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Research report

Sequential control of navigation by locale and taxon cues in the Morris water task☆

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Abstract

The neurobehavioral dissociation between place navigation and cued navigation has been central to contemporary thinking regarding the psychological processes involved in spatial behavior. In cases where locale (place) cues and taxon cues (e.g., beacons) are present it has been suggested that navigation may be controlled by either stimulus type in isolation, or, alternatively, by both simultaneously. In this report we provide evidence that place cues and beacons sequentially control navigation during a single trip to a visible goal. Rats were trained to navigate to a visible escape platform in a circular swimming pool surrounded by numerous visual cues and the kinematics and accuracy of the trajectories to the platform were analyzed. Shortly after initiating a trajectory to the visible platform, animals routinely engaged in stimulus sampling behaviors (e.g., horizontal head scans) which were consistently associated with changes in accuracy (heading error) and swim velocity. Subsequently, animals swam quickly and accurately to the visible platform suggesting that the sampling behaviors correspond to a shift in exteroceptive stimulus control. Consistent with this idea, removal or relocation of the platform disrupted navigation following the stimulus sampling behaviors, whereas the initial trajectory was unaffected. In contrast, changes in the distal cue constellation selectively disrupted the initial trajectory. The results showing that navigation to a visible goal is controlled sequentially by locale and taxon cues are discussed in relation to contemporary theories of navigation.

Keywords: Place learning; Cued navigation; Cognitive map; Morris water task; Hippocampus

1. Introduction

Animals can learn to navigate to a goal location using a variety of distinct strategies that involve qualitatively different stimulus types, psychological processes, and neural substrates (see e.g., Refs. [9] and [20]). The distinction between *cued navigation* and *place navigation* has proven useful for understanding the psychological and biological bases of navigation and has played a central conceptual role in many contemporary theories on the topic. In its simplest form, cued navigation involves finding a goal location by approaching a single cue (a beacon) that marks or is colocalized with the goal. In contrast, place navigation refers to navigation based upon the goal's fixed spatial relationship to a constellation of cues, none of which mark the goal. Both types of stimuli can control accurate (direct) navigation to a goal site, however, the precise psychological and neurobiological processes involved in each are thought to be quite distinct. For example, O'Keefe and Nadel's [20] influential *Cognitive Mapping Theory* distinguished place navigation and cued navigation (locale and taxon in their terminology) based upon their reliance on a unitary representation of space and the hippocampus. Place navigation, they argued, requires that an animal construct, store, and routinely update a cognitive map of the environment which they hypothesized to depend upon hippocampal circuitry. In contrast, cued navigation does not depend upon a cognitive map, or hippocampal circuitry, because the animal need only learn to approach a single stimulus associated with the goal. Many subsequent studies have provided data in support of this basic prediction of the theory, however, see Refs. [28] and [32] for some important exceptions.

The neurobehavioral dissociation between place and cued navigation suggests a fundamental independence between

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these forms of navigation [20,25,29]. In natural settings there are likely to be many situations in which locale and taxon cues are both present. Under such circumstances animals could engage in either type of navigation exclusively or, alternatively, they may be capable of learning about and using both types of stimuli in parallel. Laboratory investigations of small-scale navigation in rodents have yielded data in support of both possibilities. For example, Redhead et al. [22] trained animals to navigate to an escape platform marked by a visible beacon in the Morris water task [18,19]. When the beacon and platform were removed from the pool, animals did not persist in searching in the region of the pool where the platform had been, suggesting that the beacon had overshadowed the locale cues (but see Ref. [5] for a failure to demonstrate this effect in mice). Further, some researchers have reported individual differences in preference for using one form of cue over another. Such preferences have been related to sex [13], pharmacological manipulations [13,26], and brain lesions [7,17,30]. For example, Whishaw et al. [30] found that lesions of the striatum did not disrupt either place or cued navigation when only one cue type was present, however, animals with striatum lesions preferred cued navigation when both types of stimulus were available. Thus, animals appear to use only one type of cue to navigate under a broad range of circumstances.

Alternatively, some data suggest that rats learn to use both cue types when available. Whishaw and Mittleman [31] trained animals to swim to a visible platform in the presence of distal cues and subsequently tested them with the platform removed from the pool. Animals swam directly to the platform location, however, similar to the results of Redhead et al. [22] the animals did not persist in searching where the visible platform had been. Instead, they often returned to the release location and attempted to execute the same route to the platform location. Further, Whishaw et al. [30] reported that control rats learn to use both locale cues and beacons when learning to navigate to a visible platform, in contrast to the lesion results described above. More recently, Pearce et al. [21] and Hayward et al. [12] trained animals to swim to a visible cue that marked an escape platform in a triangular pool where the pool geometry provided the only cues that disambiguated spatial locations. On test trials there was no disruption in search performance when the beacon cue was removed from the pool, suggesting that animals also learned to use place cues from the pool geometry. To our knowledge, the possibility that animals use both locale and taxon strategies independently in a single trip has not yet been considered. To investigate this possibility we conducted a systematic analysis of behavior in the visible platform version of the Morris water task. Animals were trained to swim to a visible platform which remained in a fixed spatial location relative to a constellation of distal visual cues. We analyzed the accuracy and kinematics of the path to the platform and test trials with the platform removed or relocated, or with novel distal cues were conducted to assess behavioral control by each type of cue at various points during the swim path. The results obtained by Whishaw and Mittleman [31] show that if a visible platform is removed, rats can execute accurate trajectories to the former platform location based only upon distal locale cues. Therefore, the ability of rats to select a trajectory may not be disrupted when the platform is removed or relocated, whereas subsequent behaviors related to locating the visible goal may be disrupted. In contrast, alterations in the distal cues may have the opposite effect, primarily disrupting the initial trajectory.

2. Experiment 1

2.1. Materials and methods

2.1.1. Subjects

Six experimentally naive female Long-evans rats from the University of Lethbridge vivarium (originally from Charles River Stock) served as subjects. All animals were approximately 90 days old at the beginning of the experiment and weighed between 250 and 300 g. Animals were housed in plastic cages in groups of three and rat chow and water were available ad libitum except during behavioral testing (approximately 15 min per day).

2.1.2. Apparatus

A 1.5 m diameter circular pool was used for behavioral testing. The pool was approximately 40 cm in height and the inner wall of the pool was painted white. The pool was filled to a depth of 30 cm with cool water (20–22 °C) which was made opaque by adding a small amount of nontoxic powdered white tempura paint. Two testing rooms with different sets of distal visual cues were used. The escape platform was constructed of Plexiglass and the uppermost 4 cm was painted black and covered with wire mesh to assist the animals in climbing onto the platform. The top surface of the platform was 12 cm × 12 cm and extended approximately 3 cm above the surface of the water during visible platform trials.

2.1.3. Procedure

Each rat was given two visible platform trials during each of 14 daily sessions. The same room was used for all 14 sessions and the visible platform was in a fixed location in the center of the SW quadrant for three animals and the NE quadrant for the remaining three animals. Four equally spaced locations around the perimeter of the pool were used as release points. Animals were released from one of the release points closest to the platform on the first trial and from one of the release points furthest from the platform on the second trial. Occasionally a third trial was given if an animal that had been consistently navigating directly to the platform took an indirect path. Immediately following the 14th session we removed the platform from the pool and released the animals from the same location used during the previous visible platform trial. Because we were primarily

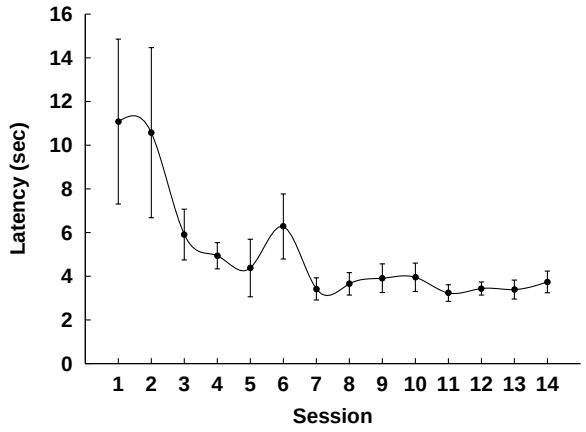

Fig. 1. Mean latency (± 1 S.E.M.) to navigate to the visible platform from the far release point (2nd trial) during each of the 14 daily sessions.

interested in the characteristics of the trajectory each animal took toward the place where the platform had been, we did not allow the animals to persist in searching for the platform as is commonly done in Morris water task probe trials. Animals were removed from the pool within 4–5 s after beginning the trial or when they passed by the former platform location, whichever occurred first.

After 72 h with no behavioral testing, a second training/testing session was conducted. Animals were first given two trials using the same environment and procedures employed in the first 14 sessions. A third visible platform trial was conducted in a new room to determine if a change in the distal room cues would disrupt navigation to the visible platform. The features of the pool, the visible platform, and the platform location within the pool were identical to those used in the first testing room, however, the distal cues in the new room were novel. Animals were given a single trial and started from a far release point.

All swim paths were video-taped by means of an overhead camera attached to a digital camcorder. For analysis purposes, Peak Motus software (Peak Performance Technologies, Inc., Englewood, CO) was used to determine the position of the rat's snout in a Cartesian coordinate system every 16 ms. Coordinates were determined for training trials only if the animal was released from a far release point and if the animal took a direct path to the platform. Coordinates were measured from the first frame in which the animal's head was visible in the pool until the animal's forepaws made contact with the platform, or, for probe trials, until the animal was removed from the pool or reached the pool wall opposite the release point. From these coordinates, we measured the heading error at various points along the path to the platform (described in more detail below), path length, distance traveled, moment-to-moment velocity, and latency to navigate to the platform. Where necessary, additional dependent measures unique to individual test trials are described in Section 2.2.

2.2. Results and discussion

All effects reported here are significant at $P < 0.05$ unless otherwise stated.

Animals began to take relatively direct paths to the platform as early as the second session and as a group had reached asymptotic latency by session 7 (see Fig. 1). Upon observing the animals' behavior we noted a consistent set of behaviors that was apparent in all subjects shortly after beginning to swim. When placed in the pool the animals would turn and begin a trajectory in the general direction of the platform. A short distance from the release point animals would perform horizontal head scans after which they would quickly swim to the visible platform (see supplementary Video 1[1]). The head scans presumably reflect attempts to sample visible stimuli and may be involved in depth estimation [15]. More importantly, these behaviors occur despite the fact that animals are already navigating more or less directly toward the location of the visible platform. Based on these observations, the trajectories to the platform can be separated into two distinct segments: An initial segment from the release point up until head scanning or trajectory correction, and a longer terminal segment in which the animal quickly navigates to the visible cue marking the platform location. One possibility is that the initial and terminal segments are separated by such distinct behaviors because they are under the control of different stimulus types. If so, we suspected that the initial segment would be controlled largely by the more global features of the environment, namely, the distal room cues, whereas, the terminal segment would be largely controlled by the visible platform. The point at which animals engage in sampling behaviors may indicate a shift in exteroceptive stimulus control from the distal locale cues to the taxon cues from the visible platform. Hence, we refer to this as a *shift point*. Fig. 2 shows the location of each animal's shift point during the final six sessions (9–14). Performance was analyzed during these sessions because all animals were at asymptotic levels of performance during the previous two sessions (7 and 8). The shift point consistently occurred approximately 25 cm into the path ($M = 26.42$, S.E.M. = 2.22). With one exception, shift points always occurred when the animal was navigating toward the general direction of, but not directly toward, the visible platform. There was also a clear relationship between moment-to-moment velocity and navigation prior to and subsequent to the shift point. Fig. 3 shows representative

[1] This video shows a single swim to a visible platform illustrating the stimulus sampling behaviors (e.g., horizontal head scans) that occur a short distance from the release point. Note that the trajectories prior and subsequent to these sampling behaviors are accurate. During the slow-motion portion of the video the animal's position and heading are marked in green prior to the stimulus sampling behaviors, in red during the stimulus sampling behaviors, and in orange and yellow during the final direct swim to the visible platform. To avoid providing a salient taxon cue in the extramaze environment (e.g., the camera), all filming of this video was performed after completion of the study using naive animals.

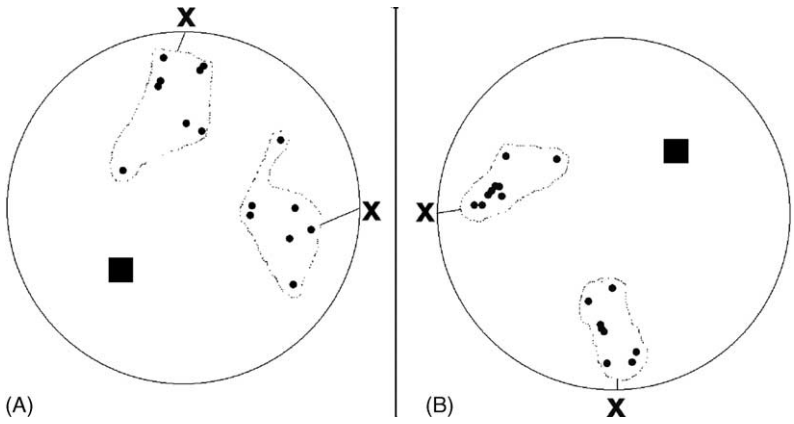

Fig. 2. Location of the shift point for all trials in which animals took a direct path to the platform during the final six sessions ($N = 36$): (A) for animals trained with the platform in the SW, and (B) in the NE. Release points are marked by xs and straight lines connect the shift point clusters with the corresponding release point.

swim paths and associated moment-to-moment velocities for each of the six subjects. The shift point was associated with a deceleration and was generally preceded by variability (sharp changes) in velocity. In contrast, velocity following the shift point increased monotonically and sharply decreased just before the animal arrived at the platform.

In order to quantify the accuracy of the swim path at various points during the swim, the angular deviation from a direct trajectory to the platform (heading error) was measured at the shift point and at two additional points (segments of the swim path 50 and 100 cm beyond the shift point). Specifically, heading error was computed relative to the release location and the platform location for the shift point, relative to the shift point and the platform location for the point 50 cm beyond the shift point, and relative to the point 50 cm beyond the shift and the platform location for the point 100 cm beyond the shift point. If the initial segment and terminal segments of the path are dissociable based upon stimulus control by the locale cues and the taxon cue from the visible platform respectively, then a comparison of heading error during the visible platform and no-platform probe trials should differ only with respect to the terminal segment. The initial segment of the trajectory to the platform was similar in the visible platform and probe trials for each animal (see Figs. 4 and 5). Subsequent to the shift point, however, all but one animal took erroneous trajectories to the former platform location. A repeated measures analysis of variance (ANOVA) with Trial Type (visible or probe) and Point in the trajectory where heading error was measured confirmed these impressions. There were significant main effects of Trial Type [$F(1, 10) = 14.27$] and Point in the trajectory at which heading error was measured [$F(1, 10) = 6.67$]. There was also a significant interaction term [$F(2, 79) = 11.51$], which resulted from the pattern of differences observed during the visible platform and probe trials at the three critical points in the trajectory. Simple comparisons revealed a non-significant effect of Trial Type at the shift point [$F < 1$], however, trajectories were significantly more accurate at the second [$F(1, 39) = 18.62$] and third points [$F(1, 39) = 48.15$] when the platform was visible. The significant interaction also occurred because heading error significantly decreased over the course of the swim path when the platform was visible [$F(2, 68) = 55.51$], but not when it was absent [$F(2, 10) = 1.28$, $P = 0.32$]. These results indicate that the visible platform was necessary to control the terminal segment of the trajectory, whereas the remaining environmental cues were sufficient to control the segment of the trajectory prior to the shift point.

We also compared navigation to a visible platform in the original training room and in a novel room with an unfamiliar distal cue constellation. If the initial trajectory segment is controlled by the distal cue constellation, then navigation should be disrupted in the unfamiliar room even though the platform is visible from the release point. Fig. 6 shows each animal's swim path during a visible platform trial in the familiar and novel environments. With the exception of one animal, navigation during the initial segment was clearly disrupted. Further, there was no kinematic evidence of a clear shift point in the novel room (data not shown), therefore, in order to directly compare performance in the familiar and novel environments, heading error in the novel room trial was measured at the same points used to compute heading error in the familiar room (i.e., the same path lengths from the release point; see Fig. 7). Due to the high variability observed in the novel room there were no significant main effects or interactions [all ps >0.31]. However, Figs. 6 and 7 clearly show that trajectories early in the swim path were more erroneous in the novel environment compared to trajectories just prior to locating the platform. The most striking effect of changing the distal cues was to increase the path length of the swim up until animals began to take a direct trajectory to the platform [$F(1, 10) = 13.68$; $M_{familiar} = 34.85$ cm, $M_{novel} = 117.68$]. Related to this effect, there was a significant increase in latency to navigate to the platform in the novel room [$F(1, 10) = 8.01$; $M_{\text{familiar}} = 3.07$ s, (S.E.M. $= 0.31$), $M_{\text{novel}} = 5.36$ s (S.E.M. $= 0.75$)]. Additionally, animals be-

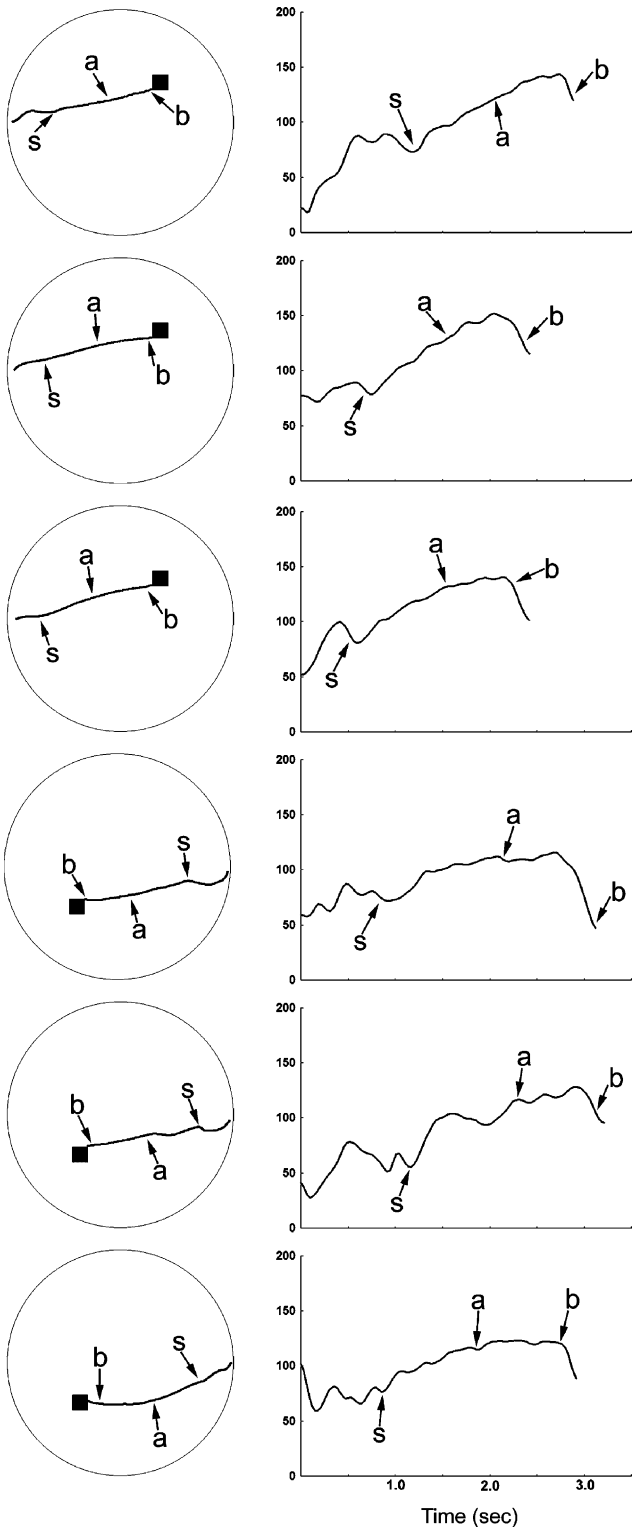

Fig. 3. Representative swim paths to the visible platform (left) and corresponding moment-to-moment velocities (right) for each rat: (s) the estimated shift point, (a) a 50 cm path segment beyond the shift point, and (b) a 100 cm path segment beyond the shift point. Deviation from a direct trajectory to the platform (heading error) was measured at each of these points (see Fig. 5). The *y*-axes of the velocity graphs are in cm/s.

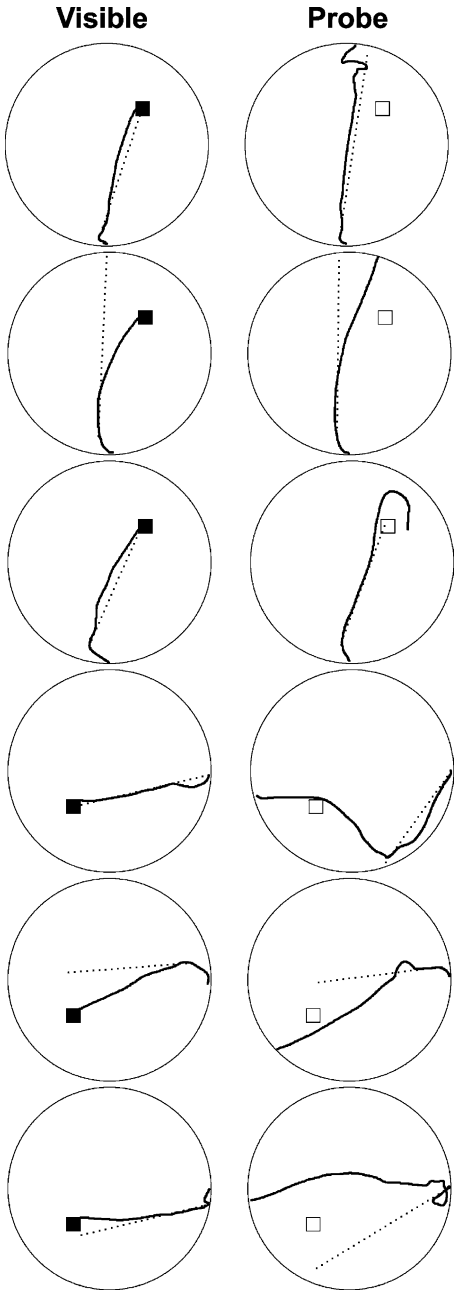

Fig. 4. Swim paths and initial headings at the shift point for each of the six rats in Experiment 1 during the session 14 visible platform and no-platform probe trial. The dotted lines indicate trajectories at the shift point.

gan taking direct paths significantly closer to platform in the novel room [$F(1, 10) = 12.87$]. In the familiar room the average distance was 96.78 cm (S.E.M. = 3.89) compared to 71.74 cm (S.E.M. = 5.80) in the novel room. Collectively, these results indicate that changing the distal cues, while holding other aspects of the testing procedures constant, was sufficient to disrupt the initial segment of the trajectory, even though the platform was visible.

Taken together, the results show that trajectories to a visible platform can be separated into two segments controlled

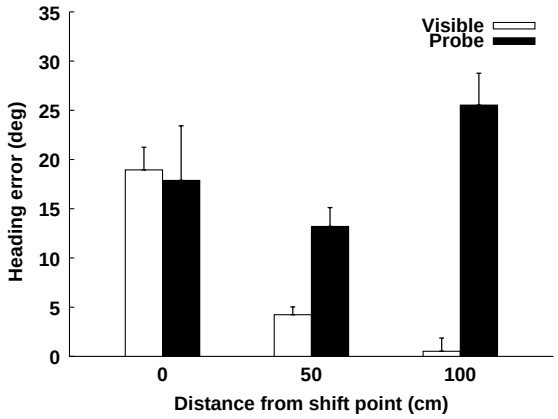

Fig. 5. Mean (+1 S.E.M.) heading error during visible platform training and the no-platform probe trial at three points during the path to the platform: 0, 50, 100 cm from the shift point. These points correspond to points s, a, and b in Fig. 3, respectively. Means during the visible platform trials were averaged over the last six training sessions.

either by distal locale cues or the taxon cues from the goal. An initial segment is controlled by the distal cues and involves orienting and executing a trajectory in the general direction of the platform. A second component of the trajectory is controlled by the local beacon cue marking the goal and is characterized by relatively fast and direct navigation to the platform following distinctive stimulus sampling behaviors. Although some studies suggest that animals preferentially use only one type of cue and others claim that both types of stimuli may be used in parallel to navigate to a goal, the present findings clearly demonstrate that animals may also use both types of cues independently and serially. If so, the present findings could have broad implications for the study of rodent spatial behavior. Before discussing these implications, however, it is necessary to assess the reliability and robustness of this behavioral dissociation. To do so, a second experiment was conducted which replicated and extended the procedures of Experiment 1 to include several additional types of test trials at various stages during training.

3. Experiment 2

The purpose of Experiment 2 was to replicate the basic behavioral phenomena reported in Experiment 1 to conduct additional tests of the hypothesis that the initial orientation and trajectory selection are based on locale cues and the terminal segment was based upon taxon cues from the visible platform. Shortly after asymptotic levels of performance were reached, animals were given test trials every 3–4 sessions. The first two tests were no-platform probe trials which were conducted earlier in the training sequence than the probe trial employed in Experiment 1. Tests in which the visible platform was relocated or in which the distal cues were unfamiliar were also conducted.

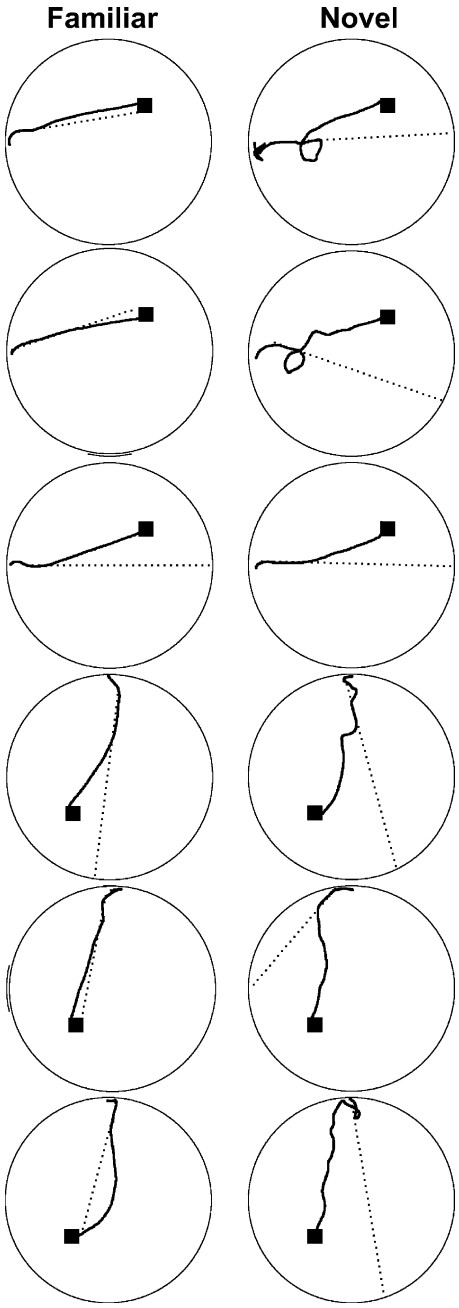

Fig. 6. Swim paths for each of the six rats in Experiment 1 during a single visible platform trial in the familiar training room and a novel room. The dotted lines represent the trajectory at the shift point.

3.1. Materials and methods

3.1.1. Subjects

Six experimentally naive female Long-evans rats served as subjects. The origin, age, weight, feeding conditions, and housing conditions were identical to those of the rats used in Experiment 1.

3.1.2. Apparatus

All materials and apparatus used in Experiment 2 were identical to those of Experiment 1.

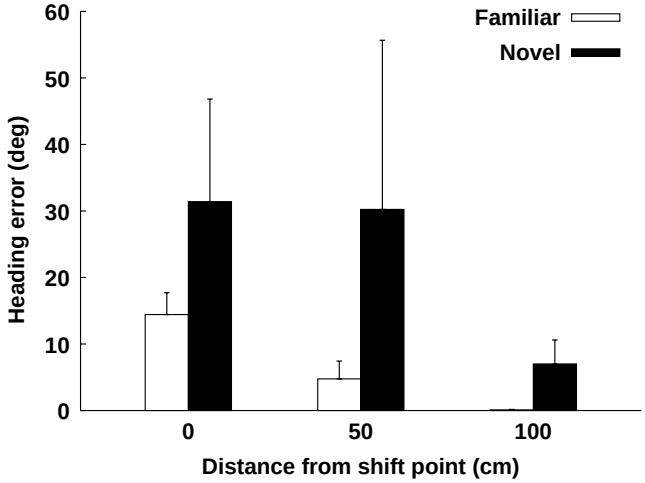

Fig. 7. Mean (+1 S.E.M.) heading error during a visible platform trial in the familiar and a novel environment. Heading error in the familiar environment was measured at three points during the path to the platform: 0, 50, 100 cm from the shift point. These points were determined using the same criteria as used to determine points s, a, and b in Fig. 3 respectively. Because a distinct shift point was not observed in the novel room, heading error was measured at the same path lengths into the trajectory as observed in the familiar room.

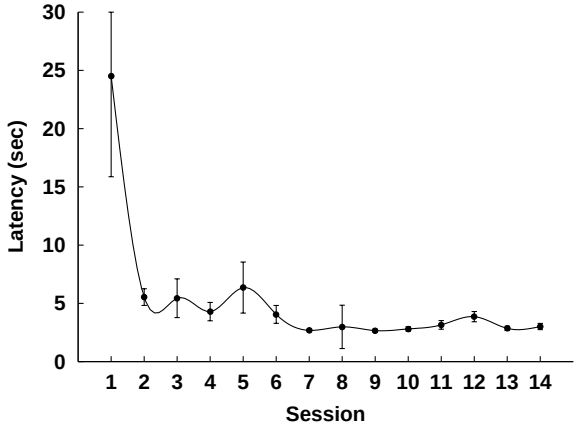

Fig. 8. Mean latency (± 1 S.E.M.) for animals to navigate to the visible platform from the far release point (2nd trial) during each of the 14 daily sessions

3.1.3. Procedure

The general procedures were similar to those employed in Experiment 1, but included multiple test trials that were conducted at various points during the training sequence. Once an animal had reached asymptotic levels of performance for two consecutive sessions (session 7 for all animals) a no-platform probe trial was conducted. The probe trial immediately followed the second visible platform trial of the session and animals were released from the same release point during the visible platform and probe trials. Three sessions later (session 10) a second no-platform probe trial was conducted in the same manner. During session 14, animals were given a test trial in which the platform was moved to a new location near the pool wall opposite the original platform location. The test trial immediately followed the visible platform training trial and used the same release location. After 72 h with no behavioral testing, animals were given two trials in the original environment followed by a single trial in an environment with unfamiliar distal cues (same as the novel environment from Experiment 1).

3.2. Results and discussion

As in the first experiment, animals reached asymptotic latency to navigate to the visible platform around day 6 (see Fig. 8). In order to make the analyses more concise, we only report data for visible platform trials that were conducted during the same session as a test trial.

During the visible platform trial of sessions 7 and 10, all animals showed clear evidence of stimulus sampling behaviors and a shift point which occurred, on average, 26.65 cm (S.E.M. = 3.54) into the path (corresponding to a distance of 26.49 cm (S.E.M. = 3.16) from the release location; see Fig. 9). Fig. 10 shows mean heading error at each of the three points for the visible platform and probe trial during both sessions. As in Experiment 1, removal of the visible platform appears to have had no effect on the swim path up until the shift point, after which the trajectory became increasingly inaccurate. A repeated measures ANOVA with Trial Type (visible or probe) and point in the trajectory (shift, shift + 50 cm, and shift + 100 cm) confirmed these general impressions. There were significant main effects of Trial Type [session 7: $F(1, 10) = 9.70$; session 10: $F(1, 10) = 3.79$] and the Point in the trajectory where heading error was measured for session 7 [$F(1, 10) = 3.79$], as well as a significant interaction term for session 7 [$F(2, 20) = 14.22$] and session 10 [$F(2, 20) = 6.10$]. The interaction occurred because heading error improved over the course of the swim path when the platform was visible [session 7: $F(2, 10) = 19.27$; session 10: $F(2, 10) = 10.68$], but during the probe trial heading error either increased (session 7: $F(2, 10) = 8.36$) or did not improve during the swim (session 10: $F(2, 10) = 2.23$, $P = .16$). Further, simple comparisons revealed no effect of Trial Type at the shift point for either session (both Fs < 1), however, trajectories were significantly more accurate at the second (session 7: $F(1, 10) = 15.95$; session 10: $F(1, 10) = 8.74$) and third points (session 7: $F(1, 10) = 11.63$; session 10: $F(1, 10) = 5.54$) during the visible platform trial. During the session 14 test sequence all animals navigated directly to the visible platform when it was in its familiar (old) location. When the platform was moved to a new location, four of the six animals began to swim to the old location and then corrected the trajectory to swim directly to the new platform location (see Fig. 11). Heading errors during navigation to the old platform location and new platform location are shown in Fig. 12). There was a main effect of Trial Type [$F(1, 10) = 8.70$] and point in the trajectory where heading error was measured [$F(1, 10) = 11.84$], as

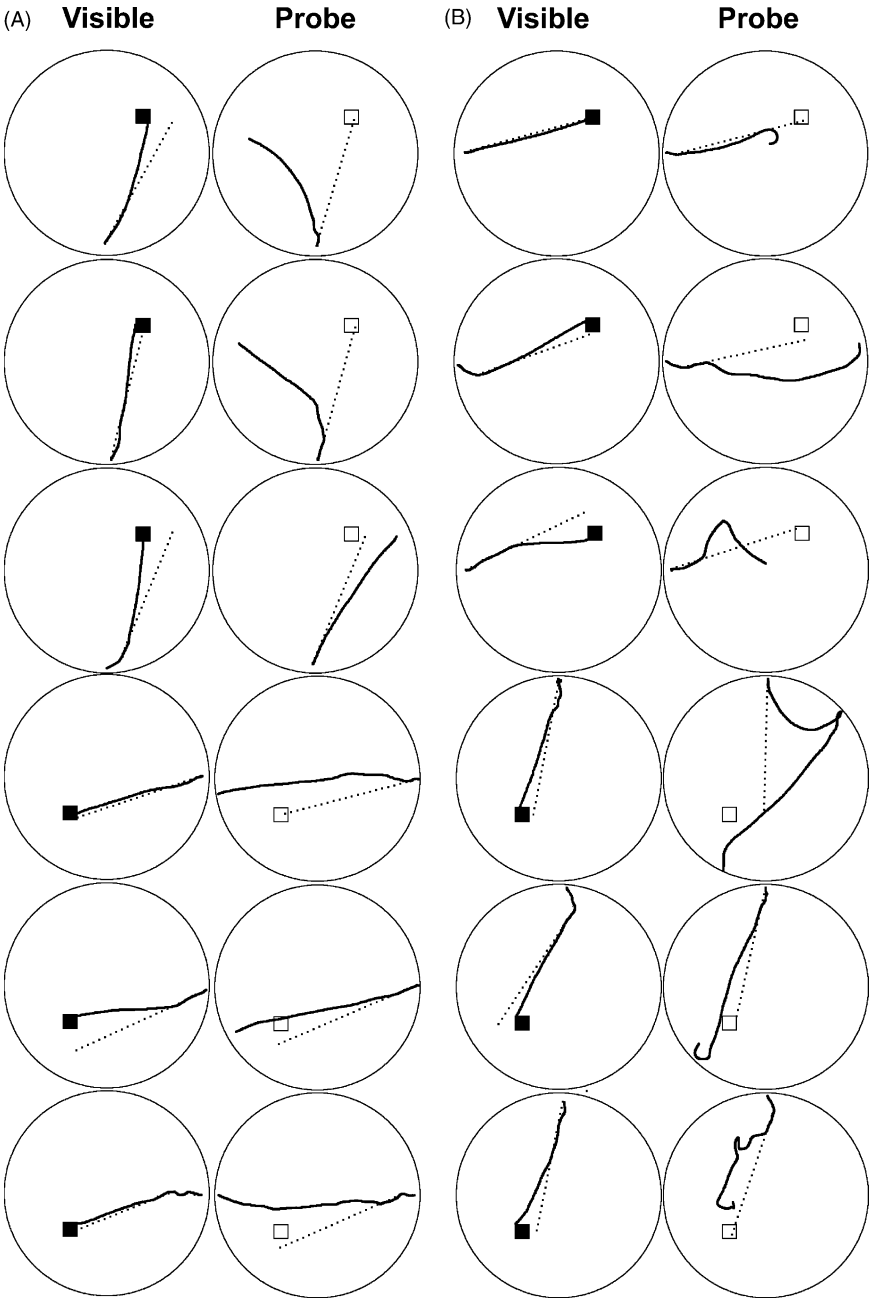

Fig. 9. Swim paths for each of the six rats in Experiment 2 during visible platform trials and no-platform probe trials during sessions 7 (A) and 10 (B). The dotted lines represent the trajectory at the shift point.

well as a significant interaction [$F(2, 20) = 4.28$]. Simple comparisons revealed that animals had significantly greater heading errors while navigating to the new location at the shift point [$F(1, 10) = 5.68$], and 50 cm beyond the shift point [$F(1, 10) = 7.16$], but not later during the swim path [$F < 1$]. The high initial heading error during the new location trial indicates that the visible platform did not control the initial trajectory, however, the relatively low heading error later during the path shows that the visible platform did control navigation subsequent to the shift point. Additionally, the disruption in navigation to the new location is indexed by the increase in latency to navigate to the platform [$M_{Old} = 3.00$ (S.E.M. = 0.24); $M_{New} = 5.48$ (S.E.M. = 1.64)], however, this difference was not statistically significant [$F(1, 10) = 2.23$, $P = .17$].

The final test consisted of two trials with a visible platform: one trial in the old (trained) environment and one trial in a novel distal cue environment. Swim paths to the platform during both trial types are shown in Fig. 13. Heading error was highly variable in the new environment and, as a result, there were no significant main effects or interactions involving Trial Type and the point at which heading error

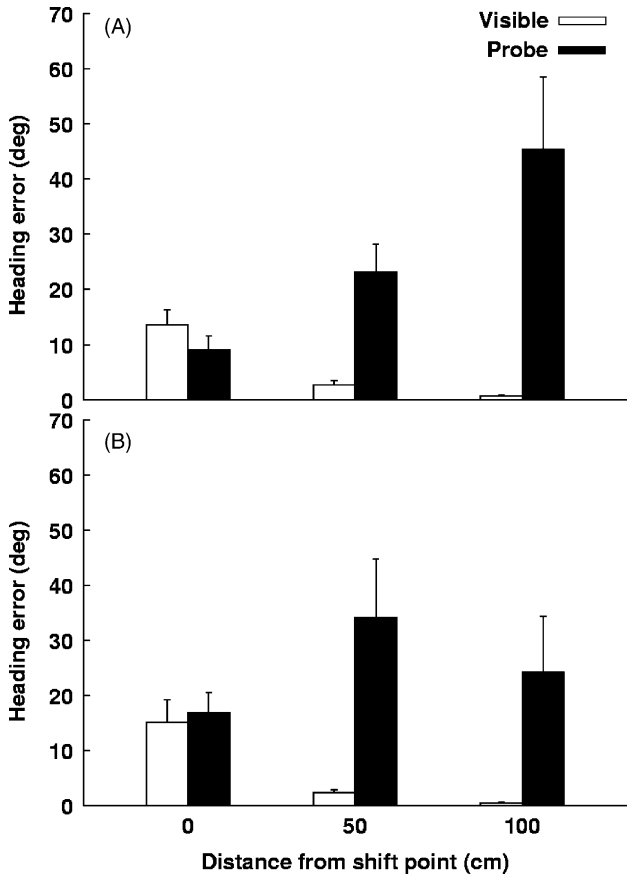

Fig. 10. Mean (+1 S.E.M.) heading error during visible platform training and the no-platform probe trial during session 7 (A) and 10 (B) at three points during the path to the platform: 0, 50, and 100 cm from the shift point.

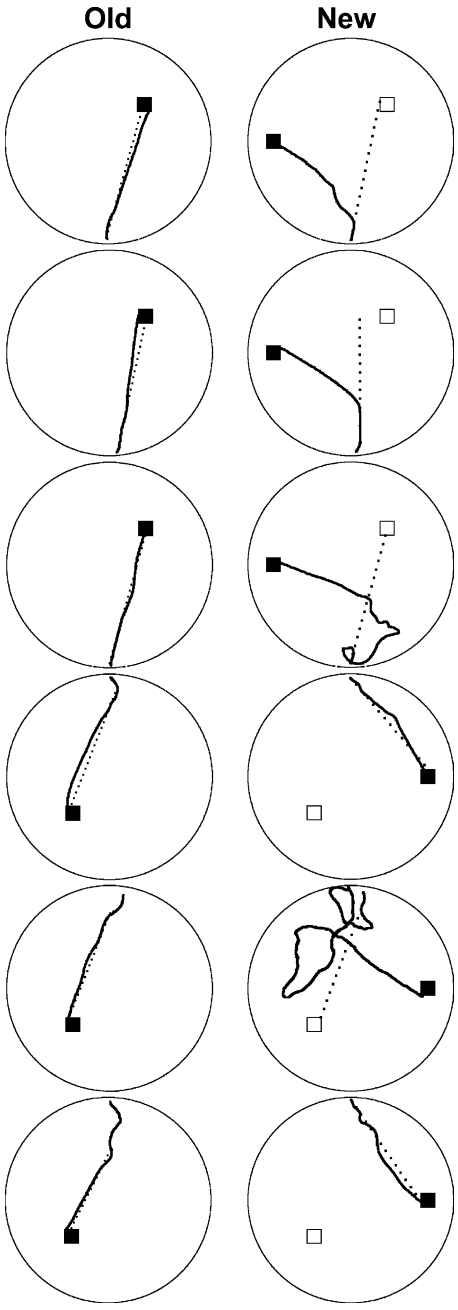

Fig. 11. Swim paths for each of the six rats in Experiment 2 during the visible platform trial in the original (left) and moved (right) location of session 14. The old platform location is marked by the open square. The dotted lines represent the trajectory at the shift point.

was measured. Nonetheless, Fig. 13 clearly shows that, as in Experiment 1, the initial trajectory was much more inaccurate in the novel room compared to heading error in the familiar room. Heading error significantly improved in the familiar room [$F(2, 10) = 5.03$], but not in the novel room [$F(2, 10) = 1.20$, $P = 0.34$]. Ultimately, however, animals did take a direct path to the visible platform during the swim in the novel room. The path length up until a direct path segment to the platform was executed was significantly higher in the novel environment [$F(1, 10) = 5.35$; $M_{familiar} = 32.55$ (S.E.M. = 2.44), $M_{novel} = 79.18$ (S.E.M. = 20.02)], and the distance from the platform at which animals initiated a direct path to the platform was significantly shorter in the novel room [$F(1, 10) = 5.41$]. In the familiar room, the average distance was 111.32 cm (S.E.M. = 5.47) compared to 82.99 cm (S.E.M. = 10.89) in the novel room. The change in distal room cues was also associated with an increase in latency [$M_{old} = 2.65$ (S.E.M. = 0.10); $M_{new} = 3.70$ (S.E.M. = 0.57)], however, this increase did not reach statistical significance [$F(1, 10) = 3.31$, $P = 0.08$]. Thus, as in Experiment 1, changing the distal cues while holding other aspects of the testing procedures constant, was sufficient to selectively disrupt navigation, particularly the initial segment of the trajectory, even though the platform was visible.

4. General discussion

The major findings of the present study suggest that locale cues and taxon cues control navigation to a visible goal in the Morris water task independently and sequentially. A

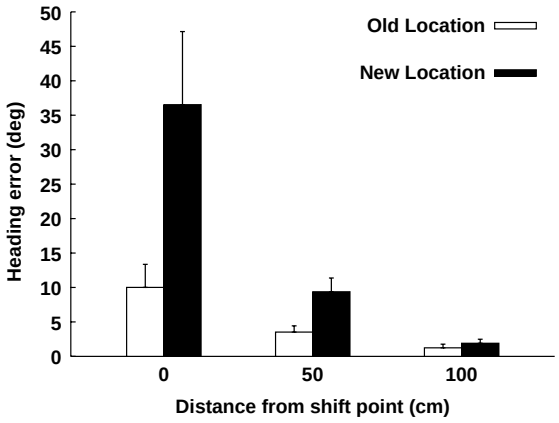

Fig. 12. Mean (+1 S.E.M.) heading error during session 14 of Experiment 2 at three points during the path to the platform: 0, 50, and 100 cm from the shift point for animals navigating to the old (trained) platform location and with the platform moved to a new location.

variety of behavioral observations indicate that rats executed an accurate initial trajectory based upon distal locale cues, engaged in stimulus sampling behaviors, and subsequently navigated directly to the visible platform based on taxon cues from the goal. These components of the swim path can be distinguished based upon kinematic markers, such as the pattern of moment-to-moment changes in velocity at and subsequent to the sampling behaviors, and the accuracy of the trajectory to the visible platform at and subsequent to the stimulus sampling behaviors. Further, test trials with unfamiliar locale cues or with the platform removed or relocated selectively disrupted either the initial or terminal components of the swim path respectively. Collectively, these results lead us to refer to the point at which animals engage in sampling behaviors as a *shift point*, in that it appears to represent the point at which exteroceptive control of navigation

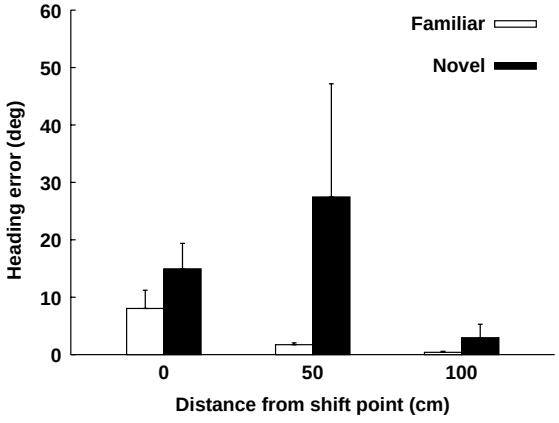

Fig. 13. Mean (+1 S.E.M.) heading error during a visible platform trial in the familiar and a novel environment. Heading error in the familiar environment was measured at three points during the path to the platform: 0, 50, and 100 cm from the shift point. Because a distinct shift point was not observed in the novel room, heading error was measured at the same path lengths into the trajectory as observed in the familiar room.

shifts from locale to taxon cues. It is important to note, however, that the mere presence of stimulus sampling behaviors is not sufficient to conclude that there is a shift in exteroceptive stimulus control. It could be argued, for example, that that presence of sampling behaviors in the absence of a conspicuous taxon cue (e.g., in the hidden platform water task) would require a revision of our interpretation. In the present study, stimulus sampling behaviors were only used to identify points in the trajectory to the platform where potentially informative behavioral measurements should be taken. It is these measurements taken during critical test trials, rather than the presence of sampling behaviors, that provide strong support for our interpretation of sequential control of navigation by locale and taxon cues. The results have several important implications for the study of spatial behavior. For example, the results indicate that locale and taxon cues independently control different aspects of navigation in the water task that are associated with distinct (yet potentially subtle) behavioral markers. This behavioral dissociation may be important for evaluating the effects of environmental manipulations involving locale and taxon cues and the effects of neurobiological manipulations on navigation.

The possibilities that animals use only one cue type or use both locale and taxon cues simultaneously have previously been suggested and supported by empirical data. For example, navigation may come under the control of only taxon cues when locale cues are also present [13,17,22,30] or both cue types may control navigation simultaneously in parallel [30,31]. To our knowledge, the possibility that navigation in the water task can be controlled sequentially by locale and taxon cues has not been considered, thus, the present findings represent a novel contribution to the literature on spatial behavior in the rat. Importantly, it should be noted that the sequential control of navigation by global and local cues is thought to operate in large-scale navigation [9] and similar analogs exist in non-spatial domains, as in the case of skilled reaching [8]. Thus, this type of independent and serial stimulus control of behavior may have generality. If so, the training and analytical methods employed here should be useful for investigating a variety of behavioral processes in the rat, for example, assessing how and when certain cues control spatial behavior.

Since Morris' initial report, there has been as increasing interest in understanding the psychological processes involved in place learning [2,14], owing largely to the widespread interest in the biological bases of this form of learning. Typically, researchers analyze escape latency during training, and search time in the platform quadrant during probe trials. While informative, these measures only provide information regarding the more molar aspects of navigation behaviors. A detailed moment-to-moment kinematic analysis may provide more sensitive data for assessing how and when stimuli control behavior than the standard measures, and appears well-suited for testing hypotheses regarding cue competition (e.g., overshadowing) in the spatial domain. For example, it has become popular

to test hypotheses regarding whether cues compete with one another for control of navigation [1,3,4,6,11,12,21,23], because such evidence for competition provides insight into the learning principles involved in place learning [3]. In some cases, latency or search persistence measures are sufficient to detect competition among cues for control over navigation, however, in some cases the effects of removing a taxon cue are not detectable using standard measures. Recently, for example, Pearce and coworkers [12,21] have reported failures to detect competition effects among taxon cues (beacons) and geometric cues using standard dependent measures, suggesting that the two cue types do not compete with one another for control over behavior and are, in fact, learned simultaneously. Geometric cues and beacons may control different aspects of navigation that could be dissociated using the type of microbehavioral analysis employed here, thus, it would be interesting to determine whether distinct kinematic markers are associated with the control of navigation by geometric and taxon cues. Such data would be informative for designing future studies and drawing conclusions regarding the learning mechanisms involved in these forms of navigation.

An interesting line of future research is also suggested by one behavioral observation which, due to its infrequency, was not reported along with the major results. All animals began to consistently turn in the same direction when released, often prior to actually being released or even being placed in the water. The development of a turning preference roughly corresponded to when animals reached asymptotic levels of performance. On several occasions, subsequent to reaching asymptote, animals turned opposite to the preferred direction. When this happened navigation was severely disrupted and these animals were given an additional trial during which they invariably turned in the preferred direction and efficiently navigated to the platform. Although few in number, these observations suggest three important possibilities. First, they underscore the idea that the initial trajectory selection is based upon cues other than the visible platform (i.e., the ambient room cues). Second, they further highlight the possibility that cued navigation in the presence of locale cues involves a sequential process. That is, the data suggest that a disruption in the initial component of the behavioral sequence can disrupt the performance of subsequent components. Third, they suggest that the distal cue constellation (as well as other exteroceptive or interoceptive cues) may control behavior at least as early as the animals begin to turn away from the pool wall, and possibly beginning as soon as they are removed from their cage. If inconsistent with the animal's expectations, stimulus control exerted during these components of the trial may lead to inaccurate navigation even though the platform is visible. This possibility fits nicely with data suggesting that nonhuman animals and humans learn to take routes to a goal within a range of familiar views encountered during training [10,24,27,31].

Of further importance, the majority of results reported here are consistent with our interpretation of sequential control of navigation by locale and taxon cues, however, behavior by a small proportion of animals on critical test trials was inconsistent with our primary interpretation. For example, in Experiment 2 we moved the visible platform to a new location and found that 4/6 animals executed an initial trajectory in the direction of the old platform location, whereas 2/6 animals navigated more or less directly to the visible platform. Although the group analyses indicated that navigation was significantly more accurate toward the old platform location (see Fig. 12), and the large majority of data from other test trials is consistent with our interpretation, this finding indicates that independent sequential control of navigation by locale and taxon cues was not observed in all animals. It is important to acknowledge such individual differences as they may represent sources of behavioral variability that could influence the outcome of experimental manipulations. Individual differences were also noted in stimulus sampling behaviors, with some animals engaging in distinctive heads scans while others made more subtle corrections in their trajectories at the shift point. Even among animals that engaged in distinctive head-scanning behaviors there could be important individual differences in navigation. For example, consider the reasons why an animal might engage in stimulus sampling behaviors. Animals may use distal cues during the initial component of the trajectory, as we have suggested, and then perform head scans in order to locate the visible platform. Alternatively, animals could navigate using the visible platform beginning at the release point and perform sampling behaviors in order to estimate the distance to the platform. Such information is particularly relevant in the procedures we employed because the distance to the platform varied from trial to trial depending upon the release location. A thorough evaluation of individual differences in the behaviors reported here may yield important clues regarding the behavioral processes involved in navigation, but will require much additional research.

As additional consideration for future studies using this methodology concerns the potential influence of training parameters. For example, in many respects, the present findings are similar to the data reported by Whishaw and Mittleman [31], however, one important difference was observed in the behavior of animals during the no-platform probe trials. Whishaw and Mittleman's animals navigated to and crossed over the platform location, whereas the majority of animals in our experiments initially navigated in the direction of the platform but subsequently took erroneous paths that did not include crossing the platform location. This may be related to the fact that Whishaw and Mittleman gave animals four trials per session while we only gave animals two trials. We are currently undertaking additional studies to characterize the factors that influence the behaviors described in the present study, of which one is the influence of the number of training trials. The influence of sex should also be investigated. In a study conducted by Kanit et al. [13] rats were trained to navigate to a visible platform in a fixed spatial location and on a test trial the visible platform was moved to a new loca-

tion. Male animals were more likely to visit the spatial location where the platform had been, whereas female rats were more likely to navigate to the visible platform. In the present study we only tested female animals, thus, it is possible that a different pattern of results would be observed in males. Because male rats appear to preferentially make use of locale cues, whereas females prefer to use taxon cues, we would predict that males would be less likely than females to show distinctive shift point behaviors or the distinctive kinematic profiles described here. Because there do not appear to be robust sex differences in place learning in laboratory rats of the type used in this study, utilization of this type of analysis may be useful for investigating sexually dimorphic spatial behavior.

That navigation based upon locale and taxon cues can be distinguished using moment-to-moment kinematics and accuracy measures also raises some interesting possibilities for future lesion and pharmacological studies. If these two forms of navigation are entirely independent and sequential, it should be possible to perform manipulations which affect behaviors associated with one type of navigation, potentially sparing the others. Thus, manipulations that disrupt place navigation might alter the initial trajectory selection, whereas those that disrupt cued navigation should only disrupt the behaviors involved with approaching a taxon cue. Further, some neurobiological manipulations may have the effect of biasing animals toward (or away from) a particular strategy which should be detectable using the methods described here without using test trials that may interact with the animal's bias. Thus, lesions that induce a bias in strategy preference may manifest in an elimination of the shift point or otherwise alter the kinematic profile in a way that would be informative regarding the effect(s) of a neurobiological manipulation. Such an analysis may provide a more sensitive measure of behavioral disruption which could be valuable in cases where there are subtle behavioral effects resulting from a particular manipulation.

In summary, the major finding of the present study is that rats appear to use locale cues and taxon cues sequentially to navigate during a cued navigation task. This behavioral dissociation is supported by a broad range of critical test trials dependent measures. The use of detailed kinematic analyses to identify, test, and describe this dissociation represents an additional contribution of this report. This type of microbehavioral analysis during navigation may yield important clues regarding how animals navigate to a goal and how cues gain control over behavior, which has been a topic of considerable interest to researchers interested in place learning [16] and its biological bases [2,20].

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