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Visual and response-based navigation in the tortoise (*Geochelone carbonaria*)

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Abstract Much research has investigated spatial cognition in mammals and birds. Evidence suggests that the hippocampus plays a critical role in this; however, reptiles do not possess a hippocampus. It has been proposed that the reptilian medial cortex plays a similar role, yet little behavioral research has directly investigated this. Consequently, this study examined the role of extramaze cues in spatial navigation by the red-footed tortoise (*Geochelone carbonaria*) using an eight-arm radial maze. In Experiment 1 the maze was surrounded by a black curtain on which geometrical shapes were attached. After the tortoise reached above-chance performance we introduced test sessions in which the cues were removed. Performance was unaffected by cue removal. The tortoise appeared to have developed a "turn-by-one-arm" strategy. In a second experiment the curtain was removed and the tortoise was allowed access to a rich-cue environment. The use of the turn-by-one-arm strategy was significantly reduced and the tortoise appeared to be using the extramaze cues to navigate around the apparatus. This type of response-based strategy, and the specific contexts in which it was used, has not been observed in mammals and birds, suggesting that the mechanisms served by the reptilian medial cortex do not parallel exactly those of the hippocampus.

Introduction

Studies of navigation in mammals and birds have shown that they are able to use a range of strategies to navigate to a specific goal. These include the use of a single salient cue (a beacon), path integration, learning a sequence of responses, and creating a spatial representation of environmental cues (a cognitive map). In the latter case the goal is defined by its spatial relation to a number of different landmarks; this may be seen as highly adaptive as the removal of any single landmark does not necessarily disrupt navigation. This behavior is thought to be dependent on the hippocampus (O'Keefe and Nadel 1978). Evidence that demonstrates the use of this navigational system has been found in a variety of mammals and birds (see O'Keefe and Nadel 1978 for a summary), and also, more recently, in fish (for a review see Broglio et al. 2005). As such it is likely that reptiles also possess a similar system, there is some evidence to support this (López et al. 2000, 2001, 2003); however, its existence in this group is much less investigated and the findings are not clear cut (Day et al. 1999, 2001).

The study of spatial behavior in reptiles has a long history (e.g., Tinklepaugh 1932; for a review see Burghardt 1977), but little is known about the mechanisms underlying their navigational ability. It is still not clear whether reptiles are capable of the forms of spatial learning that are seen in mammals and birds. For example, Holtzman et al. (1999) found that corn snakes (*Elaphe guttata guttata*) could rapidly learn the position of a hidden goal in an open field task. Their results (though not designed to test the underlying

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mechanisms) suggested that the snakes used a beacon to navigate to the goal. However, very different results have been found in lizards. Day et al. (1999) examined the different spatial abilities of two closely related lizard species whose foraging strategies differed. They found that neither species preferentially attended to either distal or local cues to navigate. The lizards (of both species) rarely approached the goal directly, suggesting that they found it through trial and error searching. This led the authors to conclude that, if spatial memory exists in reptiles it is fundamentally different from that observed in mammals and birds (Day et al. 1999).

Quite different results have been found in the study of spatial learning in chelonian (turtles, terrapins, and tortoises). López et al. (2000) showed that the terrapin (*Pseudemys scripta*) was capable of learning to approach a given location in a T maze, regardless of the starting position. The terrapins' behavior appeared to be based on extramaze cues and removal of these (using a curtain to block off parts of the experimental room) disrupted performance. The authors suggested that the terrapins were navigating using a cognitive map of the sort that is postulated in mammals and birds. Later findings revealed a flexibility in the use of this strategy. López et al. (2001) required one group of terrapins to navigate to a specific goal solely on the basis of distal cues; a second group had the same distal cues but also had a beacon (a large salient cue) that was located close to the goal. Both groups learned to successfully navigate to the goal, and probe trials revealed that only the group with just the distal cues appeared to make use of a cognitive map-like representation to do so. The beacon group did not use the distal cues and, instead, used the single beacon to locate the goal. This pattern of results suggests that reptilian learning and memory capabilities (in terrapins at least) may closely parallel those observed in mammals and birds.

Further evidence to support this conclusion comes from studies of the cerebral basis of spatial navigation in terrapins. It has been suggested that the reptilian medial cortex serves a parallel function to the mammalian hippocampus (e.g., MacPhail 1982; López et al. 2003). Experiments by López et al. (2003) revealed that lesions to the medial cortex of terrapins caused a change in performance on an open field task when the animals had to use distal landmarks to navigate to a single goal. After a number of post-operative training sessions the lesioned animals were able to learn to navigate to the correct location, with performance equaling their pre-operative level (and the level shown by sham-operated animals). Probe trials revealed that the lesioned terrapins used a modified beacon strategy to locate the goal, whereas the sham-operated animals used a map-like strategy. These results closely parallel those found in mammals and birds and further suggest that the medial cortex performs a similar function to the mammalian/avian hippocampus.

This set of results suggests that reptiles (or at least terrapins) are capable of at least some basic spatial tasks, and that the medial cortex plays an important role in this. However, little is known about the limits of their spatial ability. Previous studies have tested the ability to navigate to one specific area in which the animals were rewarded; however, a more natural task would examine their ability to remember numerous places that they have previously visited to ensure that they do not return to an area in which a food source has already been depleted. The classic task for this test is the radial arm maze.

In a recent investigation, Wilkinson et al. (2007) examined the ability of a single red-footed tortoise (*Geochelone carbonaria*) to navigate in an eight-arm radial maze. The tortoise showed reliable, above-chance performance, preferentially choosing baited arms rather than returning to arms previously visited within a trial. Tests ruled out the use of olfactory cues from either the bait (strawberries), or from the avoidance of odor trails. This suggests that, in spite of differences in brain structure, the tortoise showed spatial learning abilities comparable to those observed in mammals.

The cues that controlled this behavior remain to be determined. As suggested by López et al. (2000, 2001) for terrapins, it is possible that the tortoise is able to identify spatial locations by the configuration of visible extramaze cues that define them. But differences in the behavioral ecology of terrapins and tortoises suggest that it may be unwise to assume that the same mechanisms are used by both. Research with corvids has revealed the importance of behavioral ecology in spatial navigation (for a review see Balda and Kamil 2006). Very different spatial abilities have been observed in closely related species, and species that are phylogenetically disparate but inhabit similar ecological niches have developed similar (highly specialized) spatial memory systems (Kamil et al. 1994). The behavioral ecology of the red-footed tortoise is quite different from that of López's terrapins; the former actively forage for fallen fruit and flowers (Strong 2005; Strong and Fragoso 2006), whereas the terrapin is largely carnivorous whilst young, but as an adult eats largely plant matter (Hart 1983). Moreover, the habitat occupied by the two study species is very different. The red-footed tortoise is terrestrial and lives on the margins of tropical forests (Strong 2005), whereas the terrapin of López's experiments inhabits areas surrounding freshwater lakes, rivers, and ponds. These differences, in conjunction with the differences found within the reptile group itself makes it possible that quite different spatial abilities are present in these closely related species and that the performance of the tortoise may more closely approximate that of a mammal inhabiting a similar ecological niche.

In order to resolve this issue, it is necessary to conduct a study in which the role of extramaze cues in controlling

navigation in the tortoise can be investigated directly. In order to do this we returned to the basic procedure used by Wilkinson et al. (2007) in which the tortoise was trained in an eight-arm radial maze, but changed the nature of the cues available. In the previous study the maze was open to the room. In the present study (Experiment 1) we surrounded the maze with a curtain, but fixed to this a set of cues (simple geometrical shapes) that could be manipulated in a post-acquisition test, to determine the role of extramaze cues in controlling the animal's behavior.

Experiment 1

In this task the animal was initially trained in an eight-arm radial maze. All arms were baited with food and we expected, on the basis of previous findings (Wilkinson et al. 2007) that the tortoise would learn, in the course of a trial, to visit each arm just once. In our previous experiment the maze was open to the room. In this experiment it was surrounded by a curtain to which visual cues were attached. These cues were removed for the post-acquisition test phase.

Method

Subject

A single captive-bred, red-footed tortoise (*G. carbonaria*) participated in this study. She (formerly referred to by Wilkinson et al. 2007 as he) was approximately 4 years old and her plastron (the lower part of the shell) measured 10 cm in length at the start of the experiment. The tortoise, named Moses, had previously been the subject of a similar spatial learning experiment (Wilkinson et al. 2007). A single animal was used in this experiment because it is hard to purchase animals older than hatchlings in the UK. In the first years of life hatchlings of this species remain under leaf litter and move about very little. Moses was purchased by the first author, from a breeder, when she was young. When not involved in an experimental session, Moses was kept in a 61 cm × 30 cm × 30 cm glass tank in an office adjacent to the experimental room. The office was kept on a daily 12L:12D cycle (light on 08:00–20:00). The temperature within the tank was maintained at 29°C (±4°C); humidity was maintained at 50%. Moses had access to food (fruit and vegetables) for 60 min each day; this was given approximately 30 min after the completion of the experimental session.

Apparatus

The apparatus was an eight-arm radial maze made of opaque black Perspex. Each arm was 18.5 cm long and the width at the arm entrance was 10 cm, and widened throughout the arm to reach 25 cm at the end; this allowed the tortoise room to turn. The side walls of the maze were 10 cm high. All arms radiated out of a central octagonal platform, this measured 25 cm in diameter. During training and experimental trials white plastic bottle tops (measuring 3 cm in diameter and 1.5 cm high) were placed at the end of each arm and used as food cups. The lip of the cup prevented Moses from seeing whether food was available until she had fully entered the arm.

The maze was positioned in a small experimental room that was lit by two 60-W ceiling lights and maintained approximately 29°C by an electric heater in the corner of the room. A circular black curtain (diameter 84 cm) surrounded the maze. The length of the curtain extended 86 cm above the maze and obscured all visual cues from the surrounding room. A large circle of card (diameter also 84 cm) was fitted directly above the curtain; this obscured possible ceiling cues. The circular card had a central hole (26 cm diameter) and eight smaller holes (8 cm diameter) placed at regular intervals around the circumference, which provided light to the experimental set-up.

To observe Moses' movements in the maze, an NDS-27 Panasonic video camera was positioned directly above the maze (through the central circle in the card). The underside of the camera (excluding the lens) and beams were covered by plain brown card to prevent them being used as a cue. The camera was connected directly to a video screen in the experimental room; this allowed the experimenter (who remained in the experimental room throughout the experimental session) to view the tortoise's movements without interfering with the experimental set up.

Four brightly colored shapes were pinned to the curtain to provide potential cues for navigation. They were positioned 53 cm (measured from the floor of the maze to the center of the stimulus) above the maze and set at 90° intervals around the circular curtain. Their position on the curtain was at an equidistant point between two arms. This ensured that no single cue could be used to detect whether a specific arm had been visited, but a combination of at least two cues was required. The cues used were a yellow triangle, blue circle, red square (all 256 cm^2), and a green cross (231 cm^2).

Procedure

The experiment was run over a period of 8 weeks from July 2007 to September 2007. All trials took place in the afternoon between 13:00 and 16:00, as this was the time that Moses was most active. Prior to each experimental session Moses was removed from her tank and handled for approximately 5 min. This increased her activity level. She was then placed into a wooden holding cage and transported to the experimental room.

Moses was given 3 days of pretraining to ensure that she moved confidently around and ate readily in the maze. Each pretraining session consisted of a single trial lasting 30 min, in which the tortoise was placed in the maze and allowed to explore. The tortoise had access to all of the arms throughout the experiment. On the first day of pretraining, food (dandelions and strawberries) was scattered throughout the maze. For the following 2 days food was scattered only in the eight arms. By the third day Moses readily entered and ate from all eight arms within the 30 min trial period.

On each of the next 23 days of training, Moses received four trials separated by an intertrial interval of 5 min that was spent in the holding cage. Between each trial the maze was rotated by either 45°, 90°, or 180° to discourage the tortoise from using intramaze cues in conjunction with extramaze cues. During each trial, the experimenter observed and documented the tortoise's behavior via the video monitor. Entering an arm that had not been entered previously was scored as a correct response. At the end of each daily session the maze was wiped clean; it was not cleaned between trials.

In the first phase of training there were 15 daily sessions. At the start of each trial Moses was placed in the central area facing a randomly selected arm. Each food-cup was baited with a piece of strawberry (approximately 2 mm wide and 3 mm in length). The experimenter recorded every arm that Moses entered. She remained in the maze until she had entered all eight arms or 30 min had elapsed. An arm choice was recorded when half of the tortoise had entered the arm (although Moses rarely backed out of an arm after entering that far). After 7 days of training, there were no obvious signs of learning which raised the concern that the position of the cues might be such that they were not easily visible to the subject. At this point, therefore, the vertical position of the cues on the curtain was changed. They were fixed in a position so that the bottom of each was in line with the top of the maze wall (and 10 cm above the level of the maze floor). Moses received training with this arrangement for 8 days.

At this stage a further procedural change was made in the hope of increasing the rapidity of learning. When training rats in a radial arm maze it is common practice to restrict the number of choices allowed on a given trial (e.g., Olton and Samuelson 1976). For the next phase of training we restricted Moses to eight choices per trial, removing her from the maze at this point (or after 30 min).

After performing consistently above chance in the second phase of training in the controlled cue environment we tested the extent to which Moses used the extramaze cues. She received two test sessions. Each was made up of two test trials intermixed with two retraining trials. The first and third trials of each session were the same as in the training sessions, but in the second and fourth trials the cues were removed. Moses' performance was scored in the same manner as for a training trial. If performance was based on using any (or all) of the cues we would expect a total disruption of performance in the test trials.

Results and discussion

For the first 15 sessions of training the subject was allowed as many choices as were needed to complete the maze (enter all eight arms). We scored, for each trial, the number of correct choices in the first eight. (On 14 of the 60 trials of this phase, the subject did not complete the maze within the 30 min allowed; for these we scored the total number of correct responses made). Interestingly, performance on the incomplete trials was rarely less than on equivalent completed ones. Figure 1a presents the daily mean scores. According to Olton (1978), the number of correct responses in the first eight choices to be expected on the basis of chance, is 5.3. (Chance performance is computed assuming that every choice is made at random, without replacement). As the figure shows, mean daily scores differed little from the chance expectation. The mean number of correct responses in the first eight over all days of this stage was 5.68; a one-sample t test comparing this score against chance expectation revealed that it was approaching, but

Fig. 1 a Correct choices in the first eight trials during training in the first phase of the controlled cue environment. **b** Correct choices in the first eight trials during training in the second phase of the controlled cue environment
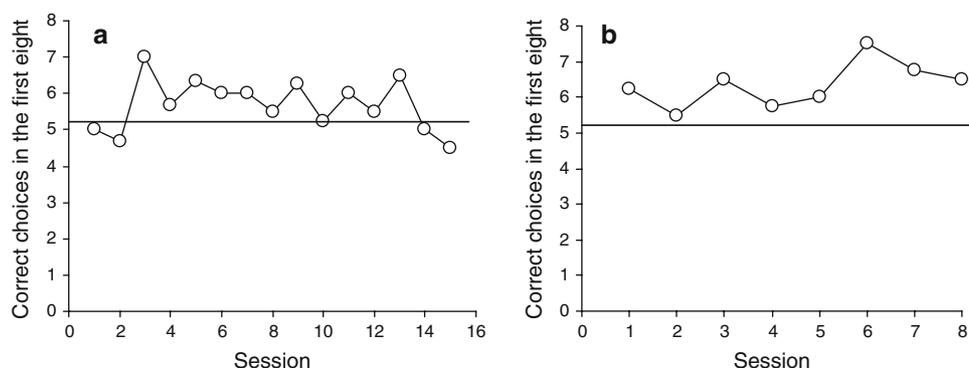
did not reach a significant difference, $t_{14} = 2.05$, $P = 0.06$. As the figure shows, there was no trend toward an improvement over the phase; a separate test of performance over the last eight trials (for which the mean correct score in the first eight choices was 5.88) again revealed no difference from chance, $t_7 = 1.44$, $P = 0.19$.

Figure 1b shows performance over the second phase of training, in which Moses was allowed only eight choices per trial. She successfully completed a total of 31 out of 32 possible trials in this phase. As the figure shows, performance was improved under this training regime. The mean number of correct choices per trial over all 8 days was 6.34, a score that differed from chance $t_7 = 4.72$, $P = 0.002$. The mean score for the last eight trials was 6.63 which again differed from chance expectation $t_7 = 5.04$, $P = 0.002$.

Table 1 shows the number of correct choices made on each trial of the test phase. It is evident that removing the cues produced no disruption of performance. Moses scored on average 7.25 (out of 8) on the test trials and 7 on the intermixed retraining trials. A one-sample t test revealed that both these measures were significantly above chance (5.3), $t_3 = 4.07$, $P = 0.03$ and $t_3 = 4.16$, $P = 0.03$, respectively. Furthermore, a paired sample test revealed that they did not differ significantly from each other $t_3 = -0.52$, $P = 0.64$. This indicates that Moses was not using the available visual cues to navigate the maze.

Examination of the details of her performance within a given trial revealed that Moses' behavior appeared to be determined by a simple, but highly effective strategy, that of turning in a given direction and entering the arm next to the one she had just left. For each of the trials of the second phase of training we scored the number of consecutive choices, after the first that were both in the same direction as the previous choice and were to an arm that was adjacent to it. Figure 2 shows these scores (mean values of the four trials in a day). The figure shows that the mean length of such a run increased dramatically over training; initially, the tendency to turn into an adjacent arm was rather low, but by the end of training the animal was regularly showing
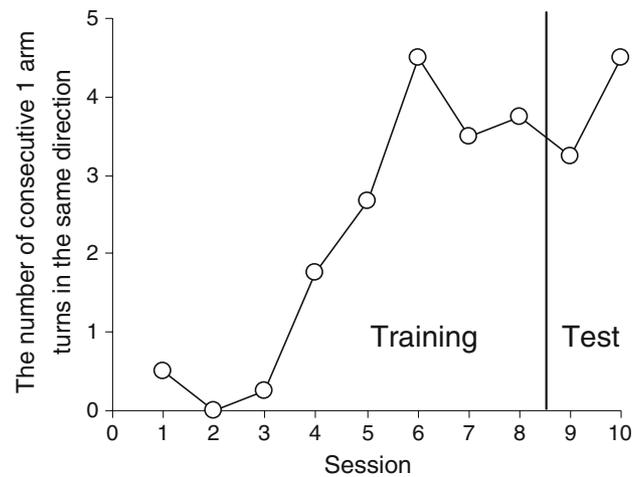
Fig. 2 The number of consecutive one arm turns moving in the same direction in the second phase of the controlled cue environment and the test

runs of four or five such turns. Analysis of the training data (comparing the first four and last four sessions) revealed a significant increase in the choice of arms that were adjacent to the arm that had just been left, and were in the same direction as the previous choice $t_3 = 5.16$, $P = 0.01$. Further analyses revealed a significant correlation between the mean number of correct choices per trial and the use of the turn-by-one-arm strategy $r = 0.58$, $n = 32$, $P = 0.001$. This suggests that this behavior did lead to greater success in the maze. Of the 32 trials in this phase of training, Moses was as likely to turn in a clockwise direction (61 choices) as in an anticlockwise direction (45 choices), $t_{30} = 0.73$, $P = 0.47$.

This response strategy was maintained on the test session. For the four test trials with the cues removed, the mean run-length score was 5.5 and the mean score on the intermixed training trials was 4.5.

In summary, Moses performed well in the radial arm maze and scored above chance for the entire second phase of training when the procedure limited her to eight choices per trial. This behavior was the result of a simple response-based strategy. This strategy was independent of the extra-maze cues as it was maintained during the test in which these were removed. Interestingly, she did not learn a turn-right, or turn-left rule; although within a trial she turned consistently in one direction, the choice of direction varied between trials. Making a choice that is one arm away from the previous choice is unusual in rats (Yoerg and Kamil 1982). This is likely to be due to the constraints imposed by the tight turning circle. These constraints will no doubt apply to the tortoise as well as the rat (perhaps more so), in which case, the strategy adopted by Moses by the end of training was acquired in spite of constraints that would tend to oppose it.

Table 1 Correct choices for each trial of the cue-use test

Retraining trials	Test trials
7	8
7	6
6	7
8	8

There were two test days each containing two retraining and two test trials. Maximum score was 8

In the previous study of Moses' maze behavior (Wilkinson et al. 2007) we found above-chance performance, but no indication that this was based on a response strategy. Exhaustive analysis of response sequences revealed only a slight tendency to preferentially choose arms that were two away from that being exited. There was no tendency to choose adjacent arms. The difference between the results of the two studies must be assumed to lie in some feature of the differing procedures. The most obvious difference is that Wilkinson et al. (2007) gave access to a rich visual environment (the room). In the present experiment the only extramaze cues available were those attached to the curtain surrounding the maze. Although tortoises have good color vision and are able to distinguish the colors that were used as cues (Quaranta 1952) the positioning of the cues with respect to the maze and to each other, or the overall sparseness of the environment (not only were there were less features available, but there was also no geometric information provided by the room) may have prevented the tortoise from using these cues successfully. The use of a response-based strategy may have been dictated by the unavailability of appropriate extramaze cues.

Experiment 2

The findings of Experiment 1 present a stark contrast to those of our previous experiment (Wilkinson et al. 2007). We have suggested that the degraded nature of the visual cues in Experiment 1 may have prevented Moses from using them to navigate, and that the use of the turn-by-one-arm strategy was a result of this. If this were the case then it is possible that, were a full range of extramaze cues made available, Moses might stop using the response-based strategy and revert to using the extramaze cues to navigate. It is also possible, of course, that the development of the response strategy seen in Experiment 1 was the result of the tortoise having had extended experience in the maze.

In order to distinguish between these possibilities we conducted a further study in which Moses was trained in a cue-rich environment that was essentially identical to that of the previous study in which she exhibited no turn-by-one-arm strategy (Wilkinson et al. 2007). If the former hypothesis is correct then we would expect the use of the turn-by-one-arm strategy to decrease when the tortoise has access to the full array of cues from the room. However, if the latter is correct then we would expect no change in behavior.

Method

This experiment began immediately after completion of the test phase in Experiment 1. The same subject was used in this experiment. All housing conditions remained the same. The fabric curtain was removed from the maze so that Moses was able to see the entire experimental room (described below). All other apparatus remained the same.

This set up was almost identical to that used by Wilkinson et al. (2007). External cues that were, in principle, visible from inside the maze included shelving upon which laboratory equipment was stored, a large poster, the experimenter, and a black door (for exact details please see Wilkinson et al. 2007). The experimenter could now observe the tortoise directly, but continued to make behavioral observations via the television screen to ensure consistency over the two experiments. In all other ways, the procedure was the same as described for the second phase of training for Experiment 1. Moses received four trials per session. There were 14 daily sessions of training and Moses completed 53 out of the 56 trials.

Results and discussion

Figure 3 shows the mean number of correct choices per trial for each training session in the cue rich environment. It is evident that performance remained above chance throughout; comparison of the overall mean for each session with chance expectation showed a significant difference, $t_{13} = 6.64$, $P < 0.001$. But analysis of the detailed pattern of responding suggests that the basis of the performance changed over the course of training. As for Experiment 1 we analyzed, for each trial, the number of consecutive selections of an adjacent arm in the same direction of movement. Mean daily scores are shown in Fig. 4. It is clear that use of the turn-by-one-arm strategy declined across days; comparing the mean score for the first four and last four sessions revealed a significant
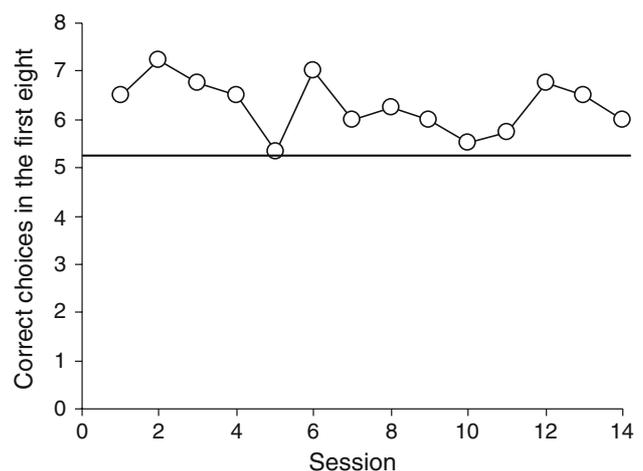
Fig. 3 Correct choices in the first eight trials in the cue rich training environment
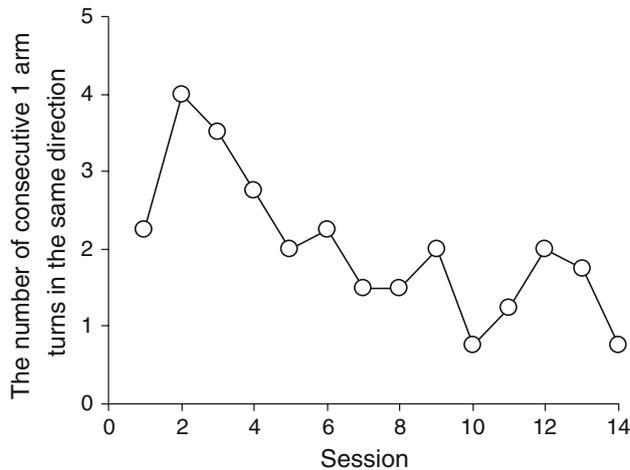
Fig. 4 The number of consecutive one arm turns moving in the same direction in the cue rich environment

difference, $t_3 = 7.13$, $P = 0.006$. Further analysis revealed that in the first four sessions accuracy correlated with the use of the turn-by-one-arm strategy $r = 0.63$, $n = 16$, $P = 0.009$; however, in the last four sessions when use of this strategy was reduced to chance levels, success no longer significantly correlated with strategy use $r = 0.33$, $n = 16$, $P = 0.22$. In fact, by the final session of training the animal's mean run length for turns into the adjacent arm was just 0.75; nonetheless, overall navigational accuracy remained above chance.

This change in performance indicates that the response-based strategy developed in Experiment 1 was a consequence of the particular cue environment used in that study; when the full set of extramaze cues was made available the animal reverted to behavior like that previously seen in the study by Wilkinson et al. (2007). It is not clear what elements of the visual environment are relevant to the change in behavior. It is possible that the turn-by-one-arm strategy was a response to the general poverty of the visual features within the environment; however, the introduction of the curtain also resulted in a change in the geometric information available. Geometric information has been shown to be a powerful environmental cue for animal spatial navigation (e.g., Cheng 1986, for a recent review see Cheng 2008). This experiment cannot clarify which environmental cues contributed to the tortoises change in behavior; however, what is clear is the intriguing flexibility of behavior displayed by the tortoise. Navigation on the basis of the visual environment appears to be in some sense the preferred option; but when appropriate visual cues are not available, the animal adopts a simple and effective response-based strategy. When visual cues are made available this strategy is abandoned.

General discussion

Wilkinson et al. (2007) demonstrated efficient radial maze performance in a tortoise. There was no evidence of a response-based strategy; rather the behavior appeared to be controlled by extramaze cues, paralleling that shown by rats in the same situation. The original aim of the present study was to examine directly the role of extramaze cues by training the tortoise in an apparatus with a restricted range of cues that could be manipulated by the experimenter. This aim could not be fulfilled as, when trained in an impoverished cue environment in Experiment 1, Moses learned to use a simple but efficient strategy to navigate through the maze—to turn consistently in one direction, selecting the arm adjacent to the one that she had just left. In Experiment 2, when the curtain was removed and the cue environment was comparatively rich (both in terms of features and the geometric information available), the use of the turn-by-one-arm strategy significantly decreased. Accurate performance was nonetheless maintained. This suggests the presence of two navigational processes in the tortoise. The use of visual cues appears to be a default behavior which is used if it is possible for the tortoise to do so. The second is a response-based strategy that allowed the tortoise to navigate the maze in a highly successful manner. It seems that by surrounding the maze with a curtain and presenting only four distal visual cues in Experiment 1, the amount of visual information available was reduced to a level that prevented the tortoise from using the extramaze cues to navigate.

This pattern of behavior is quite different from that shown by rats in a similar situation. Rats in a cue-impoverished environment (e.g., Mazmanian and Roberts 1983) and even blinded rats (e.g., Zoladek and Roberts 1978) do not normally exhibit such response-based behavior. An exception is found in studies by Einon (1980) and Roberts and Dale (1981); both experiments observed response-based strategies in a cue-rich environment, and neither saw the dramatic changes in the behavior that were observed in our tortoise. However, in the latter experiment (Roberts and Dale 1981) the effects of proactive interference between trials reduced over time, suggesting an improvement in the use of the response-based strategy. Einon (1980) systematically examined the cause of the response-based behavior and found that it was only present in immature rats. This prompts the hypothesis that the strategy observed in the maze may be related to changes in foraging behavior over the life cycle. The nutritional requirements of immature rats (those required for growth) are quite different from what is needed to maintain health at maturity (Clarke 1980). The diet of wild-living rats (*Rattus rattus*), reflects this and because of natural variation in the distributions of food types, wild foraging behavior does change with age (Clarke

1980). But whatever is true of rats in this sort of analysis cannot account for our findings in the tortoise. Moses' search behavior changed because of cue availability (or her ability to use the cues that were available); it was not a result of changes in her development, suggesting that the processes involved in her search behavior differ from those observed in rats (and other mammals).

This response-based navigational behavior has also been observed in fish (Roitblat et al. 1982; Hughes and Blight 1999). Like the rat studies (Einon 1980; Roberts and Dale 1981), the former study did not take place under limited cue conditions. However, the latter study tested fish in both a cue-rich and cue-impoverished environment. The aim was to directly test the role of behavioral ecology in spatial search behavior. The authors used two species of fish (*Spinachia spinachia* and *Crenilabrus melops*) that inhabit highly structured tidal zones in which visual cues are provided by rocks and weeds. However, rough weather frequently results in these features being obscured. Thus the authors predicted that the fish would be able to use both response-based and spatial cue-based navigational strategies.

Their experiment goes some way to supporting our data. They found that in a cue-rich environment the fish were able to use cues to navigate; however, in the impoverished cue environment the fish used a response-based strategy. Interestingly, both species were significantly less good in the non-cue than in the cue condition; this is quite different from Moses' behavior. Furthermore, their experiment was run between subjects, so it is not possible to know whether the fish would change from a successful response-based strategy to a cue-based strategy with a change in the cue environment. The authors interpreted their results as being due to the behavioral ecology of the two species that were tested (both lived in tidal zones). However, to our knowledge these specific tests have not been given to non-tidal species of fish, thus, it is possible that this behavior is common to all fish (and maybe reptiles).

The small amount of literature available on spatial behavior in reptiles does not provide any previous observations of the animals using a response-based strategy to navigate. Such evidence as there is for the use of multiple memory strategies in chelonian comes from the study of López et al. (2001) who found that terrapins were able to use both a salient (beacon) cue and a map-like representation to navigate to a single goal. The animals in this set of experiments, however, were tested in a between-subjects design, which did not allow examination of the possibility of changes between these strategies in a single animal. In contrast, in our Experiment 2 we found that Moses showed a change of navigational strategy according to environmental circumstances. It is interesting that she did not need to change her behavior to successfully navigate the maze in the cue rich environment; continuing with the turn-by-one-

arm strategy would have maintained a high level of performance. The only comparable example of such flexibility can be seen in the lesioned terrapins of López et al. (2003) that had to re-learn to navigate to a goal post-operatively. The lesions appeared to prevent them from using the map-like representation that was observed in the training phase (and in the sham-operated animals), and thus they were forced to learn a beacon-type strategy to reach the goal. It is unclear, however, why the changes in Moses' navigational behavior occurred. Our results suggest that the use of visual cues is a default strategy that will be overruled when effective visual cues are not available. It is not clear whether the same is true of the fish tested by Hughes and Blight (1999); however, there is a clear similarity in behavior between their fish and our tortoise.

In sum, these findings suggest the presence of two processes that can control navigation in our tortoise. One appears to be based on visual cues. It is apparently similar to the cognitive-map mechanism employed by rats; but our attempt to investigate this directly in Experiment 1 was thwarted by the animal's use of a different mechanism. This second mechanism involves a simple response-based strategy of a sort not usually observed in mammals, but appears to be present in at least some fish. This pattern of findings suggest that when tortoises (or at least this tortoise) navigate in a situation with poor environmental cues they use a simple, but efficient response-based strategy; but when more cues are available they switch away from this, and apparently navigate using the surrounding visual cues. This behavioral flexibility may reflect the behavioral ecology of the specific species tested, or it may be true of chelonia and possibly reptiles and fish in general.

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