Effects of dorsal-striatum lesions and fimbria-fornix lesions on the problem- solving strategies of rats in a shallow water maze

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In solving a spatial problem, animals can use a place, cue, or response strategy. The present research was designed to evaluate the role of dorsal striatum (DS) in spatial problem solving and to compare it with that of fimbria fornix (FF). Rats were trained with a place + cue task in a shallow pool, then were divided into three groups (DS, FF, control), and lesions were made in the corresponding areas. After re-training, four probe tests were given: Test 1 (start position moved), Test 2 (goal and start positions moved), Test 3 (invisible goal), and Test 4 (curtain test). The test results suggest that the DS and Control groups performed the original task by using the place strategy, whereas the FF group used the cue strategy, which strongly implies that the DS group was impaired in the use of the cue strategy. This research also provides evidence supporting the usefulness of a shallow pool in evaluating animal behavior.

Animals are thought to use a place strategy, a cue strategy, or a response strategy, depending on the availability of environmental stimuli, when they try to approach or avoid meaningful locations in their environment (O'Keefe & Nadel, 1978; Whishaw & Mittleman, 1986). The place strategy is defined as a strategy in which the allocentric spatial relationships among environmental stimuli are used. The cue strategy is a strategy in which specific landmarks or stimuli in the environment are used as a guide to approach/avoidance behavior. The response strategy utilizes egocentric cues—that is, the kinesthetic cues based on the body orientation of the animal.

Since O'Keefe and Nadel (1978) advocated the hippocampus as the structure in which the cognitive map is formed, efforts have been made to identify the brain loci responsible for the three strategies. Many experiments have demonstrated that a lesion of the hippocampus and/or its related areas causes performance deficits in tasks that require the use of the place strategy, but does not cause performance deficits in tasks that require the cue or response strategy, giving firm evidence of hippocampal involvement in the use of the place strategy (e.g., Eichenbaum, Stewart, & Morris, 1990; Morris, Garrud, Rawlins, & O'Keefe, 1982; Morris, Hagan, & Rawlins, 1986; Morris, Schenk, Tweedie, & Jarrard, 1990; Okaichi, 1987; Sutherland, Kolb, & Whishaw, 1982; Sutherland & Rodriguez, 1989; Sutherland, Whishaw, & Kolb, 1983). However, in a recent study by Whishaw and Jarrard (1996) it was found

that the hippocampus also seems to be involved in integrating movements in the water tasks. Researchers have suggested the involvement of the dorsal striatum (DS) in the use of the cue and response strategies. However, in contrast to the overall agreement on the effect of hippocampal lesions, reports on the effects of DS lesions are inconsistent: Some have recognized DS involvement in both strategies, and some have said it is involved in either one or the other of the strategies. With the use of a dry maze, such as the radial arm maze, several experiments have shown that DS lesion impairs the acquisition of a cue task but not the acquisition of a place task, indicating that the DS is involved in the use of the cue strategy (Dunnett & Iversen, 1981; McDonald & White, 1993; Packard, Hirsh, & White, 1989; Packard & White, 1991; Reading, Dunnett, & Robbins, 1991). DeCoteau and Kesner (2000) gave lesioned rats a sequential learning task and showed that medial DS-lesioned rats and hippocampus-lesioned rats exhibited deficits in egocentric-procedural and allocentric-declarative sequential information processing, respectively. Furthermore, Mitchell and Hall (1988) reported that the acquisition of a right-left response task was impaired by DS lesion.

On the other hand, DS lesions have resulted in selective impairment of the retention of an egocentric response task but not an allocentric place task or a cue task (Abraham, Potegal, & Miller, 1983; Cook & Kesner, 1988; Kesner, Bolland, & Dakis, 1993; Potegal, 1969, 1982). Packard and McGaugh (1996) trained rats with a T-maze that used three arms of a cross maze. On this task, the reward was placed on a fixed arm. After the rats were trained, lidocaine was injected into the hippocampus or dorso-lateral caudate nucleus, and the subjects were given a probe test in which the start position was rotated 180°. The results indicated that the hippocampus-inactivated rats employed a re-

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sponse strategy, and caudate-inactivated rats employed a place strategy. Colombo, Davis, and Volpe (1989) also showed that DS lesion impairs the retention of a response task, but in the same research, they showed that the DS lesion impaired the acquisition of a cue discrimination task.

With the use of the water maze, Packard and McGaugh (1992) gave DS-lesioned rats a place-discrimination task and a cue-discrimination task and reported that lesioned animals showed selective impairment in the acquisition of the cue-discrimination task. Also, McDonald and White (1994) lesioned the hippocampus or dorsal striatum, and trained the rats to swim to the visible platform placed in a fixed position. The animals were subsequently tested for which strategy they used in a situation in which both place and cue strategies were available. The DS-lesioned rats used the place strategy more often than the cue strategy, and the hippocampus-lesioned rats used the cue strategy more often than the place strategy. Devan, Goad, and Petri (1996) also trained DS-lesioned and hippocampus-lesioned rats in the water maze for place and cue tasks and reported that both lesioned groups exhibited impairment in the place task. However, according to Devan et al. (1996), the cause of the impairment shown by these two groups was different, in that the hippocampus-lesioned rats inherently could not use the place strategy, but, for the DS-lesioned rats, their thigmotactic tendency, manifested as circular swimming along the wall, prevented them from using the place strategy. Their DS-lesioned rats also showed transient impairment in the early stage of the cue-task training.

In contrast to these experiments, which show DS involvement in the cue and/or response strategies, recent reports by Devan and his colleagues (Devan, McDonald, & White, 1999; Devan & White, 1999) have suggested DS involvement in the place strategy. They reexamined the locations of the DS lesions and, based on the anatomical findings that neuronal connections exist between the medial DS and the hippocampus and between the lateral DS and the sensory cortex and the substantia nigra pars compacta (Heimer, Zahm, & Alheid, 1995; McGeorge & Faull, 1989), they have suggested that lesions in the medial DS should result in place-strategy impairment. On the basis of this hypothesis, they gave rats selective lesions in the medial or lateral DS and trained them with place and cue tasks simultaneously. After training, the rats were given the strategy probe test. The medial DS-lesioned group showed impairment in the acquisition of the place task, and in the probe test, they preferred the cue strategy. The lateral DS-lesioned group did not show any impairment in the acquisition of either task, and they preferred the place strategy in the probe test.

Considering these contradictory reports on the effect of DS lesions, the present experiments were designed to elucidate the role of the dorsal striatum in stimulus-response learning and the use of problem-solving strategies, and, at the same time, to confirm hippocampal involvement in the

use of the place strategy. We trained rats in the water maze under the condition in which both the place and cue strategies were available. After training, the DS or the fimbria fornix (FF), the major connecting pathway between the hippocampus and the forebrain area, was lesioned. The lesioned rats were retrained and then were given probe tests in order to check which strategy they had used. It is important to note that in many previous studies using the water maze, dorsal striatum lesions were made before training on the task (acquisition paradigm), whereas, in our study, the rats were trained before undergoing surgery (retention paradigm).

Before the lesion experiment, we modified the conventional water maze and tested the new version in order to see whether the results obtained from the new procedure would be equivalent to those obtained with the conventional setup. The Morris water maze (Morris, 1981) has proved to be one of the most useful tools in memory and learning research. In this apparatus, the depth of the water is usually 30–40 cm deep in order to force the rat to swim. However, this depth of water sometimes causes behavioral problems. For instance, rats sometimes show disrupted swimming behavior when they miss the invisible platform by a slight margin or when they cannot find the platform at the learned place in the no-platform probe test. This disrupted behavior could lead the experimenter to erroneous conclusions. Therefore, we employed a shallow pool in which a rat could either walk or swim. With this arrangement, rats appear to be less fearful when they cannot find the platform.

In Experiment 1, we evaluated the usefulness of the shallow pool and showed that the learning of the task by rats proceeds in the same way as in the conventional deep-water maze. In Experiment 2, using the shallow pool, we compared the role of the dorsal striatum and the hippocampus in retention of the preoperatively learned task and evaluated the results from the viewpoint of the strategy used to find the platform.

EXPERIMENT 1

Behavioral Assessment and Strategy Tests in the Shallow Pool

The main purpose of this experiment was to evaluate the usefulness of the shallow pool in assessing rats' behavior. Rats were trained for the place task with a visual cue (place + cue task). When they had learned the task, various probe tests were given in order to analyze the strategies they used.

Method

Subjects

Twenty-four experimentally naive, male Wistar albino rats were used. They were approximately 3 months old at the beginning of the experiment, with a mean weight of 330.7 g (*SD* 10.1 g). They were housed individually in wire cages with free access to water and food. The animal room was maintained at a temperature of 23° ± 1°C, with a 12:12 light:dark cycle starting at 7:00 a.m. Experiments were car-

ried out during the light cycle. All experiments were performed in accordance with the Doshisha University guidelines for animal experiments.

Apparatus

A circular polyethylene pool (142 cm in diameter with a black plastic liner) was placed in the center of the room (343 × 408 cm). There were various objects in the room including a computer, two monitors, shelves, five lamps fixed on the wall, and a rat carrier, which all served as extramaze stimuli. The height of the wall of the pool was 40 cm, and the depth of the water was 10.5 cm. The water was darkened with nontoxic black ink (30 cc/10 L) and was maintained at 22°C. The escape platform was a black cylinder 10.0 cm in height and 11.5 cm in diameter. A soft white plastic belt that was wound around the top part of the cylinder, so that the top of the belt protruded 7 mm from the surface of the water (unless otherwise stated), served as the intramaze cue. The pool was divided into four quadrants with arbitrary north-south and east-west axes, and the platform was placed in the center of the quadrant. Mounted on the ceiling above the pool, a monitor camera recorded images on a video recorder. At the same time, the images were sent to a computer (Power Macintosh 7600/132, Apple Computer) that analyzed escape latencies, swimming distance, and swimming paths with the use of the water maze path analysis system (NIH Image 1.60 WM, revized by T. Miyagawa).

Procedure

After two days of handling for 5 min each day, training with the place + cue task started. The rats were required to reach the cued escape platform from the start position at the rim of the pool. The position of the platform was fixed for each rat, and the two start positions were at the distal ends of the imaginary axes; that is, if the platform was placed in the north-east quadrant, the start positions

alternated between the west and south rims of the pool. The rat was placed in the water facing the wall at one of the start positions. The rats were trained on the place + cue task two to four trials per day. We set the learning criterion to be an escape latency of less than 10 sec, which had to be maintained for two consecutive trials. All rats attained this criterion by the 11th trial, but the training was continued through the 14th trial, after which the probe test session started.

There were four probe test conditions. One probe test was given on each test day. On the test day, the rats received two usual training trials and then two test trials. Figure 1 shows the arrangement of the start and platform positions for the training and the four tests.

Test 1 (start position moved). The start position was moved to the position opposite the escape platform. In this test, the cue strategy and the place strategy were effective, but the response strategy was ineffective.

Test 2 (goal and start positions moved). The escape platform was moved 180°, and the position opposite the platform was used as the start position. In this test, the cue strategy was effective, but the place strategy and the response strategy were ineffective.

Test 3 (invisible goal). The position of the escape platform was the same as in the training position, but the white belt was removed so that the escape platform was invisible. In this test, the place strategy and the response strategy were effective, but the cue strategy was ineffective.

Test 4 (curtain test). The pool was surrounded with a black curtain so that no extramaze cues were available. The escape platform was cued as in the training period, and the platform and start positions were unchanged. In this test, the cue strategy and the response strategy were effective, but the place strategy was ineffective.

The intertrial interval for each rat was approximately 50 min at the early stage of training, but was shortened to 20 min at the end of training. After each test, the rats were given their usual training for four tri-

Figure 1. The arrangement of the start and platform positions for the training and four probe tests. The solid small circle indicates the visible platform. The dotted small circle indicates the invisible platform. The outer large circle is the curtain in Test 4. The rats show the start positions.

als per day, until their performance recovered to the learning criterion level. After each swim, the rats were dried with a towel and returned to the cage.

Results

Figure 2 shows the mean escape latencies during the training. The latencies shortened quickly during the first 6 trials, and at the 10th trial, most subjects reached the platform within 10 sec, directly from the start position. In this shallow pool, while performing the first trial, many rats jumped to the wall of the pool and sometimes onto the rim of the pool or walked in the water instead of swimming. Owing to these behaviors, which are specific to the shallow pool, 46% of subjects could not reach the platform within 120 sec, and they were placed on the platform by the experimenter. However, swimming behavior became dominant by the 3rd trial, and the number of subjects who could not reach the platform on their own diminished drastically.

The mean escape latencies of the two training trials on the test day (baseline trials) and the two test trials are shown in Figure 3. Test 1 (start position moved) had no effect on escape latency. However, in Test 2 (goal and start positions moved), escape latency significantly increased [$t(23) = 4.10, p < .001$]. The swimming path in Test 2 revealed that the rats first headed for the training platform position, made several circles there, and then went to the new position. In Test 3 (invisible goal), the test condition did not affect escape latency. The rats headed directly toward the invisible platform from the start position. In Test 4 (curtain test), escape latency significantly increased [$t(23) = 4.71, p < .001$].

Discussion

Experiment 1 demonstrates that rats can learn a water maze task successfully in a shallow pool. This result shows

Figure 2. Mean escape latencies in seconds ($\pm$ SE) to escape onto the invisible platform during training.

Figure 3. Mean escape latencies in seconds ($\pm$ SE) for baseline trials and test trials in four probe tests.

that the shallow pool can be used as a tool to assess rat behavior in the water maze.

The results of the probe tests suggest that the rats used the place strategy first and the cue strategy when the place strategy was not available. In Test 1, in which both the place strategy and the cue strategy were effective, the unavailability of the response strategy did not affect performance. This interpretation of the unavailability of the response strategy agrees with that of Devan and White (1999). However, in Test 2, in which both the response strategy and the place strategy were not available and only the cue strategy was effective, the rats did not go directly to the visible platform. Instead, they went to the training platform position first, searched there, and then headed for the new platform position. This finding shows that the rats used a place strategy when extramaze stimuli were available, and only after confirming that the place strategy was not effective, did they use the cue strategy. Thus, there appears to be a hierarchy in the use of problem-solving strategies. The superiority of the place strategy was also confirmed in Test 3, in which the escape platform was made invisible. This condition did not affect the behavior of the rats. Although the response strategy could also have been effective in Test 3, the results of Test 3, taken together with the results of Test 1, suggest that the rats used the place strategy when extramaze stimuli were available. In Test 4, in which only the cue strategy and the response strategy were effective, the heading direction of rats showed transient disruption, and the escape latency increased. This disrupted behavior can be interpreted either as being a direct effect of the environmental change or as being the result of the unavailability of the dominant place strategy.

The results from Experiment 1 show that there is a strategy preference in rats when they are trained with a task

in which a visible escape platform is placed at a fixed location: The place strategy is the most preferred, then the cue strategy, and the response strategy the least preferred. This preference order is in agreement with former reports (Okaichi, 1996; Wishaw & Mittleman, 1986). However, the preference order may differ depending on the amount of training (Packard & McGaugh, 1996).

EXPERIMENT 2

The Problem-Solving Strategy of Dorsal Striatum- or Fimbria Fornix-Lesioned rats

In Experiment 2, the effects of dorsal striatum lesion on the problem-solving strategy was assessed after learning had occurred, and was compared with the effects of fimbria fornix lesion, with the use of the shallow pool.

Method

Subjects

Twenty-one experimentally naive male Wistar albino rats served as subjects. They were approximately 2 months old at the beginning of the experiment with a mean weight of 278 g (*SD* 8.0 g) and were housed in the same conditions as those in Experiment 1.

Apparatus

The same shallow pool used in Experiment 1 was used for this experiment.

Procedure

The basic procedure was the same as that of Experiment 1, except for the following points: After the original training on the place + cue task, the rats were divided into three groups (DS lesioned, FF lesioned, nonoperated control) according to the counterbalancing of the escape latency shown during the training period. The two lesion groups were operated on, and after a week of recovery, all rats received retraining on the original place + cue task. When their performance reached the learning criterion, four probe tests were carried out. These probe tests and the sequence of the tests were the same as those in Experiment 1: Test 1, start position moved, Test 2, goal and start positions moved, Test 3, invisible goal, and Test 4, the curtain test.

Surgery and Histology

A lesion generator (Model RFG-4, Radionics, MA) was used to create the lesions in the DS and FF groups. Rats were anesthetized with 50 mg/kg of sodium pentobarbital, i.p., and then were injected with 10 mg of atropine sulfate, i.p. The head was kept horizontal in a stereotaxis, and the electrode was inserted at four sites. For the FF lesion, the placements of the electrode from bregma were AP = -2.1 mm, ML = $\pm$ 1.2 and 2.7 mm, and DV = -3.8 mm, and the temperature of the electrode tip was maintained at 55°C for 60 sec. For the DS lesion, the coordinates were AP = 0.0 mm, ML = $\pm$ 3.8 mm, and DV = -4.5 mm; and AP = +1.5 mm, ML = $\pm$ 2.8 mm, DV = -4.2 mm, with the temperature at 56°C for 60 sec.

After behavioral testing, the lesioned rats were deeply anesthetized with sodium pentobarbital and perfused intracardially with 10% formalin, and their brains were removed. The brains were soaked in 10% formalin, 5% gelatin, and 10% sweet formalin (90 cc formalin + 10 g sucrose) for 24 h each, sectioned coronally at 25 μ m on a freezing microtome, and stained with cresyl violet.

Results

Histology

Minimal and maximal FF and DS lesions (Figure 4) were reconstructed on the Paxinos and Watson (1997)

Figure 4. Coronal sections of the lesioned rat brains reconstructed on the Paxinos and Watson (1997) atlas. Left column, fimbria fornix lesion (FF); right column, dorsal striatum lesion (DS). Dark hatching, minimum extent of the damage; dot hatching, maximum extent of the damage.

brain atlas. With the FF lesion, the fimbria fornix was completely sectioned. Additional damage to the lateral septum and part of the stria terminalis was sometimes seen. With the DS lesion, the damage was centered primarily in the medial DS, and the medial DS was damaged bilaterally in all DS-lesioned rats. The most lateral aspects of DS were spared unilaterally in 4 of the lesioned rats. Thus, although there was some damage to lateral DS, the most extensive cell loss was found in medial DS. The septum and nucleus accumbens were totally spared. No relationship was observed between the extent of the lesion and behavior.

Original Training and Retraining

The mean escape latencies during the original training in the place + cue task decreased smoothly as the training progressed. On the first retraining trial after the operation, the mean escape latency for the control group was 6.6 sec, the same level as at the end of the original training. But for the DS and FF groups, the latency was 28.7 and 49.2 sec, respectively, showing significantly increased latencies, as compared with the last training trial before the operation. However, the increase in escape latency was transient for both lesioned groups, and after three to five

trials, the latency for the lesioned groups matched that of the control group (control: 4.9 sec; DS: 5.6 sec; FF: 5.6 sec). A mixed-design analysis of variance (ANOVA) with group and trial as factors showed a significant interaction [$F(8,72) = 2.35, p < .05$]. The simple group effect was significant only for the first trial [$F(2,90) = 25.10, p < .01$].

Probe Tests

The effects of the test conditions were evaluated by escape latency, swimming distance, quadrant time, and swimming paths. Since escape latency and swimming distance showed similar results, only escape latency is shown in here.

Figure 5 shows the mean escape latencies of the two baseline trials on the test day and the two test trials for each probe test. In Test 1, in which the rats started from a new position, there was no effect of test condition or lesion. Rats in all groups took a correct heading direction at the start position and swam directly toward the escape platform. However, in Test 2, in which the cued platform was moved 180°, the groups differed from each other. The interaction between group (control, DS, FF) and session (baseline and test) was significant [$F(2,18) = 7.65, p < .01$]. The simple effects of session were significant for the DS group and the control group [$F(1,18) = 26.62$ and $12.80, ps < .01$]. The group effect on the session was also significant [$F(2,36) = 29.43, p < .001$]. The Newman-Keuls' multiple-range test revealed that the escape latency of the DS group was significantly longer than that of the control group ($p < .01$), and that of the control group was significantly longer than that of the FF group ($p < .01$), which showed no effect of test condition.

Figure 5. Mean escape latencies in seconds ($\pm$ SE) for baseline trials and test trials of the control (CONT), FF (fimbria fornix), and DS (dorsal striatum) groups in four probe tests.

In Test 3, in which the escape platform was made invisible, the escape latency of the FF group was longer than those of the two other groups. An ANOVA showed that the interaction between group and session was significant [$F(2,18) = 3.64, p < .05$]. The simple effect of session was significant only for the FF group [$F(1,18) = 16.08, p < .01$]. The simple effect of group was significant on test [$F(2,36) = 16.16, p < .01$], and subsequent Newman-Keuls' multiple-range tests showed that the escape latency of the FF group was significantly longer than those of the DS and control groups ($ps < .01$), but there was no difference between the DS group and the control group.

In Test 4, in which the pool was surrounded by a curtain, all three groups showed longer escape latencies. The main effect of session was significant [$F(1,18) = 38.83, p < .001$], but the main effect of group and the interaction between group and session were not significant.

The quadrant time for the first trial of each test is shown in Figure 6, and the representative swimming paths for each group for the first trial of each test are shown in Figure 7. The data for Test 1 was not included in Figures 6 and 7 because the test condition and the lesions did not affect performance.

Figure 6A shows the quadrant time for Test 2, both for the quadrant where the escape platform was placed during the original training and for the test quadrant, where the platform was moved during the test. An ANOVA revealed a significant interaction between group and quadrant (training quadrant and test quadrant) [$F(2,18) = 5.21, p < .05$]. The simple effect for each quadrant showed that effect of group was significant on the training quadrant [$F(2,36) = 7.34, p < .01$], but that it was not significant on the test quadrant. Newman-Keuls' multiple-range tests showed that the DS group stayed longer in the training quadrant than did the control group and that the control group stayed longer than the FF group did ($ps < .01$). The FF group did not show any sign of staying longer in the training quadrant. The swimming paths also show a conspicuous difference between the FF group and the DS and control groups. The rats in the DS and control groups started swiftly toward the former platform location. There, they made a couple of tiny circles in search of the escape platform and then headed for the current location of the cued platform. The DS-lesioned rats showed this swimming pattern more strongly than did the rats in the control group. In contrast, the rats in the FF group swam directly to the cued platform from their start position.

For Tests 3 and 4, the time in the quadrant where the platform was placed (training quadrant) and the aggregated time spent in the other three quadrants (nontraining quadrants) are shown in Figures 6B and 6C. In Test 3, in which the platform was made invisible (Figure 6B), the interaction between group and quadrant (training quadrant and nontraining quadrants) was significant [$F(2,18) = 3.77, p < .05$]. Although the simple effect of group was not significant at training quadrant, it was significant on non-training quadrants [$F(2,36) = 6.35, p < .01$]. A multiple-

Figure 6. Mean quadrant time in seconds ($\pm$ SE) spent in the platform quadrant and the other quadrants in the first test trial of Probe Tests 2 (goal and start moved), 3 (invisible goal), and 4 (curtain). CONT = control; FF = fimbria fornix; DS = dorsal striatum.

range test revealed that the FF group stayed longer in the nontraining quadrants than did the DS group ($p < .05$). As is shown in Figure 7, the rats in the control group headed directly for the escape platform from the start position, but the rats in the FF group swam along the pool wall.

In Test 4, in which the pool was surrounded by a curtain (Figure 6C), the nontraining quadrant time was significantly longer than the training quadrant time [$F(1,18) = 59.81$, $p < .001$], but the main effect of group was not significant. The training quadrant time was longest for the control group, followed by the FF group, and the DS group showed the shortest time. The order of the groups in the nontraining quadrant time was in the reverse order of the training quadrant time, but the interaction between group and quadrant showed only a tendency toward significance [$F(2,18) = 2.76$, $.05 < p < .10$].

Discussion

Test 1 was designed to evaluate the use of the response strategy; it was expected that escape latency would be lengthened and swimming paths would be affected in this test if the rats used the response strategy to find the platform. However, all three groups performed the test well, without changes in their escape latencies or swimming paths. This suggests that the rats, including the FF-lesioned and DS-lesioned animals, used something other than the response strategy as their dominant problem-solving method.

The result from Test 2 is very informative: FF-lesioned rats swam from the new start position toward the new location of the escape platform without hesitation, showing no influence of the situational change. This suggests that the rats in the FF group performed the original task with the use of the cue strategy. In contrast, the rats in the control and DS groups swam to the originally trained location, where they did not find the cued platform. Only after

searching the original location, did they head for the platform in its new location. Therefore, these rats had used the place strategy during training, and, under the test condition, they also tried to solve the problem with the place strategy. Only after they found that the place strategy was ineffective, did they use the cue strategy. This behavior was more pronounced in the DS-lesioned rats than in the control rats. The DS-lesioned rats stayed longer in the originally trained quadrant than did the control rats, suggesting that the DS group persisted in their use of the place strategy. Although the DS lesions in our subjects were focused on the medial DS and spread outward from there, our DS rats showed enhanced place learning. These results do not agree with those reported by Devan and his colleagues (Devan et al., 1999; Devan & White, 1999), who maintained that medial DS lesions result in a deficit in the use of the place strategy.

In Test 3, the use of the cue strategy was unavailable. The control group swam directly to the invisible escape platform. This evidence of the use of the place strategy by the control group is consistent with their performance in Test 2. The escape latency for the DS group was the same as that for the control group in Test 3. This suggests that the DS lesion does not cause a deficit in the use of the place strategy, which again confirms the result of Test 2. The FF group, however, spent significantly more time in the nontraining quadrants, and their escape latency was longer compared with those found in the control and DS groups. However, the swimming paths of the FF rats show that they did not make random searches; instead, they swam in concentric circles. This circular swimming is different from what Devan et al. (1996) reported, since they interpreted the swimming of their hippocampus-lesioned rats as an expression of thigmotaxis. Instead, our FF-lesioned animals swam in circles out from the wall of the pool. This is con-

Figure 7. Representative swimming path for each group in the first trial of Probe Tests 2, 3, and 4. Small dark circle shows the location of the escape platform at the time of each test. The paths for Test 2 are for the rats whose training platform position had been in the SW quadrant, and the platform was moved to the NE quadrant. In Tests 3 and 4, the test platform position was the same as in the training position. Therefore, the paths for Tests 3 and 4 are for the rats whose training position had been in the NE quadrant. Escape latencies (in seconds) and swimming distance (cm) are shown in each path figure. CONT = control; FF = fimbria fornix; DS = dorsal striatum.

sistent with our previous reports (Okaichi, 1987; Sakamoto & Okaichi, 1998) of FF-lesioned rats' using the next-to-the-best strategy for solving the task when they cannot use the best strategy. The results from Tests 2 and 3 together confirm the results of many previous reports that FF lesions impair the use of the place strategy but not the use of the cue strategy (Okaichi, 1987, 1996; O'Keefe, Nadel, Keightley, & Kill, 1975).

In Test 4, the pool was surrounded by a curtain, and the cue strategy was the best strategy for solving the task. All groups showed longer escape latencies and spent more time in the nontraining quadrants. In this test, the experimental environment had obviously changed, with the extramaze stimuli made unavailable. This drastic change in the environment may have disturbed the behavior of all of the rats. As has already been seen, the rats in the DS and control groups used the place strategy as their first choice. Therefore, it is understandable that the unavailability of the environmental stimuli resulted in disrupted behavior. However, it does not explain the disrupted behavior of the FF-lesioned rats, who did not use

the place strategy. In Test 2, they successfully solved the task with the cue strategy, but in Test 4, in which the cue strategy is the best strategy, they were as disrupted as the other rats. This suggests that the FF-lesioned rats might have paid attention to the environmental stimuli, but that they were unable to use the spatial relationship of environmental stimuli to find a goal position. In Test 4, the DS group showed the longest escape latency and the longest time spent in the nontraining quadrants. This suggests that they were more sensitive to the environmental changes than were the control and FF groups, and as a result, the observed change in behavior in the DS rats resulting from the unavailability of the place strategy was the most prominent. Furthermore, the DS group's poorest performance in Tests 2 and 4, in which only the cue strategy was effective, may suggest an impairment in their use of the cue strategy.

In summary, Experiment 2 clearly reveals differential effects of DS and FF lesions. FF lesions lead to impaired use of the place strategy, and DS lesions cause a deficit in the use of the cue strategy but not in the place and re-

sponse strategy. As pointed out in the introduction, many previous studies using water maze tasks in order to investigate the function of DS have involved operating on the animals first, and then training them (e.g., these studies involved the use of an acquisition paradigm). In the research reported here, the rats were trained on the water maze task first, and after learning had occurred, they underwent surgery and subsequently were retrained and tested (e.g., a retention paradigm was employed). It is interesting that our retention paradigm experiment had the same results as these studies using the acquisition paradigm (Packard et al., 1989; Packard & McGaugh, 1992; Reading et al., 1991).

Last, we would like to discuss the usefulness of the shallow pool. In our shallow pool, the rats did not show wild, disrupted behavior in the test situations when they could not find the escape platform in the location where it had been. The control and DS-lesioned rats made small circles at that location, and while doing so, they noticed the new location of the platform. The FF-lesioned rats switched to the concentric circular swimming that is characteristic for them. This is evidence that the use of the shallow pool can avoid unnecessary disturbance in animals' behavior and possibly allows for a better evaluation of cognitive behavior. The shallow pool should be particularly useful in evaluating the learning ability and memory of aged rats. The water maze is a task that requires swimming in the attempt to escape from water and no doubt results in considerable stress. Usually, aged rats take a longer time to find the escape platform; they are therefore forced to swim longer than are younger rats and thus they experience more stress. In the shallow pool, they do not have to swim, so they should experience less stress. In this regard, the shallow pool should prove to be a good tool for measuring the psychological and physiological function of aged rats. An added advantage is that the shallow pool requires a third to a quarter of the water necessary for the standard deep pool. This serves to reduce the trouble of maintaining the quality and temperature of water.

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