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Spatial memory in rats after 25 hours

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Abstract

We investigated the time course of spatial-memory decay in rats using an eight-arm radial maze. It is well established that performance remains high with retention intervals as long as 4 hr, but declines to chance with a 24-hr retention interval (e.g., Beatty & Shavalia, 1980b). It is possible that 24 hr reflects a genuine retention limitation of rat spatial memory. Alternatively, it may be possible to identify factors that might support memory performance even after very long delays. The current experiment was conducted to test the above two hypotheses. We evaluated performance using two intertrial intervals (24 and 48 hr) and two retention intervals (1 and 25 hr). Increasing the intertrial interval produced an approximately constant increase in performance for both retention intervals. This improvement is consistent with a trial-spacing effect (i.e., the superiority of spaced over massed trials). Rat spatial memory apparently lasts at least 25 hr.

Keywords

Spatial navigation; spatial cognition; trial-spacing effect; intertrial interval; retention interval; rat

The radial arm maze (Olton & Samuelson, 1976) has been used extensively to explore the mechanisms of spatial cognition in rats. For example, initial behavioral studies focused on the basic psychological processes responsible for the highly accurate levels of performance that are typically observed (e.g., Brown, 1992; Roberts, 1981, 1992; Timberlake & White, 1990). Subsequent experimental efforts using this approach have explored the anatomical (Davidson & Jarrard, 2004), pharmacological (Myhrer, 2003), and genetic (Ammassari-Teule, Hoffmann, & Rossi-Arnaud, 1993; Ammassari-Teule, Milhaud, Passino, Restivo, & Lassalle, 1999; Mineur & Crusio, 2002; Prior, Schwegler, & Ducker, 1997) bases of spatial cognition. In addition, performance on the radial maze has been useful for assessing hormonal and developmental contributions to spatial cognition (Jonasson, 2005; Luine, Luine, & Harding, 1994; Meck & Williams, 2003).

In the classic version of this method, eight equidistantly-spaced runways are connected to a central area, and the distal end of each arm is baited with a small piece of food. The rat is placed in the central area and permitted to explore the maze and eat the food. Optimal performance is to visit each arm once because each arm is depleted of food when a visit occurs and food is

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not replaced. In most experiments of this type, the rat is returned to the maze after a day and the next trial (with new food at each arm) is conducted.

The extensive use of the radial maze stems from the observation that rats are quite efficient at visiting each arm once without revisits (Olton & Samuelson, 1976; Timberlake & White, 1990). A basic method for studying spatial cognition in the radial maze involves interrupting the rat part way through the trial and then continuing the trial after an intervening event. For example, the initial phase of the trial might consist of presenting the rat with four randomly selected accessible arms (*study phase*), and the continuation of the trial consists of returning the rat to the maze with all arms accessible (*test phase*). Many intervening events have been shown to leave memory for the study phase locations unimpaired. For example, changes in visual, auditory, and olfactory stimuli and food consumption do not interfere with memory (Maki, Brokofsky, & Berg, 1979). More remarkably, performance on another radial maze does not interfere with memory (Beatty & Shavalia, 1980a) even when they are located in the same room (Roberts, 1981).

However, a limited number of events have been found to produce retroactive interference. For example, if the intervening events are at the exact spatial locations that were used in task, then performance declines, and performance also declines if many interpolated events occur (Roberts, 1981). Delivering electroconvulsive shock a couple of hours after the study phase is an additional effective interfering event (Beatty, Bierley, & Rush, 1985; Shavalia, Dodge, & Beatty, 1981). These observations suggest that events that reduce spatial memory in the radial maze are primarily limited to events that occur at the exact position in space or that disrupt consolidation of recently formed memories.

Consistent with the overall finding of resistance to interference in radial maze performance, memory for earlier locations appears to be uninfluenced by relatively long retention intervals between study and test. In particular, Beatty and Shavalia (1980b) showed that accuracy was uniformly high for retention intervals between 0 and 4 hr. Performance declined gradually with longer retention intervals, and was not significantly different from chance¹ when the retention interval was 24 hr. It is possible that 24 hr reflects a genuine limitation of rat spatial memory. Alternatively, it may be possible to identify factors that might support memory performance even after very long delays. The current experiment was conducted to test the above two hypotheses.

One potential explanation for chance-level performance with a 24-hr retention interval is as follows. Training procedures typically involve one trial per day, as was the case in Beatty and Shavalia's (1980b) experiment. Consequently, it is possible that the rats treated the 24-hr retention interval as a cue to reset spatial memory for locations in the earlier study phase. Indeed, accurate performance in the earlier parts of the experiment generally required resetting of spatial memory from day to day in order to maintain high levels of accuracy. The radial-maze experiment is an example of a recency discrimination because all locations have been visited in the past; therefore, accurate performance requires that the subject discriminate which locations have been visited most recently, which would be facilitated by resetting spatial memory each day. Importantly, in earlier experiments, confusion between retention interval and intertrial interval would produce chance performance with retention intervals that are approximately a day. The confusion proposal outlined above is similar to Zentall's recent observations regarding temporal processing, which focus on the potential confusion between retention intervals and intertrial intervals (Zentall, 2006, 2007).

¹The percent correct in the first four choices in the test phase of this experiment is 45% based on chance; this value is based on the conservative assumption that a rat does not enter the same arm twice in succession (Olton & Samuelson, 1976); see Beatty and Shavalia (1980b) for a brief discussion of the chance calculation.

We recently sought to examine spatial memory using a short and long retention interval of 1 and 25 hr, respectively (Babb & Crystal, 2006a). We reasoned that it might be possible to obtain above-chance performance with the long retention interval by using an even longer intertrial interval. In our experiment, the intertrial interval was at least 48 hr. We observed above-chance accuracy in the test phase using a 25-hr retention interval, which after extensive training ranged from approximately 65-75%. Above-chance performance may have occurred because the retention interval and intertrial intervals were not confusing. In addition, the use of a relatively long intertrial interval would be expected to produce high levels of performance given the extensive evidence for superior performance in spaced relative to massed trials (e.g., Cohen, Ried, & Chew, 1994; Cohen, Sturdy, & Hicks, 1996; Roberts & Dale, 1981).

To examine the influence of intertrial interval and retention interval combinations, we trained rats on an eight arm radial maze in the current experiment. The intertrial interval was 24 or 48 hr, using independent groups of rats. All rats were tested with 1-hr and 25-hr retention intervals.

Method

Subjects

Twenty male Long Evans rats (Harlan, Madison, WI) were individually housed in a colony with light onset at 0700 and offset at 1900. Upon arrival in the lab at an age of 7 weeks, the rats were given unlimited access to 5001 Rodent Diet (Lab Diet, Brentwood, MO) for one week, and then given 20 g for one day and 15 g per day on subsequent days. Water was available at all times except during testing. The rats were approximately 12 weeks old at the beginning of experiment. All rats were experimentally naive at the start of the study.

Materials

Testing was conducted in an eight-arm radial maze. The central hub (white polypropylene octagonal base [28.6 cm in diameter, 11.4 cm sides], metal walls [33.3 cm high], and a clear polycarbonate lid, MED Associates, ENV-538) was equipped with eight computer-controlled guillotine doors (ENV-540). The arms (76.2 cm long, 8.9 cm wide with 17.5-cm high clear polycarbonate walls and topped with polycarbonate) radiated from the center hub with equal spacing between each arm. A food trough (ENV-200R1M) was placed at the end of each arm. A photobeam (ENV-254, 1 cm inside each food trough, 1 cm from the trough bottom) detected head entries. A filled 45-mg pellet dispenser (ENV-203) was placed behind each food trough. Additional photobeams were located in each arm at 3.8 and 5.1 cm from the guillotine doors.

The maze was positioned on stools 81.3 cm above the floor. White noise (67 db from a speaker in the ceiling above the hub) minimized outside noise. A 500-MHz computer in an adjacent room, running MED-PC for Windows (Version 1.15), controlled experimental events (guillotine doors and food) and recorded the data (photobeam breaks) with a 10-msec resolution. A video camera in the ceiling above the center of the maze was used to observe the rats.

Procedure

Pretraining consisted of 3 days in which three 45-mg pellets (PJA/I-0045, Research Diets Inc., New Brunswick, NJ) were placed along each arm and one pellet was placed in each food trough to provide the animals with the experience of obtaining food in the maze. During the initial training (10 sessions), each rat was placed in the maze and given access to all eight arms, and one pellet was delivered to each of the accessible food troughs contingent upon the breaking of the photobeam in each of the food troughs by the first head entry. For the rest of the experiment (26 sessions), each rat received two shifts per day of training. The rats were individually placed in the maze at a fixed time of day for a study phase (forced-choice). Four

doors (randomly chosen for each rat each day) were then opened, and each of those four arms provided a pellet. After either a short or long retention interval, each animal was returned to the maze for a test phase (free-choice) in which all eight doors were open; food was available at each of the arms not previously accessible in the study phase. On trials with a short retention interval (12 sessions), the interval between study and test phases was 1 hr. On subsequent trials with a long retention interval, the interval between study and test phases was 25 hr (14 sessions). The rat was required to visit each arm to collect the remaining pieces of food after a retention interval; each test phase ended after the four pellets were collected.

During training, one group of rats ($n = 10$) had an inter-trial interval (ITI) of 48 hr (i.e., each subsequent study phase did not begin until at least two days after the previous test phase was completed). For comparison, a second group of rats ($n = 10$) had an intertrial interval of 24 hr.

Throughout the experiment, the arms of the maze were cleaned with Nolvasan (Fort Dodge Animal Health, Fort Dodge, Iowa) each day between study and test phases. This once-daily, between-phase cleaning reduced odor cues. Moreover, we note that odor cues would not provide a valid predictor of the baited status of arms because forced-choice arms in the study phase were randomly chosen for each rat and several rats were tested before a given rat was returned to the maze for its test phase. In addition, there is extensive evidence that self-generated (e.g., Olton & Collison, 1979) and other-generated (Brown, Farley, & Lorek, 2007) odor trails do not control choice behavior in the radial maze. If a rat was tested in the radial maze, it received its daily food ration approximately 1 hr after completion of its session; on days in which a rat was not tested in the radial maze, it received its daily food ration at approximately the same time of day.

Data analysis

The dependent variable was the proportion of correct locations entered during the first four choices of each test phase; a correct location was defined as one that currently had a piece of food. The proportion correct in the test phase based on chance is 0.41 on the assumption that the rats are equally likely to enter any of the eight arms on any choice. However, rats rarely visit a given arm twice in succession (e.g., Olton & Samuelson, 1976). Therefore, it is more conservative to estimate chance by assuming that the rats never reenter the arm most recently visited, which yields a proportion correct of 0.45. We used the later proportion as the estimate for chance performance.

The analysis was conducted using all sessions; two blocks of data were formed by dividing the data into two halves within each retention-interval condition. Throughout this article, the criterion for statistical significance is .05.

Results

During eight-arm training, the rats entered approximately 7 arms in the first 8 choices (mean $\pm$ SEM: 6.99 ± 0.10 and 7.03 ± 0.09 for the 24- and 48-hr intertrial interval groups, respectively), which corresponds to approximately 87.5% correct.

Accuracy in the test phase is shown in Figure 1. As can be seen in the figure, accuracy decreased as a function of retention interval, as expected. In addition, accuracy was higher in the 48-hr intertrial interval condition compared to the 24-hr condition. The pairs of lines appear to be parallel. Performance increased as a function of blocks of training, particularly in the 1-hr retention interval condition. These observations were confirmed by subjecting the data to a $2 \times 2 \times 2$ (retention interval $\times$ intertrial interval $\times$ block) mixed analysis of variance, which revealed significant effects of retention interval ($F(1,18)=81.8$) and intertrial interval ($F(1,18)=17.5$). The interaction of retention interval $\times$ intertrial interval was not significant ($F(1,18)$

<1). In addition, there was a significant effect of blocks ($F(1,18)=13.2$) and a significant interaction of retention interval x blocks ($F(1,18)=12.1$), and all other interactions failed to reach statistical significance. The retention interval x blocks interaction suggests that the block effect was larger in the 1-hr retention interval compared to the 25-hr retention interval, which was confirmed by a follow-up analysis ($F(1,19)=12.3$). Each data point in Figure 1 is reliably above chance; in addition, the overall accuracy of each individual rat was numerically above chance at each retention interval.

Discussion

The main finding in the current experiment is that increasing the intertrial interval produced an approximately constant increase in performance that did not interact with retention interval. This improvement is consistent with the extensive evidence for the superiority of spaced over massed trials. Interestingly, the improvement occurred for both the short and long retention intervals. If rats had confused 25-hr retention intervals and 24-hr intertrial intervals, then we would expect to observe a larger difference between intertrial-interval conditions for the long retention interval compared to the short retention interval. By contrast, the influence of a trial-spacing effect would be expected to be more uniform across conditions.

We note that the data in Figure 1 were above chance in all conditions. By contrast, the 24-hr retention interval data from Beatty and Shavalia (1980b) was not significantly above chance using a 24-hr intertrial interval. It is difficult to compare the amount of training in these two studies, but we note that our rats had substantially *less* training prior to testing in the long retention interval condition compared to Beatty and Shavalia's rats. However, this apparent difference is likely due to statistical power (they used only five rats) given that the data from our study (0.547 ± 0.015 ; mean $\pm$ SEM) do not differ reliably from those of Beatty and Shavalia (1980b; 0.525 ± 0.03125 , based on measurements of mean and SEM values from their Figure 1), $t(13)<1$.

We trained the rats with a 1-hr retention interval before testing them with the 25-hr retention interval. This sequence was used because we did not expect that the rats could acquire the two-phase procedure using a long retention interval without initially using a more modest retention interval. This rationale is similar to the typical strategy in which 8-arm access is trained before testing with study-delay-test sequences, which is a strategy used in many radial-maze experiments. Moreover, our sequential method follows that used by Beatty and Shavalia (1980b). We note that our conclusions are limited to the particular order in which we conducted the experiment; indeed, we expect that 25-hr performance would be lower if it were not preceded by a modest retention interval. Nevertheless, our data document a method to obtain above-chance performance with a 25-hr retention interval; lower performance may occur in other training methods. Because the effect of blocks appears to be limited to the transition from the first to the second block in the first retention-interval condition, it is unlikely that much additional training effects influenced our data. Moreover, the observation that intertrial interval did not interact with any variables suggests that the main conclusions about the interval-type confusion hypothesis generalizes to all phases of our data.

Our data suggest that the limit of rats' spatial working memory has not yet been reached by 25 hr and that confusion between retention interval and intertrial interval does not account for the observed trial spacing effect. Although other studies have documented support for interval-type confusion (e.g., Cohen & Njegovan, 1999; Santi, Keough, Gagne, & Van Rooyen, 2007), we note that earlier studies used a different scale of intervals (in the range of seconds to minutes) compared to the range of hours to days in the present study.

The question remains: why did longer intertrial intervals improve performance? A number of interesting possibilities were reviewed by Cohen and Njegovan (1999). One possibility is that the buildup of proactive interference between trials dissipates over longer intertrial intervals (Roberts & Dale, 1981). Another possibility is that the ratio of retention interval to intertrial interval determines the expectation of reward (e.g., Gallistel & Gibbon, 2000; Gibbon & Balsam, 1981). A final possibility suggested by Cohen and Njegovan is the trial tracking confusion hypothesis; according to this proposal, an animal may be confused about whether it is within or between trials when retention and intertrial intervals are similar. Applying this latter concept to the present experiment, we note that the delivery of daily rations may have influenced performance in different ways in the 24- and 48-hr intertrial interval conditions.² Delivery of a food ration at the end of a study-test sequence may signal a relatively long delay to the start of the next trial, and may also serve as a cue that the previous study information is not needed for future choice behaviors. However, in a 48-hr intertrial interval, a rat is more likely to forget that it received its post-test ration than in a 24-hr intertrial interval. In the 48-hr intertrial interval a second ration may reinstate the memory that the previous trial has ended and may serve as an extra cue that the previous study information is not needed for future choice behaviors. Although the present experiment was not designed to test the latter hypothesis, future research could vary the temporal location of food rations within intertrial intervals.

In conclusion, spatial memory in rats lasts at least 25 hr. Moreover, increasing the spacing of trials is an effective method to increase spatial memory. Given the role of the hippocampus in long-term retention of information (Hammond, Tull, & Stackman, 2004; Sisti, Glass, & Shors, 2007), behavioral techniques that promote long-term retention may facilitate future studies of its biological bases. One potential application of this method is in studies of episodic-like memory (e.g., Babb & Crystal, 2006a, 2006b; Clayton & Dickinson, 1998; Clayton, Salwiczek, & Dickinson, 2007; Naqshbandi, Feeney, McKenzie, & Roberts, 2007). Previously, we used this method to allow us to compare 1- and 25-hr retention intervals; these were approximately the minimum values that could be used to ensure that tests occurred at the same time of day after both types of retention intervals, thereby controlling time of day. However, most studies of episodic-like memory have been conducted with scrub jays and have used much longer retention intervals (e.g., 5 days). It remains to be determined if comparable retention intervals could be used with rats by further increasing the intertrial interval.

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²We thank an anonymous reviewer for suggesting the ideas in the remainder of this paragraph.

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Figure 1.
Proportion correct increased as intertrial interval increased and as retention interval decreased.
Error bars represent ± 1 standard error of the mean. ITI = intertrial interval.