .002$; $\omega^2 = .542$). Accuracy at 5- and 30-min retention intervals (0.79 ± 0.04 and 0.80 ± 0.04 , respectively) was above chance ($t(5) = 10.2$, $p = .0002$, $\omega^2 = .896$; and $t(5) = 9.5$, $p = .0002$, $\omega^2 = .882$), whereas accuracy at 24 hours (0.49 ± 0.06) was not significantly different from chance ($t(5) = 1.2$, $p = .28$, $\omega^2 = .039$); performance based on chance is 0.41 (Olton and Samuelson, 1976).

4. Discussion

The reward-contrast hypothesis predicts that accuracy will be sustained over a longer retention interval, including 24-hours when adequate contrast exists; we used a baiting pattern that recapitulated the potential contrast from Crystal and colleagues' (2013) study. Our data rule out the reward-contrast hypothesis. Accuracy significantly decreased as a function of retention interval; at 24 hours, performance was not significantly different from chance.

In the current experiment, the baiting configuration matched that used in previous studies of source memory; chow and chocolate were both available in the study phase and the test phase; more chocolate per location was provided than chow. Therefore, we expect that any contrast that developed in the current experiment matched the contrast that may have developed in the earlier source memory experiments. If reward contrast was responsible for the long-lasting memory in previous source memory experiments, then the matched contrast would be expected to have produced long lasting spatial memory in the current experiment. Contrary to this prediction, spatial memory declined to the level expected by chance after a 24-hour retention interval; spatial memory is typically degraded after approximately a day (Beatty and Shavalia, 1980; Crystal & Babb, 2008).

Two concerns about Crystal and colleagues' (2013) dissociation of memory systems have been proposed. Both concerns have been testing and rejected. Smith and colleagues' (2016) rejected the reward-value hypothesis (see Introduction for details) and the current experiment rejects the reward-contrast hypothesis. In addition to the dissociation of forgetting functions for source memory and spatial memory, Crystal and colleagues also showed, using a short retention interval, that temporary inactivation of the hippocampus selectively impaired source memory while sparing spatial memory. These lines of evidence bolster confidence in using source memory to examine neuroanatomical hypotheses about episodic memory (Crystal et al., 2013), explore binding of episodic memories (Crystal & Smith, 2014), test other cognitive hypotheses (Crystal & Alford, 2014), analyze cognitive side effects of chemotherapy (Smith et al., 2017), and characterize episodic memory impairments in animal models of aging and Alzheimer's disease.

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Highlights

- Source memory and spatial memory last at least 1 week and ~1 day, respectively
- Different forgetting functions dissociate memory systems
- Long-term retention may be caused by contrast within each trial (reward contrast)
- Tested reward-contrast hypothesis by matching baiting configurations
- Spatial memory declines after 24 hr, eliminating reward-contrast hypothesis
- Reward contrast does not explain earlier dissociation of source and spatial memory

Fig. 1.

An example baiting configuration, highlighting the simultaneous presentation of chow and chocolate flavors in a radial maze trial. Each chocolate location provided three chocolate pellets, whereas each chow location provided only a single chow pellet. In the study phase, rats received food at four randomly selected maze arms, with other arms locked by closed doors. In the test phase, rats had access to all eight arms, but food was only available at previously inaccessible arms. Revisits to unbaited arms were considered errors.

Fig. 2.

Rats performed significantly above chance (horizontal dashed line) at both 5-min and 30-min retention intervals. After a 24-hour retention interval, performance was at chance. The reward-contrast hypothesis is ruled out by the observation that spatial memory declined at 24 hours. Error bars represent ± 1 SEM.