

# Place and cue learning in turtles

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Turtles (*Pseudemys scripta*) were trained in place, cue, and control arm maze procedures. The turtles learned both tasks with accuracy. Subsequent probe and transfer trials revealed guidance and mapping strategies by the cue and the place groups, respectively. Thus, the turtles in the cue procedure solved their task by directly approaching the single individual intramaze cue associated with the goal, whereas the animals in the place task seemed to be using a maplike representation based on the encoding of simultaneous spatial relationships between the goal and the extramaze visual cues. Furthermore, the turtles in the place task were able to navigate with accuracy to the goal from unfamiliar start places, and their performance was resistant to a partial loss of relevant environmental information. The results reveal for the first time, to our knowledge, spatial learning and memory capabilities in a reptile that closely parallel those described in mammals and birds.

Throughout the last century, considerable experimental effort has been devoted to the analysis of spatial learning and memory in mammals and birds. From this analysis, it seems obvious that the spatial behaviors of mammals and birds share a number of characteristics. Mammals and birds are able to orient to and navigate in their surroundings by means of different mechanisms—as, for example, by learning a particular sequence of responses to a goal (i.e., *orientation*; Mackintosh, 1965; Restle, 1957; Scharlock, 1955), by integrating their own spatial displacements over time (i.e., *dead reckoning*; Etienne, Hurni, Maurer, & Séguinot, 1991; Mittelstaedt & Mittelstaedt, 1982; St. Paul, 1982), by learning to directly approach an individual cue as if it were a beacon (i.e., *guidance learning*; Brodbeck, 1994; Clayton & Krebs, 1994; Cook & Tauro, 1999; Deutsch, 1960; Roberts & Pearce, 1998), or by means of a variety of other egocentrically referenced representations of landmarks (i.e., *local views* or *snapshot mechanisms*; Cartwright & Collett, 1983; Leonard & McNaughton, 1990).

In addition to these discrete cue representations and nonrelational mechanisms, mammals and birds can learn the location of a goal by means of encoding its spatial relationships with a number of distant landmarks in a maplike representation that provides a stable frame of reference (i.e., *place learning*; Bingman, 1992; Gallistel, 1990; O'Keefe & Nadel, 1978; Poucet, 1993; Tolman, 1948). The use of such cartographic representations endows spatial behavior with considerable flexibility in adapting readily to environmental changes (Nadel, 1991, 1994; O'Keefe, 1991b; O'Keefe & Nadel, 1978; Thinus-

Blanc, 1996). Hence, mammals and birds that rely on such an allocentrically referenced topographic representation of their environment can navigate accurately toward a place from different directions and adopt shortcuts and novel routes from places previously unvisited, even in the absence of local cues (Bingman, 1992; Gallistel, 1990; Nadel, 1991; O'Keefe & Nadel, 1978; Thinus-Blanc, 1996; see also, for fishes, Rodríguez, Durán, Vargas, Torres, & Salas, 1994). Another remarkable property of navigation based on cognitive mapping is that it is resistant to the partial loss of relevant information. Since cognitive maps store redundant environmental information, when a subset of spatial cues become unavailable, accurate navigation can still take place on the basis of those that remain (Barnes, Nadel, & Honig, 1980; Jacobs, Thomas, Laurence, & Nadel, 1998; Mazmanian & Roberts, 1983; O'Keefe & Conway, 1978; Pico, Gerbrandt, Pondel, & Ivy, 1985; see also, for fishes, López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 1999; Rodríguez et al., 1994). In contrast, when strategies based on egocentrically referenced representations are used—for instance, approaching one particular landmark or beacon (guidance or cue learning)—the disappearance of that particular cue is sufficient to disrupt performance (O'Keefe & Nadel, 1978).

Considerable information has been obtained on the navigation mechanisms of mammals and birds. On the other hand, little is known about the spatial learning and memory capabilities in vertebrates other than mammals and birds. In particular, the scarcity of experimental works specifically aimed to investigate spatial learning mechanisms in reptiles is surprising, since amniotes (reptiles, birds, and mammals) appear to be a monophyletic group that evolved from a single stock of primitive tetrapods during the early Carboniferous (Carroll, 1988; Gaffney, 1980; Gauthier, 1994; Gauthier, Kluge, & Rowe, 1988; Hedges & Poling, 1999; Rieppel, 1995; Romer & Parsons, 1977). Within this context, the study of the spatial abilities of tur-

This work was supported by Grants PB96-1334 from Spanish DGES and CVI-242 from Junta de Andalucía. We thank Gerardo Labrador and Eduardo Cueto for technical help. Correspondence concerning this article should be addressed to J. C. López, Laboratorio de Psicobiología, Universidad de Sevilla, Avda. de San Francisco Javier, s/n, 41005 Sevilla, Spain (e-mail: jclopez@cica.es).

tles is of the utmost interest, since most hypotheses on the evolution of amniotes propose that Chelonia diverged early in evolution from the Cotylosauria or stem reptiles, the common ancestors of present-day reptiles, birds, and mammals (Benton, 1988, 1997; Romer, 1966). In addition, turtles, the only living chelonians, are thought to have retained several features from their primitive ancestors (Carroll, 1969; Gaffney, 1975, 1979; Mlynarski, 1976; Northcutt, 1970; Riss, Halpern, & Scalia, 1969). Thus, comparative research with turtles and other reptilian orders is called for, not only to elucidate the organization of the spatial learning and memory systems in living amniotes, but also to understand the evolution and adaptive importance of spatial information processing in vertebrates.

The aim of the present work was to study spatial learning and memory capabilities in turtles and to analyze the possible similarities to and differences from those described in mammals and birds. More specifically, the present experiment was designed to study whether turtles show both the capability to use simultaneously a number of distal visual cues to learn the location of a goal (place learning) and the ability to use the information provided by a single intramaze cue or beacon to reach a goal (cue learning). An additional objective of this experiment was to determine whether the turtle's place learning shares some particular properties with that of mammals and birds—that is, resistance of the performance to the partial elimination of extramaze cues and the ability to reach the goal by adopting new routes from novel start locations.

In order to obtain comparable results in turtles and other vertebrates, the use of analogous procedures was required. Among the procedures most often used to analyze spatial learning and memory are those that employ radial arm mazes (see Olton, 1979; Rodríguez et al., 1994). In these maze procedures, the spatial requirements of the tasks can be clearly defined, and transfer tests can be conducted in order to reveal the nature of the learning strategies implemented by the animals. In the present experiment, turtles were trained in one of three different procedures (place learning, cue learning, and control). Then, probe and transfer trials were conducted to analyze the characteristics of the navigational strategies used by the turtles to locate the goal.

## METHOD

### Subjects

The subjects were 24 experimentally naive turtles (*Pseudemys scripta*), 10–12 cm in shell length. For 2 months prior to the experiment, the turtles were housed in small groups in glass aquaria (100 × 50 × 75 cm) containing a 20 × 20 cm dry platform. The animals were kept on a 14:10-h light:dark cycle, at a temperature of 23°C ± 1°, and were fed twice a day during this time. Two days prior to the experiment, the animals were deprived of any food. Throughout the experiment, the turtles consumed only the three food sticks they obtained every day in the experimental session. Each stick was 20 ±

0.8 mg (mean ± SD) of dry food (Tetra pond, Ulrich Baemsch GmbH, Melle, Germany).

### Apparatus

The apparatus was an elevated four-arm maze made out of Perspex, with transparent walls and a white opaque floor. Only three of the arms were used for the training and probe trials, whereas the four arms of the maze were used during the transfer trials. Each arm was 75 cm long, 15 cm wide, and 15 cm high, with a 15 × 15 cm central platform. A guillotine door (15 cm high) made out of white Perspex, placed 15 cm from the end of one arm, was used to close the start compartment for each trial. These doors were controlled from a distance by a hand-operated pulley system. The access to the arm not used in each training trial was blocked by means of a 15-cm-high removable barrier. Before every session, the maze was filled with aerated and filtered water at 23°C ± 1°, to a depth of 3 cm. Previous observations revealed that some water in the maze facilitated the displacements of the animal. The maze was installed at a height of 50 cm on a rotatory wheeled table that enabled easy maze rotations and displacements according to experimental requirements. The maze was placed in the center of a room 4.8 m wide × 5 m long × 3.1 m high that presented abundant distal visual cues. The arrangement of the room, the various extramaze cues, and the location of the maze during training trials are shown in Figure 1.

Illumination was provided by four 100-W halogen lamps, placed equidistantly on the ceiling. In addition, the ceiling presented an anchorage device for a removable top-to-floor curtain that could surround the maze and was employed to conceal the distal extramaze cues during probe trials. To exclude the possible use of uncontrolled intramaze cues by the turtles, the maze was randomly rotated between the experimental sessions. For each training trial, removable feeders were fixed to the floor of the maze at a distance of 5 cm from the end of each of the two accessible arms. These feeders consisted of a 4-cm-high dark food cup presenting a 1.5-cm-deep cavity at the top, where a food stick could be hidden. The food was not visible, but the turtle removed it by lifting its head over the feeder. The goal arm was the one containing the baited cup.

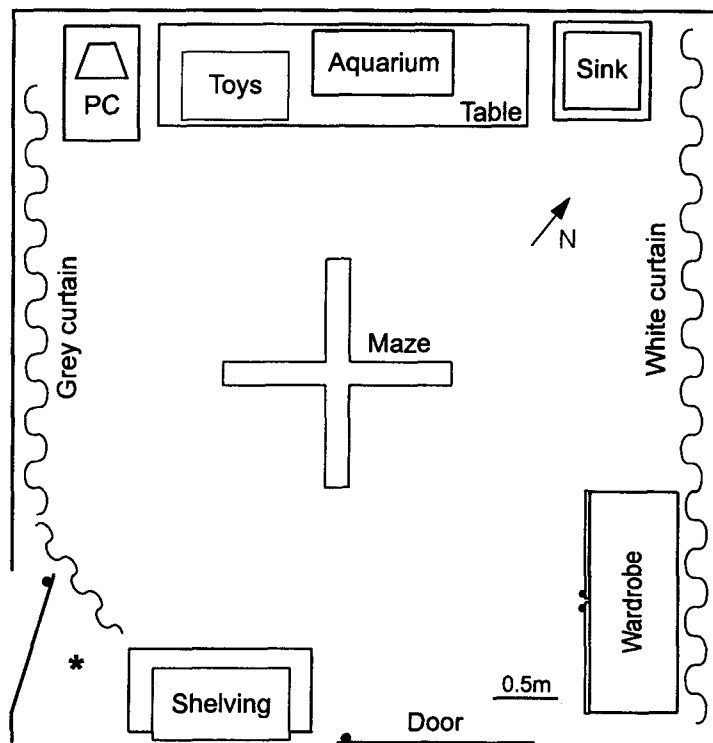
During the trials, the observer remained in an adjacent enclosure, from which he controlled the guillotine doors of the maze and observed the behavior of the turtles through a small opening.

### Procedure

**Pretraining.** Following a 2-day period of food deprivation, the turtles were trained during 4 consecutive days to obtain food from the experimental feeder. With this aim, the turtles were individually placed in a small aquarium (40 × 30 × 30 cm) provided with a food cup that was successively baited with a food pellet until the subject consumed three pellets. This aquarium was placed in a room adjoining the experimental room. Simultaneously, pretraining to the maze and to the experimental room was carried out in daily 1-h sessions, in which the animals were allowed to explore freely throughout the maze. The food holders and the opaque barriers were removed from the maze during these pretraining sessions. Following the pretraining period, the turtles were deprived of any food for 2 days prior to the experiment proper.

**Training.** The turtles were randomly assigned to one of the following experimental procedures: *place procedure* ( $n = 8$ ), *cue procedure* ( $n = 8$ ), and *control procedure* ( $n = 8$ ).

**Place procedure.** This procedure was designed to study whether turtles could learn to locate the rewarded place on the basis of the information provided by the distal extramaze cues. In this task, two opposite start points were used in a pseudorandom order (southwest [SW] arm, 50%, and northeast [NE] arm, 50%), but the goal arm remained in the same place in the room throughout the whole exper-



**Figure 1.** Plan to scale of the experimental room, showing the plus maze and the arrangement of distal visual cues. The maze is represented in the position used for training trials. The asterisk shows the position of the experimenter.

iment (see Figure 2). Note that no fixed-turn strategy was adequate to solve this task, since the animals were required to make a left or a right turn, depending on the start position. Goal location was counterbalanced, so that half of the animals in this group were trained to obtain the reward in the NW arm, as shown in Figure 2, and the remaining animals obtained the reward on the SE arm.

**Cue procedure.** This procedure was designed to determine whether the turtles could learn to identify the goal on the basis of the information provided by a single intramaze visual cue (Figure 2). Thus, the animals always obtained the reward in the arm presenting a conspicuous intramaze visual cue consisting of a red removable panel ( $14 \times 22$  cm), fixed at the end of the goal arm. For each training trial, goal location was assigned in a pseudorandom order between the two possible positions (NW arm, 50%, and SE arm, 50%), so extramaze cues were irrelevant to task solution (see Figure 2). Thus, in this procedure, the goal could be found by reference to a beacon, but not to more distant landmarks. In addition, two opposite start arms were used pseudorandomly (SW arm, 50%, and NE arm, 50%).

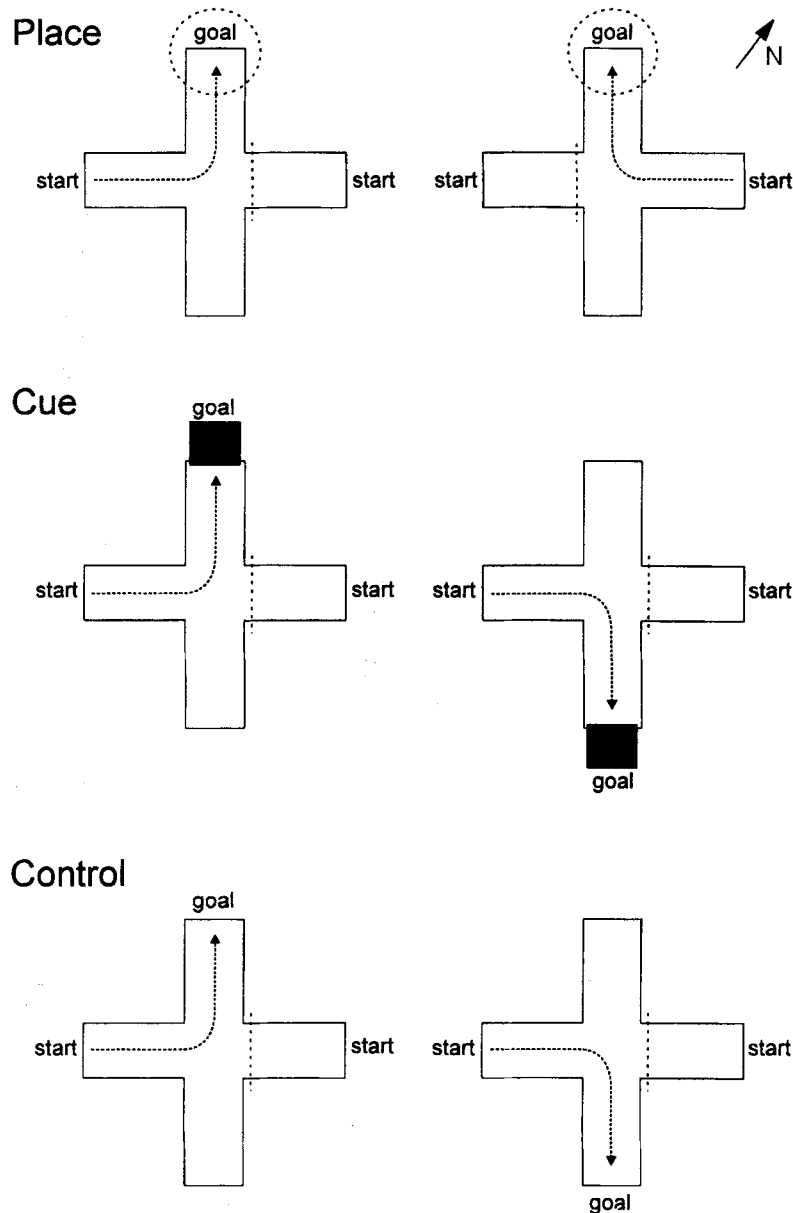
**Control procedure.** This procedure was designed to control the possibility that the turtles could find the reward by attending to odor traces or other uncontrolled variables (Figure 2). With this aim, the animals in this group were released pseudorandomly from two opposite start arms (SW arm, 50%, and NE arm, 50%), and also the position of the baited arm was pseudorandomly assigned between the two possible ones (NW arm, 50%, and SE arm, 50%) for each trial.

The animals were individually trained in daily three-trial sessions. To begin each trial, the turtle was carefully placed in the start box and confined there for 15 sec. Then, the guillotine door was raised and was lowered after the animal left the start box, allowing

the turtle to perform free displacements in the accessible arms. A choice was recorded when the turtle traveled 15 cm into the selected maze arm. The subject remained in the maze until the reward had been consumed (correction procedure) or until 20 min had elapsed. At the end of the trial, the turtle was gently removed from the maze and returned to the home aquarium for a 50-min intertrial interval. A trial was considered correct only when the first choice was correct. Error choices and time employed to obtain the reward were also recorded. The learning criterion was established as 13 correct trials out of 15 (a mean of 86.67% correct over five consecutive sessions). When the animals reached the criterion, additional postcriterion sessions were conducted, during which the probe and the transfer trials were interspersed.

**Probe and transfer tests.** These tests were aimed to determine the strategies employed by the turtles to solve the different tasks. When the animals reached the learning criterion, transfer and probe trials were interspersed in a pseudorandom order between postcriterion training trials. During transfer and probe trials, the feeders were removed from the maze; thus, reinforcement was not available. On any given session, only one transfer or probe trial was performed, and at least three training trials were conducted between any two probe or transfer trials.

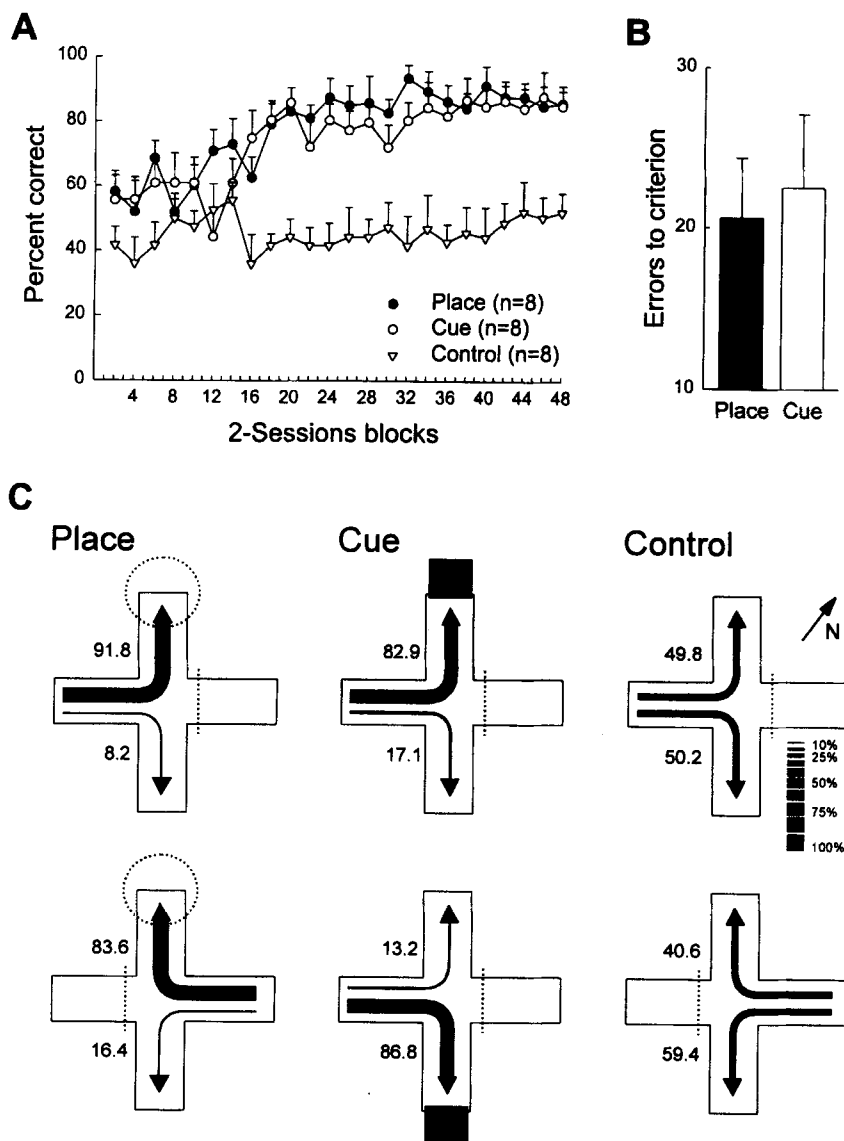
**Probe trials.** Three types of probe trial (Types I, II, and III) were performed to study the relevance of the extramaze distal cues in the solution of the place and cue tasks. See Figure 5 for a schematic representation of the probe trials. In Type I trials, all of the extramaze visual cues were simultaneously concealed by surrounding the entire maze with a curtain. In the cue group, the intramaze visual cue that signaled directly the baited feeder during training trials was maintained during these probe trials. In Types II and III



**Figure 2.** Experimental procedure: schematic diagrams of the three training procedures. *Place procedure:* The goal was maintained always in the same place in the room throughout training, but two start positions were used randomly (50% each). The diagram shows the goal location for one half of the animals in the place group; for the other half, the procedure was identical, except that the goal was placed on the opposite arm. *Cue procedure:* A conspicuous intramaze visual cue (gray panel) signaled directly the location of the goal, but the position of the cue (goal) varied in a pseudorandom order from trial to trial; in addition, two opposite start arms were used randomly (50% each). *Control procedure:* The location of the goal varied in a pseudorandom order from trial to trial; in addition, two opposite start arms were used randomly (50% each). The dotted line shows the position of the barrier blocking the access to the arm not used on a given training trial.

probe trials, the curtains concealed one half of the extramaze distal cues. During Type II trials, for the turtles trained in the place procedure, the curtains concealed the extramaze cues placed in the proximity of the goal location during training trials. For the cue group, during these trials the curtains concealed the extramaze visual cues placed in the proximity of the arm showing the intramaze visual

cue. In Type III probe trials, the most distant extramaze visual cues, relative to goal location, were excluded for the place group. Similarly, for the turtles trained in the cue procedure, in Type III probe trials, the curtains concealed the distal visual cues opposite to the arm that presented the intramaze cue. The animals in the control group were subjected to the same probe trials as the turtles in the



**Figure 3.** (A) Percentage of correct choices for each group during the training trials. For each procedure, the first 48 days of training were included, because some animals had completed the training by that time. Error bars denote *SEM*. (B) Mean number of errors to reach the criterion. (C) Schematic representation of the trajectories chosen during post-criterion training trials. The arrows' relative thickness and numbers denote the percentage of times that the choice was made. The dotted line shows the position of the barrier blocking the access to the arm that was not used. In the place procedure, the dotted circle represents the location of the goal. In the cue procedure, the gray panel indicates the position of the intramaze cue. For the cue group, the data from trials starting in the southwest and northeast arms are collapsed.

place group. In addition, Type IV probe trials were conducted with only the animals trained in the cue procedure. In these trials, the intramaze visual cue that signaled the baited arm was removed. Similar to the training trials, two start positions were used randomly during probe trials. Four probe trials of each type were conducted for each animal.

**Transfer trials.** Different transfer trials, in which the animals started from novel start positions, were conducted. These trials were designed to study whether the turtles trained in the place procedure solved the task on the basis of place strategies—that is, whether the turtles showed the capability to reach the goal regardless of start

position and whether they were able to adopt novel routes to the goal. In addition, these transfer trials were conducted to test whether the animals in the cue procedure solved the task by means of a guidance strategy, approaching the intramaze cue directly associated to the goal. See Figures 6–8 for a schematic representation of the transfer trials. In some of the transfer trials, the maze remained in the same position as that used during training trials; however, a new start position, never employed during training, was used. In the remaining transfer trials, the maze was displaced to different positions within the room in such a way that, for the animals trained in the place procedure, the end of one of the arms occupied

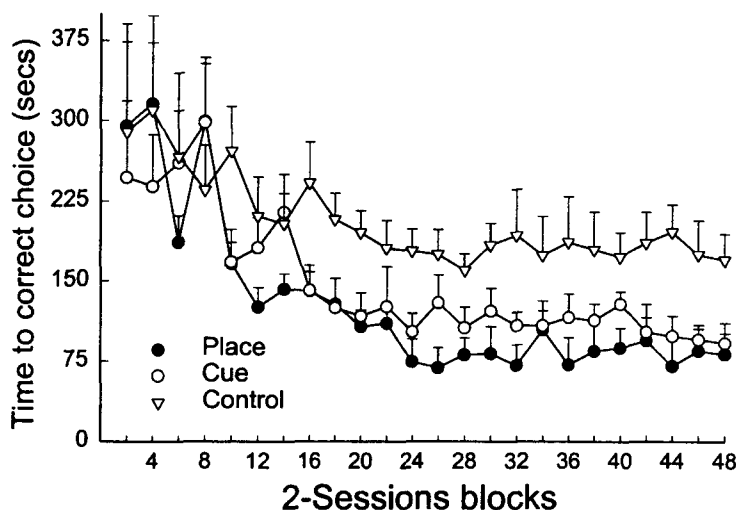


Figure 4. Mean time to obtain the reinforcer during training trials.

the same place in the room as that at which the animals obtained the reward during training trials. For the animals trained in the cue procedure, transfer trials were similar to those employed in the place procedure, except that the intramaze cue signaling the baited arm during training trials was maintained. Finally, the animals in the control group were submitted to the same transfer trials as the turtles in the place procedure. For each animal, 18 transfer trials were conducted. During transfer trials, all of the maze arms remained opened, enabling the animals to choose freely among all of them.

During probe and transfer trials, only the first choice was recorded, and then the animal was removed from the maze. A choice was recorded as a place response when, regardless of start position and turn direction, the turtle reached the place at which the reinforcement was available during training trials. A choice was recorded as a cue response when the animal selected the arm presenting the intramaze visual cue. All of the choices that could not be classified as place or cue responses were recorded as *other*.

## RESULTS

### Acquisition

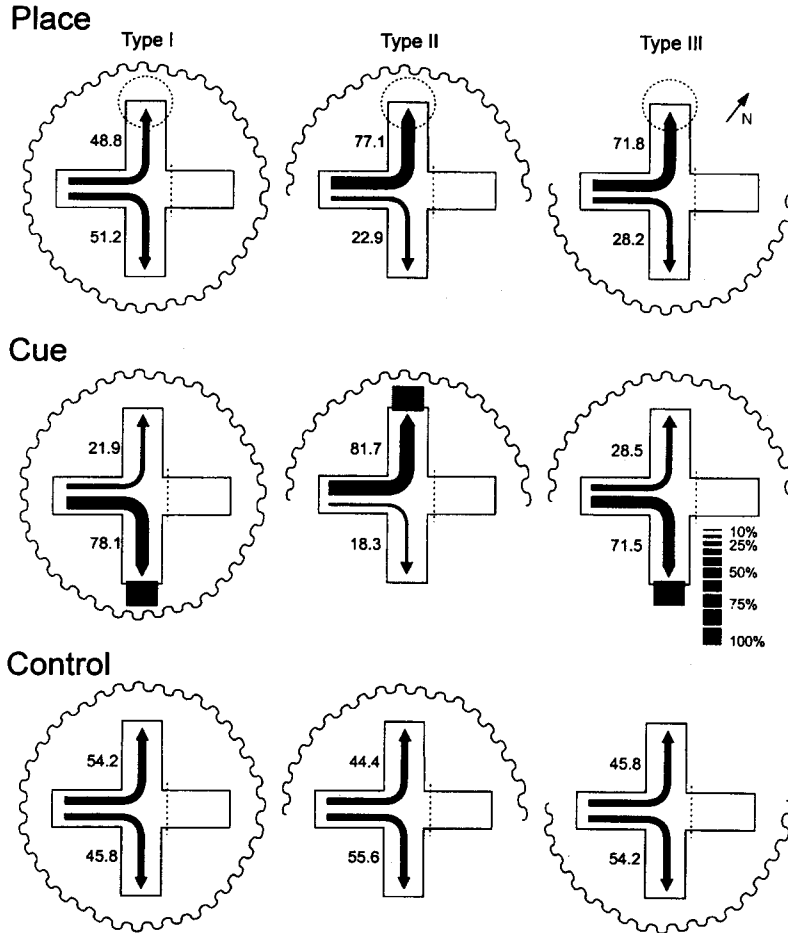
The turtles in the place and cue tasks accurately learned to find the baited arm. Figures 3 and 4 show the performance of the animals in the three groups during training. No statistically significant differences were observed between the counterbalanced conditions in the place group (Mann-Whitney, all  $U$ s > 4, all  $p$ s > .13), so these data are collapsed in the group averages.

On the initial training sessions, the percentage of correct choices by the different experimental groups was close to chance level (place: 58.49%  $\pm$  15.43%, mean  $\pm$  SEM; binomial test,  $p$  = .13; cue: 55.55%  $\pm$  27.21%; binomial test,  $p$  = .36; control: 41.67%  $\pm$  13.94%; binomial test,  $p$  = .08); thus, no significant between-groups differences were observed [Kruskal-Wallis,  $\chi^2(2)$  = 3.4,  $p$  = .18, for the three initial training sessions; Figure 3A]. On subsequent sessions, the performance of the animals trained in the control procedure remained close to chance level [Friedman,  $\chi^2(23)$  = 22.75,  $p$  = .47; Figure 3A]. In contrast, the percentage of correct responses by the turtles

trained in the place and cue procedures improved with training [Friedman,  $\chi^2(23)$  = 61.64,  $p$  < .01, and  $\chi^2(23)$  = 36.4,  $p$  = .03, for the place and cue groups, respectively; Figure 3A]. Thus, statistically significant differences were observed in the performances of the place and the cue groups, relative to the control group, from Session 15 to the end of the experiment [Kruskal-Wallis,  $\chi^2(2)$  = 10.44,  $p$  < .01; Figure 3A]. The turtles trained in the place and cue procedures reached the learning criterion approximately at the same time (place: 20.63  $\pm$  3.74 sessions; cue: 21.33  $\pm$  4.16 sessions). No statistically significant between-groups differences in the number of errors to reach criterion were observed (Mann-Whitney,  $U$  = 24.5,  $p$  = .68; Figure 3B).

During the 38 postcriterion training sessions, during which transfer and probe trials were interspersed, the turtles in the place and cue groups maintained a high and steady level of accuracy in the solution of their tasks (place: 87.74%  $\pm$  4.68% correct choices; cue: 84.86%  $\pm$  2.82% correct choices; Figures 3A and 3C). No significant differences were observed between the place and the cue groups during the postcriterion trials (Mann-Whitney,  $U$  = 18.5,  $p$  = .15; Figure 3A). Nevertheless, these two groups continued to show significantly better performance than did controls (place vs. control: Mann-Whitney,  $U$  = 2,  $p$  = .002; cue vs. control: Mann-Whitney,  $U$  = 0,  $p$  = .001), which remained close to chance level (45.21%  $\pm$  5.28% correct choices; Figures 3A and 3C). The control group data show that uncontrolled variables, such as chemosensory cues or direct visual location of food, were not responsible for the accuracy level observed in the place and cue groups.

The time it took to get food for the place and cue groups decreased quickly during training, showing a statistically significant decrement between initial sessions and subsequent training [Friedman,  $\chi^2(23)$  = 105.1,  $p$  < .01, and  $\chi^2(23)$  = 62.7,  $p$  < .01, for the place and the cue groups, respectively; Figure 4]. In contrast, the animals in the



**Figure 5.** Schematic representation of the trajectories chosen during Types I, II, and III probe trials for each group. The arrows indicate the trajectories chosen from the start position; their relative thickness and numbers denote the percentage of times that the choice was made. The dotted circle in the place procedure represents goal location during training trials. The gray panel indicates the position of the intramaze cue. The data from trials starting from the southwest and northeast arms are collapsed.

control group did not decrease significantly the time it took to obtain the food [Friedman,  $\chi^2(23) = 27.7$ ,  $p = .18$ ; Figure 4]. During the postcriterion training sessions, the time it took to obtain the reward was significantly lower in the place and cue groups, relative to the control animals (place vs. control: Mann–Whitney,  $U = 3$ ,  $p = .01$ ; cue vs. control: Mann–Whitney,  $U = 4$ ,  $p = .01$ ). No statistically significant differences were observed between the place and the cue groups (Mann–Whitney,  $U = 16$ ,  $p = .16$ ; Figure 4).

#### Transfer and Probe Trials

The results of the transfer and probe trials showed remarkable differences, relative to the strategies employed by the turtles to solve the place and the cue tasks. Figures 5–8 summarize the results obtained in the transfer and probe trials.

**Probe trials.** In Type I probe trials, in which the curtains excluded all of the distal visual cues simultaneously, important differences in the performances of the different groups were observed. In Type I probe trials, the performance of the animals trained in the place procedure decreased to random level; that is, no statistically significant differences were observed between place responses and other choices (Wilcoxon,  $Z = .01$ ,  $p > .05$ ; Figure 5). In addition, the percentage of place responses during Type I trials by the turtles in the place procedure was significantly lower than that observed during training trials (Wilcoxon,  $Z = 2.21$ ,  $p = .027$ ) and that observed during Types II and III probe trials (Wilcoxon,  $Z = 2.2$  and  $Z = 2.5$ , both  $ps < .05$ , for place responses in Type I vs. Type II and Type I vs. Type III probe trials, respectively; Figure 5). In Types II and III probe trials, in which the distal visual cues were partially excluded, the

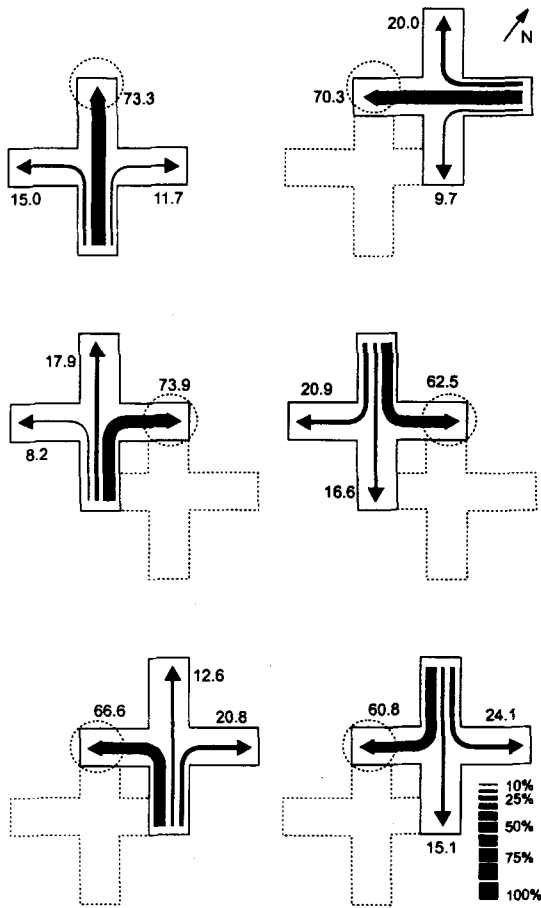


Figure 6. Schematic representation of the trajectories chosen by the place group during the transfer trials in which novel starts were used. For each start position, the arrows and the numbers indicate the percentage of times that each trajectory was chosen. The dotted circle shows the location of the goal during training trials. The position of the maze during training trials is shown in dotted lines. Note that all the arms were opened during transfer trials.

turtles in the place procedure showed a preference for the trajectory compatible with a place strategy, reaching the place at which reinforcement was available during training trials (Wilcoxon,  $Z = 2.2$  and  $2.2$ , both  $ps < .05$ , for Type II and Type III probe trials, respectively; Figure 5). Instead, the results of probe trials showed that the turtles trained in the cue procedure consistently selected the trajectory leading to the maze arm that presented the intramaze visual cue associated to the goal during training trials, irrespective of the place at which the goal was located in the room and whether or not the distal visual cues were available (Wilcoxon,  $Z = 2.02$ ,  $p = .04$ ,  $Z = 2.02$ ,  $p = .04$ , and  $Z = 2.2$ ,  $p = .02$ , for probe trials Types I, II, and III, respectively; Figure 5). In addition, in the cue group, the choice frequency of the two arms was close to chance on Type IV probe trials, in which the single intramaze cue was removed [NW arm:  $54.3\% \pm 8.3\%$ ; SE arm:  $45.7\% \pm 8.3\%$ ;  $\chi^2(1) = .66$ ,  $p = .41$ ]. In contrast with both the place and the cue groups, the animals in the control pro-

cedure did not show a preference for a particular arm in the probe trials, so the choice frequency of the two arms was close to chance level on the three types of probe trials (Wilcoxon,  $Z = 1.8$ ,  $.52$ , and  $.8$ , all  $ps > .05$ , for Types I, II, and III probe trials, respectively; Figure 5).

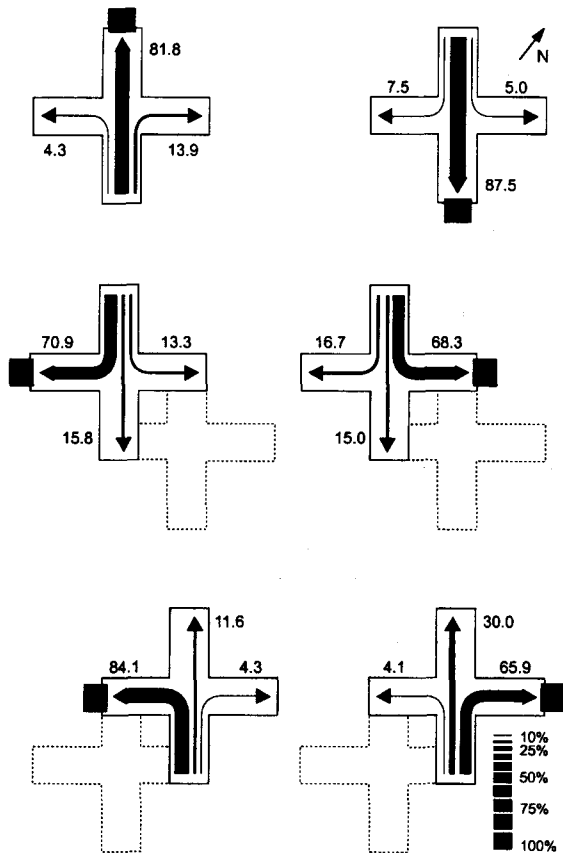
**Transfer trials.** In transfer trials, when novel start positions were used, the turtles trained in the place and cue procedures navigated accurately to the goal; nevertheless, remarkable differences were found in regard to the strategy employed by the animals in each group. Thus, the turtles in the place procedure showed a statistically significant preference for the trajectory leading to the place in the room at which the reward was available during training trials [Friedman,  $\chi^2(2) = 18.49$ ,  $p < .01$ ; Figure 6]. In this group, no statistically significant differences were found in the number of place responses between the different transfer trials—that is, the results were similar irrespective of the start position [Friedman,  $\chi^2(5) = 6.45$ ,  $p = .26$ ]. On the other hand, the animals trained in the cue procedure showed a significant preference for the trajectory leading to the intramaze visual cue that signaled the goal during training trials [Friedman,  $\chi^2(2) = 18.9$ ,  $p < .01$ ; Figure 7]. No statistically significant differences were found in the number of cue responses between the different transfer trials—that is, the results were similar irrespective of the start position [Friedman,  $\chi^2(5) = 8.84$ ,  $p = .11$ , Figure 7]. In contrast, in the control group, no statistically significant differences were found in the choice frequency of the three arms when the maze remained in the same position as that used during training trials [Friedman,  $\chi^2(2) = 2.7$ ,  $p = .25$ ; Figure 8]. However, in the transfer trials in which the maze was displaced in the room, the turtles in the control group showed a tendency to reach locations coinciding with those used as goal or start places during training trials [Friedman,  $\chi^2(2) = 6$ ,  $p = .048$ ; Figure 8].

## DISCUSSION

The present results show for the first time, to our knowledge, the presence of place learning in a reptilian species. The most noteworthy result of the present experiment is that turtles trained in the place procedure can use a maplike representation based on the encoding of the simultaneous spatial relationships between the goal and the extramaze visual cues, since they were able to navigate with accuracy to the goal from unfamiliar start places and their performance was resistant to a partial loss of relevant environmental information. In contrast, turtles trained in the cue procedure solved their task by directly approaching the single intramaze cue associated with the goal. These results reveal spatial learning and memory capabilities in reptiles that closely parallel those described in mammals and birds.

The present experiment focused on the spatial-learning strategies used by the turtles to solve place and cue tasks. The results show that turtles were able to learn both the place and the cue arm maze tasks with accuracy. In addition, the results of probe and transfer tests suggest that





**Figure 7.** Schematic representation of the trajectories chosen by the cue group during transfer trials in which novel start positions were used. For each start position, the arrows and the numbers indicate the percentage of times that each trajectory was chosen. The gray panel represents the intramaze visual cue.

although the turtles learned the place and the cue tasks at similar rates, they used different learning and memory strategies and employed different environmental information, depending on the task.

The results of the probe trials show that the turtles trained in the cue procedure used intramaze information to locate the goal: The partial or even the complete elimination of the extramaze cues had no effect on their performance (Types I–III probe trials; Figure 5); on the contrary, the removal of the single individual intramaze visual cue associated to the goal was sufficient to disrupt performance (Type IV probe trials). The results of the probe trials suggest that the sole relevant information for the animals trained in the cue task was a close and direct association between the arm and the goal. This idea is supported also by the results of the transfer trials, in which the animals consistently chose the arm signaled by the intramaze cue associated with the reinforcer, irrespective of both the start position and the location of the goal within the experimental room (Figure 7).

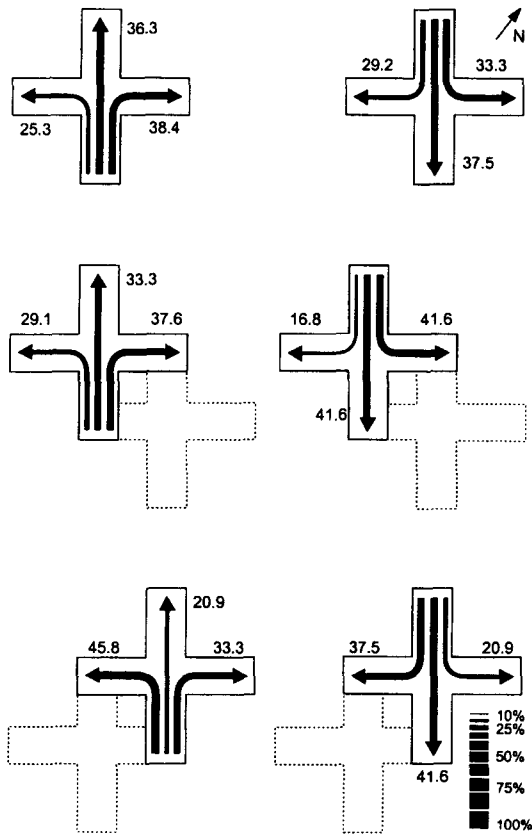
In short, the results of the probe and the transfer trials suggest that the turtles trained in the cue procedure used a guidance strategy, directly approaching the single intra-

maze cue as if it were a beacon. Similarly, it has been shown previously for mammals and birds that when a landmark is close to a goal, it is possible to find the goal solely by reference to this landmark (Brodbeck, 1994; Clayton & Krebs, 1994; Deutsch, 1960; Roberts & Pearce, 1998, 1999). This navigational strategy could be based, for instance, on the reduction of the distance between the animal's actual position and the beacon associated with the goal. It has been proposed that spatial learning is goal driven, in the sense that it depends on what information is most useful for a specific task (see Biegler & Morris, 1999). In the cue procedure, stimuli relevant to spatial learning can be classified into those that move and have no stable spatial relationships with the goal (the extramaze cues) and those that are stable with respect to the goal (the intramaze cues). Turtles more readily learn about the cues that occupy stable relationships with the goal and can therefore predict the location of it.

The performance of the place group during probe and transfer trials showed remarkable differences, relative to that observed in the cue group. Thus, the results of probe trials showed that the animals trained in the place procedure used the extramaze distal visual cues to navigate, since their performance showed a significant impairment when all of the distal visual cues were simultaneously excluded from the experimental environment (Type I probe trials; Figure 5). Nevertheless, a remarkable result is that no impairments were observed in the performance of this group when subsets of the extramaze cues were concealed (Types II and III probe trials; Figure 5). These results show that the turtles in the place group used a number of widely distributed extramaze visual cues to solve the task and that none of those cues was essential by itself to locate the goal.

These data suggest that the turtles trained in the place procedure have implemented a maplike representation of the experimental environment. A cognitive map defines the goal location by means of encoding simultaneously its spatial relationships with a number of cues or landmarks that provide a stable frame of reference (Gallistel, 1990; Nadel, 1991; O'Keefe & Nadel, 1978). Since a cognitive map stores redundant information, it is resistant to partial losses of environmental information. Evidence supporting this hypothesis has been obtained in studies with mammals and birds, which perform accurate navigation even after the removal of subsets of distal cues (Balda & Turek, 1984; Barnes et al., 1980; Clayton & Krebs, 1994; Jacobs et al., 1998; Mazmanian & Roberts, 1983; O'Keefe & Conway, 1978; Pico et al., 1985).

The data of transfer trials provided additional evidence of the flexible nature of the spatial strategies employed by the turtles to solve the place task. Thus, these animals reached the goal even when novel start positions were used and they had to adopt new trajectories (Figure 6). It should be noted that the trajectories adopted by the turtles in these transfer trials were completely novel, since in the present experiment, the maze structure had prevented the animals from traveling any route besides those used during training trials. The ability of the turtles in the present



**Figure 8.** Schematic representation of the trajectories chosen by the control group during transfer trials in which novel starts were used. For each start position, the arrows and the numbers indicate the percentage of times that each trajectory was chosen.

experiment to spontaneously navigate toward the goal location from novel start positions and to use new routes or shortcuts without previous reinforcing experience (see the trajectories in Figure 6) is similar to that observed in mammals and birds (Chapuis, Durup, & Thinus-Blanc, 1987; Chapuis & Varlet, 1987; Keith & McVety, 1988; Matthews & Best, 1997; Morris, 1981; Morris, Garrud, Rawlins, & O'Keefe, 1982; Poucet, 1985; see also, for fishes, Rodríguez et al., 1994; Salas, Rodríguez, Vargas, Durán, & Torres, 1996) and suggests that turtles possess the capacity to discriminate and encode the environmental spatial relationships by means of allocentric frames of reference that depend on a cognitive map (Gallistel, 1990; O'Keefe & Nadel, 1978; Tolman, 1948).

Observe also that the animals in the control group, in the transfer trials in which the maze was displaced in the room, showed a tendency to go more frequently to the arm coinciding with locations used as goal or start positions during training trials (see Figure 8), indicating that these animals have learned about the places used during training and, as the animals in the place group, are able to reach them from new start positions. Thus, present findings strongly suggest map-based navigation in turtles

and could indicate the use of allocentric spatial reference frameworks into which environmental features are encoded. Such a hypothetical cognitive mapping system would allow the animals to determine their actual spatial position and would mediate the computations required to navigate accurately in their environment (for recent models of the mechanisms of the cognitive mapping system in rodents, see, e.g., Burgess & O'Keefe, 1996; Gallistel, 1990; McNaughton et al., 1996; Muller, Stead, & Pach, 1996; O'Keefe, 1991a; O'Keefe & Burgess, 1996; Poucet, 1993; Redish & Touretzky, 1997; Samsonovich & McNaughton, 1997; Worden, 1992; for revisions, see Redish, 1999; Thinus-Blanc, 1996).

However, possible alternative interpretations of the present data should be considered. The use of strategies other than those of the cognitive mapping by the turtles in the place procedure—for instance, a guidance or *snapshot* strategy (i.e., approaching an individual distal visual cue or cluster of cues associated with the goal; Chapuis et al., 1987; McNaughton, Leonard, & Chen, 1989)—cannot account for the performance observed in the probe and transfer tests in the present study. If these animals used a guidance strategy, performance should have deteriorated significantly in the Type II probe trials to a level similar to that observed in the Type I probe trials. In contrast, the turtles continued choosing the trajectory leading to the goal location, regardless of the subset of distal visual cues excluded at any given time (see Figure 5). Also, the results in the transfer trials enable us to rule out this possibility, since during these trials, the local views of the room perceived from the start location or even from the crossroad of the maze were completely new for these turtles, inasmuch as they had never visited those locations before. In addition, in the transfer trials, the animals trained in the place task did not approach directly any individual distal cue or snapshot behind the goal location. Instead, in these trials, the turtles navigated in a reverse direction, in order to reach the place where they were reinforced during training.

The results enable us also to disregard the possibility of the use of a geomagnetic sense or any other *direction sense* (Lohmann, 1991; Mrosovsky, 1978; Salmon & Lohmann, 1989) by the turtles trained in the place task in the present experiment. Of course, other simple alternative explanations to the present results—for example, that the animals could have solved their respective tasks by approaching olfactory cues, by means of the direct vision of the reinforcer, or by any other uncontrolled cue—can be disregarded, because the animals in the control procedure did not improve their performance level with training.

Another possibility is that the precise performance of the place group during training could have been based on a conditional response strategy: (1) When starting from one start arm, turn to the right, and (2) when beginning from the other, turn to the left (Blodgett & McCutchan, 1947; McNaughton et al., 1989; Thinus-Blanc & Ingle, 1985). However, again the results of transfer tests rule out

this possibility (see also Olton, 1979; Rodríguez et al., 1994), given that the turtles navigated to the goal irrespective of starting point and turn direction (see Figure 6).

Thus, the results of the present experiment suggest that reptiles, like mammals and birds, can use both guidance strategies by encoding individual cues in close proximity to the goal as beacons and place or mapping strategies by encoding the spatial relationships between the goal and multiple environmental distal landmarks to locate this goal (Balda, Bunch, Kamil, Sherry, & Tomback, 1987; Brodbeck & Shettleworth, 1995; Cheng, 1986; Cheng & Sherry, 1992; Clayton & Krebs, 1994; Cook & Tauro, 1999; Greene & Cook, 1997; Jacobs et al., 1998; Kamil & Balda, 1985; Leonard & McNaughton, 1990; Olton & Samuelson, 1976; Roberts & Pearce, 1999; Sherry, 1984; Shettleworth, 1995; Shettleworth & Krebs, 1982; Spetch & Edwards, 1988; Strasser & Bingman, 1996; Suzuki, Augerinos, & Black, 1980).

Regarding mammals and birds, a great amount of functional and anatomical evidence suggests that their spatial learning and memory capabilities are based on homologous neural mechanisms. For instance, in mammals and birds, damage to the hippocampal formation, which is considered homologous in both taxa on the basis of anatomical evidences (Bingman, 1992), produces selective impairments in spatial tasks that require the encoding of reciprocal relationships among environmental features (place learning), but not in tasks requiring the subject to approach a single cue or requiring nonspatial discriminations (Bingman & Mench, 1990; Fremouw, Jackson-Smith, & Kesner, 1997; Good, 1987; Morris et al., 1982; Nadel & MacDonald, 1980; Okaichi, 1987; Olton & Papas, 1979; Pearce, Roberts, & Good, 1998; Sherry & Vaccarino, 1989). However, a feature can be considered homologous in two or more taxa only if it can be traced back to the presumptive common ancestor of these taxa (Simpson, 1961; Striedter & Northcutt, 1991; Wiley, 1981). Modern reptiles, including chelonians, cannot be viewed as the ancestral stock from which living birds and mammals evolved, since the actual evolutionary history of modern reptiles spans a time period that is as long as that of the therapsid radiation that led to mammals. In addition, for characteristics such as brain and behavior, little evidence has remained in the fossil record. Consequently, any hypothesis of homology concerning learning and memory systems in vertebrates must be inferred from the distribution of characteristics observed in the extant species on the base of a principle of parsimony, according to which the phylogenetic scenario that most likely represents the actual course of the evolutionary history is that which requires the smallest number of phyletic transformations (Eldredge & Cracraft, 1980; Hennig, 1966; Northcutt, 1984, 1995; Patterson, 1982; Wiley, 1981).

Although more comparative studies in turtles and other reptilian taxa are needed, the present data reveal, in a reptilian species, the presence of spatial learning and

memory capabilities that closely parallel those described in mammals and birds. This result suggests that the presence of these memory systems could be a primitive characteristics in amniotes and could have been present in the common reptilian ancestor of modern turtles, mammals, and birds that inhabited the earth in the Mesozoic era, some 200 million years ago. If this reptilian spatial memory system is actually homologous to those described in mammals and birds, it should also be based in the same neural mechanisms.

The reptilian dorsomedial cortex is considered to be homologous to the hippocampal formation of mammals and birds on the basis of anatomical and physiological evidence (Nieuwenhuys, ten Donkelaar, & Nicholson, 1998; Northcutt, 1981; Schwerdtfeger & Smeets, 1988; Ulinski, 1990). That is, if the cognitive map system herein described in turtles is homologous to those described in mammals and birds, it should be based on the dorsomedial cortex function. Further psychobiological studies are needed to reveal whether the reptilian dorsomedial cortex, like the hippocampal formation in mammals and birds, is selectively implicated in cognitive mapping strategies.

In summary, the results of the present study suggest that turtles, like mammals and birds, besides orienting by means of egocentrically referenced mechanisms, are able to navigate on the basis of allocentric frames of reference. Present results show that turtles possess the capacity to use the information provided by a number of distal visual cues as a whole, to select the correct trajectories to the goal without previous training, and to navigate efficiently to the goal even from start places never visited before. The present data reveal spatial learning and memory capabilities in reptiles that closely parallel those described in mammals and birds and encourage a search for their comparative peculiarities and neural substrata. The present data lead to the notion that multiple spatial learning and memory systems may have evolved early in amniote evolution, being already present in the common reptilian ancestor of modern reptiles, mammals, and birds, and have been retained throughout the evolution of each, independent lineage.

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