Spatial Learning and Memory in the Tortoise (*Geochelone carbonaria*)

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Abstract

A single individual of the species *Geochelone carbonaria* was trained in an eight-arm radial maze, with the apparatus and general procedures modelled on those used to demonstrate spatial learning in rats. The tortoise learned to perform reliably above chance, preferentially choosing baited arms, rather than returning to arms previously visited on a trial. Test sessions that examined control by olfactory cues revealed that these did not affect performance. No systematic, stereotyped response patterns were evident. In spite of differences in brain structure, the tortoise showed spatial learning abilities comparable to those observed in mammals.

Key words: tortoise, *Geochelone carbonaria,* spatial learning, radial maze

Spatial Learning and Memory in the Tortoise (*Geochelone carbonaria*)

Nonavian reptiles, birds, and mammals all evolved from a common amniotic ancestor and it is therefore possible that these classes share common behavioral traits and capabilities. Equally, since the putative common ancestor lived as long as 280 million years ago, there is ample time for evolutionary paths to have diverged and for quite different capacities and mechanisms to have evolved in the different classes. Certainly, brain structures appear to differ in important respects – for example the forebrain of the reptile, with its thin cortical layer is very different from the multilayered structure seen in mammals.

The study of spatial learning in chelonia (turtles, terrapins, and tortoises) has a long history (for a review see Burghardt, 1977). It started early with Yerkes (1901), who demonstrated that the speckled turtle (*Clemmys guttata*) could learn a multiunit maze “with surprising quickness” (quoted by Macphail, 1982), a result confirmed for the common wood turtle (*Clemmys insculpta*) by Tinklepaugh (1932). Acquisition and reversal of a T-maze task by the terrapin *Chrysemys picta picta* was demonstrated by Kirk and Bitterman (1963), and the ability of this species to show serial reversal improvement in a (slightly different) spatial task was confirmed by Holmes and Bitterman (1966). What these various studies do not reveal is whether chelonians are capable of forms of spatial learning shown by mammals. In mammals, some forms of spatial learning are thought to be dependent on the hippocampus (a structure that reptiles lack). It is possible, then, that the chelonians learned the mazes using a system (e.g., by learning to make a

given turn or sequence of turns) different from some more advanced, hippocampally dependent, navigational system used by mammals.

This issue has been addressed directly in a series of experiments by López and his colleagues. López et al. (2000), working with the terrapin *Pseudemys scripta*, showed that this species could learn, in a T-maze, to approach a given location in space regardless of which of the other two arms they started from. The animals maintained this performance even when the entire maze was rotated, so that the starting point was some quite novel location. The ability appeared to depend on navigation by means of extramaze (room) cues, in that it was disrupted by the introduction of shielding curtains around the maze. López et al. suggested that the turtles were using a "cognitive map" of the sort postulated for mammals. They went on to show that lesions of a forebrain area, the medial cortex, taken on anatomical grounds to be a parallel of the mammalian hippocampus, disrupted performance on these tasks (López, Vargas, Gomez, & Salas, 2003).

The results just described encourage the view that chelonians (with an intact medial cortex) should be capable of coping successfully with other tasks that have been used to demonstrate the spatial learning abilities of mammals. To this end we have studied the performance of a red-footed tortoise (*Geochelone carbonaria*) in an eight-arm radial maze (Figure 1).

This species is a land-dwelling chelonian, unlike the semi-aquatic terrapins that were tested in the experiments just described. Previous work with the desert tortoise (*Gopherus agassizii*) by Fink (1954, cited by Burghardt 1977) has shown that the performance of this species on a spatial reversal task is comparable to that of terrapins. However, its behavioural ecology is

different from that of the red-footed tortoise; the latter species eats fallen fruit, and flowers whereas the desert tortoise is largely a grass grazer. It is possible that the differences in their foraging strategy may have more influence on their performance than evolutionary proximity. The red-footed tortoise is a relatively active species, and is capable of travelling up to 85 meters an hour (Moskovits, 1985, cited by Strong & Fragoso 1987). This liveliness, in addition to their foraging behavior makes this species an ideal subject for our study.

The radial arm maze was pioneered for use with rats by Olton and Samuelson (1976) and consists of a central area from which eight arms radiate. Food is available at the end of each arm. A well trained rat will visit each arm to collect the food, and rarely return to arms that it has previously visited, exhibiting an ability to discriminate among the various spatial locations, and remember which places have been visited on a given trial. The procedure provides an excellent test of an animal's spatial learning capacities and its working memory. It can readily be adapted for use with many species and provides a useful tool for making direct comparisons across species.

In the present experiment we examined the performance of a tortoise in the radial maze asking, first, whether this animal could achieve efficient performance. To anticipate, we found that he could. We then went on to investigate the nature of the mechanisms responsible for its performance by carrying out a series of tests designed to exclude the contribution of non-spatial factors. We hoped to reveal the extent to which the tortoise's behavior is comparable to that of a mammal.

Method

Subject

The subject (named Moses) was a male captive-bred red-footed tortoise (*Geochelone carbonaria*). He was approximately 2 years old and his plastron (the base of his shell) measured 7.5 x 6 cm at the start of the experiment. He was experimentally naïve. During the study Moses lived in a tank in an office adjacent to the experimental room. The office was kept on a daily 12L:12D cycle (light on: 0800-2000). The tank measured 61 x 30 x 30 cm and was maintained at 29^{o}C (+/- 4^{o}C); humidity within the tank was maintained at 50%. The tortoise was given access to food (fruit and vegetables) for 60 min each day, approximately 30 min after that day's experimental procedures had been completed.

Apparatus

The apparatus was an eight-arm radial maze made of opaque black Perspex (see Figure 1). Each arm was 10 cm wide, 20 cm long, and the sides and one end had walls 7 cm high. The arms radiated from a hexagonal central platform, 24 cm across. Removable guillotine doors could be placed at the junction between the arm and central platform. During the training and testing phases a white plastic food cup, 3 cm in diameter and 1.5 cm high was placed in a central position at the end of each arm. The maze was positioned on a table in a small experimental room, that was lit by two 60-W ceiling lights and maintained at approximately 27-29°C. External cues that were, in principle, visible from within the maze, included shelving on which laboratory equipment was stored (adjacent to arm 7 of the maze disposition shown on the left of Figure 1), and a poster on the opposite wall (above arm 3). The wall adjacent

to arm 1 contained a door, to the left of which (adjacent to arm 8), the experimenter sat. The experimenter remained in the room for the entire session. Two experimenters were involved in conducting experimental sessions. Experimenter 1 observed the tortoise from the beginning of the experiment up until midway through the training phase "Assessing the influence of odor trails" (see below). The second experimenter completed the experiment.

Procedure

The experiment took approximately 5 months and was conducted from 25th January 2006 - 17th June 2006. Procedures took place in the afternoon, as this was the time when Moses was most active. He was removed from his tank and handled for approximately 5 min prior to experimentation. During this time he was allowed to walk around the office space or the experimenter's lap. This served to increase his activity level. He was then placed in a holding cage and taken to the experimental room. On each day he received several trials (detailed below), each separated from the next by an intertrial interval (ITI), usually of 5 min, spent in the holding cage. The maze was wiped clean at the end of each day but not between trials.

Familiarization to the maze. Extensive pretraining was needed in order to ensure that the tortoise would locomote around, and eat readily in, the maze. The procedures, which involved trial-and-error learning, as much on the part of the experimenters as on the part of the tortoise, are detailed in Table 1. By the end of this phase of pretraining the subject would, on most occasions, visit all 8 arms within a 30-min trial, to obtain the reward (a small piece of strawberry) that was visible at the end of each arm.

Basic radial arm maze training. There were 12 daily sessions in the first phase of training, each consisting of 4 trials. At the start of each trial Moses was placed on the central platform, facing an arm selected at random. Each arm of the maze contained a food cup baited with a piece of strawberry. Choice of an arm was recorded whenever half of Moses had advanced into an arm, so that half his shell was within the arm. This measure was used as Moses rarely backed out of the maze once he had entered this far and we felt that this measure was suitably conservative as to ensure all errors were included in analysis. The trial ended when all eight rewards had been consumed, or after 30 min. A record was kept of which arms were entered and in what order.

Assessing the influence of food odor. This 2-day phase introduced test trials designed to assess whether or not Moses was using odor cues from food in the food cups to guide his behavior. Sessions were organised as before, except that on trials 2 and 4, only four of the arms were baited. On trial 2 of the first test day and trial 4 of the second, these were arms 1, 3, 5, and 7; on trial 4 of the first test day and trial 2 of the second they were arms 2, 4, 6, and 8. If performance is guided by odor cues, we might expect Moses to show a preference for the baited arms on these test trials.

Assessing the influence of odor trails: Training. During this phase, which lasted 9 days, each trial was divided into two parts. In the first, four arms (equally often the even- or odd-numbered arms) were blocked by the guillotine doors, and Moses was allowed to take food from the food cups of all four of the available arms. (A maximum of 30 min was allowed for this part of the trial.) He was then removed from the maze and placed in the holding cage

for 30 s. During this time the doors were removed, and the other four arms were baited. Moses was then replaced in the maze and allowed to enter any arm (although he only received reward when he entered an arm not visited during the first part of the trial). The trial was terminated when all four rewards had been eaten or after 60 min. The procedure of removing the tortoise and then replacing him proved to be somewhat disruptive and on occasion Moses failed to take all rewards in the time allowed. Over the course of the 9 days Moses successfully obtained all the rewards on 17 of the 36 trials.

This procedure was introduced principally to provide a baseline against which the effects of the test procedure, to be described next, could be assessed. But it also allows the possibility of testing the animal's memory – efficient performance in the second part of the test requires that information acquired in the first part should survive the retention interval and the disturbance it involved.

Assessing the influence of odor trails: Test. This test lasted 9 days and consisted of four retraining days interspersed among which were 5 test days. On retraining days the procedure was identical to that described above for the odor trail training phase. Test trials were similar except that, when Moses was removed from the maze having visited the four available arms, the maze was rotated through 45 degrees (clockwise on half the trials, anticlockwise on the rest) with the result that an arm not previously visited was now in the same spatial location as one visited in the first part of the trial (see Figure 1). Food was made available only in arms in spatial locations that had not previously been visited (i.e., in order to perform efficiently Moses needed to return to arms that he had traversed in the first part of the trial). This procedure allows

us to test whether the tortoise had learned a strategy of avoiding arms that he had previously visited, and had perhaps marked by means of some sort of odor. (Such a strategy would result in poor performance in the rotated maze.) This procedure also constitutes a test of the extent to which the animal's behavior is controlled by extra-maze cues. We take up these matters in the final Discussion.

Results

Basic radial arm maze behavior. In spite of the extensive familiarization, the tortoise's movement around the maze was often slow; on 15 of the 48 trials of the first training phase, the time limit was reached and testing was terminated before the animal had made eight choices. Our analysis will be confined to the remaining 33 trials, on each of which at least eight choices were made. According to Olton (1978), the number of correct responses in the first eight choices, to be expected on the basis of chance performance, is 5.3. (A correct response is entering an arm that had not been entered previously; chance performance is computed assuming that every choice is made at random, without replacement). The mean number of correct responses in the first eight choices of the 33 trials available for analysis was 5.88 (*SEM* = 0.16; range 4-8). A one-sample *t* test comparing this score against chance expectation revealed a significant effect, $t(32) = 3.59$, $p < .01$.

To obtain a more detailed picture of Moses' performance we focused our analysis on those trials on which he successfully visited all eight arms. There were 18 such trials; the first occurred on day 2 of training and there was at least one such trial on all succeeding days. Table 2 presents a full list of all the choices made on these 18 trials. For each trial we calculated the

probability that the task would be completed in the number of choices actually made, on the assumption that choices were made at random and with replacement. This probability is given in the far right column of the table. This shows that, although accuracy of performance fluctuated substantially from trial to trial, it was consistently at a level unlikely to be achieved on the basis of chance. Particularly, good performance was as likely to be seen on early trials as on later trials; that is, there was no indication of a gradual acquisition process.

It is possible that Moses adopted stereotyped response patterns (e.g., a pattern of always turning into the next arm on the left would ensure perfect performance). To examine this we scored each of the responses he made after the first choice on each of the trials detailed in Table 3. There were 203 of these. Table 3 breaks these down into choices of arms that were 1, 2, or 3, positions, either clockwise or anticlockwise, from the arm just left, and those that were choices of the arm directly opposite. A strategy of a sort is immediately apparent as on none of the trials did Moses reenter the arm that he had just exited. Random choice among the remaining 7 possible turns would result in 29 choices of each of these possibilities. Table 3 reveals a tendency for choices of arms two positions away from that being exited to be overrepresented, at the expense of choices of arms 3 positions away. A one-sample chi-squared test on the scores presented in the table showed the deviation from chance expectation to be significant, chi-squared = 18.96, df = 6, $p > .01$

Assessing the influence of food odor. This test was designed to assess if Moses' performance was based on odor cues. If it were, we might expect

him to choose preferentially those arms that were baited on the four test trials of this phase on which four of the arms were left unbaited. Performance on these test trials turned out to be very similar to that shown on the four standard trials with which they were intermixed. Scoring a correct response as choice of an arm not previously visited (whether it contained food or not) showed that he made a mean of 6.25 (95% CI = +/-.49) correct responses in the first eight choices on the standard trials, and a mean of 5.75 (95% CI = +/-.49) on the test trials. Critically, correct choices on test trials were as likely to be made by entering unbaited as by entering baited arms; of the total of 23 correct responses under consideration, 10 were to unbaited arms and 13 to baited arms, chi-squared = 0.39, *df* = 1, *p* >.50.

Assessing the influence of odor trails: Training. In this phase of training, the guillotine doors forced Moses to enter four of the arms before a 30-s interval; after this all eight arms were made available. Moses performed rather poorly during the forced-choice trials of this procedure and on several occasions failed to visit the four arms available during the 30 min allowed for the first part of the trial. This seemed to be caused by the introduction of the barriers which he spent a large amount time trying to push, a pattern of behavior that became more pronounced as training proceeded. This behavior is commonly observed in tortoises. If barriers either have visible gaps or move when pushed, tortoises spend a great deal of time trying to get through. These trials were abandoned and were excluded from the analysis. We analyzed the 17 trials in this phase on which Moses succeeded in visiting all eight arms. On these trials the first four baits were collected efficiently (the mean number of choices required was 5.88). When returned to the maze after

the interval he took a mean of 9.59 (range 5–15; see Table 4) choices to collect the remaining four baits. For comparison we looked at the number of trials taken to obtain the final four baits on the 18 trials of phase-1 training on which this was achieved (see above). In this latter case the mean number of trials required was 7.78. These scores differed significantly, $t(33) = 2.07$, $p < .05$.

Evidently performance was rather poor on these trials, but despite performance being disrupted, it did not decline to a level that might be expected on the basis of random choice. Table 4 shows the number of choices required to visit the remaining four arms on each trial of this stage and, for each such trial, the probability that the task would be completed in the number of choices actually made, on the assumption that choices were made at random and with replacement.

Assessing the influence of odor trails: Testing. In this final test the maze was rotated after the retention interval so that arms that had previously been visited were now in spatial locations that had not previously been visited. The score is the number of trials taken, after the retention interval, to visit the four unvisited spatial locations. The scores were 11, 9, 7, and 15 trials, with a mean of 10.50. This is not markedly worse than that (9.59) reported for the second training phase. Had his performance in that phase been based on the avoidance of the odor of a previously visited arm we would have expected a total disruption in performance.

Discussion

Basic radial arm maze behavior. In spite of the extensive familiarization, the tortoise's movement around the maze was often slow.

Accuracy of performance fluctuated substantially from trial to trial; it was, however, consistently at a level unlikely to be achieved on the basis of chance. There was no indication of a gradual acquisition process. This is perhaps not surprising. Although the food was visible during the extensive familiarization phase, the general procedures used in that phase matched those used in the basic radial arm maze training. The results of the familiarization phase revealed a sharp learning curve. It is possible then that, during pretraining, Moses acquired strategies that he could then use in the training phase. This would allow the immediate above-chance performance that we observed, even when the food was hidden from view by the food cups.

The rest of the study was intended to elucidate the nature of the strategies involved in Moses' performance. One possibility was that Moses adopted stereotyped response patterns (e.g., a pattern of always turning into the next arm on the left would ensure perfect performance). As we have noted, our analysis showed that on none of the trials did Moses reenter the arm that he had just exited. The analysis also revealed a tendency for choice of arms two positions away from that being exited; rats show a similar pattern (Olton, Collison, & Wertz, 1977). The factors controlling this behavior in rats were investigated by Yoerg & Kamil (1982), who manipulated the size of the central platform of a radial arm maze. They found that this had no effect on the accuracy of performance, but the use of adjacent arms significantly increased with a larger platform. They suggested that this could be due to the increased cost of choosing a nonadjacent arm. However, it is possible (as they acknowledged) that the sharp angles of adjacent arms in a small maze

make it hard to negotiate and make it easier to choose a non-adjacent arm in such a maze. Both of these hypotheses could account for our tortoise's arm choice behavior. No other simple response patterns were discerned.

Assessing the influence of food odor. If Moses' performance was based on odor cues from the food we might expect him to preferentially choose those arms that were baited on the test trials over those that were left unbaited. Performance on these test trials turned out to be similar to that shown on the four standard trials with which they were intermixed. There is no evidence, therefore, of control by food odor.

Assessing the influence of odor trails: Training. This phase of training was conducted in preparation for testing whether Moses learned to avoid his own odor trails. It also allowed examination of the extent to which information acquired in the first part of the trial survived the interval (and the disruption consequent on removal from and return to the maze). Performance on this part of the task was compared with that of the last four arms of the basic radial arm maze training. There was some disruption following the retention interval, however it did not decline to a level that might be expected on the basis of random choice. This suggests that performance in the second part of the trial was controlled, to some extent, by memory of the first part of the trial.

Assessing the influence of odor trails: Testing. In this final test the maze was rotated after the retention interval so that arms that had previously been visited were now in spatial locations that had not previously been visited. Moses' performance was not markedly worse than that reported for the training phase. Had his performance in this phase been based on the avoidance of the odor of a previously visited arm, rotation of the maze (which

required the animal to return to a location previously visited) would have produced a total disruption. We tentatively conclude, therefore, that his performance is based, at least in part, on information about the spatial location of the maze arms.

Conclusions. The study of a single individual cannot tell us what is generally true of some larger grouping (such as reptiles, or chelonians, or members of the species *Geochelone carbonaria*). It does, however, set some limits on assertions about what that group is or is not capable of. Our study allows the conclusion that a tortoise is capable of showing fairly efficient performance in a radial maze. Its performance is less efficient than that of rats (see Olton & Samuelson, 1976) (for whatever reason – this may reflect an inadequacy in our procedure rather than a lack of capacity in the animal), but it is, none the less, above the level to be expected on the basis of chance. As is true for rats, the performance of the tortoise does not appear to depend on the acquisition of stereotyped response strategies; nor is it controlled by odor cues or the following (or avoidance) of odor trails. As for the rats, the evidence points to an ability to learn about spatial locations, to remember which have been visited, and to adopt a strategy of going to those that have not been visited previously (or of avoiding those that have). Exactly what cues control this ability remains to be determined. It is tempting to suppose that the tortoise identifies spatial locations by the configuration of extramaze cues that define them. Direct support for this proposal requires studies in which the relationship of the maze arms to the extramaze cue is explicitly manipulated.

We can further conclude that hippocampal formation of the mammalian brain is not essential for adequate performance on this sort of spatial task.

This may mean that some quite different brain structure is capable of carrying out the same functions, but perhaps by way of quite a different mechanism. Alternatively it may be taken to support the view that the reptilian medial cortex is functionally equivalent, even analogous, to the mammalian hippocampus. In the latter case, further studies could reveal the operation of similar mechanisms in reptiles and mammals.

In summarising his study, Tinklepaugh (1932) wrote as follows: “This report on the maze running of a single turtle is made not because this lowly subject learned the maze, but rather because of the nature of its behavior during the process…” (p. 201). The same holds for our report. Tinklepaugh went on to say: “In my estimation, the learning of the turtle equalled the expected accomplishment of a rat in the same maze …” (p.206). We would not want to make the same claim for our own subject; we have already noted ways in which his performance fell short of what might be expected of a rat trained in the same maze. But we would want to say that his performance was not fundamentally different from that of the rat – that any difference appears to be quantitative rather than qualitative. His movements around the maze may have been slow, but satisfactory learning was ultimately achieved. To that extent we can endorse the conclusion reached by Tinklepaugh, that “…the physical sluggishness and awkwardness of the turtle may have earned him an undeserved reputation for stupidity” (p. 206).

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Table 1

Overview of the experimental procedure

Procedure	Description	Criteria	ITI	Total no. days	Total no. trials	No. trials/day
Familiarization 1	1 arm open. Tortoise placed in the center; needs to enter the arm to get food.*	5 min or completion	1 min	4	52	4-16
Familiarization 1a	No arms open. Dandelion and strawberry placed in central platform.	30 min or all food eaten	5 min	3	28	2-14
Familiarization 1	1 arm open. Tortoise placed in the center; needs to enter the arm to get food.	15 min or completion	1 min	13	145	8-48
Familiarization 2	All arms open. Food visibly available at the end of each arm.	30 min or completion	5 min	15	60	4
Familiarization 3	All arms open. Food available, but hidden in cups at the end of each arm. Tortoise allowed to accustom himself to eating from food cups.	30 min or completion	5 min	1	4	4
Basic RAM training	All arms open. Food available, but hidden in cups at the end of each arm.	30 min or completion	5 min	12	48	4
Food Odor Test	All arms open. Food available in four of the arms. Intermixed with normal training trials.	30 min or completion	5 min	2	4 test 4 retraining	4
Odor Trails Training	**a**: 4 arms open, other 4 arms blocked. **b**: 30-s retention interval. **c**: All arms open, food only available in the arms not previously visited.	**a**: 30 min or completion **c**: 60 min or completion	5 min	9	23	1-4
Odor Trails Test	**a**: 4 arms open, other 4 arms blocked. **b**: 30-s retention interval during which the maze is rotated by 45°. **c**: All arms open; food only available in unvisited arms spatially.	**a**:30 min or completion **c**: 60 min of completion	5 min	9	5 test 4 retraining	1

Note. *After four days of training on this procedure, Moses was not eating readily. Phase 1a was include to encourage him to eat in the maze; RAM: Radial arm maze; ITI: Intertrial interval.

Table 2

Sequence of choices in the 18 trials of the first phase of training on which all arms were visited.

Day	Trial	Choices	No. choices to completion	Probability
2	4	[2,5,4,7,1,**2**,**1**,8] 7,6,5,1,3	13	.139
3	3	[3,4,8,7,5,6,**5**,1] **7**,**5**,**8**,2	12	.093
4	2	[1,6,8,**6,8,6,8,**7] 5,**6,8**,2,4,3	14	.192
5	2	[2,6,4,3,1,7,5,**7**] 8	9	.011
6	1	[2,4,5,8,3,7,1,**2**] **8**,6	10	.028
6	2	[5,8,2,6,1,**2**,**1,**7] 4,**5,8,7,6,**3	14	.192
6	3	[4,5,2,8,6,3,7,1]	8	.002
6	4	[4,7,1,5,**7**,**1**,2,8] 6,3	10	.028
8	3	[5,1,8,2,**8**,6,7,3] 4	9	.011
8	4	[4,8,**4**,7,1,**8**,6,**8**] 2**,1,8**,5**,6,1**,3	15	.248
9	2	[7,8,6,**7**,1,2,**8**,3] **8,6,**5**,7,3,8,**4	15	.248
9	3	[6,4,8,**6**,1,7,**6**,5] **1,**2,**6,8,6,**3	14	.192
9	4	[6,5,3,7,**6**,8,**7,8**]1,**8,7,8,**4,**1,7,5,**2	17	.366
10	2	[3,1,**3**,8,2,6,7,**1**] **8**,4,**3**,5	12	.093
10	3	[2,7,3,8,**2**,6,4,**2**] **4,**5,**3**,**8**,1	13	.139
10	4	[4,8,3,5,7,6,**4**,2] **8,2,**1	11	.056
11	4	[3,8,4,5,1,**5**,6,**8**] 2,**5,6,8**,7	13	.139
12	4	[4,7,6,**7**,8,2,1,3] **8,1,3,**5	12	.093

Note. The numbers in the Choices column refer to the arms of the radial maze. The first eight choices made are enclosed in square brackets. Choices in bold indicate errors (returning to an arm already visited). The probability given for each trial is that associated with the number of choices to completion assuming that every choice is made at random, with replacement of choices already made.

Table 3

Classification of type of turn for choices made in the 18 trials of the first phase of training on which all arms were visited.

Type of turn	Number	Percentage of total
1 arm anticlockwise	30	14.8
2 arms anticlockwise	42	20.7
3 arms anticlockwise	15	7.4
1 arm clockwise	33	16.3
2 arms clockwise	37	18.2
3 arms clockwise	19	9.4
Opposite	27	13.3

Table 4

Number of choices required to complete the task for the 17 trials of the second phase of training on which this was achieved.

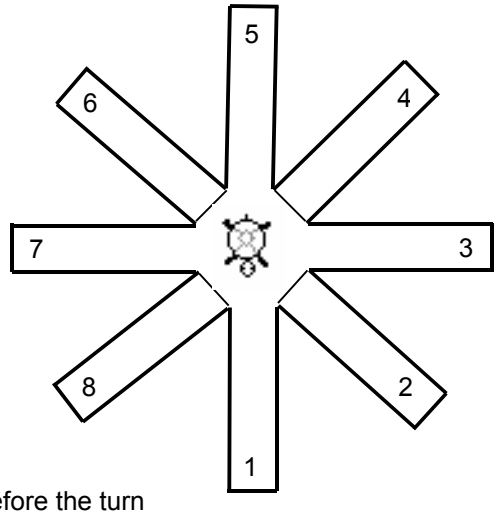
Day	Trial	No. choices to completion	Probability
1	2	9	.192
1	3	7	.089
1	4	8	.137
2	2	9	.192
2	3	5	.022
2	4	10	.250
3	1	13	.429
3	2	15	.539
3	4	9	.192
4	1	11	.310
4	3	14	.485
4	4	13	.429
5	2	11	.310
6	1	10	.250
7	2	5	.022
8	1	11	.310
9	1	5	.022

Note. In this phase of training the subject had received forced trials with four of the maze arms; choices to completion refers to the number of choices required to visit the remaining four arms when all eight were made available. The probability given for each trial is that associated with the number of choices to completion assuming that every choice is made at random, with replacement of choices already made.

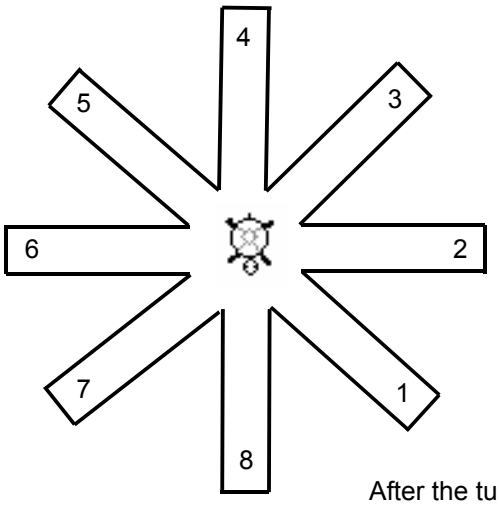
Figure Caption

Figure 1. Layout of the maze in the two phases of a trial when testing the influence of odor paths. Before the turn, guillotine doors blocked access to four of the arms, allowing access to food only in the other four (those numbered 1, 3, 5, and 7 in this example). After rotation of the maze the doors were removed and food was available again only in arms 1, 3, 5, and 7. The tortoise was therefore required to enter same arms as had been visited before, these now being in different spatial locations.

Figure 1



Before the turn



After the turn