Performance of *Betta splendens* in a radial arm maze

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Siamese fighting fish (*Betta splendens*) were tested in aquatic versions of radial arm mazes. In the first experiment, the fish were trained to find tubifex worms in an eight-arm maze in which the optimal strategy was to choose each arm once without repetition. After initial training, the fish entered approximately 6.63 different arms in eight choices, showing a strong tendency to choose sequences of adjacent arms, moving about the maze in a stereotypic direction. This algorithmic response pattern was not, however, sufficient to predict the high performance level of the fish. In the second experiment, a delay of .5 or 5 min was interposed between the fourth and fifth choices. Similar stereotypic patterns continued in Experiment 2, but choice accuracy following the longer delay declined to a level not significantly above chance. In the third experiment, different fish were tested in a three-arm maze, reinforced either for returning from the second arm to the arm in which they had most recently been fed (win-stay) or for visiting a third arm (win-shift). The fish were significantly faster at acquiring the win-shift contingency than the win-stay contingency. These results demonstrate that solution of spatial tasks depends on the interaction of appropriate behavioral strategies and cognitive capacities that may have little generality across species.

The importance of a memory for places (spatial memory) to an animal's survival has often been noted. For example, nectar feeding birds such as the amakihi (*Loxops virens*) studied by Kamil (1978) appear to use spatial memory to improve their foraging efficiency. Within their own territory, they were less likely than would be expected by chance to return to flower clusters on which they had previously fed. Amakihi intruding on the territory under observation, however, neither affected nor were affected by the distribution of flowers on which the resident birds fed, thereby ruling out any role for cues produced by the presence of nectar or by the visitation of an amakihi. Other means for avoiding repeat visits, such as stereotypical search patterns, were also not detected.

Similar memory abilities have also been found in rats performing in a radial arm maze in which each of the arms extends from a common central platform like spokes from a wheel. Typically, a single piece of food is placed at the end of each arm at the start of a trial and the animal is allowed to enter a number of arms. Once an arm is visited, no more food is available there, so the optimal strategy is to enter each arm exactly once before repeating any choices.

When trained on a four-arm maze, rats perform

perfectly after about 10 training trials (Olton, 1978). In a maze with 17 arms, rats reach an asymptotic level of choosing about 15 arms in the first 17 choices after about 50 tests (Olton, Collison, & Werz, 1977). Like the amakihi, rats' performance on radial arm mazes appears to be memory based. In one experiment, for example, the arms of the maze were rotated to new spatial locations and rebaited after the third choice. The rats continued to enter arms in previously unvisited *spatial locations* even if those arms (in their former locations) had been previously depleted (Olton & Samuelson, 1976), thus indicating that external cues emanating from the food itself (e.g., odor) or from the passage of a rat (scent markers left on the maze) played a negligible role in controlling performance (see also Olton & Collison, 1979).

Also similar to the amakihi, rats' performance is not usually dependent on consistent response patterns. Although there was enough regularity in response patterns to reject the hypothesis that the rats were choosing randomly among the arms without replacement (Olton, 1978), the regularities were not sufficient to account for the high accuracy obtained. Furthermore, when rats were confined to the central platform of a 17-arm maze for 20 sec following each choice, performance remained high while the regularity virtually disappeared (Olton, Collison, & Werz, 1977). Finally, performance remained high when the first four choices were forced to arms chosen by the experimenter, leaving the last four as free choices (Roberts & Dale, 1981). These data and others suggest that rat radial-arm-maze performance is

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based on internal representations of spatial information (Roitblat, in press a).

Similar memory capacities have also been reported in a fish—the jumping goby (*Bathygobius soporator*) by Aaronson (1951). These fish swim over a tidal area during high tide and apparently learn the topography of the substrate. At low tide levels, they jump from one tide pool to another even though unable to see neighboring pools. They rarely, if ever, jump onto dry land, passing through as many as six or seven pools while jumping over ledges and rocks on their way to the open sea.

In the present study, Siamese fighting fish (*Betta splendens*) were tested for their ability to perform a spatial task based on the radial arm maze. The individuals typically maintained by aquarists were originally derived from wild stock living in Southeast Asia in various habitats, including slow-moving streams and other aquatic environments in which their favorite food, mosquito larvae, can be found (Smith, 1958).

EXPERIMENT 1

Method

Subjects. Six experimentally naive *Betta splendens*, three males and three females, approximately 6 months of age at the start of the experiment, served as subjects. They were maintained in male-female pairs in separate compartments of a standard 30-gal tank. The floor of the tank was covered with 5-8 cm of aquarium gravel. Water was constantly filtered and maintained between 21° and 28°C at pH 7. Approximately one-third of the water in the tank was changed every other week. During a pretest, the fish were given access to a large number of tubifex worms, of which they consumed 20-25 within an approximately 10-min period.

Apparatus. An eight-arm maze was constructed of .3-cm white Plexiglas. Each arm was 5 cm wide, 23 cm long, and 15 cm high, equally spaced around a central platform 14.5 cm in diameter. The end of each arm opposite to the central platform was closed by fine nylon mesh. A plastic feeding cup (5.08 cm in diameter and .64 cm high) was attached to the floor of each arm 1.25 cm from the distal end and equidistant from the sides. The maze was submerged in a large Plexiglas tank filled to a depth of 10 cm. A motorized filter forced water through a diffused opening in the center of the central platform, creating a flow of water outward from the center toward the arms. The entire apparatus was illuminated by overhead incandescent and fluorescent lamps. Maze temperature was maintained at about the same level as in the home tank. The water was changed approximately every other week.

Procedure. The fish were transferred to the maze in a small net and confined to the central area for approximately 2 min in a white cylinder, 11 cm in diameter and 15 cm high, while a single live tubifex worm was placed in the feeding cup at the end of each arm. The cylinder was then raised and the fish were allowed to make eight choices (arm entries). A choice was counted when the base of the fish's tail passed the entrance to the arm. Each fish was tested twice daily, with a minimum of 15 min intervening between trials, for a total of 55 trials.

Results

After the first few trials, all fish were entering the arms and readily consuming the bait. During the first five trials, the fish chose an average of 5.70 arms in the first eight choices. The accuracy of performance

Figure 1. Performance of *Betta splendens* in an eight-arm radial maze during acquisition, Experiment 1. Choice accuracy refers to the number of different arms entered in the first choices. Chance is the value that would be expected if the fish were sampling randomly with replacement from among the arms (5.23).

is displayed in Figure 1. Chance is the level predicted on the basis of random sampling with replacement (Olton, 1978).

The fish showed a strong tendency to choose sequences of adjacent arms, moving about the maze in a single direction, clockwise for some fish and counterclockwise for the others. This tendency is illustrated in Figure 2 in the form of the percentage of choices at each displacement. The arm entered on any particular choice was designated arm 0. The adjacent arm in the clockwise direction was called displacement +1, the second arm +2, etc. Similarly, the adjacent arm in the counterclockwise direction was designated displacement -1, etc. Displacement 4 in either direction was the arm directly opposite to the chosen arm.

Figure 2. Proportion of arms chosen at each distance and direction from the current arm. Data for each curve are averages of all fish during the last 20 sessions of Experiment 1 and the two phases of Experiment 2. Arms in the positive direction were removed from the current arm in the clockwise direction. Negative displacements are in the counterclockwise direction.

Figure 3. Average number of different arms entered by fish during the first eight choices of the last 20 trials of Experiment 1 and the number expected from a simulation based on the assumption that the fish were using only transition probabilities and no memory to determine their radial maze performance.

A new arm 0 was designated on each choice, so the figure displays choices relative to the immediately previous choice rather than in terms of absolute physical locations.

Clockwise turns accounted for 78% of all choices made. Choices of displacements +1 and -1 accounted for 63.6% and 17.1% of the choices, respectively. To evaluate the effect of turning bias on the obtained choice accuracy, we performed a Monte Carlo simulation. Choice distributions analogous to Figure 2 were computed separately for each fish during the last 20 trials of the experiment. These choice probabilities were then used to determine the next choice in the simulated sequence without any contribution from previous choices. That is, we assumed in the simulation that the fish used no memory of any pre-

vious choices in making its next choice. Figure 3 shows that the observed performance of the real fish was always superior to that obtained from the simulated no-memory fish [paired comparison $t(5) = 12.14$, $p < .01$]. The average choice accuracy of the simulated fish was 5.82, not significantly above the chance accuracy of 5.23 [$t(5) = 1.57$, $p > .05$].

The probability of repeating a previously chosen arm (making an error) as a function of the ordinal position of that choice was also determined for the live fish. After considering the differing number of opportunities available, errors were no more likely to arms visited early in the trial than to arms visited later in the trial. See Table 1.

Discussion

The performance of the fish in this experiment showed a strong algorithmic component that played a role in determining the direction and the displacement of the sequential choices. This algorithmic component was not sufficient, however, to account for all of the behavior observed. Simulations based only on the algorithmic component did not differ from an expectation based on random choice with replacement. Real fish, however, differed not only from this expectation, but also from the performance of the simulated fish. Because the simulation was based on the performance of individual fish, the difference between simulated and live fish could not have been due to averaging several fish together and so distorting the algorithm for any one fish. The simulation did combine data from the same fish obtained on 20 sessions. If the fish were using one algorithm during one session and another algorithm on a second session, both consistent within a day, but different across days, then the model would predict lower performance than would be obtained. No solution is available for this difficulty using these techniques, however.

The difference between the simulated and the real fish suggests that some small amount of memory was involved in determining the real fish's choice. The most obvious kind of memory that might be used would be a list (e.g., a pushdown stack) in which each arm is placed on the list as it is entered. Partial memory would correspond to maintenance of only the most recent part of the list. Arms on the list would be avoided, and arms not on the list might be entered. No difference was found in the likelihood to reenter an arm as a function of serial position, meaning either that the list was very short or that performance was controlled not by a memory for the arms already visited, but by a memory for the arms remaining with food (see Roitlat, in press a). Alternatively, this pattern of choices may represent strategic choices rather than memory limitations. That is, even though the fish could remember more information, their pre-

Table 1
Conditional Choice Frequencies in Experiment 1

Error on Choice	Frequency of Revisit to Arm Most Recently Visited on Choice							Sum
	1	2	3	4	5	6	7	
2	0							0
3	13	0						13
4	1	11	0					12
5	7	7	13	0				27
6	5	8	5	15	0			33
7	7	5	6	3	10	0		31
8	12	10	1	4	5	11	0	43
Sum	45	41	25	22	15	11	0	
N	7	6	5	4	3	2	1	
Sum/N	6.8	6.8	5	5.5	5	5.5	0	

Note—N = number of opportunities to revisit that position. The row corresponds to the choice on which the error occurred; the column corresponds to the choice on which that arm was last entered.

ferred pattern of movement in the maze "overshadowed" their use of memory and resulted in the pattern observed.

These results are similar to those obtained with pigeons (Bond, Cook, & Lamb, 1981) in a radial arm maze. Pigeons entered an average of 6.28 different arms in their first eight choices, a value significantly above that expected by chance and by a simulation similar to ours based on turn bias. The best predictor of pigeons' performance was based on the assumption that the birds were remembering a maximum of approximately 3.2 of their most recent choices.

EXPERIMENT 2

Brief confinement following each choice (Olton, Collison, & Werz, 1977) or a single, longer confinement between choices 4 and 5 (Maki, Brokofsky, & Berg, 1979) both disrupt the regularities of the rat's response pattern, but fail to disrupt choice accuracy. In contrast, the fish in Experiment 1 showed stronger algorithmic patterns than did the rats. Accurate algorithm-based performance depends on an unbroken chain of responses; any interruption of the algorithm would reset it. If the animal "loses its place," it cannot resume the algorithm from the most recent choice because it does not "remember" its previous choice. The effectiveness of disruption should be great if performance depends only on an algorithmic strategy and less, and time dependent, if performance has a memory component. Experiment 2 was conducted to assess the effects of delay on radial arm maze performance.

Method

Subjects and Apparatus. The subjects and the apparatus were the same as in the first experiment. One fish died before completing Phase 2 of the experiment.

Procedure. Experiment 2 was conducted in two phases, each involving a delay interpolated between the fourth and fifth choices. During the delay, the fish were confined to the central platform inside the "holding" cylinder. During the 20 trials of Phase 1, the fish were confined for 30 sec following the fourth choice. During the 20 trials of Phase 2, the duration of the confinement was increased to 5 min. In all other respects, the procedure was the same as that used in the first experiment. The arms were not rebaited after the start of a trial.

Results and Discussion

Confinement clearly interfered with accurate performance. Overall choice accuracy (number of different arms entered during the first eight choices) declined with increasing delay [a repeated-measures ANOVA with days nested in delay condition yielded $F(2,8) = 4.50$, $p < .05$, for delay]. An average of 6.63 different arms were entered on each of the last 20 trials of Experiment 1, 6.02 during Phase 1 and 5.63 during Phase 2 of Experiment 2 (both pre- and post-confinement choices are included). Choice accuracy on trials including the 30-sec confinement was sig-

Figure 4. The number of novel arms entered on the first (left panel) and on the last (right panel) four choices of each trial in Experiments 1 (last 20 trials) and 2. Novel arms refer to those not previously entered in that trial (i.e., including both those entered in the first and on the last four choices).

nificantly above chance [$t(5) = 7.60$, $p < .001$], but accuracy on trials involving a 5-min delay was not [$t(4) = 2.00$, $p > .05$].

Performance during the first four choices was next analyzed separately from the performance for the last four choices (postconfinement in Experiment 2). The effect of the delay was mainly to interfere with the maintenance of the algorithm during the delay. Choice accuracy, of the first four choices, displayed in the left panel of Figure 4, was not significantly different in either delay condition from that observed in Experiment 1 (both t values less than 1). These results were not surprising, since the first four choices were made under similar conditions for the three phases. Performance on the last four choices, seen in the right panel of Figure 4, did drop significantly relative to that obtained with no delay [Phase 1, $t(5) = 3.17$, $p < .05$; Phase 2, $t(4) = 3.83$, $p < .05$]. Recall that reentries to arms visited before the delay are also counted as errors.

During the confinement period, the fish were active, moving about the holding cylinder. The proportion of times each arm, at each displacement, was entered on the fifth choice is displayed in Figure 5, relative to the arm chosen on the fourth choice. The obtained distributions differed from a uniform distribution in which each arm is chosen with equal frequency when no delay ($\chi^2 = 211.958$, $p < .005$) or a .5-min delay ($\chi^2 = 22.667$, $p < .005$) occurred, but not when a 5-min delay ($\chi^2 = 7.594$, $p > .05$) intervened between the fourth and fifth choices. These distributions indicate that the fish were maintaining information about their fourth choices for some time during the delay. We do not know, however, how that information was represented (e.g., memory, postural attitude, etc.; see Roitblat, in press a).

Figure 5. The distribution of locations of fifth choices relative to the arm chosen on the fourth choice. Displayed are the data from the last 20 trials of Experiment 1 and from the two phases of Experiment 2. The format is analogous to that of Figure 2.

Whatever role memory played in controlling performance in the first experiment, it was effectively removed by the longer confinement condition. As Figure 2 shows, the fish continued to choose adjacent arms during Experiment 2, but during the confinement the fish were apparently increasingly likely to "lose their place," and so to choose randomly (compare the distributions of fifth choices as a function of confinement duration, Figure 5). These results confirm the important role played by a combination of memory and algorithmic response strategies in the control of fish spatial performance. The issue of strategic control was further pursued in Experiment 3.

EXPERIMENT 3

Rat and fish spatial memory performance is controlled by a combination of memory ability and compatible response strategy. In the radial arm maze, animals are reinforced for adopting a win-shift strategy; once food has been obtained in a particular location, no more is available there, so the best strategy is to search elsewhere. Rats seem to prefer discrimination problems that are compatible with this strategy to situations involving a win-stay contingency. In win-stay situations, reinforcers are delivered in consistent locations, so once food is found in a particular location, it pays to return there.

A number of examples of rats' preference for win-shift situations are available, including spontaneous alternation in a T-maze (Dember & Fowler, 1958) and avoidance of locations already visited in a complex maze constructed of three concentric hexagonal alleys interconnected by shorter alleys (Battig, Driscoll,

Schlatter, & Ulster, 1976; Uster, Battig, & Nageli, 1976) and in the "towers of Baltimore" problem (Olton, Walker, Gage, & Johnson, 1977), in which rats were tested in a large enclosure containing three towers. On any given day, one of the towers, chosen randomly, had a number of food pellets placed on top of it; the other towers were empty. The rat could not tell, without climbing a tower whether that tower had food on that day. Instead of following the optimal strategy of searching the towers until food was discovered and then removing the food from that tower, the rats visited each tower each day, even after they had taken some of the food from the single tower that had any. In fact, the probability of revisiting the tower with food remained at chance level until the other two towers had been visited. Thus, in this situation, the rats were employing a win-shift as well as a lose-shift strategy.

Rats also learn a discrimination task more easily when the task requires a win-shift as opposed to a win-stay strategy. Rats have been tested (Olton, in press; Olton, Handelmann, & Walker, 1981) in a variation of the three-table problem introduced by Maier (1932). At the beginning of each trial, the rats were fed a small amount of food on one of three interconnected tables. A different table was chosen each day in random order. After a delay, spent in its home cage, the animal was placed on one of the other two tables and allowed to choose between the original table on which it had been fed and the third table. The rats that were reinforced for choosing the third table (whose location also varied from day to day) learned to perform this task much more quickly and accurately than did the rats reinforced for returning to the table on which they had originally been fed (Olton, in press).

Although the fish in Experiments 1 and 2 relied heavily on algorithmic strategies, and only lightly on memory, to perform the task, it is possible that if we had asked the question differently, the fish would have shown the same magnitude of memory seen in rats. For example, rats required to return to the same arms of an eight-arm maze from which they had recently obtained food perform very poorly (Olton, in press), while rats required to visit different arms perform very well. If the rats' ability to remember the arms depleted of food in one context were not known, it might be possible to mistake the poor performance in the other for a lack of memory. For this reason, we ran another group of *Betta splendens* on an aquatic version of the three-table problem. If the strategic preferences present in fish are different from those in rats, then we would expect to see faster acquisition of a win-stay than of a win-shift discrimination. On the other hand, the fish could be indifferent to the strategic aspects of the task, perhaps because these strategic aspects evolve only in conjunction with a well-developed spatial memory capacity.

Method

Subjects. The subjects were 12 experimentally naive female Siamese fighting fish, otherwise similar to those serving in the first two experiments, maintained under the same conditions.

Apparatus. An aquatic version of the three-table apparatus was constructed of white Plexiglas. Three arms were arranged in a Y shape around a triangular central compartment, 7.6 cm per side. Each arm was 23 cm long, 15 cm high, and 7.6 cm wide. The distal end of each arm was terminated by nylon mesh. A food cup, 2.54 cm in diameter and .6 cm high, was fastened 1.25 cm from the rear of each arm. Guillotine doors were placed at the entrance and 10 cm from the rear of each arm, dividing the arm into a "food" and a "holding" compartment. In order to ensure that the fish were able to discriminate the three arms, colored plastic forms were attached to the floor of each arm. One arm had red circles (5 cm diam), one arm had black squares (4 × 4 cm), and the third had yellow triangles (3 cm per side). Each arm had five forms equally spaced. The apparatus was submerged in the same tank and aerated and illuminated as in the first two experiments.

Procedure. At the start of each trial, each arm was randomly designated "placement," "start," or "goal." The fish were confined (by means of the guillotine door at the arm's entrance) in the placement arm and allowed to consume a single tubifex worm with which the arm had been prebaited. The fish were then transferred by net to the start arm and confined in the holding compartment. Confinement in the start arm was sufficient to allow (re)baiting of one of the other two arms and never longer than 5 sec. Following this confinement period, the fish were released and allowed to choose one of the two available arms: the placement arm or the goal arm.

The fish were divided into two experimental squads of six fish each. Squad 1 was exposed to a win-stay contingency in which the placement arm was rebaited during the confinement in the start arm and the animals were reinforced for returning to that arm. Squad 2 was exposed to a win-shift contingency in which the goal arm was baited during confinement in the start arm and the fish were reinforced for visiting the novel arm. Animals in each squad were tested on the designated contingency until reaching a criterion of 8 choices of the baited arm in 10 trials or for a maximum of 70 trials. On reaching criterion, each fish was transferred to the opposite task (i.e., from win-shift to win-stay, or vice versa).

Results

Two of the fish died during the course of the experiment, one from Squad A and one from Squad B. The data from the remaining fish are displayed in Table 2. The first column of the table shows the total

number of trials each animal received under the win-shift contingency; the second column shows the total number of trials each animal received under the win-stay contingency. Fewer trials were necessary to reach criterion in the win-shift condition than in the win-stay condition (Mann-Whitney $U = 4.75$, $p < .01$). Under the shift contingency, 9 of 11 animals (82%) reached criterion, while under the stay contingency, only 4 of 10 animals reached criterion.

Discussion

Similar to rats, *Betta splendens* also appear to prefer win-shift over win-stay strategies, learning the former more readily. Similar win-shift preferences have also been seen in several other species, including Hawaiian honeycreepers (Kamil, 1978) and bumblebees (*Bombus sonorus*) foraging for nectar from *Chilopsis linearis* flowers (Witham, 1977).

On the other hand, at least two species of birds foraging for earthworms and other small terrestrial invertebrates have exhibited win-stay strategies in unconstrained (at least by the experimenter) situations. Smith (1974a, 1974b) has described the pattern employed by English thrushes searching in a meadow. On finding prey, the birds increased their rate of turning and decreased their rate of forward motion, staying in the vicinity of the discovered prey. Similar performance has been obtained from ovenbirds (*Seiurus aurocapillus*) when searching for mealworms hidden in a large enclosure on a forest floor (Zach & Falls, 1976). Although the situations in these studies are not precisely comparable to the three-table problem, they suggest that employment of a win-shift strategy is unlikely to be an inherent property of searching for food.

GENERAL DISCUSSION

Numerous approaches are available to explain the differences in performance and capacities observed across species. Some of these approaches favor some sort of phylogenetic scale, perhaps based on neural complexity or phylogenetic ancestry (e.g., Bitterman, 1965). More recent approaches (e.g., Roitblat, in press b) emphasize the evolution of cognitive capacities in the context of the animal's ecology. According to this latter view, each species' cognitive capacities evolve as adaptive specializations relative to the species' ecological niche. One of the questions inherent in the adoption of this view of cognitive capacities concerns the capacities and strategies that co-occur either because each is necessary for the other to be of benefit (e.g., because one is a precursor or component of the other) or because they are both a product of the same mechanism. It is clear from the present series of experiments that a high level of performance in a radial arm maze does not depend on the presence of a high-capacity memory system, but

Table 2
Number of Trials to Reach Criterion in the Three-Arm Task

Fish	Win-Shift	Win-Stay
A1	12	70
A2	70	70
A3	59	
A4	46	70
A5	45	15
A6	10	70
B1		47
B2	57	70
B3	38	12
B4	17	70
B5		
B6	13	70

Note—Fish in Group A were tested first in the shift condition and next in the stay condition. Fish in Group B were tested first in the stay condition and then in the shift condition. A blank indicates that the fish died before completing that condition.

rather that performance depends on the interaction of strategic preferences and memory. That these fish demonstrate little use of working memory, but compensate through the use of strong algorithmic patterning suggests that memory and strategic preferences are complementary and are not necessary concomitants of one another.

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