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Research report

Differences between appetitive and aversive reinforcement on reorientation in a spatial working memory task

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Abstract

Tasks using appetitive reinforcers show that following disorientation rats use the shape of an arena to reorient, and cannot distinguish two geometrically similar corners to obtain a reward, despite the presence of a prominent visual cue that provides information to differentiate the two corners. Other studies show that disorientation impairs performance on certain appetitive, but not aversive, tasks. This study evaluated whether rats would make similar geometric errors in a working memory task that used aversive reinforcement. We hypothesized that in a task that used aversive reinforcement rats that were initially disoriented would not reorient by arena shape and thus make similar geometric errors. Tests were performed in a rectangular arena having one polarizing cue. In the appetitive condition water consumption was the reward. The aversive condition was a water maze task with reinforcement provided by escape to a hidden platform. In the aversive condition rats returned to the reinforced corner significantly more often than in the dry condition, and did not favor the diagonally opposite corner. Results show that rats can use cues besides arena shape to reorient in an aversive reinforcement condition. These findings may also reflect different strategies, with an escape/homing strategy in the wet condition and a foraging strategy in the dry condition.

Keywords: Geometric module; Delayed-matching-to-sample; Working memory; Disorientation

1. Introduction

Effective navigation requires an animal to maintain knowledge of its current position and a goal location. When this knowledge is uncertain, a mechanism for reorientation is necessary to avoid an extended random search. Reorientation is needed when an animal has been relying on internal cues that are subject to cumulative errors, or when perceptual access to the surrounding environment is restricted (reviewed in [7]).

Researchers have proposed that reorientation is based on the macroscopic shape of the environment [8]. The idea that reorientation is related to environmental shape originated from studies showing that rats [4,5,10,18], toddlers [12–14], and to a lesser degree birds [23] are unable to distinguish the diagonally opposite corners inside a rectangular arena following various forms of disorientation. Subjects in these studies were equally likely to search for a reward at the correct or diagonally opposite corner in a rectangular arena. Diagonally opposite corners in a rectangle are congruent, and thus are geometrically equivalent following a 180° rotation of the arena. This pattern of confusing the geometrically equivalent corners persists even when salient non-geometric cues can be used to unambiguously define the correct corner [13,18].

The tendency to confuse geometrically equivalent corners in rectangular arenas may indicate the operation of a specialized cognitive module (geometric module) for reorientation that is unresponsive to sensory information other than environmental shape [4,18]. This viewpoint implies that subjects should confuse the geometrically equivalent corners regardless of the type of reinforcement (appetitive or aversive) because the behavioral pattern is due to the ambiguous information provided by the rectangular shape.

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All of the previous studies that have documented the tendency to confuse geometrically equivalent corners have used appetitive reinforcers (such as food or water consumption). Recent studies show that the influence of a disorientation procedure on subsequent performance in spatial learning tasks can vary depending on the type of reinforcement given [6,9,19]. The Dudchenko et al. [6] and Martin et al. [19] studies both showed that in appetitive tasks rats that were disoriented by slow spinning inside an opaque box before each trial were impaired relative to controls that were not disoriented. In contrast, when the same tasks and procedures were conducted using aversive reinforcement (swimming to an escape platform), animals that were given the disorientation procedure learned the task normally. Differences between appetitive and aversive tasks have also been observed when task difficulty was similar [9].

The purpose of the present set of experiments was to test the hypothesis that reorientation by environmental shape is contingent upon the type of reinforcement. Because the Martin et al. [19] and Dudchenko et al. [6] studies showed that disorientation impaired performance in appetitive, but not aversive, tasks, we predicted that rats would perform a spatial task well in a rectangular-shaped arena when the task employed aversive reinforcement. Thus, under these conditions we predicted that rats would be able to approach the correct corner and avoid the diagonally opposite corner.

2. Materials and methods

Two experiments were conducted to examine the influence of reinforcement condition on response choice in two similar working memory tasks. The major difference between the two tasks was the type of reinforcement (appetitive vs. aversive). In the aversive (wet) condition, rats escaped from a water maze onto a hidden platform. In the appetitive (dry) condition, water restricted rats were reinforced by consuming drops of water. In each experiment the same rats were run in both conditions; the only difference between the two experiments was the order of testing. In the wet–dry experiment (Experiment 1) rats were first run on the wet maze version followed by the dry condition, while in the dry–wet experiment (Experiment 2) the order of conditions was reversed.

2.1. Subjects

Seven female Long–Evans rats were used in Experiment 1. Six out of seven rats run in the wet version were included in the dry condition. Data from one rat in the dry condition were not included because the rat became ill and died after completing the wet condition, but before finishing the dry condition. Ten female Long–Evans rats were used in Experiment 2 for both the dry and wet versions of the task. Rats from both experiments were 3–4 months old at the start of training.

The rats were individually housed in standard cages in an animal vivarium. In the dry conditions rats were water restricted before testing and given 10–30 min ab lib access to water after daily testing. All procedures were in accordance with a protocol approved by the Institutional Animal Care and Use Committee of Dartmouth College.

2.2. Apparatus

Training and experiments were conducted within a white plastic rectangular arena ($118 \times 59 \times 59$ cm high) on an elevated (40 cm) platform. A black Plexiglas panel (59×59 cm) was attached to the inside of one of the short walls. This panel served as the only intentional landmark for orientation within the arena. Four 50 watt lights, one above each corner facing the center of the arena, provided the only source of illumination in the room in Experiment 1. Experiment 2 was conducted in a different room with eight 50 watt lights arranged overhead in an octagon. For both experiments, the arena was placed inside a black circular curtain ($\sim$2.5 m diameter), spanning from floor to ceiling. A white sheet provided a uniform surface on the ceiling, and a video camera was centered above the arena to record the test sessions.

2.2.1. Wet condition

The arena was filled to a height of $\sim$23 cm with room temperature water mixed with white powder tempera. Circular weighted Plexiglas platforms (12.5 cm diameter, 21 cm height) were used as start and escape platforms (see Training and Experimental Procedures, below) and the platform tops were 2 cm below the water surface.

2.2.2. Dry condition

A white Plexiglas board (118×59 cm) was placed 21 cm above the bottom of the arena to serve as a floor. This height was chosen in order to control for available sensory stimuli by approximating the position of the rat's head within the arena during the wet condition. Identical opaque water cups ($4.5 \times 4.5 \times 1.0$ cm) were placed in each corner.

2.3. Pretraining

The rats were handled for $\sim$15 min/days for 5 day before behavioral testing. In both conditions each rat was removed from its cage and brought into the room in a closed box.

2.3.1. Wet condition

Five platforms were placed inside the arena: one start platform in the center, and one platform in each corner. Each rat was placed on the center platform for 1 min. Then, the rat was picked up while the platform was submerged on its side, and replaced in the center of the arena facing one of the walls. Because the start platform was now inaccessible, the rat swam until it encountered one of the corner platforms. After standing on a corner platform for 30 s the platform was submerged on its side, and the rat was replaced in the same corner and permitted to swim to one of the remaining corner platforms. This procedure was repeated until the rat had visited all four corners. Each rat received two pretraining sessions per day, separated by ~ 4 h. Rats in both experiments received 3–4 days of pretraining in the wet condition.

2.3.2. Dry condition

Water restricted rats were placed inside a transparent Plexiglas corral (28.5×28.5 cm, height 28.5 cm) positioned in the center of the arena for 1 min. The rat was then picked up, the corral removed, and the rat was replaced in the center of the arena facing one of the walls and permitted to approach the corners. Each cup contained a 0.1 ml drop of water as a reinforcer. After consuming the water in each corner the rat was removed from the arena. Rats were given 6 (Experiment 1) and 10 (Experiment 2) days of pretraining in the dry condition.

2.4. Experimental design and procedures

In both the wet and dry conditions rats performed a delayed match-to-sample spatial working memory task. Rats were given a pair of trials—a sample trial and a test trial (described below). A block consisted of a pair of sample and test trials. Two blocks were conducted each day, one between 9:00 a.m and 12:00 p.m. and one between 2:00 and 6:00 p.m. Each block was performed at least 4 h after the previous block to reduce proactive interference. Fifty blocks were performed over 25 consecutive days.

In the sample trial rats searched for the one corner containing a reinforcer (an escape platform in the wet condition, a drop of water in the dry condition). In the following test trial the animals approached one corner, and were reinforced if they returned to the corner that contained the reinforcer in the previous sample trial. The corner that was reinforced varied randomly across blocks.

Before entering the arena rats were given a disorientation procedure in an attempt to encourage the rats to orient relative to the arena and landmark cue. Using this procedure was important because otherwise rats could have maintained their orientation throughout the experiment by either monitoring their movements, via path integration, from their home cage or from the entrance/exit locations of the sample trial, and thus avoided the use of the arena and cue card for orientation [7,16,22]. Rats were first placed inside an opaque box and slowly spun (~ 3–$6°$/s) for 1 min while the experimenter slowly walked a circuitous route around the room. The experimenter then placed the box down adjacent to the middle of one wall of the arena. The direction the box was spun and the location where it was finally placed were randomized across blocks. These procedures were conducted for both the wet and dry conditions prior to each trial block.

2.4.1. Wet condition

Sample trials began when the rat was removed from the holding box and placed on the platform in the center of the arena for 30 s. The platform was then submerged on its side, and the rat was released into the water while directly facing one of the walls. The wall the rat faced was randomly varied across trials. The rat swam from corner to corner until it located the platform and climbed onto it. The rat stayed on the platform for 30 s and was then placed inside the holding box. The box top was closed, and the holding box was rotated slowly a total of 90 or 180° in either the clockwise or counterclockwise direction and then placed outside a different wall from where it was placed before the sample trial. The speed of box rotation was ~ 3–$6°$/s and was intended to be subthreshold for vestibular activation. This procedure was designed to create a discrepancy between the animal's orientation and the arena during the test trial, a discrepancy that could be resolved by using the landmark cue for reorientation. The amount of box rotation (90 or 180°), direction of box rotation (clockwise, counterclockwise), and box location before the test trial were randomly varied across trials.

For test trials the rat was placed on the start platform for 30 s and then released into the water facing one wall. If the rat swam to the correct corner it was allowed to stay on the platform for 30 s before it was returned to the holding box. If the rat approached an incorrect corner it was blocked from swimming to another corner by a piece of wood held by the experimenter. The rat swam for an additional 15 s before it was removed from the arena. This procedure was used because we did not want to reinforce the selection of an incorrect corner choice by immediately taking the rat out of the pool. Each block of sample-test trials lasted ~ 4 min, and the inter-trial interval was ~ 60 s.

2.4.2. Dry condition

In the dry condition rats were reinforced in both the sample and test trials with a drop of water (0.1 ml). The elapsed time for the different parts of each trial were identical to those described above for the wet condition, with the following differences: (1) instead of being placed on a start platform, rats were placed inside the transparent corral, and (2) in the test trial rats were removed from the arena after consuming the water drop. Rats were only permitted to approach one corner per test trial. In a previous study using similar procedures [10], rats showed a significant bias during test trials for approaching the correct and rotational corners, compared with the near and far corners.

After pretraining in the dry condition of the wet–dry experiment (Experiment 1), rats were first given 24 blocks without the disorientation procedure between sample and test trials. Rats were then run on 50 trials with the disorientation procedure between sample and test trials, as described above. The main findings in the dry condition from the wet–dry and dry–wet experiments were the same (see Results); thus, differences in pretraining between the two groups run in the dry condition did not appear to affect the results.

2.5. Data analysis

The primary measure in the experiments was the corner the rats approached in the test trial, relative to the location of the reinforced corner in the sample trial. There were four possible responses in the test trial: (1) correct (return to reinforced corner in sample trial): (2) rotational (choosing the corner diagonally opposite the correct corner): (3) near error (corner adjacent to the correct corner along a short wall): (4) far error (corner adjacent to the correct corner along a long wall). The diagonally opposite corner is labeled 'rotational' because this location would be congruent with the correct corner following a 180° rotation of the arena. After pretraining the rats reliably approached one corner after release, which enabled the unambiguous classification of responses.

Chi square tests were used to compare the relative frequencies of each response type. Repeated measures analysis of variance (ANOVA) tests were used to compare differences in the acquisition of correct responses. For all statistical tests significance was set at the $P < 0.01$ level to help correct for multiple tests.

3. Results

3.1. Response choices in wet and dry conditions

The mean percent of trials for each response type are shown in Fig. 1 for Experiments 1 (A) and 2 (B). Chi square comparisons within each condition for the wet–dry and dry–wet experiments are shown in Table 1. In both wet conditions correct responses were significantly more frequent than near, far, and rotational responses (all P values < 0.001). There was also a subtle difference that appeared to depend on the order of the wet and dry

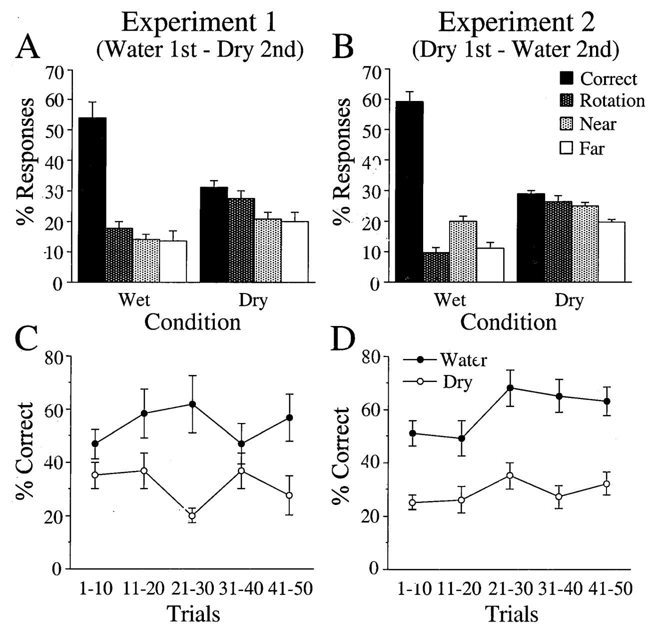

Fig. 1. Mean percent of response types (correct, rotational, near, far) as a function of condition (wet, dry). (A) Percent of responses for Experiment 1. Wet trials were conducted first, followed by dry trials in the same animals. (B) Percent of responses for Experiment 2. Dry trials were conducted first, followed by wet trials in the same animals. (C, D) Percentage of correct responses as a function of trial block in Experiment 1 (C) and Experiment 2 (D). The percentages in the dry condition of Experiment 1 were calculated from nine, rather than ten, trials in the 41–50 block.

conditions. In the wet condition that followed the dry condition, near responses were significantly more frequent than rotational and far responses (both P values < 0.001), a result not observed when the wet condition was tested first.

To determine if rats were more likely to approach correct corners located near the cue, we conducted a Chi square analysis of correct responses as a function of the location of the reinforced corner relative to the cue (two adjacent vs. two opposite corners). There were no significant differences between adjacent and opposite locations in either experiment (see Table). There were also no significant differences between adjacent and opposite locations, relative to the cue, for rotational, near, or far responses (data not shown).

In contrast to the wet conditions, for both dry conditions there were no significant differences between correct responses and either near or rotational responses (Table 1). The only significant response differences in the dry conditions were between the percent of correct ($\sim 30\%$) and far ($\sim 20\%$) responses (both P values $<$ 0.01). In order to test for any bias towards approaching the geometrically equivalent corners, responses in the dry conditions were analyzed in terms of the number of geometrically equivalent (correct, rotational) versus geometrically incorrect (near, far) responses. There was a significant difference between geometrically

Table 1
Comparison of behavioral responses across conditions (wet, dry)

Condition	Comparison	Experiment 1 (wet–dry)			Experiment 2 (dry–wet)		
		n	X^2	P value	n	X^2	P value
Water	Correct-rotation	191/65	62.0	< 0.001	296/48	178.8	< 0.001
	Correct-near	191/50	82.5	< 0.001	296/100	97.0	< 0.001
	Correct-far	191/44	92.0	< 0.001	296/56	163.6	< 0.001
	Rotation-near	65/50	2.0	ns	48/100	18.3	< 0.001
	Rotation-far	65/44	4.1	ns	48/56	0.6	ns
	Near–far	50/44	0.4	ns	100/56	12.4	ns
	Correct adj vs. opp	91/100	0.4	ns	153/143	0.3	ns
Dry	Correct–rotation	92/81	0.7	ns	145/132	0.6	< 0.001
	Correct-near	92/62	5.8	ns	145/125	1.5	ns
	Correct-far	92/59	7.2	< 0.01	145/98	9.1	< 0.001
	Rotation-near	81/62	2.5	ns	132/125	0.2	ns
	Rotation-far	81/59	3.5	ns	132/98	5.0	ns
	Near–far	62/59	0.1	ns	125/98	3.3	ns
	C+R vs. N+F	173/121	9.2	< 0.01	277/223	5.8	ns
	C+N vs. R+F	154/140	0.7	ns	270/230	3.2	ns

Correct: adj vs. opp = adjacent vs. opposite location of correct corners, relative to cue location for correct responses only, C+R = sum of correct+rotational responses, N+F = near+far, C+N = correct+near, R+F = rotational+far. The n values match the order of response categories in the corresponding row in the left column (ex. 191/65 indicates 191 correct and 65 rotational responses). The water-dry experiment had a total of 350 responses in the water condition (seven rats × 50 trials), and 294 responses in the dry condition (six rats × 49 trials). The dry-water experiment had a total of 500 responses (ten rats × 50 trials)for water and dry conditions.

equivalent (59%) and incorrect (41%) responses in the wet–dry experiment ($P < 0.01$). In the dry–wet experiment, differences between geometrically correct (55%) and incorrect (45%) responses nearly attained significance ($P < 0.02$). Across all trials the percent of correct and rotational responses in individual subjects ranged from 53 to 69% (Experiment 1) and 50 to 62% (Experiment 2). Percentages were similar when examining just the last 20 trials; only 1/16 subjects (Experiments 1 and 2) approached the correct and rotational corners on > 70% of the trials.

Thus, the overall results show that the subjects were capable of approaching the correct corner, but only when escaping from the water. In the dry condition, conducted within the same environment as the wet condition, subjects were unable to approach the correct corner more often than the near and rotational corners. This result was observed even in subjects that had previous experience approaching the correct corner in the wet condition (Experiment 1).

3.2. Acquisition

Acquisition was examined by dividing the 50 trials in each condition into five consecutive ten trial blocks (trials 1–10, 11–20, etc.) and measuring the number of correct responses. Separate repeated measures ANOVA tests were performed for the wet–dry and dry–wet experiments using factors of condition (wet, dry) and trial block (five blocks). In the wet–dry experiment we only analyzed the results from the six rats that completed both the wet and dry conditions. For both experiments there were significant differences between conditions (wet–dry: $F_{(1,\ 5)} = 16.8$, $P < 0.01$; dry–wet: $F_{(1,\ 9)} = 73.1$, $P < 0.0001$), with more correct responses in the wet condition relative to the dry condition. In both experiments there were no significant differences across trials, and the condition × trial interaction was also not significant (Fig. 1C, D). These findings show that acquisition in the wet version was rapid, with correct responses in ~50% of the first ten trials for both experiments, as compared with a mean of ~50–65% for trials 11–50. Although the percent of correct responses increased somewhat for subsequent trials, this increase did not attain significance. The percent of correct responses was low in the dry condition, and did not significantly improve across trials.

4. Discussion

These findings demonstrate that after a disorientation procedure rats are able to acquire a spatial delayed match-to-sample task when escaping from water, but perform nearly at chance in a dry version of the same task. These results are consistent with other reports showing that disorientation impairs performance in reference memory tasks under dry, but not water maze, conditions [6,19].

The observation that rats were able to approach the correct corner in the wet condition suggests that the proposal that rats cannot distinguish the correct from rotational corners following disorientation may need to be qualified based on the type of task that is used.

Previous studies in rats [4,5,10,18] and toddlers [13,14] that reported an equal bias for geometrically equivalent corners (correct and rotational) employed appetitive reinforcers. In both of the current experiments rats approached the correct corner far more often than the other corners in the wet condition. Because training in water mazes is considered to use aversive reinforcement [15], the present findings suggest that the confusion between geometrically equivalent corners may apply to appetitive tasks, but may not be present in aversive tasks, such as the water maze. Although the two tasks were similar, they were not identical on one or more dimensions. For example, the nature of the environment (water vs. dry) and type of locomotion (running vs. swimming) were different and there may be strategy differences when rats are swimming in water versus locomoting on dry land. Thus, additional studies designed to compare appetitive and aversive reinforcement while maintaining similar environmental conditions and locomotor responses would further test the notion that the differences observed here are due to the type of reinforcement.

Unexpectedly, rats did not demonstrate a significant preference for either the correct or rotational corners in the dry condition, a result that does not support the notion that rats were using arena geometry to determine their corner choice in the present study. However, based on previous results showing a significant preference for correct and rotational corners in similar appetitive tasks [4,5,10,18], and the significant difference between correct and rotational responses versus near and far responses in the dry condition, the use of arena shape appears to be an important cue for defining corner choice in tasks using appetitive reinforcers. The most important finding of this study is that in the wet condition rats clearly did not base their choices solely on arena shape, because most responses were directed to the correct corner. Presumably the cue was used to define the correct corner, but additional study is required to test this hypothesis.

We consider two hypotheses, that are not mutually exclusive, that are relevant to the different findings in the wet and dry conditions. First, differences in the type of reinforcement (appetitive vs. aversive) may relate to differences in performance across the two conditions. Somewhat different brain processes may be engaged during memory tasks that employ appetitive versus aversive reinforcement. For example, long-term memory recall is facilitated when memorizing material with a strong emotional component, compared with more neutral items [3]. The amygdala and the release of stress-related hormones, which are associated with fear conditioning and other emotionally arousing situations, have an important role in the modulation of long-term memory. Thus, these systems may facilitate better performance in the wet condition than the dry condition. This explanation is tentative, however, because most studies that examined the role of stress hormones and the amygdala measured long-term memory rather than working memory, and there is some evidence that the amygdala may not modulate working memory in rats [2].

A second possibility for the performance differences between the wet and dry conditions is that the animals were employing different behavioral strategies in each condition to solve the same task. In a study of spontaneous alternation in wet and dry conditions, Whishaw and Pasztor [26] suggested that rats utilize a strategy based on an array of visual cues (cognitive mapping) when foraging, and an escape or homing strategy when returning to their nest. Reinforcement type is related to these different strategies because foraging behavior is appetitively motivated, and escape or homing behavior is emitted to avoid harm.

Cognitive mapping can be used in foraging tasks [21], and cognitive mapping may in turn depend on environmental shape [7]. In contrast, an escape strategy may rely on non-geometric cues rather than cognitive mapping to define a goal location [26]. If an escape strategy was operative in the wet condition, this would suggest the rats were using non-geometric cues, such as the position of the landmark cue, to define the correct corner. In this manner, the rats would not confuse the geometric equivalent corners because they were using a strategy other than cognitive mapping, and consequently would not have depended on environmental shape for orientation.

Indirect evidence that water maze tasks may not necessarily require cognitive mapping is provided by studies showing that animals with hippocampal lesions can be taught under certain conditions to find a hidden platform in a water maze task [24,25]. Since the hippocampus is thought to be crucial for supporting a cognitive mapping strategy [21], accurate performance without a hippocampus implies the use of a strategy other than cognitive mapping. In contrast, in the dry version of the task, the rats may be more likely to engage a cognitive mapping strategy based on landmarks, such as environmental shape, and thus be more prone to rotational errors. Hippocampal lesions have been shown to impair performance on a dry version of the water maze task [17], but additional study is needed to determine if, as in the typical water maze, hippocampal animals given extensive pretraining can perform an appetitive spatial task well.

Strategy differences may also lead to greater difficulty in the dry, versus wet, condition. In delayed-match-to-sample tasks rats must overcome the tendency to alternate locations in the dry condition to receive reinforcement, while the wet condition is consistent with the tendency to return to previous locations in water mazes [26]. A comparison of delayed non-match-to-sample and delayed-match-to-sample tasks could be used to evaluate the influence of potential strategy differences in the wet and dry conditions.

4.1. Absence of notable correct-rotational bias in dry condition

An unexpected finding was the absence of a strong bias towards approaching the geometrically equivalent corners, relative to the geometrically incorrect corners, in the dry conditions. There was a small, but significant, bias towards the geometrically equivalent corners only when the total number of correct and rotational responses were compared with the total number of near and far responses, but this effect was smaller than we expected. In previous studies rats chose the correct or rotational corners on $\sim 70\%$ of the trials (67%, Margules and Gallistel, 1988 [18]; 73%, Golob et al., 2001 [10]), compared with $< 60\%$ of the responses in the present study. It is important to note that in previous studies there were subgroups of rats that did not acquire the task [10] (Experiment 3), or were not tested [18] (Experiment 3). This procedure would have increased the apparent performance scores in these previous studies.

What differences across these studies led to the absence of a strong correct/rotational bias in our dry condition? One possibility is that in our rectangular arena the corners were smooth and continuous, which did not provide sharp demarcations between the walls. The arena we used may not have provided adequate spatial cues to allow the rats to adopt a geometry-based response strategy in the dry condition. Another possibility follows from the observation that the task includes a delayed matching component, in addition to reorientation. Accuracy in two-choice spatial delayed matching paradigms in rats typically ranges from ~ 70 to 90% correct for delay intervals comparable to those in the present experiments (~ 60 s) (e.g. [1,11,20]). Thus, a long delay could obscure the tendency for rats to approach geometrically equivalent corners.

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References

[1] Aggleton JP, Hunt PR, Rawlins JN. The effects of hippocampal lesions upon spatial and non-spatial tests of working memory. Behav Brain Res 1986;19:133–46.

[2] Bianchin M, Mello e Souza T, Medina JH, Izquierdo I. The amygdala is involved in the modulation of long-term memory, but not in working or short-term memory. Neurobiol Learn Mem 1999;71:127–31.

[3] Cahill L, McGaugh JL. Mechanisms of emotional arousal and lasting declarative memory. Trends Neurosci 1998;21:294–9.

[4] Cheng K. A purely geometric module in the rat's spatial representation. Cognition 1986;23:149–78.

[5] Cheng K, Gallistel CR. Testing the power of an animal's spatial representation. In: Roitblat HL, Tever TG, Terrace HS, editors. Animal cognition. Hillsdale, NJ: Lawrence Erlbaum Assoc, 1984.

[6] Dudchenko PA, Goodridge JP, Seiterle DA, Taube JS. Effects of repeated disorientation on the acquisition of spatial tasks in rats: dissociation between the appetitive radial arm maze and aversive water maze. J Exp Psychol Anim Behav Process 1997;23:194–210.

[7] Gallistel CR. The organization of learning. Cambridge, MA, USA: The MIT Press, 1990.

[8] Gallistel CR, Cramer AE. Computations on metric maps in mammals: getting oriented and choosing a multi-destination route. J Exp Biol 1996;199:211–7.

[9] Gibson BM, Shettleworth SJ, McDonald RJ. Finding a goal on dry land and in the water: differential effects of disorientation on spatial learning. Behav Brain Res 2001;123:103–11.

[10] Golob EJ, Stackman RW, Wong AC, Taube JS. On the behavioral significance of head direction cells: neural and behavioral dynamics during spatial memory tasks. Behav Neurosci 2001;115:285–304.

[11] Hampson RE, Heyser CJ, Deadwyler SA. Hippocampal cell firing correlates of delayed-match-to-sample performance in the rat. Behav Neurosci 1993;107:715–39.

[12] Hermer L. Internally coherent spatial memories in a mammal. Neuroreport 1997;8:1743–7.

[13] Hermer L, Spelke ES. A geometric process for spatial reorientation in young children. Nature 1994;370:57–9.

[14] Hermer L, Spelke E. Modularity and development: the case of spatial reorientation. Cognition 1996;61:195–232.

[15] Hodges H. Maze procedures: the radial-arm and water maze compared. Brain Res Cogn Brain Res 1996;3:167–81.

[16] Hynes CA, Martin GM, Harley CW, Huxter JR, Evans JH. Multiple points of entry into a circular enclosure prevent place learning despite normal vestibular orientation and cue arrays: evidence for map resetting. J Exp Psychol Anim Behav Process 2000;26:64–73.

[17] Kubie JL, Sutherland RJ, Muller RU. Hippocampal lesions produce a temporally graded amnesia on a dry version of the Morris swimming task. Psychobiology 1999;27:313–30.

[18] Margules J, Gallistel CR. Heading in the rat: determination by environmental shape. Anim Learn Behav 1988;16:404–10.

[19] Martin GM, Harley CW, Smith AR, Hoyles ES, Hynes CA. Spatial disorientation blocks reliable goal location on a plus maze but does not prevent goal location in the Morris maze. J Exp Psychol Anim Behav Process 1997;23:183–93.

[20] Mumby DG, Pinel JP, Wood ER. Nonrecurring-items delayed nonmatching-to-sample in rats: a new paradigm for testing nonspatial working memory. Psychobiology 1990;18:321–6.

[21] O'Keefe J, Nadel L. The hippocampus as a cognitive map. Oxford, UK: Clarendon Press, 1978.

[22] Sharp PE, Kubie JL, Muller RU. Firing properties of hippocampal neurons in a visually symmetrical environment: contributions of multiple sensory cues and mnemonic processes. J Neurosci 1990;10:3093–105.

[23] Vallortigara G, Zanforlin M, Pasti G. Geometric modules in animals' spatial representations: a test with chicks (*Gallus gallus domesticus*). J Comp Psychol 1990;104:248–54.
[24] Whishaw IQ, Jarrard LE. Similarities vs. differences in place learning and circadian activity in rats after fimbria–fornix section or ibotenate removal of hippocampal cells. Hippocampus 1995;5:595–604.
[25] Whishaw IQ, Jarrard LE. Evidence for extrahippocampal involvement in place learning and hippocampal involvement in path integration. Hippocampus 1996;6:513–24.
[26] Whishaw IQ, Pasztor TJ. Rats alternate on a dry-land but not swimming-pool (Morris task) place task: implications for spatial processing. Behav Neurosci 2000;114:442–6.