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Remembrance of places lasts: Proactive inhibition and patterns of choice in rat spatial memory

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A series of experiments was carried out to evaluate the notion that rats given a sequence of massed daily trials on the radial maze reset working memory at the end of each trial by deleting its contents. Although curves presented by D. S. Olton [*Scientific American*, 1977, 236, 82-98: In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*, 1978, Hillsdale, N.J.: Erlbaum] show that rats return to errorless performance at the beginning of each trial after the first, the fact that accuracy falls less rapidly over choices on Trial 1 than on subsequent trials suggests a proactive inhibition (PI) effect. In Experiment 1, Olton's findings were replicated, and a PI effect was observed on Days 1-2 of testing. On Days 3-5, overall accuracy improved significantly and was associated with the development of a strong tendency for rats to enter adjacent alleys, which became particularly marked on the final trials of a day's testing. In order to prevent rats from achieving accurate performance by using an adjacent alleys pattern, a procedure was used in Experiment 2 which involved initial forced random choices followed by a retention test consisting of free choices. Repeated daily trials with this procedure yielded a significant PI effect, which was more marked at a 60-sec delay than at a 0-sec delay. Experiments 3 and 4 showed this PI effect to be robust and resistant to manipulations designed to produce release from PI. Both the PI effect and a strong tendency found in Experiment 1 for animals to avoid on the initial choices of Trial *n* those alleys most recently entered on Trial *n* - 1 argue that rats do not reset working memory between trials.

Recent investigations of spatial memory in the rat, using the radial maze, have revealed some interesting facts. The radial maze consists of eight or more alleys projecting from a central platform, with food placed at the end of each alley. After a small amount of initial training, rats placed on the central platform will collect all of the rewards on the alleys, with few reentries into previously visited alleys. The strong tendency of rats not to reenter alleys previously traveled has been attributed to spatial memory or an ability of the rat to keep track of places visited in a two-dimensional space [for reviews, see Olton (1977, 1978, 1979)]. Prominent characteristics of spatial memory in the rat are that it involves a capacity for retention of a large number of places visited (Olton, Collison, & Werz, 1977; Roberts, 1979), that it persists for 4 hr or longer (Beatty & Shavalia, 1980), that it is based upon retention of extramaze visual cues (Olton & Collison, 1979; Olton & Samuelson, 1976; Zoladek & Roberts, 1978), that retention of sequentially visited alleys shows a recency effect (Roberts & Smyth, 1979), and that a number of sensory events interpolated between runs on the maze and a test of retention creates little interference with memory (Maki, Brokofsky, & Berg, 1979).

As a theoretical model for spatial memory in the rat, Olton (1978) has suggested that memory for alleys visited is held within a limited-capacity working memory. Further, it is held that the

working memory may be reset at the end of each trial by deleting its contents; in this way, proactive inhibition (PI) from a just-completed trial will not interfere with retention of events within a subsequent trial. Evidence for this assumptions comes from an experiment in which rats were tested repeatedly for eight trials, with a 1-min interval between trials. Within each trial, animals made eight or more entrances into alleys. Each entrance was defined as a choice, with entrances into previously unentered alleys being correct choices and entrances into previously entered alleys being errors. When performance was plotted across choices made on each trial, it was found that accuracy dropped as a function of choices within each trial but returned to errorless performance on the initial choices of the subsequent trial (Olton, 1977, 1978). This return to errorless performance at the beginning of each trial after the first was interpreted as evidence for the resetting mechanism.

In this paper, we argue that there is suggestive evidence of PI in Olton's data and that a return to errorless performance at the beginning of each trial in a massed sequence of trials is not strong evidence for absence of PI or a resetting mechanism. This position is based on the observation that Olton's (1977, 1978) curves which plot accuracy as a function of choices decline sooner and more precipitously as trials progress. For example, on Trial 1, animals were errorless on Choices 2-7 and accuracy declined only slightly at Choice 8. On subsequent trials, errors began to appear at Choice 6 and eventually as early as Choice 3, and the drop in accuracy found was substantially greater than that found in Trial 1. This pattern of results is exactly what one might expect from studies of PI in human subjects. Keppel and Underwood (1962) studied the short-term retention of verbal items over successive trials and found that rate of forgetting increased as trials progressed. Importantly, differences in retention on successive trials were small at a short retention interval but marked at longer retention intervals. In the case of spatial memory in the rat, the initial choices of each trial are made when the retention interval is short and the memory load is light. When the final choices are made, the retention interval since initial choices in longer and the potential interference from an increased memory load is greater. These are precisely the conditions which the human literature suggests should produce maximal PI. Hence, the return to errorless performance on initial choices of successive trials may represent a ceiling effect in which the memory task is so easy that it does not reveal PI effects: when the task is made more difficult on later choices, PI effects become apparent.

Evidence regarding the resetting mechanism is potentially available from the initial choices of successive trials, even though these trials involve errorless performance. Since rats show a strong tendency to avoid reentering alleys previously chosen within trials, it is possible that this tendency would persist between trials. That is, the initial alleys chosen on Trial n might reveal an avoidance of the final alleys chosen on Trial n - 1. If this were the case, it would indicate the retention of choices from Trial n - 1 during performance on Trial n. No such behavior should be observed according to the resetting notion, however, since the contents of working memory should have been deleted at the end of Trial n - 1.

Experiment 1

The first experiment was designed to replicate Olton's (1977, 1978) experiment. Rats were tested on an eight-arm radial maze for five trials each day, with a 60-sec intertrial interval (ITI). The data were examined for changes in accuracy over choices within each trial and for any tendency to avoid choice of the alleys most recently entered on the preceding trial.

Method

Subjects

The subjects were 10 naive male hooded rats, which ranged in age from 100 to 125 days at the beginning of the experiment. They were maintained at 80% of free-feeding weight throughout this and the subsequent experiments.

Apparatus

An elevated, eight-arm radial maze was used, which consisted of a circular central platform, 35.5 cm in diameter, and eight identical arms, each 76 cm long × 9 cm wide. The arms extended outward from the central platform, and adjacent arms were separated by 45° angles. The maze was painted black and stood 63.5 cm above the floor. Attached to the end of each arm was a rectangular metal food cup, 7.5 cm long × 5 cm wide × 2.5 cm deep. Adjacent to the central platform, each alley contained a door frame within which was mounted a transparent acrylic door. When raised, each door left a space, 11 cm high × 9 cm wide, through which an animal could gain access to an arm. These doors could be raised and lowered by individually weighted cords attached to a control board situated 1.8 m from the central platform.

The maze was situated in the center of a room, 3.8 m long × 3.2 m wide, which contained a counter along one wall, two windows, and a single door. Also in the room were a small writing table, two high-back stools, and a wastepaper basket. Illumination was provided by two enclosed, overhead fluorescent lighting units.

Procedure

After an initial period of preliminary handling and weight reduction, each subject was allowed to explore the maze freely for about 10 min each day. The doors to all arms were open, and food was placed at the end of each arm. Throughout preliminary training and all further experimentation, arms were baited with one 45-mg Noyes pellet prior to each subject's placement in the maze. After 3 days of free exploration, animals were entering alleys readily and consuming pellets. For the next 4 days, animals were allowed to choose freely among the arms on one trial each day. On each trial, an animal was allowed to enter alleys until all eight food pellets had been collected, and the experimenter recorded the specific alleys entered. An alley entrance was defined as an animal placing all four feet on the alley.

Following the fourth day of preliminary training, the experiment was begun. Each animal was tested for five successive trials each day, with a 60-sec ITI. On each trial, an animal was placed

on the central platform with all eight alley doors open and a food pellet available at the end of each alley. The subject was allowed to enter alleys freely until all eight food pellets were collected. When the animal had returned to the center platform after obtaining the eighth pellet, all alley doors were closed, and the animal was kept on the central platform for the 60-sec ITI. During the ITI, the experimenter rebated each food cup with one pellet. At the end of the ITI, all alley doors were raised simultaneously to initiate the next trial. Testing according to this procedure proceeded for 5 days, at which point the experiment was terminated. It had been intended to carry out the experiment for a more extended period, but testing was terminated after 5 days for reasons which will become apparent in the presentation of the results.

Throughout these experiments, effects were considered significant only if $p < .05$.

Results

During the 4 days of preliminary training, all subjects showed a strong tendency to avoid entering alleys previously visited. The mean number of different alleys entered on the first eight choices was 7.3, 7.5, 7.6, and 7.6, respectively, for Days 1-4.

Over the initial 5 days of testing, animals showed improvement in choice of unentered alleys. The mean percentages of choices of correct (unentered) alleys on the first eight choices of a trial were 88.0, 85.8, 94.2, 93.8, and 93.2 on days 1-5, respectively. The effect of days was significant [$F(4, 36) = 5.31$], and a Newman-Keuls test showed that performance on Days 1-2 was lower than on Days 3-5 but that performance did not differ within these blocks of Days.

An examination of the specific sequences of alleys chosen by animals on each trial of each day provides information relevant to the significant improvement in performance across days. This analysis revealed that animals adopted a pattern of choosing alleys adjacent to one another. In order to quantify this behavior, the number of entrances into an alley adjacent to the one just entered was counted for Choices 2-8 for each animal on each trial. In Fig. 1, the percentage of adjacent alley entrances is plotted as a function of trials within days, with a separate curve for each day. The point on the far left indicates that adjacent alleys were entered 40% of the time during the 4 days of preliminary training (PT). The curves show that the tendency to enter adjacent alleys increased markedly across days and across trials within days, particularly on Days 3-5. By the final trials of Days 4 and 5, 90% or more of the choices were of adjacent alleys, and all 10 rats were showing this pattern. Percentages of adjacent alley entrances were subjected to a Days × Trials × Subjects analysis of variance, which yielded significant effects of days [$F(4, 36) = 11.49$] and of trials [$F(4, 36) = 9.49$] but not of the Days × Trials interaction [$F(16, 144) = 1.64$]. A Newman-Keuls test showed that the percentage of adjacent alley entrances was significantly higher on Days 3-5 than on Days 1-2 and did not differ significantly within either of these blocks of Days.

A high percentage of adjacent alley entrances could arise from animals making a few choices in one direction and then doubling back in the opposite direction. This pattern of behavior would

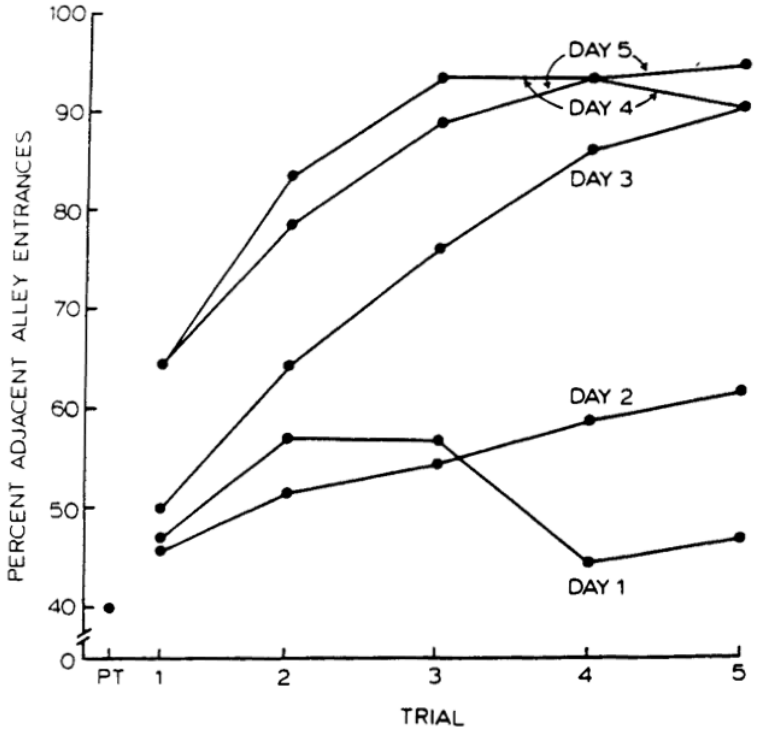

Fig. 1. Percentage of adjacent alley entrances plotted as a function of trials for each of Days 1-5 in Experiment 1. [The initial point on the left represents level of adjacent alley entrances in preliminary training (PT).]

not lead to the low level of errors observed and was rarely the case in these observations. In the vast majority of cases, animals entering adjacent alleys circled the maze continuously in the clockwise or counterclockwise direction. Over the 5 days of testing, there was a total of 96 trials on which animals entered seven adjacent alleys after the initial alley chosen. Of these 96 cases, animals went in the same direction on every choice on 85 trials, there was one reversal of direction on 8 trials, there were two reversals of direction on 2 trials, and only one trial involved three turns in one direction and four in the other.

Since animals demonstrated a strong tendency to enter adjacent alleys on Days 3-5, and there was a corresponding increase in correct choices so that very few errors were made, little evidence of PI effects could be revealed. Given this turn of events in the experiment, only the data from Days 1-2, in which patterning had not yet strongly developed, were analyzed for PI. Within Days 1-2, accuracy of choices dropped from Trial 1 to Trial 2 and remained constant over Trials 2-5. The percentages of correct choices on Trials 1-5 were 93.1, 85.0, 85.0, 86.2, and 85.0, respectively. In Fig. 2, the percentage of correct responses is plotted as a function of choices 2-8 within Days 1-2, with separate curves for Trial 1 and Trials 2-5. In agreement with Olton's (1977, 1978) data, the curves drop progressively over choices, and the curve for Trials 2-5 drops more rapidly than the curve for Trial 1.

A Trials × Choice × Subjects analysis of variance was performed on the data in Fig. 2. Significant effects were found for both trials [$F(1, 9) = 6.73$] and choice [$F(6, 54) = 21.57$], and the Trials × Choice interaction fell just short of significance [$F(6, 54) = 2.18$].

Although a PI effect suggests that memories persist between trials, further evidence of intertrial retention might be found in a comparison of the orders of choices made on Trials *n* and *n* - 1. If the known tendency of rats to avoid choosing alleys most recently entered within trials persists between trials, we would expect animals to avoid the alleys most recently entered on Trial *n* - 1 when making initial choices on Trial *n*. For each successive pair of trials within days, three overlap scores were determined for each subject. These scores were the number of alleys in common among (a) the first four different alleys entered on Trial *n* - 1 and the first four different alleys entered on Trial *n*, (b) the last four different alleys entered on Trial *n* - 1 and the first four different alleys entered on Trial *n*, and (c) the last four different alleys entered on Trial *n* - 1 and the last four different alleys entered on Trial *n*. Each score could take on a value from 0 (no alleys in common) to 4 (complete overlap). Comparison of scores (a) and (b) indicates which alleys entered on Trial *n* - 1 were most frequently entered on the initial choices of Trial *n*, and comparison of scores (b) and (c) indicates where within Trial *n* the final alleys entered on Trial *n* - 1 tended to be chosen. The overlap or number of alleys in common should be equivalent for (a), (b), and (c) if animals deleted the contents of working memory between Trial *n* -1 and Trial *n*, since the sequence of choices on successive trials should be random relative to one another. On

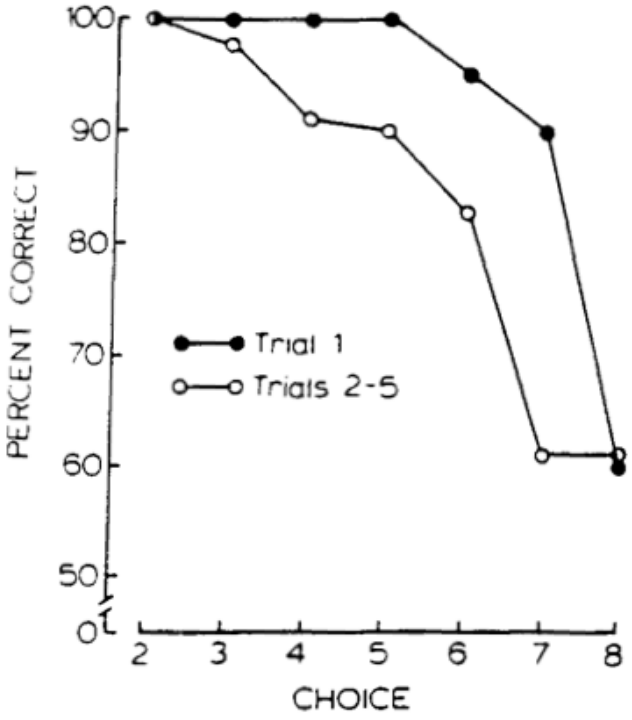

Fig. 2. Percentage of correct choices on Days 1-2 plotted as a function of choice for Trial 1 and Trials 2-5 in Experiment 1.

the other hand, if animals retained memory of the final choices on Trial *n* - 1 and avoided entrance into these alleys on the initial choices of Trial *n*, overlap scores (a) and (c) should be higher than score (b). Mean overlap scores for successive pairs of trials averaged over all 5 days of testing are presented in Table 1. It is apparent that overlap scores (a) and (c) are sizably larger than overlap score (b) at all four comparisons of Trial *n* and Trial *n* - 1. Statistical analyses showed that the means of the three overlap scores differed significantly for comparisons of Trials 1-2, 2-3, 3-4, and 4-5 [*F*'s (2, 18) = 5.25, 14.36, 8.85, 7.10, respectively]. Further, *t* tests revealed that, for all pairs of trials, score (a) was significantly higher than score (b) and score (c) was significantly higher than score (b). Comparisons of scores (a) and (c) showed no significant differences.

The argument may be raised that the pattern of overlap scores seen in Table 1 arose from a tendency of subjects to enter the same alleys on the initial choices of each trial. That is, if animals had strong preferences for initial choices, this could lead to a low level of overlap between the final choices of Trial *n* - 1 and the initial choices of Trial *n*. If this were the case, we would expect to find the same pattern of overlap scores among trials which did not follow one another within days. In order to test this possibility, the sequences of choices on the first trial of each day were compared. Overlap scores (a), (b), and (c) were determined for the first trials of Days 1-2, 2-3, 3-4, and 4-5. The means of these scores were 1.80, 2.10, and 1.92 for (a), (b), and (c), respectively. The pattern of these scores is clearly not in agreement with that of the scores seen in Table 1, and the scores do not differ significantly ($F < 1.0$). The hypothesis that animals fail to choose the alleys most recently entered on the preceding trial because of strong initial alley preferences is not supported.

Discussion

The data presented in Fig. 2 clearly resemble those reported by Olton (1977, 1978), since curves which plotted performance across choices within trials declined more sharply as trials progressed. The significant drop in accuracy seen on Days 1-2 from Trial 1 to Trials 2-5 suggests that repeated testing of animals created a PI effect. Further, the PI effect appeared to reach its maximum extent on Trial 2, since performance dropped no lower than that on Trial 2 over the subsequent three trials.

Table 1. Overlap Scores

Pairs of trials	(a)	(b)	(c)
1-2	2.26	1.60	2.24
2-3	2.46	1.58	2.40
3-4	2.48	1.52	2.34
4-5	2.22	1.64	2.38

Note: Overlap scores comparing the number of alleys in common between (a) the first four different alleys entered on Trial *n* - 1 and the first four different alleys entered on Trial *n*, (b) the last four different alleys entered on Trial *n* - 1 and the first four different alleys entered on Trial *n*, and (c) the last four different alleys entered on Trial *n* - 1 and the last four different alleys entered on Trial *n*.

It may be hypothesized that the development of an adjacent alleys pattern across days and trials within days represents an adaptation to conditions which make retention of recently entered alleys difficult. If repeated massed testing generated strong PI with retention of recently entered alleys within a trial, adoption of an adjacent alleys pattern would be an ideal strategy for overcoming this problem, ince this pattern requires retention of only the most recently entered alley. The significant increase in use of the adjacent alleys pattern across trials within days is particularly notable in this regard, since PI should become stronger as trials progress. Further, the finding that all rats in this study clearly used a pattern is surprising, in light of the general absence of patterns reported by Olton and Samuelson (1976). However, Einon (1980) also has reported finding that rats follow an adjacent alleys pattern on an eight-arm maze. This pattern was most common in rats that were young (54 days), male, and reared in the company of other rats. Possibly, a number of variables (memory, sex, age, and society) may affect the tendency to use patterns.

The analysis of overlap scores indicated clearly that animals tended to make initial choices on Trial *n* which avoided the final alleys chosen on Trial *n* - 1. These findings leave little doubt that animals remembered alleys entered on Trial *n* -1 while running the maze on Trial *n* and that memories of Trial *n* - 1 influenced choices made on Trial *n*. Such results argue strongly against the notion that subjects delete the contents of working memory after each trial.

Experiment 2

Beyond the first 2 days of testing in Experiment 1, a major difficulty with the demonstration of a PI effect was the development of an adjacent alleys pattern of choice. This pattern of behavior raised the level of correct responses and attenuated PI effects. In Experiment 2, a procedure is used in which the adoption of an adjacent alleys pattern will not lead to accurate performance. Rats were tested on three massed trials each day over a series of days, and each trial involved four forced runs to randomly selected alleys, followed by free choices among all eight alleys. The free-choice phase of each trial was a retention test, in which errors were entrances into alleys already entered, and accurate choices were entrances into alleys not previously entered. Since animals were forced down four randomly chosen alleys, use of an adjacent alleys pattern during free choices would lead to frequent errors and a poor retention score.

In addition to trials as a major variable in this study, the retention interval or delay between forced and free choices was varied between 0 and 60 sec. If PI effects are more prominent at a long retention interval than at a short one, we might expect to find a greater decline in performance across trials at the 60-sec delay than at the 0-sec delay.

Method

Subjects and apparatus

The same subjects and apparatus were used in this experiment as were used in Experiment 1.

Procedure

Each subject was tested on three trials each day, for a period of 12 days. Trials within days were separated by a 60-sec ITI. Before each trial, each arm of the maze was baited with one 45-mg food pellet. At the start of each trial, the rat was placed on the center platform with all doors to alleys closed. The animal then was allowed to enter four alleys, which were chosen as a random sequence from a table of 1000 random orders of the numbers 1 through 8 (Underwood, 1969). As soon as an animal had entered one alley, collected its reward, and returned to the center platform, the door to the just-entered arm was lowered, and the door to the next arm was raised. Following the fourth forced choice, the doors to all eight alleys were raised simultaneously either immediately (0-sec delay) or after a 60-sec delay spent on the center platform. The animal was allowed to freely enter alleys until the four remaining food pellets had been consumed. All doors then were lowered, and the subject remained on the center platform during the ITI. The same delay, 0 or 60 sec, was used on all three trials of a given day; for five subjects, the 0-sec delay was used on odd-numbered days and the 60-sec delay was used on even-numbered days; this assignment of delays to days was reversed for the remaining five subjects.

Results

Accuracy of retention on each trial was measured by counting the number of previously unentered alleys chosen on the first four free choices. Thus, performance on any trial could vary from a perfect score of 4 correct to a score of 0. The percentage of correct choices is presented as a function of trials in Fig. 3, with separate curves plotted for 0- and 60-sec delays. These curves reveal that accuracy generally was lower at a 60-sec delay than at a 0-sec delay. At the 60-sec delay, it can be seen that performance dropped sharply from Trial 1 to Trial 2 but showed no further decline at Trial 3. By contrast, performance at the 0-sec delay showed only a slight drop over trials. A Delay × Trials × Blocks of Days (two blocks of 6 days each) × Subjects analysis of variance revealed significant effects of delay [$F(1, 9) = 57.89$], trials [$F(2, 18) = 11.24$], and blocks of days [$F(1, 9) = 5.73$]. The effect of blocks of days resulted from improved accuracy from Block 1 (70.0%) to Block 2 (75.4%). The only significant interaction found in the analysis was that of Delay × Trials [$F(2, 18) = 6.71$]. Separate Trials × Subjects analyses of variance were performed on the data from each delay, and it was found that accuracy dropped significantly over trials at both the 0-sec delay [$F(2, 18) = 4.13$] and the 60-sec delay [$F(2, 18) = 10.50$]. Further tests showed that the drop in accuracy from the 0-sec delay to the 60-sec delay was significant at Trails 1, 2, and 3 [t's (9) = 3.34, 6.95, and 5.16, respectively].

Since the tendency to choose adjacent alleys had been so prevalent at the end of Experiment 1, sequences of free choices in Experiment 2 were examined for use of this pattern. On each trial, the number of adjacent alley choices were counted on the second, third, and fourth free choices. The percentage of adjacent alley entrances is plotted as a function of days of testing in Fig. 4. Separate curves are presented for each of the daily trials, and data from days of testing with 0- and 60-sec delays are shown in the left and right panels, respectively. Two aspects of these data are particularly prominent: The first is a much higher level of adjacent alley entrances at the 60-sec delay than at the 0-sec delay, and the second is a clear decline in adjacent alley entrances

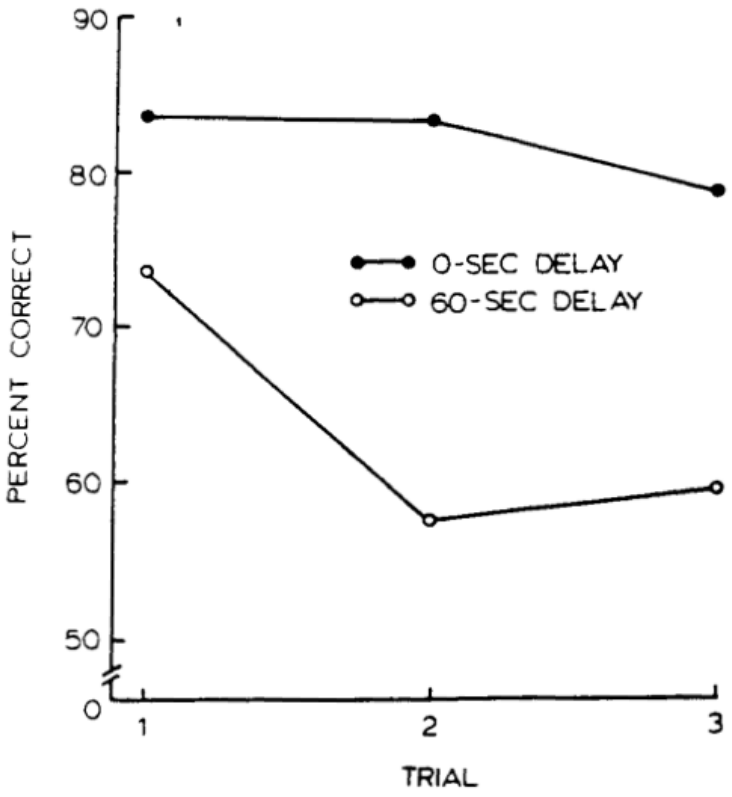

Fig. 3. Percentage of correct responses on free choices presented as a function of daily trials, with delay as the parameter (Experiment 2).

across days of testing. An analysis of variance was carried out on the frequency of adjacent alley entrances, with delays, trials, days, and subjects as factors. Only two effect were significant, delay [$F(1, 9) = 27.50$] and days [$F(5, 45) = 7.46$].

Discussion

The significant decline in accuracy of retention across trials indicates that later trials in this series of spatial memory tests suffered PI from earlier trials. This decline in accuracy over massed trials with a forced choice procedure also has been reported recently by Maki, Beatty, Berg, and Lunn (1980). In agreement with data from the human literature on PI (Keppel & Underwood, 1962), the interaction of trials and delay found here suggests that PI effects are more marked at a relatively long retention interval than at a short interval. The 60-sec delay curve in Fig. 2 suggests that the PI effect may be maximal after one trial, since the curve drops steeply from Trial 1 to Trial 2 but does not drop any further at Trial 3. This finding agrees with the observation of Experiment 1 that PI reached its maximal extent on Days 1-2 after only one trial. The 60-sec curve does resemble curves which plot the development of PI in human short-term memory (STM) experiments, since the greatest loss in retention is typically between Trials 1 and 2. In fact, Loess (1964) found that PI had developed to its maximum extent between Trials 1 and 2.

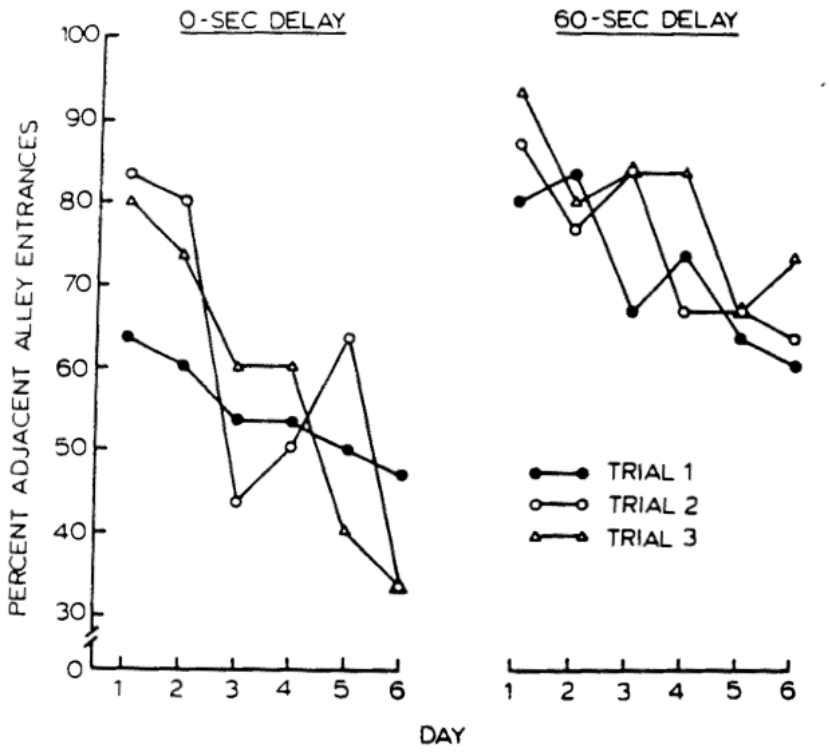

Fig. 4. Percentage of adjacent alley entrances plotted as a function of days of testing, with separate curves presented for Trials 1, 2, and 3 within days in Experiment 2. (The left panel presents data from days when the delay was 0 sec, and the right panel presents data from days when the delay was 60 sec.)

Although the drop in accuracy between trials observed in Experiments 1 and 2 has been interpreted as a PI effect, an alternative account could be offered in terms of a loss of motivation. This account would argue that running the maze and consuming reward pellets on Trial 1 reduces an animal's hunger and hence the motivation to choose accurately on subsequent trials. The interaction of delay and trials seen in Fig. 3 argues against a motivational hypothesis, since the insertion of a delay of only 60 sec led to a far sharper decline in retention than found with a 0-sec delay. Presumably, little motivational change would occur over a 60-sec delay. Further evidence against a motivational explanation comes from the retroactive inhibition studies of Maki *et al.* (1979), in which interpolated feeding on the central platform of the maze caused no drop in performance on a subsequent retention test.

The development of an adjacent alley pattern of responding in Experiment 1 may have arisen as an adaptation to conditions which promote PI, but this strategy could not be effective in Experiment 2. Fig. 4 indicates that the tendency to enter adjacent alleys was strong at the beginning of Experiment 2, as it was at the end of Experiment 1, but animals gradually abandoned this pattern of behavior with repeated days of testing in the second experiment. The observation that animals tended to enter adjacent alleys more frequently at the 60-sec delay than at the 0-sec delay may indicate that animals were more prone to use this pattern when memory for preceding alleys entered was weak or absent.

Experiment 3

Given that PI effects in spatial memory are demonstrated in Experiments 1 and 2, the next two experiments were devoted to an assessment of the parameters of this effect. More specifically, these experiments were concerned with conditions which could be introduced to alleviate the PI effect.

In several studies of PI in human short-term memory (STM) it has been found that extending the time interval between successive trials leads to a release from PI (Cermak, 1970; Kincaid & Wickens, 1970; Loess & Waugh, 1967). Experiment 3 was designed to evaluate the effect of ITI variation on the PI effect observed in Experiment 2. The same procedures were used as in Experiment 2, and the ITI was set at 60, 120, and 240 sec.

Method

The same subjects and apparatus were used as in the first two experiments. The experiment was carried out over a period of 12 days, with each subject being tested for two trials on each day. Each trial involved four initial forced rewarded choices of randomly selected alleys, followed by a 60-sec delay and then an opportunity to choose freely among all eight alleys until the four remaining food pellets had been collected. The ITI between the first and second daily trials was varied between days: three ITI lengths were used, 60, 120, and 240 sec. When an animal had returned to the center platform after collecting the last food pellet of the first daily trial, all alley doors were lowered, and the subject was held on the center platform for the duration of the ITI. The experimenter rebated all eight alleys during the ITI; when the ITI had elapsed, the second daily trial was initiated by opening the door to one alley for the initial forced choice of Trial 2. Each ITI was tested once within a block of 3 days, and the orders in which the ITI values were tested varied between animals and between 3-day blocks.

Results and Discussion

The percentage of correct choices on the first four free choices is shown as a function of daily trials in Fig. 5, with ITI as the parameter. Performance dropped from Trial 1 to Trial 2 at each ITI, but the curves are essentially parallel, which suggests that the length of the ITI had little effect on the extent to which Trial 1 interfered with retention on Trial 2. An analysis of variance was performed on these data, which incorporated the factors of trials, ITI, blocks of days (two blocks of 6 days each), and subjects. Two significant effects were revealed, trials [$F(1, 9) = 22.07$] and blocks of days [$F(1, 9) = 38.34$]. Neither the effect of ITI [$F(2, 18) = 1.17$] nor the Trials × ITI interaction ($F < 1.0$) was significant. The effect of blocks of days resulted from considerable improvement from Block 1 (71.0%) to Block 2 (86.5%).

The percentages of adjacent alley entrances on the first four free choices were calculated for Trial 1 and Trial 2 at each ITI. For the first block of 6 days of testing, the percentage scores at ITIs of 60, 120, and 240 sec were 50.0, 48.3, and 46.7, respectively, on Trial 1 and 63.3, 61.7,

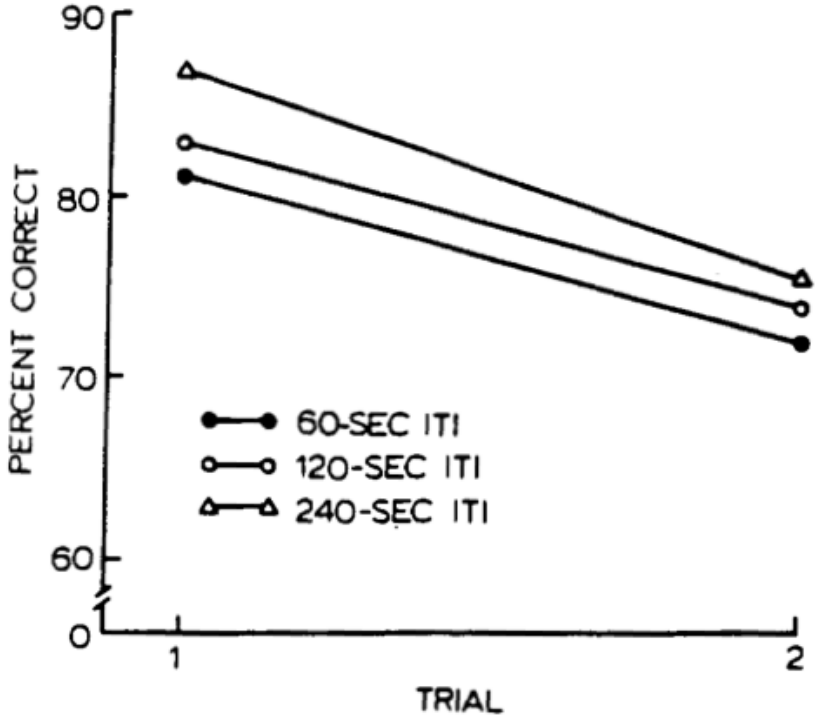

Fig. 5. Percentage of correct responses on free choices presented as a function of daily Trials 1 and 2, with ITI value as the parameter (Experiment 3).

and 63.3, respectively, on Trial 2. The corresponding scores on the second block of 6 days were 51.7, 46.7, and 43.3 on Trial 1 and 43.3, 51.7, and 48.3 on Trial 2. Statistical analysis revealed no significant effects of trials [$F(1, 9) = 3.68$], ITI ($F < 1.0$), or blocks of days [$F(1, 9) = 3.96$]. Only the Trials × Blocks of Days interaction was found to be significant [$F(1, 9) = 13.89$]. Further tests showed that the overall percentage of adjacent alley entrances on Trial 2 was significantly higher than that on Trial 1 for the first block of days [$t(9) = 2.86$] but not for the second block of days ($t < 1.0$). These data suggest that the tendency to increase adjacent alley entrances across trials within a day, which was found in Experiment 1, reappeared on the first block of days in Experiment 3 but disappeared by the second block of days.

These results replicate those of Experiments 1 and 2, in that there was a significant decline in accuracy from Trial 1 to Trial 2. Although a PI effect is clearly indicated, the failure to find an interaction between trials and ITI indicates that increasing the ITI did not lead to a release from PI. That a much longer ITI leads to release from PI was shown by Maki *et al*. (1980); a decline in Trial 2 performance seen at a 0-sec ITI was eliminated at a 4-hr ITI. It is interesting, however, that the present results are at variance with those of human PI studies, when the absolute lengths of ITIs are compared. In human studies of PI in STM, PI decreases rapidly with an increase in the ITI and is largely dissipated after a 120-sec ITI (Kincaid & Wickens, 1970; Loess & Waugh, 1967).

Experiment 4

A factor which might be particularly important in determining the appearance of a PI effect is the extent to which an animal can discriminate one trial from the next. If the termination of one trial and the initiation of the next are not clearly demarcated, these trials may be easily confused. In Experiments 1-3, the subject always was left on the center platform of the maze during the ITI. This procedure may have acted to minimize discrimination between trials and to maximize the PI effect. In Experiment 4, the procedure used in the first three experiments was compared with a procedure in which the subject was demoed from the maze and kept in a separate chamber during the ITI. The hypothesis tested is that spending the ITI in a place separate from the maze may allow the subject to more easily segment one trial from the next in memory, thereby reducing the PI effect.

Method

The subjects and apparatus were the same as those used in the preceding experiments. The experiment lasted for a period of 8 days, with each subject being tested on three successive trials each day. On each trial, the same procedure was used as in Experiments 2 and 3; that is, subjects were given forced choices of four randomly selected alleys, followed after a delay by free choices among all eight alleys. Since there had been strong improvement in performance across blocks of days in Experiment 3, the delay within each trial was increased to 120 sec in order to make the task more difficult and thus avoid a potential ceiling effect on performance. The ITI used throughout the experiment was 60 sec. The major variable of interest in this study was the place in which the subject spent the ITI. On half of the days, an animal spent both of the ITIs on the center platform of the maze, just as in the earlier experiments. On the other days, an animal's home cage was removed from the housing rack and brought into the test room; during the ITIs, the animal was placed in its cage, with a metal cover placed on top to prevent the animal's escape. At the end of the ITI, the subject was returned to the center platform with all alley doors closed, and forced choices were initiated immediately. Half of the subjects spent ITIs on the maze on odd-numbered days and were placed in the cage during ITIs on even-numbered days; the reverse assignment of ITI chamber to days was in effect for the remaining half of the subjects.

Results and Discussion

The percentage of correct choices on the free-choice phase of each trial is plotted as a function of daily trials in Fig. 6, with a separate curve presented for each ITI condition. Retention scores dropped sharply between Trials 1 and 2 but remained constant between Trials 2 and 3, just as was the case in Experiment 1 and in the 60-sec delay condition in Experiment 2. It can be seen further than the curves for the maze and cage ITI conditions differ very little from one another. Analysis of variance revealed significant effects of trials [$F(2, 18) = 62.27$] and of block of days [$F(1, 9) = 12.53$], but neither the effect of ITI condition ($F < 1.0$) nor any of the interactions were

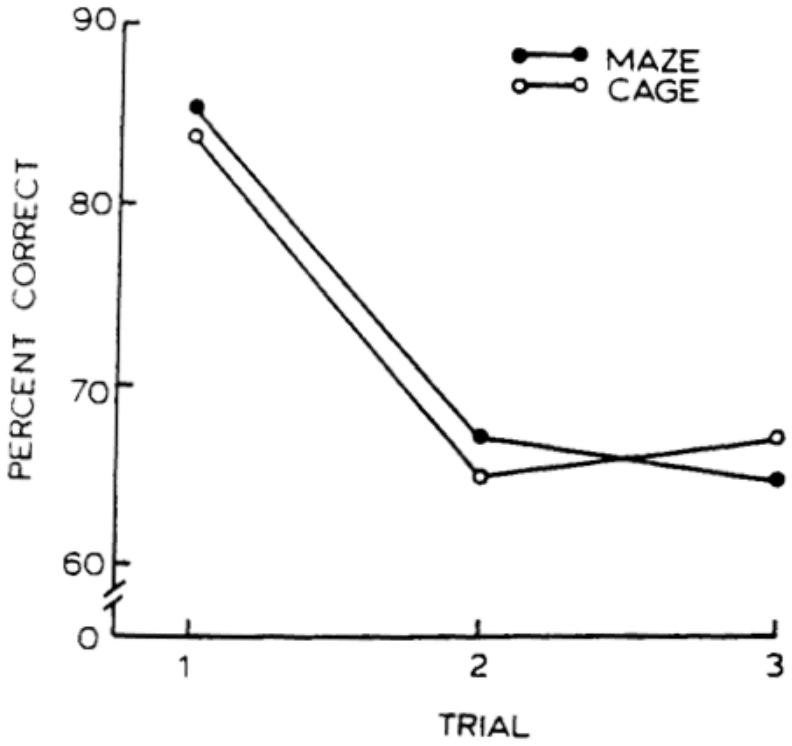

Fig. 6. Percentage of correct responses on free choices plotted as a function of daily trials, with separate curves presented for days on which animals spent the ITI on the maze and days on which animals spent the ITI in a cage (Experiment 4).

significant. The blocks of days effect was the result of improvement in performance from the first 4 days of testing (69.4%) to the second 4 days of testing (74.8%).

The percentages of entrances into adjacent alleys on free choices were 50.8, 50.0, and 51.7 for Trials 1, 2, and 3, respectively, on days when animals were left on the maze during the ITI. On days when animals were placed in the cage during the ITI, the corresponding percentages of adjacent alley entrances were 50.8, 51.7, and 59.2. Analysis of variance performed on adjacent alley entrances indicated no significant effect of trials, ITI condition, or blocks of days, and no interactions between these factors were significant.

It must be concluded that placing an animal in its cage during the ITI did not alleviate or even reduce the PI effect. Either this procedure did not aid in the discrimination of trials, or, if it did, discrimination between trials may not provide a release from PI.

General Discussion

The experiments presented in this article originated as a means of testing our doubts that (a) rats given repeated massed trials on the radial maze reset working memory after each trial by deleting its contents (Olton, 1977, 1978) and (b) as a consequence of resetting, rats suffer no PI with

retention on the final trials of a series. Olton (1977, 1978) was led to suggest that rats reset working memory by the observation that curves which plotted accuracy against choices on successive trials fell on the later choices of a trial but always returned to errorless performance on the initial choices of a subsequent trial. Our doubts were created by the fact that these curves fell sooner and more steeply as trials progressed. We suspected that these curves might represent a typical pattern of PI found in studies of human STM. Given repeated STM tests on verbal items at varying retention intervals, PI was strongly apparent at long retention intervals but relatively weak at short retention intervals (Keppel & Underwood, 1962). In rat spatial memory, errorless performance on initial choices of a trial may represent minimal susceptibility to PI at a short retention interval. At the later choices of a trial, the retention interval since initial choices is longer, and the differential drop seen here may represent a PI effect.

In an attempt to replicate Olton's (1977, 1978) findings in Experiment 1, rats were tested on five successive trials per day. Performance on the initial 2 days of this experiment resembled Olton's findings and revealed a PI effect, in that accuracy of choices dropped off more rapidly within Trials 2-5 than within Trial 1. Overall accuracy improved significantly between Days 1-2 and Days 3-5. Further analysis showed that animals had adopted a strategy of entering adjacent alleys within trials, which became more prominent over days, and over trials within days. This pattern of choices could represent a striking adaptation, which maximizes reward-collecting efficiency int he face of conditions which create strong interference with retention.

In order to prevent a ceiling effect on performance caused by use of an adjacent-alleys pattern of choice, a procedure was used in Experiment 2 which made an adjacent-alleys pattern inappropriate. On each trial of a daily set of three, rats were forced to enter four randomly selected alleys, and, following a delay or retention interval, were tested for retention of the forced alley entrances. Evidence of PI or a drop in accuracy over trials clearly was apparent with this procedure.

Two aspects of the findings of Experiments 1 and 2 were similar to PI effects in human STM experiments. One was the fact that the loss in retention over trials was clearly in evidence at a longer retention interval but was minimal at a short retention interval (Keppel & Underwood, 1962). The other was the observation that the PI effect reached its maximum extent on Trial 2, with no further drop in performance on subsequent trials (Loess, 1964).

In a further series of studies (Experiments 3 and 4), the procedure used in Experiment 2 was repeated in conjunction with manipulations designed to produce a release from PI. The PI effect seen in Experiment 2 was replicated and found to be quite robust. Although lengthening the ITI to a value of 120 sec has been found to produce almost complete release from PI in human studies (Kincaid & Wickens, 1970; Loess & Waugh, 1967), variation in the ITI between values of 60 and 240 sec had no effect on the magnitude of the PI effect in Experiment 3. Attempts to make successive trials more discriminable by having the animal spend the ITI in its home cage in the experimental room in Experiment 4 failed to attenuate the PI effect.

Two findings from these experiments may be used to argue that rats do not reset memory at the end of a trial by deleting the contents of working memory. The robust PI effect demonstrated in all four experiments indicates that memories of an initial trial persist over an ITI and interfere with retention on subsequent trials. The other finding, revealed in Experiment 1, is that rats' initial choices on all trials after the first of a daily series involve an attempt to avoid entrance into those alleys most recently entered on the preceding trial. Overlap scores revealed that subjects were less likely to enter the alleys chosen at the end of Trial n - 1 during their initial choices on Trial n than during their final choices on Trial n. Avoidance of the final alleys entered on Trial n - 1 suggests that animals remembered entrances into these alleys during Trial n.

As an alternative to the notion that rats hold the events of a trial in a limited-capacity working memory, which deletes its contents at the end of the trial, working memory could be conceived of as the storage of more permanent information in a long-term memory representation of the radial maze. Access to the appropriate working memory would involve activation of a permanent representation of the radial maze at the time of daily tests (Atkinson & Shiffrin, 1971; Lewis, 1979; Roberts, 1979). As alleys are entered on the maze, temporal markers may be placed on the appropriate alleys in the memorial representation. These markers allow the animal to discriminate the order in which alleys were entered. However, the more closely in time alleys are entered, the more difficult it becomes to discriminate the order in which they were entered. When two trials are given in close succession, entrances or non entrances into alleys on Trial n may be difficult to discriminate as more recent than entrances into alleys on Trial n - 1. As a consequence, alleys which were entered on Trial n - 1 but not on Trial n may be erroneously avoided, and the result of this confusion will be a PI effect. This model suggests that PI arises primarily from a failure of temporal discrimination, and this mechanism has been used successfully in prior applications to STM in animal experiments using the delayed matching procedure (D'Amato, 1973; Worsham, 1975).

This model accounts nicely for the Trials × Delay interaction found in Experiment 2. As the delay was increased from 0 to 60 sec, the ratio between the retention intervals for the events experienced on Trials 1 and 2 decreases, and temporal discrimination between trials should become worse. As a consequence, more PI should be seen at the 60-sec delay than at the 0-sec delay. Unfortunately, the findings of Experiments 3 and 4 fail to support this model. It clearly would be expected that lengthening the ITI from 60 to 240 sec in Experiment 3 would enhance discrimination between memories of Trials 1 and 2, and it could be argued that removal from the apparatus during the ITI in Experiment 4 should also serve to differentiate trial memories.

The resistance of spatial memory to release from PI creates a problem for temporal discrimination theory and is surprising when compared with other forms of STM in other species. Human subjects show clear release from PI when the ITI is lengthened by a few min, and a change in the class of verbal material presented for retention leads to marked release from PI (Wickens, 1970). In delayed matching experiments with visual or auditory stimuli, pigeons (Grant, 1975; Maki, Moe, & Bierley, 1977), monkeys (Jarrard & Moise, 1971), and a dolphin (Herman, 1975) have all shown improved retention as the ITI was lengthened, and these effects

have been attributed to release from PI. Spatial memory in rats appears to be developing a list of characteristics which differentiate it from other types of memory which involve a single exposure to information. Two of these are its capacity for information (Olton, *et al.*, 1977; Roberts, 1979) and its temporal persistence (Beatty & Shavalia, 1980). A robust PI effect which is very resistant to elimination may have to be added to that list.

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