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Research report

Water maze versus radial maze: differential performance of rats in a spatial delayed match-to-position task and response to scopolamine

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Abstract

Studies rarely assess treatment effects across tasks; the present experiments addressed this issue. In Experiments 1 and 2, rats ($n = 12$) were trained and then tested with variable delays on a spatial match-to-position task sequentially in the water and radial mazes (in counterbalanced order). Experiment 1 compared the effect of 0-, 60- and 1440-min delays on performance in both mazes. Rats required fewer ($P < 0.05$) mean ($\pm$S.E.M.) sessions to reach criterion performance in the water (11.0 ± 1.0) versus radial maze (19.3 ± 2.2). In test sessions, performance was impaired delay-dependently when scores were averaged across the two tasks ($P < 0.05$) but no significant effect of task or task $\times$ delay interaction was found. In the second experiment, the same rats were retrained and tested with 0-, 1-, 3- and 5-min delays in both mazes and testing followed the administration of scopolamine (0, 0.1, 0.4 and 0.8 mg/kg). The mean ($\pm$S.E.M.) number of acquisition sessions was similar in the radial (6.33 ± 0.34) and water maze (6.08 ± 0.46). On the sample portion of trials, performance was impaired at the 0.8 mg/kg dose of scopolamine ($P < 0.02$) in the radial maze only. On the recognition portion of trials in the radial maze, the 0.4 and 0.8 mg/kg doses of scopolamine impaired performance whereas in the water maze task the 0.8 mg/kg dose impaired performance. The pattern of results may reflect different natural tendencies of rats to alternate (win-shift) versus not alternate (win-stay) in dry land versus swim tasks.

Keywords: Water maze; Radial maze; Scopolamine; Recognition memory; Working memory; Reference memory

Many tasks have been used in the radial maze and the water maze to study the neuroanatomical and neurochemical substrates of learning and memory (for review see [2,25,26,39,40]), however, performance on the same task has not been directly compared in both mazes. One of the challenges faced by memory researchers is to ascertain the specificity of a treatment effect on memory relative to its effects on performance (motivation, motor activity, sensory processing, etc.) in the task used. Heise [17] has suggested that performance be assessed across differentially motivated tasks putatively sensitive to the memory system under investigation to dissociate the effects of a treatment on memory from its effects on performance (also see [36]).

Delayed matching tasks are useful for dissociating the mnemonic effects of a treatment from its non-mnemonic effects [20]. In these tasks, subjects must retain information from the sample component of a trial to accurately perform the recognition component of that trial (e.g. [13,18]). Treatment-induced delay-dependent impairments are interpreted as mnemonic whereas delay-independent impairments may be interpretable as non-mnemonic [13,20]. Mnemonic effects are more convincing if the animals tested have engaged in numerous training trials to a pre-established performance criterion at which asymptotic levels of responding are observed [17,34] to confirm that the rules of the task have been incorporated into reference memory

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[13,14,29,38]. The subsequent observation of variable delay-dependent impairments increases the validity of recognition memory tasks [36].

Various treatments have been reported to impair recognition memory in water maze delayed match-to-position tasks. For example, 192 IgG-saporin lesions of p75 receptor-bearing basal forebrain cholinergic neurons [1,16], entorhinal cortex lesions [32] and intraseptal muscimol injections [31] have been shown to impair rats' performances in a delay-dependent manner in match-to-position water maze tasks. However, the rats in the control condition of each of the aforementioned studies were not impaired in a delay-dependent manner with the intervals used [1,31,32]. This may raise some doubt with respect to interpreting treatment-induced deficits as indicative of recognition memory impairments.

In contrast, studies utilizing delayed non-match-to-position radial maze tasks (also termed delayed spatial win-shift tasks) have described delay-dependent working memory impairments in the control condition and further impairments following drug treatments. For example, rats made more entry errors on a win-shift radial maze task when a 5-min delay was inserted mid-session and the delay-dependent impairment could be enhanced by scopolamine, among other drugs [5,6]. A few studies have used single trial delayed match-to-position tasks in the radial maze to assess recognition memory. For example Kesner et al. [22] pretrained rats on a spatial delayed match-to-position task and then retrained after lesioning various structures. Rats given access to a single baited arm on the sample component made more errors following delays (1–4, 15 or 30 s) on the two-choice recognition component of trials; hippocampus lesions exacerbated this effect. In these radial maze tasks [5,6,22] the delays impaired the performance of rats in the control condition suggesting that the tasks were indeed assessing recognition memory, which was further affected by scopolamine or hippocampus lesions.

Water maze and radial maze tasks differentially tax motivation (the water maze is aversive and the radial maze is appetitive) and motor systems (running versus swimming), which could produce different results among control groups. However, the number of water maze and radial maze training trials also often differs. Studies utilizing the delayed match-to-position water maze task report training rats over 4–24 trials often after they have completed standard Morris water maze training trials [1,31,32]. Alternatively, rats are typically trained to asymptotic performance (40–180 trials in published reports [5,6,22]) on delayed radial maze tasks. Thus, the differential performance of rats in the control conditions of water maze versus radial maze delayed matching tasks could reflect differential training levels. Indeed, Lydon and Nakajima [23] report that scopolamine differentially affects reference memory in a working/reference memory radial maze task depending upon the level of training that rats receive.

The purpose of the present study was twofold: (1) To modify a match-to-sample task for use in the two differentially motivated radial and water mazes so that we could assess delay-dependent recognition memory decrements in untreated rats on each task. We hypothesized that with extensive training rats' performances would similarly diminish at longer delays on both tasks, indicating that the tasks validly assessed recognition memory. (2) To assess the effect of scopolamine on recognition memory performance of rats in both versions of our match-to-position task. Reports of scopolamine's effect on learning and memory have been equivocal. Both delay-dependent [5,6,8,13,24] and delay-independent effects [9,10,30,35] of scopolamine on performance of various working memory tasks have been reported. By testing the effect of scopolamine on the performance of a similar recognition memory task in two differentially motivated mazes (radial versus water maze) with different motor requirements (running versus swimming), we could assess the possibility that task type interacts with the effects of scopolamine. In Experiment 2, we hypothesized that delay-dependent recognition memory decrements in both tasks would be exacerbated by the centrally active muscarinic receptor antagonist scopolamine.

1. Methods

The Queen's University Animal Care Committee approved these experiments. All animals were treated in accordance with the guidelines set forth by the Animals for Research Act, the Guidelines of the Canadian Council on Animal Care and relevant University Policies.

1.1. Subjects

Twelve male Sprague–Dawley rats (Charles River, Quebec), 225–250 g at the time of arrival, were housed individually on cedar bedding in transparent plastic cages. The cages were kept in a temperature-controlled room (20 ± 1 °C) with a 12-h light:12-h dark cycle; lights on at 07:15 h. Prior to training, the rats were handled for 5 min each day over 7 days, and given food (Purina rodent Lab Chow #2001) and water ad libitum. All training and testing was done during the light cycle and was carried out at about the same time daily. While water maze training and testing was conducted, rats were given free access to both food and water. However, 4 days before radial maze training commenced, food deprivation (85–90% of free feeding weight, adjusted for growth) was initiated and main-

tained for the duration of training and testing. On each of the 4 days preceding radial maze training, rats were given five Kellogg's Froot Loops™ in their home cages.

1.2. Drug preparation

For Experiment 2, scopolamine hydrobromide (RBI Biochemicals Inc., Natick, MA) was prepared daily about 1 h prior to testing. Amounts of 0, 0.1, 0.4 and 0.8 mg scopolamine were dissolved in 1.0 ml of 0.9% saline and were injected intraperitoneally in a volume of 1.0 ml/kg. Each recognition component of a trial commenced 20 min after the administration of scopolamine. Each dose was administered in a block so that all delays (in random order) were tested at one dose before another dose was administered (e.g. Rat # 8 was tested at a 0-, 1-, 3-, and then 5-min delay after receiving 0.1 mg/kg and then was tested at a 1-, 3-, 5- and then 0-min delay after receiving an 0.8 mg/kg dose of scopolamine). Although eight different patterns of dose administration were chosen, delays were administered randomly.

1.3. Apparati

The water maze was a plastic pool (180 cm diameter; 40 cm depth) filled with water (temperature 25.5 ± 1 °C) to a depth of 24 cm. The water was made opaque with 250 ml of white non-toxic tempera paint (Demco) to prevent visual localization of a platform 2 cm below its surface. The plexi-glass platform was 10 cm in diameter. The maze was divided into sextants (1 through 6) and three concentric annuli (diameters = 60 [release annulus], 120 [in annulus] and 180 [out annulus] cm) for the purposes of the allocation of platform positions during training and testing (Fig. 1A). The temperature-controlled (25.5 ± 1 °C) water maze room was painted white and several distinct extra-maze cues were visible to the rat (e.g. pool toys, experimenter, and table). Placement of the maze and cues was consistent for the duration of the experiment.

The radial maze was constructed of varnished plywood and consisted of an octagonal central platform (30 cm wide) surrounded by eight equally spaced radial arms (65 cm long × 10 cm wide); it was positioned 50 cm above the floor (Fig. 1B). Plastic food cups, 2.0 cm deep and 1.5 cm in diameter, were placed at the end of the arms to conceal the position of the whole Kellogg's Froot Loop™ (approximately 3 g). The radial maze was housed in a white painted room (approximately 25% the size of the water maze room), with several distinct extra-maze cues visible to the rat (e.g. shelf, door, filing cabinet, experimenter). Placement of the maze and cues was consistent for the duration of the experiment.

Separate flags composed of green labeling tape wrapped around a cotter pin that was secured to a small plastic suction cup were used to either signal the location of the hidden water maze platform or to signal a baited radial maze arm. The flags were used to facilitate learning of the platform position or baited arm on sample portions of trials. The dependent variables were time to find the hidden platform or hidden food. On the radial maze task, arm entry errors were also recorded.

1.4. Procedure

1.4.1. Spatial match-to-position task

In both Experiments 1 and 2, rats were trained and tested with variable delays in one maze and were then trained and tested in the other maze (i.e. the same six rats were trained and tested in the water maze and then in the radial maze in both experiments and vice versa for the other six rats). All training and testing trials of the spatial match-to-position task consisted of a flagged sample component and an unflagged recognition component. During the sample component, a flag was affixed to the center of the platform in the water maze or to the right side of the baited arm entrance in the radial maze (defined by the observer facing the distal end of the arm from the central hub). Rats were released from the center of the water maze (facing the border between annuli 1 and 2, Fig. 1A) or the radial

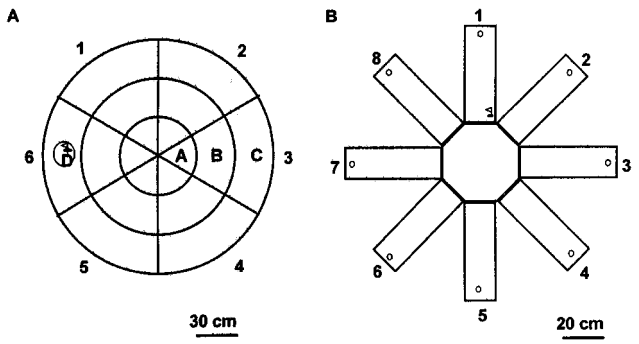

Fig. 1. Schematic of the water maze and the radial maze. (A) The water maze. The water maze was partitioned into sextants 1 through 6 and the annuli A ($d = 60$ cm), B ($d = 120$ cm) and C ($d = 180$ cm). Rats were always released from the center of the maze facing the intersection between sextants 1 and 2 (where the experimenter stood upon releasing the rats). The platform was always positioned either at the outside edge of annulus B or annulus C in the middle of the sextant arc. D represents one of the 12-fixed platform positions used during testing (6 out; marked by a flag during the sample component of trials). (B) The radial maze. Rats were always released from the center of the maze facing the end of arm 1 (where the experimenter stood upon releasing the rat). One food cup (open circle) located at the end of an arm (1 through 8) was baited with a Froot Loop during the sample component of a trial (and marked by a flag on the right side of the entrance) and then rebaited during the recognition component of the same trial (the unflagged portion of the trial).

maze (facing the end of arm 1, Fig. 1B) and given 1 min to find the flagged platform or traverse the flagged baited arm. If the rat failed to locate the flagged platform in the allotted time, it was guided to the platform and permitted to remain upon it for 5 s. If the rat failed to traverse the flagged arm, it was placed upon the entrance to the arm and gently urged toward the food cup. The rats received reward when they got to the flagged platform (escape from water) or to the baited food cup (1 Kellogg's Froot Loop™). To promote immediate entry to the flagged arm, the rat was given an additional piece of Kellogg's Froot Loop™ (approximately 1.5 g) if it traversed the baited arm first, unassisted.

After completing the sample component of the trial in either maze, the rat was placed into its opaque plastic carrying cage for a period of 30 s during training (which was equal to the time required to eliminate odor cues from the surface of the radial maze with a 1:6 solution of acetic acid:water) or for the duration of the delay interval during delay testing (i.e. 5-, 60- or 1440-min in Experiment 1). Retaining rats in their transport cages over the trial delay presumably minimized the probability that rats could use a mediating strategy to recall the response made on sample trials and therefore, likely increased the probability that rats used recognition memory to return to the spatial location of the hidden platform or baited radial maze arm (see [38]). After removing the flag the recognition component of the trial commenced.

The recognition component began when the rat was released in either maze (release was conducted exactly the same way in the sample and recognition components of each trial). In either case, the rat received reward when it reached the platform (escape from aversive water) or the end of the target arm (1 Kellogg's Front Loop™) that was flagged in the sample component of the trial. As for the sample component of trials, the rat was given an additional piece (approximately 1.5 g) of Kellogg's Fruit Loop™ if it traversed the correct arm first, unassisted.

After releasing the rats on both the sample and recognition components of the trial, the experimenter always returned to the same position in the room. Following completion of the recognition component of a trial, the rat was returned to its home cage; the rat was towel dried following a water maze trial and the radial maze was wiped with the acetic acid solution following a radial maze trial.

Latency, the time the rat required to locate the hidden platform or baited food cup, was recorded for the sample and recognition components of each trial. "In addition, arm entry errors (four legs on the baited arm) were recorded during recognition trial components in the radial maze".

1.4.1.1. Experiment 1: training. Training sessions were administered daily and consisted of seven spatial match-to-position trials, with an intertrial interval of up to 10 min. The first trial was administered to re-familiarize the rat with the task and was not counted. A new platform position or baited arm was chosen for each trial. The delay between the sample and recognition components of each trial was about 30 s.

Training (in either the water or radial maze) continued until the rats achieved a performance criterion of latency equal or less than 10 s for 83% (5 of 6) of the counted recognition components of trials over three consecutive sessions. In addition, each rat had to participate in at least five training sessions before delay testing began.

1.4.1.2. Experiment 1: delay testing. Rats participated in one trial every 48 h. The three delays (repeated three times) used were 5, 60 and 1440 (24 h) min. After completing the sample component of the trial, the rat was returned to its carrying cage for the duration of the delay. After completing the recognition component of the trial, the rat was returned (towel dried if in the water maze) to its home cage.

The delays were administered in a Latin square format to randomize any effect of order. In addition, platform positions and arm entrances were selected so that they would be equally represented. For example, 12 fixed platform positions were used nine times each during Experiment 1 so that no rat swam to the same platform position more than once at the same delay interval or more than twice throughout assessment. Similarly, four arms were baited 13 times and four arms were baited 14 times throughout assessment so that no rat approached the same baited arm more than once at the same delay interval and more than twice throughout assessment.

We chose to analyze latencies on the recognition components to facilitate comparison of performance between mazes. Our pilot work demonstrated that rats could traverse a baited unflagged radial maze arm or swim directly to a hidden platform in less than 10 s after adequate training. Frick, Baxter, Markowska, Olton and Price [15] performed a principal components analysis on variables (swim latency, swim distance and heading angle) assessed in a place discrimination (reference memory) and a match-to-position task (working memory) in the water maze. They found that latency (component loading = 0.809) and distance (component loading = 1.040; where loading > 0.50 is significant) loaded heavily into working memory and were highly correlated ($r = 0.80$). Thus, latency was a reasonable measure to compare between mazes.

1.4.1.3. Experiment 2. Rats were trained as described in Experiment 1 and then participated in a single drug

trial every 48 h. Delays of 0-, 1-, 3- or 5-min were inserted between the sample and recognition components of trials (note that the 0-min delay was the minimum time required to remove the rat from the maze, wipe it with the acetic acid solution, remove the flag and re-bait the arm, about 30 s). At each delay, performance was tested following the administration of scopolamine doses of 0 (saline), 0.1, 0.4 and 0.8 mg/kg. Rats were given a single undrugged trial with a 0-min delay on the days between scopolamine trials (day-after trials).

2. Results

2.1. Data analyses

Unless stated otherwise, the analyses performed were within-subjects (to test the effects of delay and drug dose) or mixed design (to test the effect of training order) analyses of variance (ANOVA) and post-hoc tests utilized Newman–Keuls ($\alpha = 0.05$). For some between-maze analyses, latencies were converted to z-scores to facilitate comparison (see below). Since we were interested in investigating the effect of delays on performance of the spatial delayed match-to-position task, planned comparisons were also performed separately on latencies derived from each maze.

2.2. Experiment 1

2.2.1. Sessions to reach criterion

Rats learned the water maze faster than the radial maze (Fig. 2A); an order × maze ANOVA on the number of sessions to criterion revealed a significant main effect of maze ($F_{(1,10)} = 12.16$, $P < 0.01$). The ANOVA also revealed a significant order × maze interaction ($F_{(1,10)} = 7.782$, $P < 0.02$). Post-hoc tests revealed that rats first trained in the radial maze took significantly more sessions to criterion in the radial maze than in the water maze ($P < 0.005$) or than the other group of rats in either the water maze ($P < 0.05$) or the radial maze ($P < 0.05$; see Fig. 1B). Rats trained first in the water maze required about the same amount of sessions to criterion in the radial maze (the task they learned second) as they did in the water maze ($P > 0.05$; see Fig. 2B).

In summary, fewer sessions were required to reach criterion performance in the water maze than in the radial maze. Rats initially trained in the radial maze learned the water maze version of the task in fewer sessions while rats trained in the water maze first achieved criterion performance in both versions of the task in approximately the same number of sessions. By the final day of training average water maze latencies and average radial maze latencies were less than 10 s.

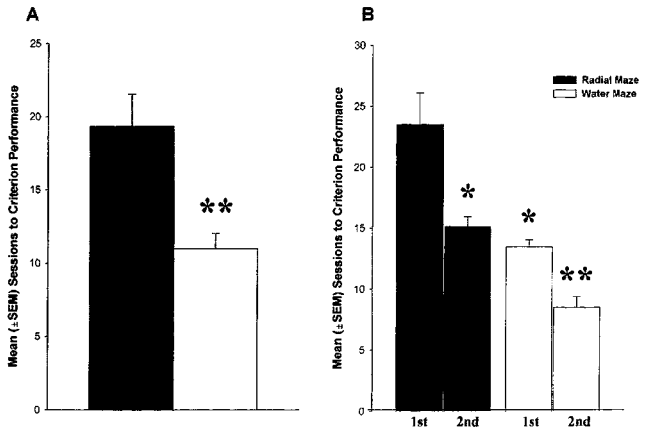

Fig. 2. Mean (±S.E.M.) number of training sessions to performance criterion (latency < 10 s in 83% of trials over three sessions) in Experiment 1. Black bars represent radial maze performance while open bars represent water maze performance. (A) Mean number of training sessions required in the radial versus water maze. Rats required significantly fewer sessions to achieve target performance in the water maze versus the radial maze ($P < 0.01$). (B) Mean number of training sessions required in the radial versus the water maze as a function of training order. Rats trained first in the radial maze took significantly more sessions to achieve criterion performance in the radial maze than in the water maze ($P < 0.005$) or than the other group of rats in either the water maze ($P < 0.05$) or the radial maze ($P < 0.05$).

However, average (±S.E.M.) radial maze latencies (3.77 ± 0.43) were significantly shorter than average water maze latencies (5.83 ± 0.56; $t_{(11)} = 4.48$, $P < 0.001$). No rat made an arm entry error on the final day of acquisition.

2.2.2. Acquisition latencies over the first five training sessions

All rats were tested for a minimum of five sessions making it possible to analyze the groups together over these sessions. Performance on both mazes improved over sessions but the effect was larger for the radial maze than for the water maze (Fig. 3). An order × maze × session ANOVA revealed a significant main effect of session ($F_{(4,40)} = 3.14$, $P < 0.001$) and significant maze × session ($F_{(4,40)} = 13.70$, $P < 0.001$) and order × maze ($F_{(1,10)} = 5.501$, $P < 0.05$) interaction effects on z-scores of latencies. Post-hoc analyses of the maze × session interaction revealed that radial maze ($P < 0.001$) but not water maze ($P > 0.10$) performance improved over sessions. Radial maze scores were significantly larger during session 1 ($P < 0.001$) and smaller on session 5 ($P < 0.01$; see Fig. 3) compared with water maze scores. The order × session interaction reflects the slower learning in the radial maze when it was the first training apparatus as discussed in the earlier paragraph.

In summary, z-scores of latencies decreased over the first five acquisition sessions but the effect was largely

due to performance on the radial maze. Rats trained first in the radial maze showed a significantly greater change in z-scores over the first five radial maze acquisition sessions than did rats trained first in the water maze.

2.2.3. Delay testing: sample component

As would be expected, the latency to enter the flagged arm or platform was not significantly different for trials that subsequently involved delays of 5, 60 or 1440 s; however, rats took longer on these sample components in the radial maze than in the water maze (Fig. 4, inset). Thus, an order × maze × delay ANOVA on latencies revealed a significant effect of maze ($F_{(1,10)} = 51.95$, $P < 0.001$; Fig. 4, inset). When latencies were converted to z-scores, the order × maze × delay ANOVA revealed neither significant main effects nor interactions (Fig. 4).

In summary, performance on the sample component of the match-to-position trial did not vary across delay in either maze. However, rats took longer to enter the flagged arm on the radial maze than to swim to the flagged platform in the water maze.

2.2.4. Recognition component

Latencies increased with delay in both mazes; as was the case for the sample component, radial maze latencies were longer than water maze latencies (Fig. 5, inset). An order × maze × delay ANOVA on latencies revealed significant main effects of maze ($F_{(1,10)} = 326.62$, $P < 0.001$) and delay ($F_{(2,20)} = 3.90$, $P < 0.05$). A Newman–Keuls test found that mean latencies averaged across maze type at the 5-min delay were significantly shorter than latencies at the 60-min delay ($P < 0.05$) and the 1440-min delay ($P < 0.05$). There were no significant main effects or interactions involving training order. As expected, the order × maze × delay ANOVA on z-scores of latencies revealed an effect of delay ($F_{(2,20)} = 4.99$, $P < 0.05$) and the Newman–Keuls test found that mean z-scores at the 5-min delay were significantly lower than at the 60-min ($P \leq 0.037$ 0.05) and 1440-min ($P \leq 0.015$) delays (Fig. 5).

Planned one-way ANOVAs for radial and water maze latencies were performed separately. The effect of delay was non-significant for both the radial maze ($F_{(2,22)} = 2.86$, $P \leq 0.08$) and the water maze ($F_{(2,22)} = 2.76$, $P \leq 0.065$). Thus, although the delay effect was significant in the overall ANOVA when both mazes were considered together, individual analysis of either maze alone failed to reveal a significant delay effect.

Using arm entry errors as the dependent variable in the radial maze, ANOVA with delay as the variable

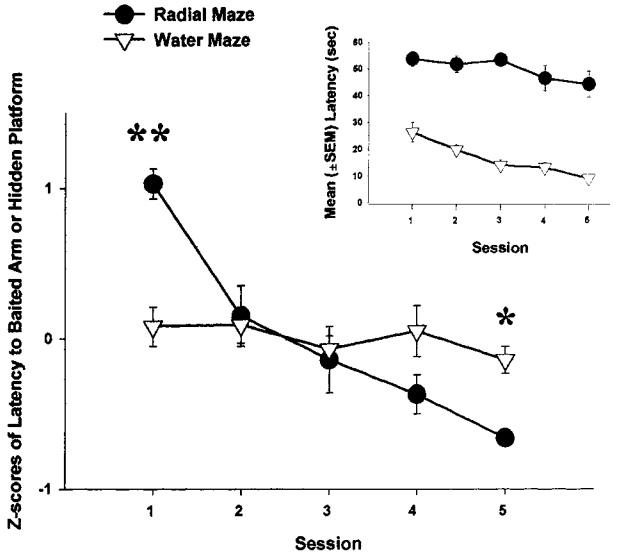

Fig. 3. Mean ($\pm$ S.E.M.) z-scores of latency to the baited food cup (black circles) or to the hidden platform (open triangles) during the first five sessions in Experiment 1. Z-scores of latency to the baited food cup were larger on the first session ($P < 0.001$) but smaller during the fifth session ($P < 0.01$) than z-scores of latency to the hidden platform. In addition, combined z-scores were highest during the first session relative to all other sessions ($P < 0.001$) and decreased steadily across the second, third and fifth sessions ($P < 0.05$). Inset: Mean ($\pm$ S.E.M.) latency (s) to the unflagged baited food cup and to the unflagged platform.

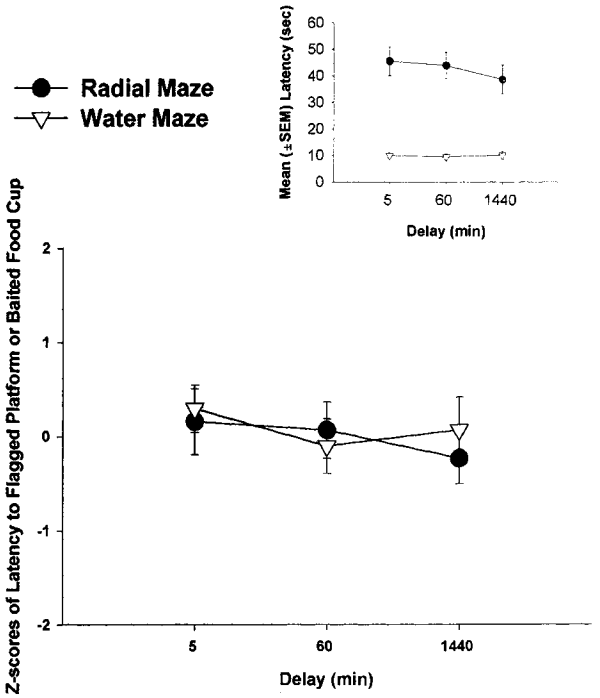

Fig. 4. Mean ($\pm$ S.E.M.) z-scores of latency to the flagged platform (open triangles) and to the flagged baited food cup (black circles) on the sample component of spatial match-to-position trials in Experiment 1. The flagged portion of the trial was followed by a delay of 5, 60 or 1440 min. There was no effect of delay on performance. Inset: Mean ($\pm$ S.E.M.) latencies to the flagged platform and to traverse the flagged baited arm. There was a significant effect of maze on latency such that rats took longer to enter a flagged arm for food than to swim to a flagged platform to escape from water ($P < 0.001$).

analyzed similarly revealed a non-significant effect ($F_{(2,22)} = 2.18$, $P > 0.10$). Mean ($\pm$S.E.M.) arm entry errors across the 5-, 60- and 1440-min delays were 1.22 ($\pm$0.25), 1.89 ($\pm$0.32) and 1.78 ($\pm$0.35), respectively. To facilitate comparison between arm entry errors and latency, data derived from the first replication of each delay were analyzed where rats initiated at least one arm entry choice in 60 s (10 rats at the 5-min delay, 11 rats at the 60-min delay and 10 rats at the 1440-min delay; no single rat failed to choose an arm more than once). Latency was significantly correlated with number of arm entry choices at the 5- ($r_{(10)} = 0.93$, $P < 0.001$), 60- ($r_{(11)} = 0.74$, $P < 0.01$) and 1440-min ($r_{(10)} = 0.81$, $P < 0.005$) delays.

In summary, delays of 60- and 1440-min resulted in significant increases in latency compared with the 5-min delay when mazes were combined in the omnibus ANOVA.

2.3. Experiment 2

2.3.1. Sessions to reach criterion

Rats took fewer sessions to achieve criterion performance in Experiment 2 than in Experiment 1 (compare Figs. 2 and 6 noting the differences in scale) and sessions to criterion were fewer in either maze when it was the second apparatus retrained. Thus, an order $\times$ maze ANOVA on number of sessions to achieve criterion performance in Experiment 2 did not reveal a significant effect of maze (Fig. 6A) but a significant order effect ($F_{(1,10)} = 35.11$, $P < 0.001$) was found. A post-hoc test revealed that rats took fewer sessions to achieve criterion in the version of the task that they reacquired second ($P < 0.001$; Fig. 6B).

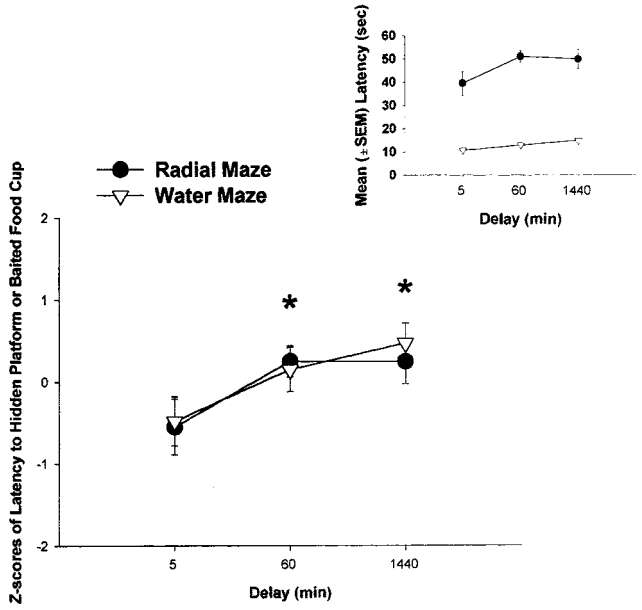

Fig. 5. Mean ($\pm$S.E.M.) z-scores of latency to the unflagged platform (open triangles) or to the unflagged baited food cup (black circles) on the test component of spatial match-to-position trials in Experiment 1. The unflagged portion of the trial followed a delay of 5, 60 or 1440 min. The main effect of delay on z-scores of combined latencies to the hidden platform or baited food cup was significant ($P < 0.05$). Inset: latency to reach the unflagged platform and to traverse the unflagged baited radial maze arm. There was a significant main effect of delay when radial and water maze latencies were combined ($p < 0.05$). When latencies were analyzed for each maze separately, the delay effect tended to be significant in both the water and radial mazes ($0.05 < ps < 0.10$).

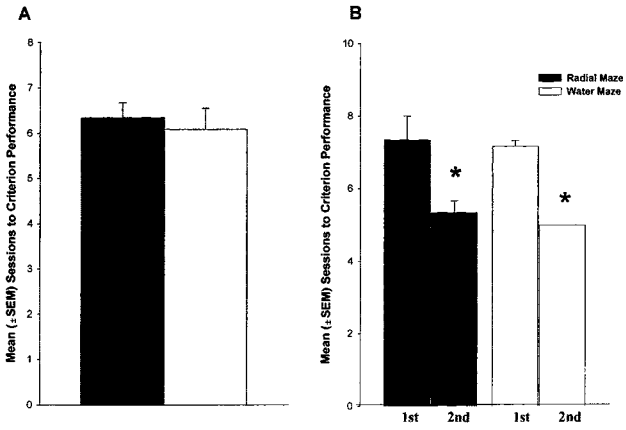

Fig. 6. Mean ($\pm$S.E.M.) number of sessions to reach criterion performance (latency < 10 s over 83% of trials on 3 consecutive days) in Experiment 2. Solid black bars represent radial maze performance and open bars represent water maze performance. (A) Mean ($\pm$S.E.M.) number of sessions to reach criterion performance in the radial maze and the water maze. The number of sessions taken to criterion performance did not differ between mazes. (B) Mean number of training sessions taken in the radial versus the water maze as a function of training order. Rats required fewer sessions to reach criterion performance on the version of the task that they reacquired second ($P \leq 0.01$).

2.3.2. Acquisition latencies over the first five sessions

Performance improved over the first five sessions (the minimum number of sessions over which criterion performance could be achieved) but the effect was larger for the radial maze than for the water maze (Fig. 7). An order $\times$ maze $\times$ sessions ANOVA revealed a significant main effect of sessions ($F_{(4,40)} = 37.48$, $P < 0.001$) and significant maze $\times$ session ($F_{(4,\ 40)} = 8.54$, $P < 0.001$) and order $\times$ maze ($F_{(1,10)} = 5.35$, $P < 0.05$) interactions on z-scores of latencies. Post-hoc tests of the maze $\times$ session interaction revealed that the effect was due to improved performance over sessions on the radial maze ($P < 0.05$) but not the water maze ($P > 0.05$; Fig. 8), as was seen in Experiment 1. Post hoc analysis of the order $\times$ maze interaction revealed that while order of training did not affect acquisition of the water maze task (Fig. 8A), rats trained in the water maze first had significantly larger z-scores over the second, third and fourth radial maze acquisition trials than rats trained first on the radial maze ($P < 0.04$, $P < 0.001$ and $P < 0.005$, respectively; Fig. 8B).

On the final training session, rats performed the recognition component of trials in the radial maze and water maze in less than 10 s. Mean ($\pm$S.E.M) latencies tended to be shorter ($t_{(11)} = 2.06$; $P \leq 0.06$) on the recognition component of trials in the radial maze (4.87 ± 0.85) relative to the water maze (6.66 ± 0.44). One rat made an arm entry error during the recognition component of a trial on the final day of testing.

In summary, latencies decreased over the first five acquisition sessions but the effect was largely due to performance on the radial maze. With respect to radial maze performance, rats trained first in the radial maze had significantly shorter latencies over the first five radial maze acquisition sessions than did rats trained in the water maze first. With respect to water maze performance, the order of testing on the two mazes did not influence latencies. By the final acquisition session, rats could obtain a hidden piece of food on the radial maze or swim to a hidden platform in the water maze in less than 10 s.

2.3.3. Delay and scopolamine testing: sample component

As would be expected because delay follows the sample component, there appeared to be no systematic effect of delay on performance in either maze; higher doses of scopolamine appeared to increase latencies in the radial maze (Fig. 9). A dose $\times$ delay ANOVA of latencies revealed an effect of dose on performance in the radial maze ($F_{(3,33)} = 3.26$, $P \leq 0.05$). This effect was found when latencies were averaged across delay yielding means ($\pm$S.E.M.) of 48.42 ($\pm$5.02), 52.17 ($\pm$3.89), 53.58 ($\pm$4.33) and 57.89 ($\pm$0.96) at 0, 0.1, 0.4 and 0.8 mg/kg doses of scopolamine, respectively. A Newman–Keuls test found latencies at the 0.8 mg/kg dose of scopolamine to be significantly longer than at the other three doses ($P < 0.02$; Fig. 9A). In contrast, a dose $\times$ delay ANOVA of latencies in the water maze yielded neither an effect of dose nor an effect of delay (Fig. 9B). No effect of dose on latency in either the radial maze or the water maze was observed on those trials administered on the day-after scopolamine trials (data not shown).

In summary, performance on the visually guided (flagged), delay independent sample component was impaired at the highest dose of scopolamine in the radial maze but not in the water maze. No general scopolamine-induced performance impairments (motor, sensory or motivation) were observed during trials administered the day after scopolamine was injected.

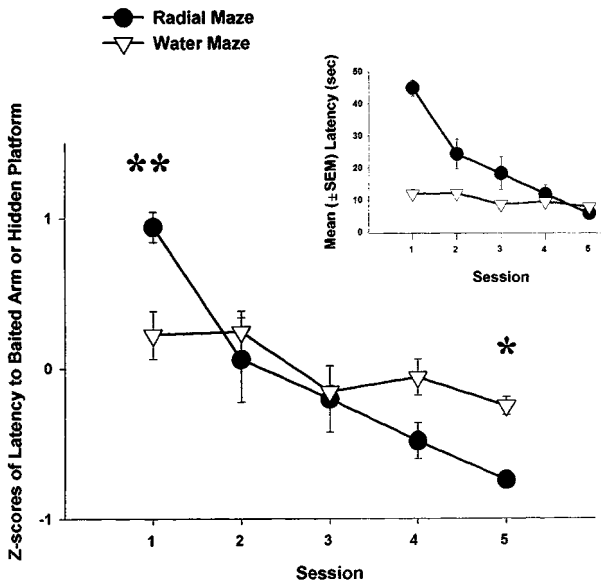

Fig. 7. Mean ($\pm$S.E.M.) z-scores of latency to the flagged baited food cup (black circles) or to the flagged platform (open triangles) over the first five training sessions of Experiment 2. Z-scores of latency to traverse the flagged radial maze arm were higher during the first session ($P < 0.001$) but lower during the fifth session ($P < 0.05$) than z-scores of latency to the flagged platform. In addition, combined z-scores were highest during the first session relative to all other sessions ($P < 0.001$) and decreased steadily across the second, third and fifth sessions ($P < 0.05$). Inset: latency to traverse the flagged radial maze arm and to approach the flagged platform.

2.3.4. Recognition component

Latencies increased with delay and with dose of scopolamine in both mazes and in both mazes the effect of higher doses of scopolamine appeared to be largest at the 0-min delay (Fig. 10). A delay $\times$ dose ANOVA on latencies in the radial maze revealed significant main effects of delay ($F_{(3,33)} = 5.15$, $P < 0.005$) and dose ($F_{(3,33)} = 18.70$, $P < 0.001$; Fig. 10A) but no interaction. Mean latencies ($\pm$S.E.M.) collapsed across delay were 32.77 ($\pm$6.42), 45.30 ($\pm$5.59), 52.32 ($\pm$4.42) and 55.36 ($\pm$3.20) s at 0, 0.1, 0.4 and 0.8 mg/kg doses of scopolamine, respectively. A Newman–Keuls test found that rats in the control condition (0 mg/kg) found the food reward significantly faster than they did in all other conditions ($P < 0.001$). After receiving either 0.4 or 0.8 mg/kg of scopolamine, rats took significantly longer to find the food reward than they did after receiving the 0 mg/kg ($P < 0.05$) or the 0.1 mg/kg ($P < 0.01$) dose. Mean latencies ($\pm$S.E.M.) collapsed across dose were 40.18 ($\pm$ 5.40), 41.97 ($\pm$4.74), 48.69 ($\pm$3.74) and 54.92 ($\pm$3.49) s at the 0-, 1-, 3- and 5-min delays, respectively. A Neuman–Keuls test found that performance was poorer at the 5-min delay relative to the 0-min ($P < 0.01$) and the 1-min ($P < 0.01$) delays.

Table 1 shows arm entry errors made during the recognition component of trials at each dose and delay interval. Arm entry errors increased across delay but decreased across dose of scopolamine and were significantly correlated with latency at the short delays in the control condition. A planned comparison demonstrated that latencies increased delay-dependently in the control condition ($F_{(1,11)} = 6.92$, $P < 0.02$) such that latencies

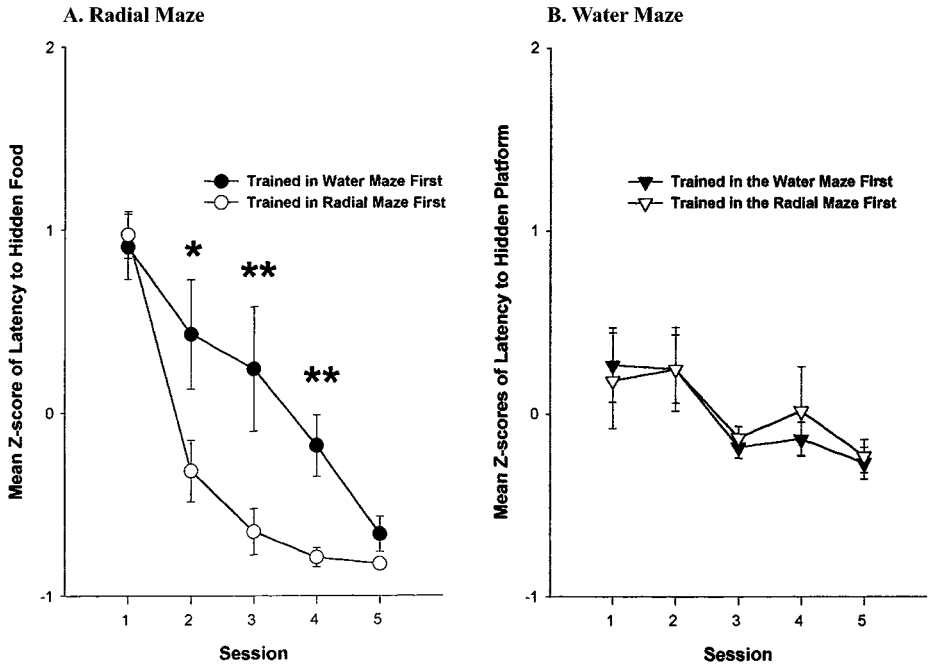

Fig. 8. Mean ($\pm$S.E.M.) z-scores of latency to the hidden platform (triangles) or to the baited food cup (circles) as a function of training order in Experiment 2. Z-scores of rats trained first in the water maze are depicted by black symbols and z-scores of rats trained first in the radial maze are depicted by open symbols. (A) Mean z-scores of latency to the hidden platform. Z-scores do not vary as a function of training order. (B) Mean z-scores of latency to hidden food. Z-scores of rats trained first in the water maze are higher than those of rats trained first in the radial maze across the second, third and fourth acquisition sessions ($P < 0.04$, $P < 0.0007$ and $P < 0.005$, respectively).

were shorter at the 0- and 1-min delays relative to the 5-min delay ($ps < 0.02$).

The delay $\times$ dose ANOVA on latencies on the recognition component of spatial match-to-position trials in the water maze revealed significant main effects of delay ($F_{(3,33)} = 2.90$, $P < 0.05$) and dose ($F_{(3,33)} = 3.65$, $P < 0.02$; Fig. 10B) but no interaction. The failure to observe a significant interaction indicated that the higher latencies observed with scopolamine doses of 0.4 and 0.8 mg/kg at the 0-s delay were non-significant. Mean latencies ($\pm$S.E.M.) collapsed across delay were 10.0 ($\pm$2.89), 11.81 ($\pm$3.41), 16.31 ($\pm$4.71) and 18.28 ($\pm$5.28) s at the 0, 0.1, 0.4 and 0.8 mg/kg doses, respectively. A Newman–Keuls test found that rats had significantly longer latencies to the hidden platform in the 0.8 mg/kg condition than they did in the control (0 mg/kg) condition ($P < 0.05$). Mean latencies ($\pm$S.E.M.) collapsed across dose were 17.28 ($\pm$4.82), 9.67 ($\pm$5.24), 14.33 ($\pm$5.98) and 15.69 ($\pm$5.60) s at the 0-, 1-, 3- and 5-min delays, respectively. A Newman–Keuls test found that latencies to the hidden platform were significantly shorter at the 1-min delay relative to the 0-min delay ($P < 0.05$). Latencies tended to be longer at the 3- and 5-min delays relative to the 1-min delay ($P \leq 0.08$ and $P \leq 0.07$, respectively). A planned comparison revealed delay-dependent performance impairments of rats in the control condition ($F_{(1,11)} = 9.136$; $P = 0.012$) with significantly shorter latencies at the 0- and 1-min delays relative to the 3- ($P < 0.012$ and $P < 0.06$, respectively) and 5-min ($P < 0.005$ and $P < 0.02$, respectively) delays. No effect of dose on latencies in either the radial maze or the water maze was observed in day-after trials (data not shown).

In summary, dose- and delay-dependent impairments on the recognition component of the spatial match-to-position trial in both mazes were observed. These effects were more pronounced in the radial maze than in the water maze. In particular, radial maze performance was impaired at the higher doses of scopolamine whereas water maze performance was impaired only at the highest dose. Interestingly, performance appeared to be more impaired at the 0-min delay in the water maze when rats had received the high doses of scopolamine, although the interaction effect was non-significant. In the radial maze, performance was impaired at the longest delay. Planned comparisons revealed that rats in the control condition of each task were impaired delay-dependently with longer delays. Mnemonic impairments were not observed the day after scopolamine was administered in either the radial maze or the water maze (data not shown).

3. Discussion

3.1. Acquisition of spatial match-to-position differed in the radial versus water maze

The present study demonstrated that rats are able to learn similar versions of a spatial match-to-position task in the water maze and the radial maze. Accurate performance in this type of recognition memory task requires the acquisition and use of two types of information [13,14,29,38]. First, the rule about how to respond in order to obtain reward must be consolidated and recalled from reference memory to perform the task accurately (i.e. traverse the arms of the radial maze or swim away from the walls of the water maze, and returning to the same arm or platform position results in reward [28]). Second, trial-specific information derived from the sample component of the trial must be maintained in working memory to be matched with choice stimuli presented during the recognition component of the trial (platform position or specific radial maze arm) in absence of a mediating strategy [38]. Rats demonstrated asymptotic performance on the recognition component of trials in the water maze in this study after 66 training trials and in the radial maze after 114 training trials. These results are in good agreement with earlier findings from the radial maze (40–160 trials [22]) but greater than the standard number of trials given in similar versions of the water maze match-to-position task (4–24 trials [1,31,32]).

Although average latencies approached 10 s on the fifth training session in the water maze, rats did not reach criterion until they participated in an average of 11 training sessions (66 trials). The relatively short latencies observed over the first five water maze sessions in this (Fig. 3), and other studies, may reflect the motivational demands of the swimming task rather than accurate recognition memory. This observation might indicate that without sufficient training in water maze tasks, the putative effects of drugs or delays on working memory might reflect effects on acquisition learning or some other variable.

This idea is further substantiated by the performance observed on recognition memory trials. Thus, rats in the current study (Fig. 5) and rats in a similar radial maze task [22] were impaired delay-dependently on test trials. However, rats in the control conditions of water maze match-to-position tasks utilizing fewer training trials performed erratically when delays were introduced [1,31,32]. Thus, rats trained over a fixed set of training trials rather than to asymptotic levels of responding may not have learned the task sufficiently leading to erratic performance when delays were introduced.

In Experiment 1, rats reached criterion more rapidly in the water maze (11 sessions or 66 trials) than on the radial maze (19 sessions or 116 trials; Fig. 2). Different rates of acquisition may be related to differential motivation in the two tasks; the water maze is aversively motivated (rats swim to escape) whereas the radial maze is appetitively motivated (rats run to obtain

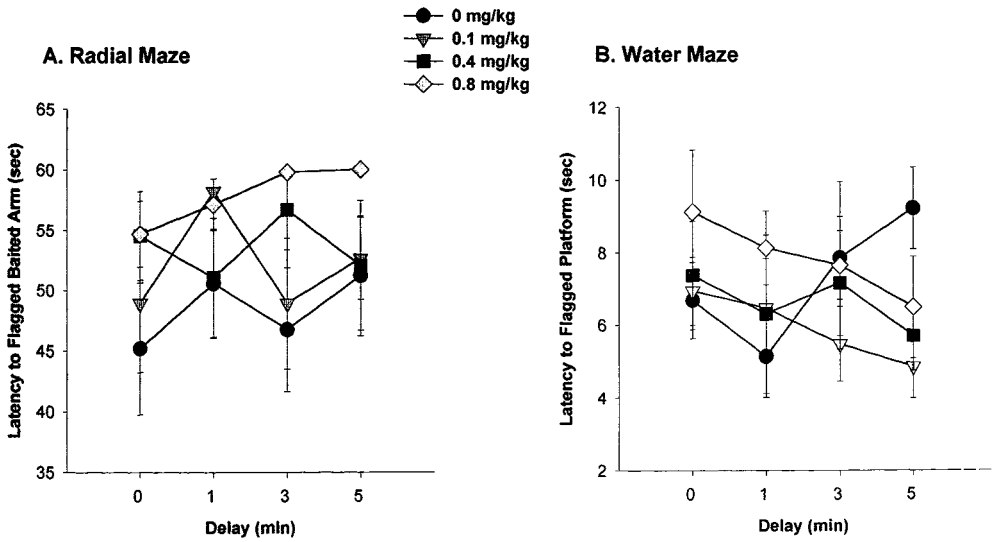

Fig. 9. Mean (±S.E.M.) latency (s) to traverse the flagged radial maze arm or to approach the flagged platform on the sample component of spatial match-to-position trials in Experiment 2. The flagged portion of the trial was followed by a delay of 0, 1, 3 or 5 min and the administration of a 0, 0.1, 0.4 or 0.8 mg/kg dose of scopolamine. (A) Mean (±S.E.M) latency (s) to the flagged baited food cup. An ANOVA on latencies in the radial maze revealed that while there was no effect of delay on latency, performance was impaired at the 0.8-mg/kg dose of scopolamine relative to all other doses ($P < 0.02$). (B) Mean (±S.E.M) latency (s) to the flagged platform. Performance was impaired neither delay- nor dose-dependently.

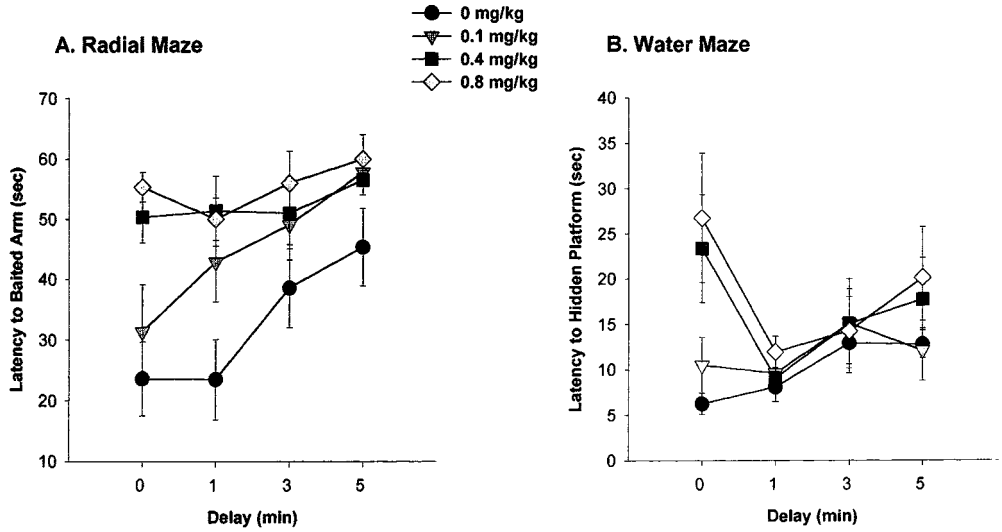

Fig. 10. Mean (± S.E.M.) latency (s) to the traverse the unflagged radial maze arm or swim to the unflagged platform on the test component of spatial match-to-position trials in Experiment 2. The unflagged portion of the trial followed a delay of 0, 1, 3 or 5 min and following the administration of a 0, 0.1, 0.4 or 0.8 mg/kg dose of scopolamine. (A) Mean (± S.E.M) latency to the unflagged baited food cup. An ANOVA on latencies in the radial maze revealed a delay- ($P < 0.005$) and dose- ($P < 0.001$) dependent effect. (B) Mean (± S.E.M) latency to the unflagged platform. Delay ($P < 0.05$) and dose ($P < 0.02$) produced significant effects in the ANOVA.

food). Indeed, studies manipulating motivation have demonstrated effects on performance in both mazes. For example, Kirkby, Jones and Higgins [21] found that prefeeding increased errors of omission and task latencies on a delayed match-to-position operant task and Hodges [19] described a prefeeding-induced shift in strategy on an optimum foraging radial maze task. Seldon, Cole, Everitt and Robbins [37] found that cold water could impair the acquisition of a cued water maze task. These studies demonstrate that changes in motivation can alter performance within each task. Thus, the differences in motivation between mazes may have led to the differential number of acquisition trials to reach criterion in Experiment 1. In Experiment 2, the task was re-acquired in fewer sessions in either maze but there was no significant difference between mazes (Fig. 6) suggesting that performance may be less influenced by motivation as learning progresses.

Alternatively, the radial maze task may have produced a different learning curve than the water maze task over the first five training sessions in Experiment 1 (Fig. 3) because the radial maze contains intramaze cues, such as odor trails and arm entrances that can be used associatively [3,4,27]. Although precautions were taken to eliminate odor trails in the radial maze, it is possible that rats could have used intramaze cues. To our knowledge, only one other study has directly compared the performance of the same rats on similar versions of a task in different contexts. Whishaw and Pasztor [45] trained rats to approach two different food locations that could be reached by either swimming (in the filled water maze) or running (in the empty water maze). The rats used different spatial strategies in each task, an alternation strategy in the dry task and a non-alternation strategy in the water task. A number of related results support this distinction [11,12,27,43–45]. Perhaps the different learning curves from the two tasks over the first five sessions of Experiment 1 and Experiment 2 reflect these different strategies. Thus, the present match-to-position task would favor the non-alternation (win-stay) tendency seen in rats required to swim to a goal and would conflict with the alternation (win-shift) tendency seen in rats required to run to a goal. This provides a basis for understanding the slower acquisition of the task on the radial maze. Of course, our data merely supports the work of Whishaw and Pasztor [45] as we did not undertake the difficult task of assessing the tendency of rats to alternate in the water maze version of our task.

3.2. Effects of delays

The delays used in Experiment 1 (5, 60 and 1440 min) produced delay-dependent impairments in performance when the results from both mazes were combined; rats retained information about the location of food or a hidden platform better at 5 min than at either 60 or 1440 min (Fig. 5). However, when performance on each maze was analyzed separately, there was no effect of delay. Although rats were kept in their transport cages over the delay interval of each trial during training and testing (to establish the context of a single trial) the context of 'trial' may not have been retained over the 24 h delay. Nevertheless, others have reported

that overtrained rats had significantly longer latencies at a 1440-min delay relative to a 1-,60- or 240-min delay in a match-to-position water maze task [33] and perhaps the effects of long delays interact with the amount of training. Alternatively, we may have been too conservative in setting the trial duration at 60 s to see an effect of delay at 24 h.

In Experiment 2, we assessed the effects of shorter delays of 0, 1, 3 and 5 min and observed delay-dependent increases in latencies in both tasks across control conditions (Fig. 10, 0 mg/kg dose). We found a significant positive correlation between arm entry errors and latency at the 0- and 1-min delays and a tendency for the measures to be correlated at the longer delays further indicating the duration-dependent negative influence of delays on maze performance. These results confirmed the validity of both versions of the spatial delayed match-to-position task as a test of recognition memory.

3.3. Effects of scopolamine

On sample trial components (reference memory), the 0.8 mg/kg dose of scopolamine impaired performance on the radial maze version (Fig. 9A) but not in the water maze version of the spatial match-to-position task (Fig. 9B). Other studies utilizing appetitive delayed matching and non-matching tasks have also found delay-independent scopolamine-induced performance decrements [9,30,35]. Kirkby, Jones and Higgins [21] found that either prefeeding or scopolamine (1 mg/kg) impaired choice accuracy on an operant delayed match-to-position task, suggesting that scopolamine may reduce motivation to respond on appetitively-motivated tasks. In support of this idea Watts, Stevens and Robinson [42] and Stevens [41] found that responding on a radial arm task under the influence of scopolamine could be enhanced if the reward was changed from solid food pellets to chocolate chips. In the present study, rats were observed to initiate their choices on the radial maze more slowly at high doses of scopolamine, which may explain why the correlation between latency and entry errors diminished at higher doses (Table 1). Combined with the absence of a scopolamine-induced impairment on the sample portion of trials in the water maze the hypothesis linking scopolamine effects to changes in motivation on appetitive tasks seems plausible.

On the recognition component in both the water and radial maze in the present study scopolamine impaired performance at doses that had no significant effect on the sample component (Figs. 9 and 10). Results suggest that scopolamine affected performance and are in agreement with other studies reporting that scopolamine impairs recognition memory by enhancing delay-dependent performance impairments [5–7,13,21].

Differences in performance impairments emerged between the tasks. In the radial maze, the delay-dependent decrements were enhanced by scopolamine in a dose-dependent manner (Fig. 10A). In the water maze only the 0.8 mg/kg dose significantly affected performance (Fig. 10B). In the water maze, only the 0.8 mg/kg dose of scopolamine significantly impaired performance. Although neither the interaction of dose $\times$ delay nor the effects of the 0.4 mg/kg dose were significant, it appeared that the 0.4 and 0.8 mg/kg doses of scopolamine produced their greatest effects on latency at the 0-s delay (Fig. 10B). Perhaps the disruptive effects of high doses of scopolamine on swim latency synergize with the stressful effects of particularly short inter-swim intervals (approximately 30 s) that occur at the 0-min delay condition. Clearly, further experiments are necessary to replicate and understand this effect.

The differential sensitivity of the two versions of the task to scopolamine may be related to the interaction of task type with response type discussed earlier (cf., [45]). Thus, the radial maze task required rats to learn a response (win-stay) that was in conflict with their natural tendency to alternate on dry land whereas, in the water maze, the win-stay strategy is the preferred one. The effects of scopolamine were greatest on the task requiring the incongruent response.

Table 1
Correlations between latency and mean ($\pm$S.E.M) arm entry errors on the recognition component of the radial maze version of the spatial match-to-position task across delay and dose of scopolamine

	0-min	1-min	3-min	5-min
0.0 mg/kg	0.75 ± 0.37, $r = 0.815$**	0.67 ± 0.35, $r = 0.717$**	1.08 ± 0.39, $r = 0.513$	1.17 ± 0.32, $r = 0.364$
0.1 mg/kg	0.42 ± 0.29, $r = 0.487$	0.75 ± 0.28, $r = 0.040$	0.75 ± 0.31, $r = 0.418$	1.41 ± 0.41, $r = -0.110$
0.4 mg/kg	0.42 ± 0.19, $r = -0.123$	0.33 ± 0.14, $r = 0.312$	0.41 ± 0.07, $r = -0.172$	0.83 ± 0.29, $r = -0.156$
0.8 mg/kg	0.12 ± 0.16, $r = 0.120$	0.50 ± 0.26, $r = 0.058$	0.25 ± 0.13, $r = 0.174$	0.33 ± 0.26, $r = 0.188$

Mean ($\pm$S.E.M) arm entry errors are shown. The table shows that errors increased across delay but decreased across dose. Furthermore, arm entry errors were most correlated with latency in the control condition and the correlations reached significance at the short delays (0- and 1-min).
**Indicates $P \leq 0.01$.

4. Summary and conclusions

Rats trained to asymptotic levels on a spatial match-to-position task could perform the task in both the radial and water maze. When delays of 5, 60 or 1440 min were inserted between the sample and recognition components of the task, rats demonstrated delay-dependent performance decrements. In Experiment 2, delay intervals of 0, 1, 3 and 5 min produced delay-dependent performance decrements that were enhanced by scopolamine. Comparisons of results from the sample and test components on each maze suggest that the effects of scopolamine are attributable to an impairment of memory. Furthermore, scopolamine differentially affected performance in the radial versus water maze. These results may reflect the differential demands that the two versions of the match-to-position task made on the animals' natural strategies in water versus dry land tasks. Results emphasize the importance of considering the natural tendencies of animals in behavioral testing.

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