

Radial-Arm-Maze Behavior of the Red-Footed Tortoise (*Geochelone carbonaria*)

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The radial-arm maze is an established method for testing an animal's spatial win-shift behavior. Research on mammals, birds, and fish has shown that the mastery of this task is commonly mediated, to different degrees, by two types of strategy: those based on external cues and those based on response stereotypy. In the present study we trained four red-footed tortoises (*Geochelone carbonaria*) to navigate an eight-arm radial maze while providing different levels of access to visual room cues. The results indicate that response stereotypy is the more prevalent mechanism in these tortoises, although navigation based on landmarks can also occur if learned initially. The findings suggest that tortoise spatial navigation may be more similar to that observed in mammals and birds than previously thought.

Keywords: spatial cognition, radial-arm maze, tortoises, cognitive map, response stereotypy

The ability to orient around complex environments (an aspect of spatial cognition; Reber & Reber, 2001) is considered an essential survival tool for almost all species, as it allows efficient movement between feeding grounds, hiding places, and sleeping areas (Day, Crews, & Wilczynski, 1999). Despite the universal nature of spatial cognition, its study has largely focused on the behavior of mammals, birds, and fish. This has led to a fair understanding of their capabilities (Bond, Cook, & Lamb, 1981; López, Bingman, Rodríguez, Gómez, & Salas, 2000; Vargas, López, Salas, & Thinus-Blanc, 2004). However, to gain a clear understanding of the evolution of vertebrate cognition, it is important to examine this ability in reptiles (Mueller, Wilkinson, & Hall, 2011; Wilkinson & Huber, in press). The amniotes (mammals, birds, and reptiles) have common evolutionary roots and can, therefore, be

expected to share certain behavioral traits and capabilities. Yet, because the evolutionary split between the different classes took place several million years ago, there is ample time for quite different capacities and mechanisms to have evolved (Zardoya & Meyer, 2001). Thus, the exploration of differences and similarities among the amniotes is likely to provide insight into the evolution of spatial cognition.

Several different methods of spatial orientation have been identified in mammals, birds, and fish. Some strategies rely on use of external stimuli as the basis for orientation. One example that is commonly seen in mammals and birds is the use of a distinctive cue located near the goal as a beacon on which to home. Another is the orientation based on an array of different *landmarks* in relation to each other. In this case no one cue needs to be located near the goal. Landmark use is considered the dominant orientation strategy in mammals and birds (O'Keefe & Nadel, 1978). Another, quite different mechanism involves the development of a *response strategy*, in which a goal is reached by performing a specific sequence of responses—for example, an animal may show a stereotyped pattern of always turning left at a choice point. With a strategy of this kind, no external cues are needed to reach the goal successfully. A potential disadvantage of such a strategy may be that it might imply an inability to adapt to a changing external environment. It has been argued response stereotypy generally appears in conjunction with other mechanisms (Bond et al., 1981). Strategies based on external cues will impose a load on the animals' memory (Dale & Innis, 1986), something that could be alleviated if such strategies were supplemented by the development of effective stereotyped response patterns.

Spatial navigation in chelonia (turtles, terrapins, and tortoises) has been a topic of interest for over a century. Early studies demonstrated a general ability to solve basic spatial problems such

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as multiunit and T mazes (for a review see Burghardt, 1977); later studies have focused on the mechanisms underlying spatial learning (for a review see Mueller et al., 2011). For example, López et al. (2000) trained the terrapin *Pseudemys scripta* to approach a specific location in a T maze. They found that, regardless of their starting position, the terrapins successfully used a configuration of distal cues to locate the goal. Partial obstruction of the cues did not negatively affect performance. However, when the cues were completely obscured, a drop in performance was observed. Similarly, López et al. (2001) trained two groups of terrapins to navigate to a specific goal and showed that they could use either landmark-based representations or a single beacon, depending on cue availability during training. These findings suggest a close resemblance between the spatial learning mechanisms observed in chelonia and those seen in mammals and birds.

Most research on spatial cognition in reptiles has used tasks requiring navigation toward a single goal (win-stay tasks). Win-shift tasks in contrast require the animal to move around from one goal to another and to retrieve rewards from a number of different locations that must not be revisited within a trial. The classic test of this is the radial-arm maze (Olton & Samuelson, 1976), which has been used extensively in the study of rat spatial navigation. Rats have been found to be extremely successful in learning to choose the novel arms of a radial mazes (Olton, Collison, & Werz, 1977; Olton & Samuelson, 1976). It appears that their primary orientation mechanism is a memory strategy relying on extramaze cues (Olton & Collison, 1979; Suzuki, Augerinos, & Black, 1980). This technique seems likely to impose a substantial cognitive load in that the animals must not only form a long-term representation of the relation of the goals to a range of extramaze cues, they must also use working memory to hold information about which arms have recently been visited. To adopt stereotyped response patterns would ease this load, and maplike strategies can be accompanied by secondary response stereotypy (Dale, 1986; Dale & Innis, 1986) that can take different forms, ranging from a weak tendency toward turning into every other arm to a stable succession of one-arm turns (Suzuki, Augerinos, & Black, 1980). Whether or not response stereotypy is shown seems to depend on factors such as the cost of errors (Yoerg & Kamil, 1982), the availability of extramaze cues (Suzuki et al., 1980), the experimental setup (Magni, Krekule, & Bure, 1979), and the number of trials already experienced during a session (Roberts & Dale, 1981).

Radial maze studies with other species have produced varying results. In some studies, pigeons have been found to have success rates well below that of rats and to rely strongly on response stereotypy (Bond et al., 1981; Olson & Maki, 1983; Walcott, 1996); others have found them to be proficient when provided with an appropriate setup (Roberts & Van Veldhuizen, 1985). The Siamese fighting fish (*Betta splendens*) studied by Roitblat, Tham, and Golub (1982) were able to solve an eight-arm radial maze successfully. The fish showed a strong tendency toward the stereotyped response of sequentially visiting adjacent arms, but this was not sufficient to explain the high levels of performance they achieved. The authors suggested that a memory-based mechanism acted to supplement the behavior supported by the response strategy component. Hughes and Blight (1999) report an interesting dissociation in two intertidal fish species (*Spinachia spinachia* and *Crenilabrus melops*). Both species showed response stereotypy when no visual cues were provided. However, a second group of

each species, which was provided with spatial cues in the form of colored tiles, navigated using a memory-based strategy.

To our knowledge only three studies have been conducted to date to examine the mechanisms underlying radial-arm maze behavior in reptiles. A single jeweled lizard (*Timon lepidus* studied by Mueller-Paul, Wilkinson, Hall, and Huber (submitted for publication), was found to display the stereotyped response pattern of emitting a sequence of turns by one arm. A more complex behavior pattern has been observed in a red-footed tortoise (*Geochelone carbonaria*). Wilkinson, Chan, and Hall (2007) found that the tortoise learned to navigate an eight-arm radial maze achieving a level performance only slightly below that shown by rats and comparable to that of pigeons (Bond et al., 1981). The tortoise did not exhibit any response stereotypy and its performance was not based on olfactory cues. Rather, navigation appeared to rely on a memory strategy based on extramaze cues. In a follow-up study the same tortoise was trained with a curtain surrounding the maze that obscured all room cues; the only extramaze cues available were four cut-out shapes pinned to the curtain (Wilkinson, Coward, & Hall, 2009). In this sparse environment the tortoise changed its strategy and began to use a stereotyped response pattern. It turned sequentially into adjacent arms and rarely changed direction during a trial. However, some flexibility was shown in that the turning direction varied between one session in the maze and the next. This stereotyped pattern persisted when the cues were removed leaving a black curtain, but was abandoned when the curtain itself was removed giving visual access to the extramaze cues of the room.

The results of Wilkinson et al. (2007, 2009) suggest that the tortoise's primary response strategy may be response-based under poor cue conditions, but that a landmark-based strategy can appear when a rich cue environment is provided. Such a clear separation between mechanisms (which is uncommon in rats; Dale & Innis, 1986) might indicate the existence of two separate processes that control navigation in the tortoise. These conclusions, however, are based on the behavior of just one individual. The present set of studies sought to replicate and extend the findings of Wilkinson and colleagues. In particular, we examined whether learning to navigate around a radial arm maze was an ability that was common to all red-footed tortoises and we sought to determine the ability of the tortoise to switch from one method of solution to another according to circumstances.

Experiment 1: Can Red-Footed Tortoises Learn To Navigate a Radial-Arm Maze?

Introduction

The aim of this study was to replicate the basic radial-maze procedure used by Wilkinson et al. (2007) but to test the performance of more animals to establish the generality of the effects observed.

Methods

Subjects. Four juvenile red-footed tortoises (*G. carbonaria*), Esme, Molly, Quinn, and Emily took part in the study. Their plastron lengths were 12.5, 12.5, 11, and 10 cm respectively. They had a minimal age of 3 years at the beginning of the experiment.

The tortoises' sex was unknown, as this species only develops unambiguous sexual dimorphic traits closer to sexual maturity. All four tortoises were captive bred and purchased from licensed pet shops in Austria. The tortoises were housed as a group in a 120 × 70-cm enclosure, at 28 ± 2 °C and approximately 60% humidity, with permanent access to fresh water, shelter, UV light, and heat lamps. During experimental sessions the tortoises were rewarded with small pieces (approximately 0.5 × 0.5 cm) of preferred fruit and vegetables, such as strawberry, sweet corn, and mushroom. They were fed with a variety of less preferred food types, such as apple, pear, and cucumber, in their enclosure after training. In accord with standard husbandry practice, they experienced 1 day a week without food. None of the animals was experimentally naïve (see Wilkinson, Künstner, Mueller, & Huber, 2010; Wilkinson, Mandl, Bugnyar, & Huber, 2010; Wilkinson, Mueller-Paul, & Huber, submitted for publication), but they had never previously been involved in a maze task.

Apparatus. The apparatus was an eight-arm radial maze (Figure 1) with 14-cm-high opaque, plastic walls. The maze floor was covered with grip-ensuring rubber lining, and the whole maze was covered by a 1.5-cm² wire mesh. The central area was an octagon with a diameter of 23 cm. Each arm was 18 cm long, 10 cm wide at the opening, and 25 cm wide at the back wall. This arm shape was used to ensure that the tortoises could turn easily within the arm. A small, opaque, yellow food bowl (diameter 3 cm × height 1.5 cm) was located centrally at the end of each arm. The rim of the bowl prevented the tortoises from seeing the reward until they had fully entered the arm. The maze was not cleaned thoroughly between trials. This is because multiple arms are entered during each trial, and thus, leaving the maze with many odor cues increased the difficulty of identifying odor information from the present trial. It was thought that this would decrease the value of using odor trails as cues. In the rare cases that the animals defecated or urinated in the maze, this was removed and affected area was cleaned after the trial was completed.

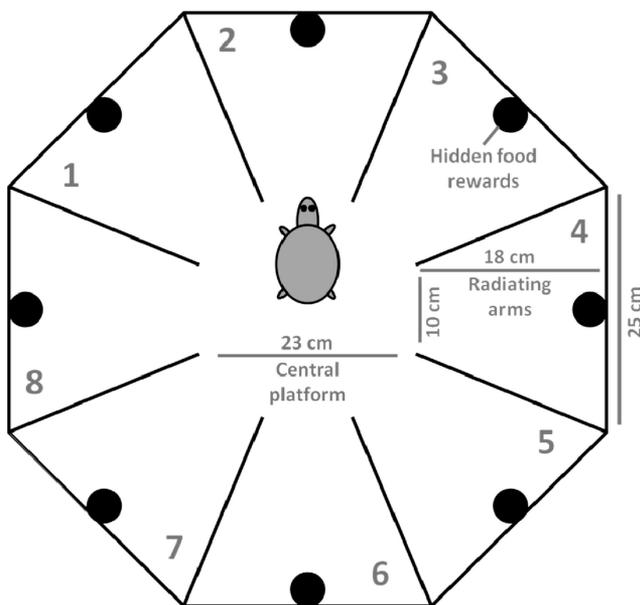


Figure 1. Radial-arm maze apparatus.

The maze was placed centrally in a 2.24 × 2.24-m room which was lit with two 25-W fluorescent tube lights. Each wall of the room contained a variety of visual stimuli that the tortoises could potentially use as cues during navigation. All the walls were white. One contained two sinks and soap dispensers, a large strip of beige newspaper ran across the entire wall, and there were two posters. A second contained a blue shelf, a lilac towel, a black, hanging plastic bag, two pictures, and a black door with a blue poster. The third white wall showed an array of many posters, a green, hanging plastic bag, and an open doorway to an illuminated white-tiled wall and a black door. The fourth wall had an open doorway, leading to a dark room, a shelf containing several boxes, a yellow, hanging plastic bag, and a beige electric hand dryer.

Procedure. Experiment 1 was run over a period of 27 weeks between September 7, 2009, and March 12, 2010. The animals were tested 5 days a week, trials being given between 9.00 a.m. and 5.00 p.m.

Pretraining. To habituate them to the apparatus, the animals were placed into the maze individually for 30 min with openly visible food items in each arm. Pretraining was considered complete when the animals had moved around and eaten readily for three sessions.

Training. Throughout the training phase each of the eight arms was baited with one hidden reward. Reward type varied across trials, but within one trial all eight rewards were identical. At the start of each trial, a tortoise was individually placed into the maze facing a randomly selected arm. The tortoise was allowed to move around the maze freely and to collect the food rewards from the different arms. Throughout each trial, the experimenter observed and documented the tortoise's behavior on a monitor from a room adjacent to the testing room. A video setup above the maze provided a live feed of the animal's behavior for this purpose. The order in which each animal entered the arms was recorded. Entry into an arm was counted when half the animal's body was inside the arm. Entering an arm that had not previously been visited was counted as a correct choice, and a repeat visit within a trial was considered an error. The tortoises were run between one and five times per day. A trial was terminated when eight arms (regardless of whether the choices were to novel or previously visited arms) had been visited. Trials were terminated and rerun later if the animal failed to move for 15 min or after 30 min (extended to 40 min if the animal was actively foraging) even though fewer than eight choices had been made. Behavior observed on such incomplete trials was scored but not analyzed further.

To ensure reliable observation of arm choice behavior, interobserver reliability was tested on 240 potential arm choices made by three different tortoises over 10 sessions each. These reliability test trials were analyzed both by the experimenter and by an additional observer who was blind to the hypothesis of the study. Interobserver reliability was 100%.

All the animals, apart from Emily, received training until they had completed 120 trials; Emily's performance was successful and stable from early in training, and she received only 40 trials. After completing this first phase of training, all animals received two different tests designed to examine what cues they were using to navigate around the maze.

Food odor test. This test examined whether the tortoises used the scent of the rewards to guide their selection of novel arms. Test sessions consisted of a training trial followed by a test trial. One to

two test sessions were run per day. Test trials were identical to training trials except that only four arms were baited. Four test trials were run for each animal with the bait being presented in arms 1, 3, 5, and 7 and in arms 2, 4, 6, and 8 on alternate trials. Following this food odor test, the tortoises received retraining until they achieved eight successful trials before being undergoing the next test.

Scent trail test. This test was designed to examine whether the tortoises used scent trails as a cue to avoid a previously visited arm. The test trials resembled training trials in that all arms were baited but the maze floor was flooded with a 5-mm layer of warm water to disperse olfactory cues. The water remained in the maze throughout each scent trail test trial but was exchanged between trials. Each tortoise received eight test trials with a maximum of two trials per day.

Results

All four tortoises readily explored the maze during the pretraining phase and required only three to five trials to meet habituation criterion.

Training. In the course of a trial of eight choices, the chance expectation is that 5.3 would be novel arm choices (Olton & Samuelson, 1976). By the end of training all animals were performing above this chance level. One-sample *t* tests comparing the mean number of novel arm choices over the last 20 trials to the chance expectation (5.3 arms) showed that all four tortoises visited significantly more novel arms than could be expected on the basis of chance. For Molly, the mean score was mean 6.0, $t(19) = 2.772$, $p < .05$; for Esme, 5.9, $t(19) = 2.676$, $p < .05$; for Quinn, 6.0, $t(19) = 2.207$, $p < .05$; and for Emily it was 7.3, $t(19) = 10.251$, $p < .001$.

Food odor test. Figure 2a shows, for each subject, the number of novel arms entered over all four test trials, distinguished according to whether the chosen arm was baited or not. It is evident that there was no tendency to preferentially choose arms that were baited. Chi-square tests showed no significant difference in the likelihood of a visit to a baited versus an unbaited arm for any of the tortoises, with Molly $\chi^2(1) = 0.39$, $p > .05$; Esme $\chi^2(1) = 0.18$, $p > .05$; Quinn $\chi^2(1) = 0.04$, $p > .05$; and Emily $\chi^2(1) = 0.04$, $p > .05$.

Scent trail avoidance test. Figure 2b shows, for each subject, the mean number of novel arms chosen over the eight test trials in

the flooded maze. Also shown, for comparison, is the mean number of novel arms chosen over the last eight trials of the training phase (i.e., in the dry maze). It is evident that flooding the maze had little effect on performance. Paired sample *t* tests comparing the test performance to the performance during the last eight training trials found no significant differences for any tortoise, Molly, $t(7) = -1.16$, $p > .05$; Esme, $t(7) = 1.00$, $p > .05$; Quinn, $t(7) = 0.21$, $p > .05$; and Emily, $t(7) = -0.764$, $p > .05$.

Turning behavior. For each completed trial for each tortoise, a record was made of the exact pattern of turns made. This allowed us to score the number of turns between adjacent arms (one-arm turns) that occurred in succession in a given turning direction. Such a response strategy would constitute an efficient way of behaving in the radial maze. We also scored the number of two-arm, three-arm, and four-arm turns in a row in given direction for each trial. Figure 3, a–d, shows, for each subject, the mean number of turns of each type throughout successive four-trial blocks of the training phase. It is evident that Emily and Quinn readily developed a turn-by-one arm strategy. For Esme, there was a slight tendency for turns by two arms to predominate, whereas Molly showed no clear pattern.

For statistical analysis we concentrated on the performance shown on the first 20 and last 20 trials of training (see Table 1). For each tortoise on each of these blocks, we conducted a chi-square test looking at the proportional use of the four different turn types. The results of these tests are reported at the top of the column labeled SR in Table 1. In every case but one (that of Molly for the beginning of training) a significant effect was obtained, indicating that the various turn types were being used differentially. Analyses of the standardized residuals (SR) revealed which turn types contributed to the significant results of the chi-square analyses. SRs were calculated from the observed (*O*) and expected (*E*) values of each cell with the following formula: $SR = (O - E)/E^2$. SRs of above 1.96 indicated a significantly larger than expected contribution of the cell, SRs below -1.96 a significantly lower than expected contribution, and SRs between 1.96 and -1.96 a non-significant contribution. This analysis confirmed that Quinn and Emily showed a significantly enhanced tendency to perform one-arm turns and correspondingly, a reduced tendency to make other types of turns during both the first and the last 20 trials of training. Esme produced a larger-than-expected number of two-arm turns both during the first and the last 20 trials. Molly showed no very

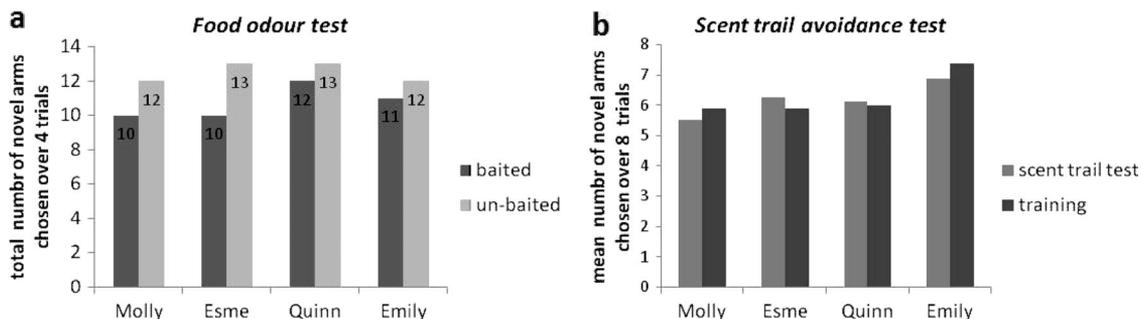


Figure 2. Performance of four red-footed tortoises on two olfactory tests. (a) Total number of visits to baited versus unbaited arms. (b) Mean number of novel arms chosen during the last eight training and the eight scent trail avoidance test trials.

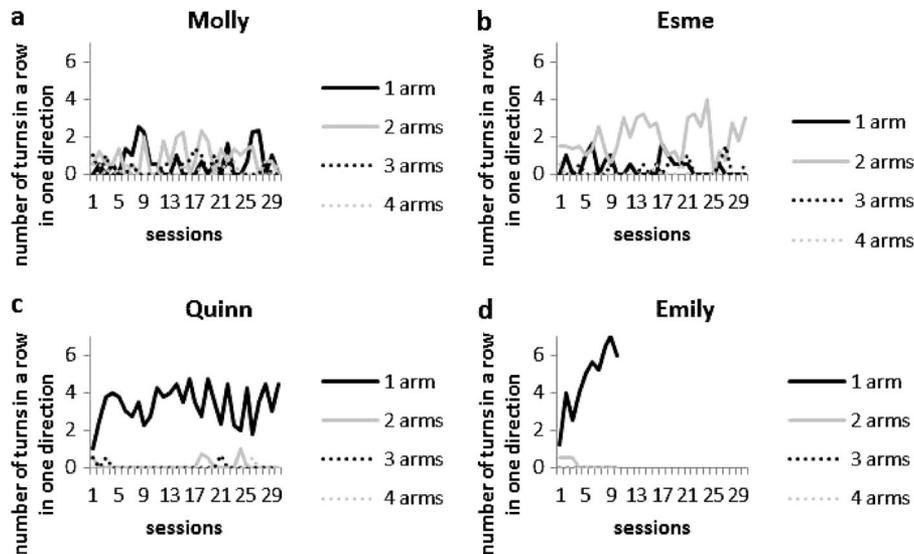


Figure 3. (a–d) Turning behavior during Experiment 1: the number of turns in a row in one direction for each turn type in blocks (sessions) of four trials.

clear pattern, although there was a significant tendency to favor two-arm turns at the end of the training.

Differences between the use of each turn type during the first and last 20 trials were analyzed by repeated-measures *t* tests. They revealed that Molly significantly reduced the number of three-arm turns, $t(19) = 2.540, p < .05$, and Esme significantly reduced the number of one-arm turns, $t(19) = 4.931, p < .05$, while increasing the number of four-arm turns, $t(19) = -2.162, p < .05$. Both Quinn and Emily significantly increased the number of one-arm turns, Quinn: $t(19) = -2.266, p < .05$; Emily: $t(19) = -4.094, p < .05$, and significantly decreased the number of two-arm-turns, Quinn: $t(19) = 2.668, p < .05$; Emily: $t(19) = 3.559, p < .05$.

Discussion

The results show that all four red-footed tortoises were able to perform in the eight-arm radial maze at a level significantly better than chance. This suggests that mastering a radial-arm maze task lies within the general capabilities of red-footed tortoises and is not a peculiarity of the one tortoise previously tested by Wilkinson et al. (2007, 2009). Over the last 20 trials of training, all had scores (mean number of novel arms entered in eight choices) that differed significantly from the chance level (the poorest performing subject had a score of 5.9; the best, of 7.3). The tortoises were thus slightly less proficient than rats in this task (Olton & Samuelson, 1976), but they performed at a level similar to that shown by pigeons (Bond et al., 1981), by the jeweled lizard studied by Mueller-Paul et al. (submitted), and the red-footed tortoise tested previously by Wilkinson et al. (2007, 2009). Maze orientation did not appear to be based on odor cues emanating from the rewards, as the tortoises did not choose baited arms more often than unbaited ones, nor was performance likely to depend on scent trails left by the tortoises themselves, as no disruption in behavior was observed during the scent trail avoidance test when scent cues were dispersed by water. Even if flooding the maze might not have entirely

removed all scent cues, the tortoises' movement around the maze would have dispersed them in a manner sufficient to introduce a clear decrease in performance had the animals relied on scent trails to any major degree when solving the task. It is further unlikely that the animals were leaving scent cues in the form of defecation or urination in the maze as these behaviors were only infrequently observed, and marks were removed immediately after the trial during which they occurred. In summary, the tortoises' behavior regarding navigation based on scent is in line with the behavior found in rats (Olton & Collison, 1979).

In other respects, the behavior of the tortoises was very different from that shown by rats. All of the tortoises performed at a high level from the beginning of training, and only one showed a significant improvement over time. For two of the subjects, their successful performance was the consequence of the rapid development of a turn-by-one arm strategy. Turning by one arm is a response strategy that will obviously lead to a high success rate (Dale & Innis, 1986). In so far as the other two animals developed a response strategy, it tended to involve turning by two arms. Clearly, a continuous sequence of two-arm turns in an eight-arm radial maze can lead to no more than four correct choices. The consistent, above-chance, level of maze performance shown by these subjects thus indicates that additional mechanisms must have been operating. This could have involved some reliance on the extramaze cues, or it may have involved additional response rules (such as performing a different turn type as soon as an empty aisle is encountered or after every three choices). Evidence favoring the former interpretation comes from the behavior shown by the tortoise tested by Wilkinson et al. (2007, 2009). When extramaze cues were not available, it used one-arm turns, whereas two-arm turns prevailed when such cues were numerous. One possibility, then, is that when navigation is largely based on the extramaze cues, the two-arm turning behavior predominates simply because such

Table 1
Turning Behavior of Four Red-Footed Tortoises Based on Chi-Square Calculations and Analyses of the Resulting Standardized Residuals

Turn types	Experiment 1				Experiment 2				Experiment 3				Experiment 4			
	First 20 trials		Last 20 trials		First 20 trials		Last 20 trials		First 20 trials		Last 20 trials		First 20 trials		Last 20 trials	
	SR	Turns used	SR	Turns used	SR	Turns used	SR	Turns used	SR	Turns used	SR	Turns used	SR	Turns used	SR	Turns used
Molly	$\chi^2(3) = 5.06$ $p > .05$		$\chi^2(3) = 11.67$ $p < .05$		$\chi^2(3) = 5.06$ $p < .001$		$\chi^2(3) = 126.10$ $p < .001$		$\chi^2(3) = 86.11$ $p < .001$		$\chi^2(3) = 41.68$ $p < .001$		$\chi^2(3) = 59.85$ $p < .001$		$\chi^2(3) = 15.68$ $p < .001$	
	-0.86	More	-0.69	More	4.52	More	9.62*	More	7.77*	More	4.99*	More	6.10	More	1.82	More
	1.89	Less	2.76*	More	0.52	Less	-2.15*	Less	-0.84	Less	-2.29*	Less	0.55	Less	1.50	Less
	-0.17	Less	-1.84	Less	-2.06*	Less	-3.06*	Less	-2.75*	Less	0.57	Less	-3.05	Less	-0.06	Less
Esme	-0.86	Less	-0.31	Less	-2.92*	Less	-4.42*	Less	-4.18*	Less	-3.33*	Less	-3.61	Less	-3.19	Less
	$\chi^2(3) = 41.93$ $p < .001$		$\chi^2(3) = 66.32$ $p < .05$		$\chi^2(3) = 39.53$ $p < .001$		$\chi^2(3) = 109.60$ $p < .001$		$\chi^2(3) = 106.63$ $p < .001$		$\chi^2(3) = 116.71$ $p < .001$		$\chi^2(3) = 149.23$ $p < .001$		$\chi^2(3) = 142.53$ $p < .001$	
	0.06	More	-3.54*	Less	-2.75*	Less	-2.32*	Less	-2.53*	Less	-2.94*	Less	-5.92*	Less	-5.58*	Less
	5.23*	More	6.93*	More	5.32*	More	9.04*	More	8.89*	More	9.35*	More	3.72*	More	3.38*	More
Quinn	-2.68*	Less	-1.84	Less	-0.66	Less	-3.36*	Less	-2.29*	Less	-3.21*	Less	-5.07*	Less	-5.41*	Less
	-2.68*	Less	-1.56	Less	-1.85	Less	-3.36*	Less	-4.02*	Less	-3.21*	Less	-5.92*	Less	-5.92*	Less
	$\chi^2(3) = 147.50$ $p < .001$		$\chi^2(3) = 197.45$ $p < .05$		$\chi^2(3) = 156.00$ $p < .001$		$\chi^2(3) = 245.37$ $p < .001$		$\chi^2(3) = 233.39$ $p < .001$		$\chi^2(3) = 305.30$ $p < .001$		$\chi^2(3) = 136.80$ $p < .001$		$\chi^2(3) = 126.01$ $p < .001$	
	10.50*	More	12.14*	More	10.82*	More	13.54*	More	13.20*	More	15.11*	More	10.07	More	9.47	More
Emily	-3.50*	Less	-4.22*	Less	-3.61*	Less	-4.67*	Less	-4.12*	Less	-4.79*	Less	-2.32	Less	-1.27	Less
	-3.00*	Less	-4.22*	Less	-3.61*	Less	-4.24*	Less	-4.56*	Less	-5.18*	Less	-3.87	Less	-3.68	Less
	-4.00*	Less	-3.74*	Less	-3.61*	Less	-4.67*	Less	-4.56*	Less	-5.18*	Less	-3.87	Less	-4.56	Less
	$\chi\chi^2(3) = 163.17$ $p < .001$		$\chi^2(3) = 360.00$ $p < .05$		$\chi^2(3) = 341.27$ $p < .001$		$\chi^2(3) = 211.50$ $p < .001$		$\chi^2(3) = 294.00$ $p < .001$		$\chi^2(3) = 369.00$ $p < .001$		$\chi^2(3) = 280.92$ $p < .001$		$\chi^2(3) = 290.31$ $p < .001$	
11.04*	More	16.43*	More	15.97*	More	12.56*	More	14.85*	More	16.61*	More	14.51	More	14.75	More	
-2.70*	Less	-5.48*	Less	-5.46*	Less	-3.09*	Less	-4.95*	Less	-5.55*	Less	-4.71	Less	-4.65	Less	
-4.15*	Less	-5.48*	Less	-5.09*	Less	-4.51*	Less	-4.95*	Less	-5.55*	Less	-4.71	Less	-5.05	Less	
-4.15*	Less	-5.48*	Less	-5.46*	Less	-4.92*	Less	-4.95*	Less	-5.55*	Less	-5.10	Less	-5.05	Less	

Note. SR = standardized residuals; SR = (Observed - Expected)/Expected².
* Significant at .05 (SR > +1.96 or < -1.96).

turns are considerably easier than turning by one arm (Yoerg & Kamil, 1982), particularly for a physically inflexible animal like a tortoise. This suggestion is investigated in the next experiment.

Experiment 2: What Determines Navigation Mechanisms Used by the Red-Footed Tortoise?

Introduction

In Experiment 1, the tortoises with a preference for one-arm turns were the two smaller ones, whose neck lengths are approximately 2 cm shorter than those of the two larger tortoises. Thus, the smaller tortoises' heads were lower in the maze, which might have prevented them from detecting visual cues from the room that were more readily available to the larger tortoises. This could have resulted in the smaller tortoises' relying on response strategy, whereas the larger tortoises were able to see the room cues clearly and to use a memory strategy accompanied by the easier turn type.

To test the hypothesis, the differential visual access to the extramaze has resulted in the different navigations methods chosen by the tortoises, we designed a second experiment in which the maze walls were raised for the larger tortoises and lowered for the smaller tortoises. These amendments should provide better visual access to cues for the smaller tortoises and reduce the cue information accessible to the larger tortoises. The question of interest was whether the latter would then resort to a turn-by-one-arm strategy, whereas the former would abandon this strategy.

Methods

The experiment was run over a period of 10 weeks between February 22, 2010, and May 5, 2010. The animals were tested 5 days a week between 9 a.m. and 5 p.m. until they had received 80 trials each. The same four juvenile red-footed tortoises that participated in Experiment 1 took part in this experiment. No changes were made to training procedure.

Apparatus

The apparatus consisted of two eight-arm radial mazes of identical size and design to that used in Experiment 1. The only difference was in the height of the maze walls. The outer walls of the large tortoises' maze were raised by 5 cm to a total height of 19 cm by attaching black cardboard to the outside of the maze. The floor of the small tortoises' maze was raised by inserting a 5-cm-thick layer of firm rubber foam covering the entire maze floor. The rubber foam was covered with the same grip-ensuring rubber lining as before so that there was no apparent difference from the previous maze floor. The resultant wall height of this maze was 9 cm. The maze position and the testing room were kept identical.

Results

Training. Maze performance compared to chance (mean 5.3 arms) during the first and last 20 trials of radial-arm maze training was analyzed using one-sample *t* tests. These showed above chance performance for all four tortoises, Molly: first 20 trials: mean 6.1, $t(19) = 4,198, p < .001$; last 20 trials: mean 6.2, $t(19) =$

4,500, $p < .001$; Esme: first 20 trials: mean 5.8, $t(19) = 2,500, p < .05$; last 20 trials: mean 6.2, $t(19) = 4,230, p < .001$; Quinn: first 20 trials: mean 6.4, $t(19) = 7,998, p < .001$; last 20 trials: mean 6.3, $t(19) = 3,963, p < .001$; and Emily: first 20 trials: mean 7.5, $t(19) = 14,009, p < .001$; last 20 trials: mean 6.6, $t(19) = 5,086, p < .001$. A comparison of the tortoises' performance during the first and the last 20 trials showed a significant decrease only for Emily, $t(19) = 2.93, p < .05$.

Turning behavior. For each completed trial for each tortoise, a record was kept of the exact pattern of turns made and the number of one-arm, two-arm, three-arm, and four-arm turns in a row in one direction was counted. The tortoises' turning behavior was analyzed as described in Experiment 1. Figure 4, (a–d), shows, for each subject, the mean number of turns of each type throughout successive four-trial blocks of the training phase. It is evident that Emily and Quinn maintained a turn-by-one arm strategy and Esme appeared to develop a strong preference for two-arm turns. When presented with restricted room cues Molly developed a clear preference for one-arm turns.

Chi-square tests revealed a highly significant difference in number of turn types for the first and last 20 trials for all four tortoises (Table 1). Analyses of the SRs showed that Molly, Quinn, and Emily used significantly more one-arm turns than all other turn types, whereas Esme used significantly more two-arm turns during both the first and last 20 trials (see Table 1). Differences between the turning behavior of the first and last 20 trials analyzed by repeated-measures *t* tests revealed that Molly significantly increased the number of one-arm turns, $t(19) = -2.861, p < .05$, and Esme significantly increased the number of two-arm-turns, $t(19) = -2.430, p < .05$. Quinn significantly increased the number of one-arm-turns, $t(19) = -4.003, p < .05$, whereas Emily significantly decreased the number of one-arm-turns, $t(19) = 3.187, p < .05$, and increased the number of two-arm-turns, $t(19) = -2.131, p < .05$.

Discussion

All four tortoises maintained above-chance performance in the changed conditions of this experiment. Analyses of their turning behavior revealed that Molly changed her choice behavior. When visual access to the room cues was impaired by raising the maze walls by 5 cm, she started using a response strategy of sequentially turning into adjoining arms. This change in behavior suggests that Molly might initially have been using a strategy that relied on visual cues but that when access to these cues was reduced, she adapted by adopting a response strategy of one-arm turns. This is demonstrated by the significant increase in the number of one-arm turns toward the end of the experiment. Her behavior corresponds with that of the red-footed tortoise tested by Wilkinson et al. (2009). The second large tortoise, Esme, did not abandon her preferred two-arm turn strategy; indeed she showed an increased tendency to make such turns.

The other two tortoises, the smaller animals, Quinn and Emily, did not show a strategy change in response to the increased visual access to the room cues resulting from the lowering of the maze walls. Both maintained high levels of response stereotypy in the form of one-arm turns (although Emily's overall performance and continuous turning behavior decreased somewhat toward the end of the experiment as she increased the use of two-arm and reduced

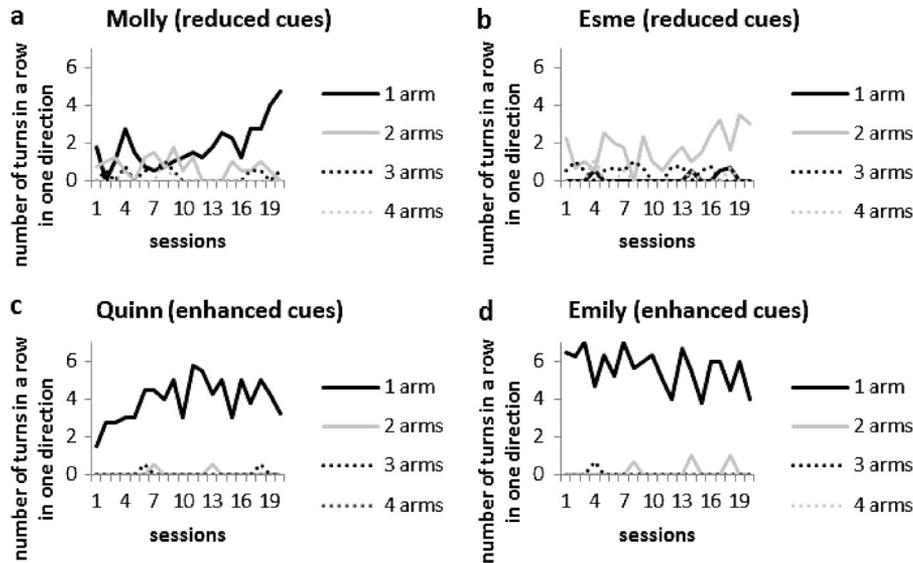


Figure 4. (a–d) Turning behavior of four red-footed tortoises during Experiment 2 with reduced and enhanced cues, respectively: the number of turns in a row in one direction for each turn type in sessions of four trials.

the use of one-arm turns). In neither animal, therefore, was there evidence of a shift to a strategy that made use of the extramaze cues. It seems, therefore, that a response-based strategy, once established, is difficult to change. This matter was investigated further in the next experiment.

Experiment 3: Can Existing Response Stereotypy Be Modified?

Introduction

We had anticipated that Quinn and Emily might abandon their response-based strategy when, in Experiment 2, the extramaze cues were made more accessible. That they did not do so may indicate only that our technique for increasing the availability of these cues was not powerful enough. Accordingly, in this experiment, we continued training them in the modified maze, but enhanced the properties of the room cues. We also continued training with Molly and Esme in the presence of these cues, but with the maze used in Experiment 1. The question of interest in this case was whether Molly, who had changed to a turn-by-one-arm strategy in Experiment 2, would revert to her previous pattern of behavior.

Methods

The experiment was run over a period of 13 weeks between May 20, 2010, and August 23, 2010. The animals were tested 5 days a week between 9 a.m. and 5 p.m. until they had reached 80 trials each. The same four juvenile red-footed tortoises that participated in Experiments 1 and 2 took part in this experiment. No changes were made to the training procedure.

Apparatus

The apparatus consisted of the radial mazes that were used in Experiment 2. They differed only in that the outer walls of the

large tortoises' maze were reduced back to their original height of 14 cm. The floor of the small tortoises' maze remained raised with the wall height of 9 cm. However, the cue environment in the testing room was changed. Although room cues such as doors, sinks, and posters remained in place, additional cues were moved closer to the maze. Specifically, two additional shelves stacked with a variety of colorful 3-D cues were placed at a distance of 25 cm from each side of the maze.

Results

Training. One sample *t* tests analyzing maze performance compared to chance (mean 5.3 arms) during the first and last 20 trials of radial-arm maze training showed that the mean number of arm visits was significantly higher than expect based on chance for all four tortoises, Molly: first 20 trials: mean 6.3, $t(19) = 6.104$, $p < .001$; last 20 trials: mean 6.0, $t(19) = 3.647$, $p < .05$; Esme: first 20 trials: mean 6.3, $t(19) = 4.396$, $p < .001$; last 20 trials: mean 6.2, $t(19) = 4.344$, $p < .001$; Quinn: first 20 trials: mean 6.2, $t(19) = 2.669$, $p < .05$; last 20 trials: mean 6.6, $t(19) = 5.557$, $p < .001$; and Emily: first 20 trials: mean 6.9, $t(19) = 7.015$, $p < .001$; last 20 trials: mean 7.3, $t(19) = 8.675$, $p < .001$. A comparison of the tortoises' performance during the first and the last 20 trials did not show a difference in overall performance.

Turning behavior. For each completed trial for each tortoise, a record was kept of the exact pattern of turns made, and the number of one-arm, two-arm, three-arm, and four-arm turns in a row in one direction was counted. The tortoises' turning behavior was analyzed as described in Experiment 1. Figure 5, a–d, shows, for each subject, the mean number of turns of each type throughout successive four-trial blocks of the training phase. Emily and Quinn maintained a turn-by-one arm strategy, and Esme, apparently, maintained a turn-by-two-arm strategy. Molly, however, returned to showing no obvious pattern of preferred arm types.

Chi-square tests revealed a highly significant difference in number of turn types for the first and last 20 trials for all four tortoises

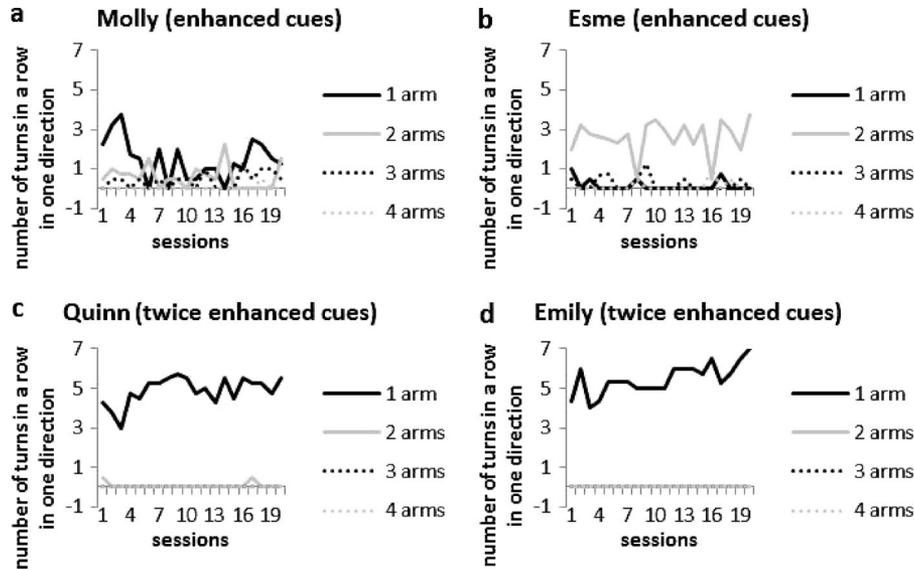


Figure 5. (a–d) Turning behavior of four red-footed tortoises during Experiment 3 with enhanced cues and twice enhanced cues (additional room cues and low maze walls), respectively: the number of turns in a row in one direction for each turn type in sessions of four trials.

(Table 1). Analyses of the SRs showed that Molly, Quinn, and Emily used significantly more one-arm turns and Esme significantly more two-arm turns than expected on the basis of chance (Table 1). Differences between the turning behavior of the first and last 20 trials analyzed by repeated measures t tests revealed no significant changes for either Molly or Esme. Quinn significantly reduced the number of two-arm turns, $t(19) = 2.463$, $p < .05$, whereas Emily significantly increased the number of one-arm turns, $t(19) = -3.584$, $p < .05$ and decreased the number of two-arm turns, $t(19) = -4.067$, $p < .05$.

Discussion

The attempt to enhance the effectiveness of extramaze cues had no effect on the behavior shown by Emily and Quinn, who continued with the turn-by-one-arm strategy. This suggests that for them visibility and availability of visual cues might not play the deciding role in their navigational mechanism or at least, that when it has been established initially (and remains successful), a response-based strategy is relatively impervious to changes in the environmental conditions.

Esme, too, continued with the strategy (in her case, turn-by-two-arms) that was evident at the end of Experiment 2. Only Molly showed a degree of sensitivity to the changed conditions. Although there was some tendency for the turn-by-one-arm strategy to dominate over others, her behavior in this study reverted to that shown in Experiment 1. It seems unlikely that her slight preference for one-arm turns constituted the primary source of her successful overall performance. Combinations of memory strategies with stereotyped response strategies have repeatedly been observed in rats (Bond et al., 1981; Dale, 1981; Dale & Innis, 1986). However, to demonstrate that external cue use is an important factor in Molly's navigation, it is necessary to test her without access to any visual cues. We took up this issue in Experiment 4.

Experiment 4: Are the Tortoises Using Response Strategies or Memory Strategies?

Introduction

In Experiment 4 the role played by extramaze cues was examined by testing the animals while the maze was entirely surrounded by a black curtain, thus eliminating such cues. Animals whose behavior is determined primarily by response-based strategies (i.e., Quinn and Emily) might be expected to continue to perform well in these conditions. A reduction in level of performance might be taken to indicate that their primary, response-based strategy was supplemented by a secondary strategy requiring access to visual cues (although it would also be consistent with generalization decrement brought about by the general change in conditions).

Potentially more informative is the effect that this manipulation might have on the behavior of Molly and Esme; at the end of Experiment 3, neither of these animals had response strategies fully capable of generating the overall performance they showed. To the extent that their behavior depended on the use of external cues, performance levels should drop, and use of other strategies, such as stereotyped responding, might well increase.

Methods

The experiment was run with Esme over a period of 9 weeks between September 8, 2010, and October 11, 2010, and with Molly, Quinn, and Emily over a period of 8 weeks from December 6, 2010, to January 28, 2011. Because of the break between Experiments 3 and 4 for Molly, Quinn, and Emily, these three tortoises received eight retraining trials to regain previous performance levels. The tortoises were tested 5 days a

week between 9 a.m. and 5 p.m. until they had reached 40 trials each.

Apparatus

The apparatus was the eight-arm radial maze as described for Experiment 1. The maze was entirely surrounded by a black curtain. An additional light was attached to the ceiling above the maze to compensate for the reduction in illumination produced by introduction of the curtain.

Procedure

No changes were made to the training procedure. After the 40 trials of the training phase, the animals were given the two odor tests (the food odor and the scent trail test) exactly as described for Experiment 1. Finally, the animals received a further food odor test consisting of four trials (as before) but in which the bait was alternately presented in arms 1, 2, 5, and 6, and in arms 3, 4, 7, and 8 (the test in which alternate arms are baited allows a possible confound when animals have adopted a turn-by-two arm strategy).

Results

Training. One sample *t* tests analyzing maze performance compared to chance (mean 5.3 arms) during the first and last 20 trials of radial-arm maze training showed that the mean number of arm visits was significantly higher than expect based on chance of all four tortoises, with Molly: first 20 trials: mean 5.9, $t(19) = 3.667$, $p < .05$; last 20 trials: mean 5.9, $t(19) = 3.736$, $p < .001$; Esme: first 20 trials: mean 6.2, $t(19) = 4.500$, $p < .001$; last 20 trials: mean 6.2, $t(19) = 3.847$, $p < .001$; Quinn: first 20 trials: mean 6.2, $t(19) = 3.141$, $p < .05$; last 20 trials: mean 6.4, $t(19) = 4.491$, $p < .001$; and Emily: first 20 trials: mean 6.6; $t(19) = 4.895$, $p < .001$; last 20 trials: mean 7.0, $t(19) = 7.813$, $p < .001$.

Turning behavior. For each completed trial for each tortoise, a record was kept of the exact pattern of turns made, and the number of one-arm, two-arm, three-arm, and four-arm turns in a row in one direction was counted. The tortoises' turning behavior was analyzed as described in Experiment 1. Figure 6, a–d, shows, for each subject, the mean number of turns of each type throughout successive four-trial blocks of the training phase. Given the complete obstruction of external cues Emily, Quinn, and Esme maintained their previously developed strategies of turning by-one arm and by-two arms, whereas Molly showed no clear pattern.

Chi-square tests revealed a highly significant difference in number of turn types for the first and last 20 trials for all four tortoises (Table 1). Analyses of the SRs showed that Esme used significantly more two-arm turns than expected on the basis of chance, whereas Quinn and Emily used significantly more one-arm turns than any other turn types during both the first and the last 20 trials. Molly used significantly more one-arm turns during the first 20 trials but showed no above-chance turn use during the last 20 trials (Table 1). Differences between the turning behavior of the first and last 20 trials analyzed by repeated-measures *t* tests revealed that Molly significantly reduced the number of one-arm turns, $t(19) = 2.372$, $p < .05$, and increased the number of two-arm-turns, $t(19) = -2.483$, $p < .05$.

Food odor test. Chi-square tests showed no significant difference for either tortoise (Figure 7a) for neither the first, Molly: $\chi^2(1) = 2.33$, $p > .05$; Esme: $\chi^2(1) = 1.64$, $p > .05$; Quinn: $\chi^2(1) = 0.00$, $p > .05$; Emily: $\chi^2(1) = 0.04$, $p > .05$, nor the second round of testing, Molly: $\chi^2(1) = 3.52$, $p > .05$; Esme: $\chi^2(1) = 0.00$, $p > .05$; Quinn: $\chi^2(1) = 0.00$, $p > .05$; Emily: $\chi^2(1) = 0.04$, $p > .05$. Both test rounds combined revealed that Molly chose the baited arms significantly more often than the unbaited arms, $\chi^2(1) = 5.82$, $p < .05$, whereas no significant difference was found for the other three tortoises, Esme: $\chi^2(1) =$

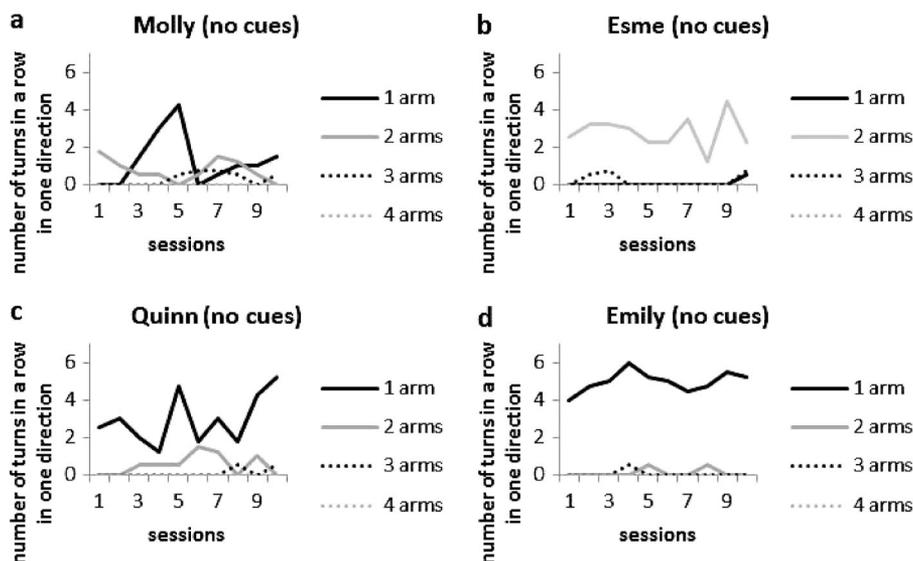


Figure 6. (a–d) Turning behavior of four red-footed tortoises during Experiment 4 with no cues visible: the number of turns in a row in one direction for each turn type in sessions of four trials.

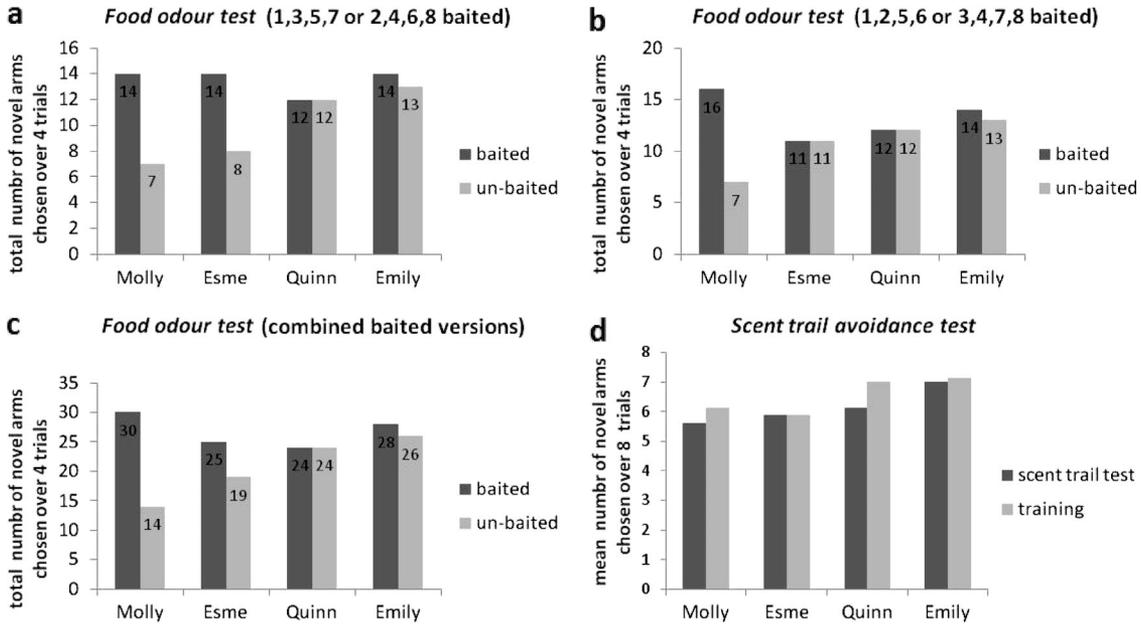


Figure 7. Performance of four red-footed tortoises on two olfactory tests. (a–c) The total number of visits to baited versus unbaited arms in the first test round, the second test round, and the test rounds combined. (d) The mean number of novel arms chosen during the last eight training and the eight scent trail avoidance test trials.

0.82, $p > .05$; Quinn: $\chi^2(1) = 0.00$, $p > .05$; Emily: $\chi^2(1) = 0.07$, $p > .05$.

Scent trail avoidance test. Paired sample t tests comparing test performance to the performance during the last eight training trials found no significant differences for any tortoise with Molly, $t(7) = 0.00$, $p > .05$; Esmé, $t(7) = -1.18$, $p > .05$; Quinn $t(7) = -1.51$, $p > .05$; and Emily $t(7) = -0.24$, $p > .05$ (Figure 7b).

Discussion

In the no-cue condition the maze performance of all four tortoises remained above chance. Quinn and Emily’s turn-by-one arm performance remained high, and Esmé maintained a significant preference for two-arm turns. That no changes in overall performance or turning behavior appeared when all visual cues were removed strongly indicates that the response stereotypy displayed by Esmé, Quinn, and Emily is likely to be a primary mechanism based on a response strategy rather than a secondary mechanism accompanying a memory strategy.

A change of behavior following the removal of all visual cues was observed in Molly, in that her tendency to (slightly) prefer a turn-by-one arm strategy, evident at the end of Experiment 3, was no longer shown. She did not preferentially choose any turn-type but seemed to have developed a strategy based on the smell of the reward that enabled her to keep performance above chance level. The reduction in turn-by-one-arm behavior in response to the total loss of visual cues is in contrast to the increase in this behavior that was shown in response to a partial obstruction of visual stimuli in Experiment 2. Though not conclusive, this pattern of results may indicate that Molly was using the response strategy as a secondary method to facilitate memory-based navigation. It is therefore possible that she used visual, cue-related navigation strategies during

the first three experiments. When no extramaze cues were available during Experiment 4, Molly may have started to use olfactory cues from the reward to solve the task. When cue availability was diminished in Experiment 2, this potential cue-based strategy was not abandoned, but given the increased difficulty of the task, was supplemented by an increase in turn-by-one-arm behavior. This technique for reducing task demands and memory load has also been observed in rats (Dale & Innis, 1986). There is no obvious reason why Molly should have behaved differently from the other three subjects (all of whom showed a tendency to rely on stereotyped responding), but it is noteworthy that Molly was the only tortoise to show a learning curve during Experiment 1, which suggests that she applied a different approach to the other three tortoises from the beginning of the test series.

General Discussion

The results of these experiments indicate that efficient eight-arm radial maze navigation is within the general capabilities of red-footed tortoises. Further, their performance, although slightly inferior to that observed in rats (Olton & Samuleson, 1976), appeared to be similar to that of pigeons (Bond et al., 1981), of another red-footed tortoise (Wilkinson et al., 2009), and a jeweled lizard (Mueller-Paul et al., submitted). Analyses of the tortoises’ choice behavior revealed a preference for response strategies for maze navigation in three of the four animals tested. Thus tortoises, like fish (Hughes & Blight, 1999), appear to have a slightly greater preference for the use of primary response strategies in comparison with pigeons (Bond et al., 1981) and rats (Dale & Innis, 1986), which tend to prefer memory strategies accompanied by secondary response stereotypy. The source of this difference between the behavior of the tortoises and that of birds and mammals may lie in

a difference in error costs. Yoerg and Kamil (1982) have tested rats in mazes of different sizes. They found that increasing the size of the central platform, and with it the cost of errors, increases the use of response stereotypy. This is possibly because response stereotypy, as a primary mechanism, is highly successful in a stable experimental setting. When comparing the ease and speed of moving around the maze rats are likely to be the fastest followed by pigeons, and tortoises are expected to be slowest. Assuming that greater walking ease and speed correspond with lower error cost and a low rate of response strategy, one might expect rats to show the least reliance on response strategies and tortoises the most, with pigeons somewhere in the middle. This is exactly the picture that we found. Future studies could attempt to vary the error cost for the three different species systematically by, for example, adjusting the distance between the arms or the ease of walking in the maze, to test for changes in mechanism preferences.

The studies by Wilkinson et al. (2007, 2009) and the results of Molly in the present study show that at least some tortoises are able to use a memory strategy to successfully navigate in a radial arm maze and that they do possess a certain degree of flexibility in respect to navigation mechanisms. It is possible that this sort of behavior may be characteristic of the natural foraging behavior of tortoises—to rely on a stereotyped response strategies could be disadvantageous of in the wild where circumstances are likely to change frequently. Reliance on a response strategy could be a consequence of the experimental setting in which conditions are highly stable, and such strategies lead to high levels of success while providing the shortest routes and requiring low levels of working memory involvement. This hypothesis could be tested by increasing the level of variability within the experimental setup. Regular variations might encourage the use of memory strategies and demonstrate a more general degree of flexibility in the behavior of the red-footed tortoise.

In conclusion, the radial maze behavior of red-footed tortoises shows strong parallels to that of mammals and birds, in that both response stereotypy and memory strategies can be used. However, in the experimental setup used here, tortoises appear to have a stronger preference for the primary use of response stereotypy than is seen the other amniotes. It is possible that part of this difference can be explained by the cost of errors when navigating the maze.

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