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Route finding by rats in an open arena

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Abstract

Rats were repeatedly exposed to an open arena containing two depletable food sources in a discrete-trials procedure. Their movement patterns were recorded and compared to adaptive foraging tactics such as minimizing distance or energy expenditure, thigmotaxis, and trail following. They were also compared to the predictions of the associative route-finder model of Reid and Staddon [Reid, A.K., Staddon, J.E.R., 1998. A dynamic route finder for the cognitive map. Psychol. Rev. 105 (3), 585–601]. We manipulated the presence/absence of food, goal cups, and a wooden runway to determine the influence of local and distal stimuli (visual, olfactory, and tactile) on movement patterns. Increased experience in the arena produced decreases in travel distance and time to the food sources. Local and distal stimuli influenced movement patterns in ways compatible with visual beacons and trail following. The route-finder model accurately predicted movement patterns except those that were influenced by local and distal stimuli. These results show how certain stimuli influence movement and provide a guide for the incorporation of local and distal stimuli in a future version of the dynamic route-finder model.
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1. Introduction

In the last few decades, spatial navigation has stimulated substantial research, especially following O'Keefe and Nadel (1978) classic work proposing the hippocampus as a cognitive map. Biegler (2003) identifies three current approaches to the study of spatial navigation that have different assumptions and goals: (a)

The ethological or adaptationist approach tends to concentrate on species-specific adaptations, whereas the (b) cognitive approach and the (c) associative approach aim to discover general principles underlying behavior. Biegler argues that the cognitive approach assumes that different species may perform qualitatively different types of computation during spatial navigation, whereas the associative approach generally assumes that the computations are only quantitatively different across species and task domains. The main goal of the current study was to contrast explanations of spatial foraging patterns based on species-specific adaptations

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with the predictions of the Reid and Staddon (1998) associative route-finder model.

Reid and Staddon (1998) point out that spatial orientation has two logical parts, knowledge and action. Their route-finder model was designed to explain action — it was not intended to explain how the organism acquired spatial knowledge, or how the animal knows where it is. Nevertheless, most recent research in spatial navigation has centered on the mechanisms that permit the acquisition of spatial knowledge. Such knowledge includes learning the location of a goal in relation to landmarks or beacons (e.g., Benhamou and Poucet, 1998; Mackintosh, 2002; Poucet, 1993; Roberts and Pearce, 1998), computation of position based on path integration (e.g., Etienne, 2003; Gallistel, 1990; Wallace et al., 2003; Wehner and Srinivasan, 2003) or the geometric properties of the environment (e.g., Cheng, 1986), the creation of a cognitive map (e.g., O'Keefe and Nadel, 1978), and various other processes. The current debate about the existence of a cognitive map is centered on the knowledge that enables spatial orientation. For the interested reader, the various chapters in Jeffrey (2003), Healy (1998) and Wang and Spelke (2002) provide comprehensive overviews of the acquisition of spatial knowledge and discussions of the various systems or modules (including species-specific adaptations) involved in acquiring spatial knowledge.

The Reid and Staddon (1998) route-finder focuses on action — the means by which spatial knowledge is used to produce movement patterns, such as when animals forage for food in a well-learned environment. It simply assumes the existence of an orientation process sufficient to locate the animal in space. The underlying "map" could be quite detailed, or it could be rudimentary and incomplete, and it could change dynamically as the animal forages or encounters barriers. By "map" Reid and Staddon mean only that for every spatial location, there must be one and only one node (which will have a defined state) and adjacent locations in space would be represented by a connection between nodes. This model promises, "If you can provide certain details of the animal's knowledge of space, the model will show how the animal's history of reward and non-reward in that space will produce dynamic step-by-step movement patterns as the animal forages."

Just as systems and modules have been proposed for acquiring spatial knowledge (e.g., Cheng, 1986; Gallistel, 1990; Rodrigo, 2002; Wang and Spelke,

2002, 2003), modules have also been proposed for action. The most well-known approach, represented extensively in the ethology and adaptationist literature, is the assumption that different movement patterns represent different adaptive behavioral modules, or search tactics, that may combine to produce elaborate movement patterns. Examples of these tactics in rats are thigmotaxis, distance minimization, trail following, detour avoidance, central-place foraging, area-restricted (focal) search, and other win-shift or win-stay strategies compatible with the maximization of net rate of energy gain (e.g., Hoffman et al., 1999; Krebs and McCleery, 1984; Olton and Samuelson, 1976; Rodrigo, 2002; Stephens and Krebs, 1986; Timberlake et al., 1999). This conceptual approach has considerable appeal because these behavioral tactics are normally assumed to be independent of each other, yet they may be simultaneously expressed in many environments. It is easy to imagine evolutionary selection pressures that would favor or suppress each of these foraging strategies in a known environment, eventually resulting in highly adaptive foraging patterns. This conceptual approach implies that: (a) the separate behavioral modules may have evolved independently of one another; (b) they may represent the interactions of multiple motivational systems (such as foraging and predator avoidance); and (c) they may be influenced by different characteristics of the environment (such as distance, walls, trails, sounds, and odors).

Surprisingly, the Reid and Staddon (1998) route-finder model produces most of these behavioral tactics in a single one-parameter model, based on the well-known process of diffusion, without the need of additional modules. Their goal was to identify the most parsimonious mechanism that would generate movement patterns consistent with those observed in a variety of species in the open field and in mazes, such as area-restricted search, avoiding barriers, finding shortcuts, and radial maze behavior. Thus, their model fits squarely within the associative approach. Their dynamic model is based on stimulus generalization in which an elementary diffusion process produces a landscape of reward expectancy, and the simplest hill-climbing algorithm produces movement toward areas of higher expected reward (see Reid and Staddon, 1998; Staddon, 2001; Staddon and Reid, 1990 for additional details). Thus, the model has only two parts: the diffusion of reward expectancy along adjacent nodes

(with only one parameter representing the rate of diffusion) and the simplest local movement rule. This unrealistically simple model successfully generates movement compatible with each of the behavioral tactics described above, even though none of the tactics are explicitly built into the model (see Biegler, 2000; Reid and Staddon, 1998; Staddon, 2001 for demonstrations of movement patterns produced by the model). That is, the model produces behavior commonly classified as thigmotaxis, distance minimization, area-restricted search, win-shift and win-stay strategies, spatial "insight", short cuts, and detours even though only the unitary process of diffusion of reward expectancy creates the model's landscape and produces movement.

As Reid and Staddon's goal was to create the most parsimonious model possible, diffusion acts only as a local process on adjacent locations. They purposely limited the model to local connections between nodes (representing adjacent locations), and reward expectancy diffuses only along these connections. Therefore, the model does not include the visual detection of beacons or any distal stimuli other than the unspecified stimuli that allow the organism to know where it is in space. Reid and Staddon (1998) demonstrated that no detection of distal stimuli, "insight", or overview of the situation as a whole is required to reproduce the foraging tactics listed above. They explicitly compared the predicted step-by-step movement patterns of their simulated organism with the actual movement patterns of rats, badgers, dogs, insect larvae, and ants in published studies that provided detailed figures of these movements. Subsequently, additional comparisons have been carried out by Staddon (2001) involving vervet monkeys and Robles (2003) with humans in a virtual maze. The model was not intended to be a complete model of action (much less a model of knowledge acquisition), but they concluded that it might be an essential ingredient in any comprehensive model of spatial orientation in animals. Recently, Biegler (2000, 2003) has extended this route-finder model into a more powerful, biologically compatible neurophysiological model of action.

The theoretical issue of concern is whether we should conceptualize each of these behavioral tactics as independent species-specific action modules to be employed in a given environment (the ethological/adaptationist approach). Or, might they be teleological categories imposed on an observed stream of behavior that is produced by a simpler mechanism, potentially denying the validity of these categories as separate behavioral modules? Should we expect evolutionary selection pressures to act on each of these behavioral tactics independently, or to act on a single process (such as a diffusion process) that produces each of these descriptive categories of behavior?

What type of evidence would allow us to answer these questions? It is not clear that these two conceptual approaches can be reconciled experimentally in spatial navigation studies. But we can test the adequacy of the Reid and Staddon (1998) route-finder model in foraging situations that normally produce the behavioral tactics described above. Thus, one goal of the current study was to identify the behavioral tactics observed during foraging in a well-learned environment that cannot be accounted for by the route-finder model.

In this experiment, we exposed rats to an open rectangular arena in which food was located at two fixed positions in each trial. We measured the step-by-step movement patterns of rats in a well-known environment and compared them to the predictions of the route-finder model. We also examined how these movement patterns changed across trials as subjects became more familiar with the task. The local-process route finder does not contain a learning rule or the ability to detect goal stimuli from a distance. It contains no distal stimuli at all, other than unspecified landmarks used by the organism to orient itself in space. Therefore, two additional goals of this experiment were to identify the changes in movement patterns: (a) in successive trials in the same environment, and (b) in the presence and absence of distal food cups, which could serve as visual beacons, while keeping the olfactory cues constant by delivering the same amount of food at the same location whether the cups were present or not.

A final goal of this experiment was to increase our understanding of the "trail-following" tactic described by Timberlake et al. (1999). They measured the movement patterns of rats exposed to a radial arm maze located on the floor (rather than elevated above the floor) — thus, shortcuts across arms were quite possible. They demonstrated that spatial navigation was more strongly influenced by the edge of a maze arm than by its surface, and clipping the whiskers decreased this foraging tactic. The Reid and Staddon (1998) route finder does not include stimuli such as surfaces and edges of arms. If these stimuli are important influences

on foraging patterns, then we need to determine which part of spatial navigation they affect: knowledge or action. Therefore, in some trials we added a board (with a wooden surface and prominent edges) to see if the strength of the "trail-following" tactic was sufficient to alter the direction of movement in the arena.

2. Materials and methods

2.1. Subjects

Five adult female Long Evans rats (*Rattus norvegicus*), approximately nine months old at the beginning of the study (mean weight 302 g), were used as subjects. Although the rats were maze-naïve, they had previous experience in a laboratory project (rat basketball, e.g., http://www.wofford.edu/psychology/ratBasketball.asp) for approximately 3 months, which involved daily handling by various students, exposure to relatively open areas in a noisy environment, and reinforcement with the same 45 mg Noyes pellets used in this study. The rats were housed individually in standard polycarbonate cages in a room with relatively constant temperature and humidity with a 12:12 light/dark cycle. Water was continuously available in the home cages. After completing the daily session, the rats were provided with unlimited access to food for 1 h (Teklad Rodent Diet) in their home cages to maintain a 23 h deprivation level for each daily experimental session.

2.2. Apparatus

The open-area arena (see Fig. 1) was constructed by placing 38 cm high polystyrene walls (Owens Corning Extruded Polystyrene Insulation Foamular 150) around a table (96 cm × 183 cm). The tabletop was covered with plastic sheeting and covered with 32 kg of clean sand (Bonsal Play Sand) spread to a uniform thickness of approximately 2 cm. The locations of the starting position and goals can be most easily identified by describing the arena in Cartesian coordinates with 1 in. units (2.54 cm). Thus, the bottom left corner would be represented as position (0, 0), and the upper right corner would be (72, 38). An 8 in. (20.3 cm) circular block cut from 1/2 in. (1.3 cm) plywood was used as the starting position, centered and placed on top of the sand against the short wall on the left side of the arena, centered at position (4, 19). Two 3.7 cm × 1.5 cm aluminum bottle
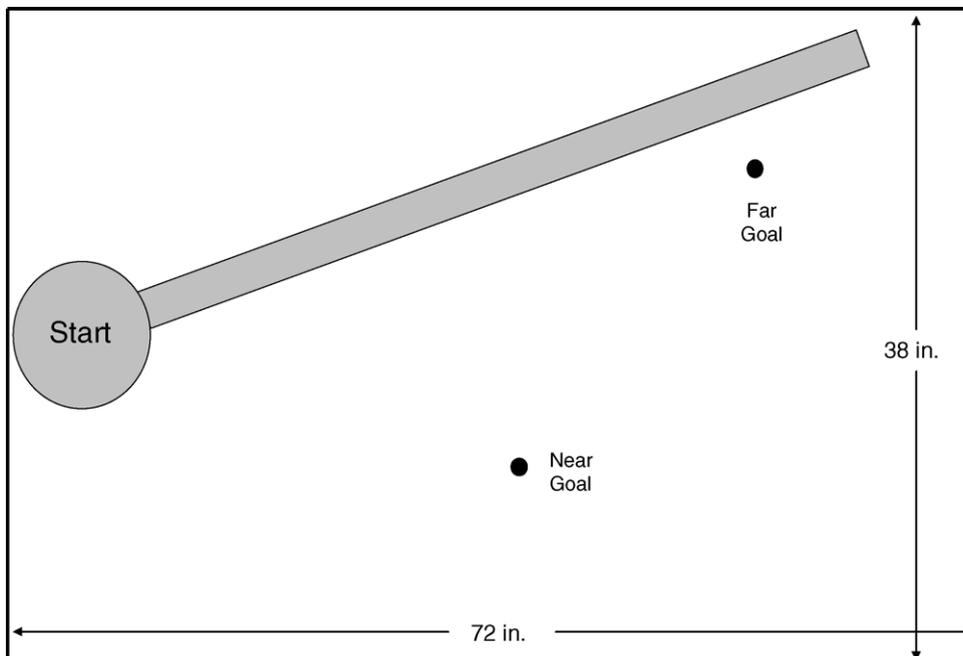

Fig. 1. The dimensions and spatial layout of the open arena.

tops served as the two goal cups to hold the food pellets. The two goals were placed at unequal fixed distances from the starting position. The near goal was 10 in. (25.4 cm) from the lower long wall at position (36, 10), and the far goal was located 10 in. (25.4 cm) from the opposite wall at position (54, 28). Thus, the distance between the middle of the starting position and the near goal was 33.2 in. (84.3 cm), and the distance to the far goal was 53.1 in. (134.9 cm). In some trials, a 158 cm × 6.6 cm × 2 cm poplar board, cut to abut the circular starting platform, was present in a fixed location shown in Fig. 1. The board was partially buried in the sand to ensure that its surface was the same height above the sand as the starting platform (1.3 cm). The sand was carefully smoothed around the board after each trial to ensure that its vertical edges would provide a consistent stimulus to the rats' whiskers.

Three 1 in. PVC pipes were used to create a tripod, which supported a Pro Video CVC-770PH color miniature camera with a conical pinhole lens. The camera looked down through a 5 cm washer placed inside the metal shell of a Hubbell Twist-Lock 20 Amp connector taped to the tripod, which supported the camera 2.44 m above the arena. This arrangement allowed the camera to be rotated manually inside the stationary connector, and three screws on the connector adjusted the position of the washer to provide fine-grain adjustments of the camera's viewing angle. The camera fed into a Sony Dual-Deck VHS Recorder and a 24 in. Metravox television so the images from the camera would appear on the television screen during each trial and could be recorded onto RCA standard grade VHS tapes.

The maze was in a fixed position in the room during the study. The room was an empty circular planetarium, 21.5 ft in diameter, with a white spherical ceiling normally used for projecting images of star constellations. The room was dimly illuminated with a single 60 W bulb in a clamp-on aluminum reflector that directed light in a forward direction. This room configuration allowed tight control of extra-maze stimuli that could serve as landmarks for orientation. For this experiment, we provided abundant extra-maze visual stimuli of several types. The light source was stationary on one wall of the room, and it illuminated the tripod and apparatus in such a way as to produce a large distinctive shadow on the wall and ceiling. The tripod itself could also be used for orientation since two legs were over the bottom wall of the arena and only one was over the top

wall. An air conditioner (turned off) was visible on the wall nearest the bottom left corner of the arena. During every trial, one experimenter stood motionless approximately 3 ft from one end of the arena in a position visible from most locations in the tabletop arena. Finally, the geometry of the rectangular arena and fixed position of the starting platform and goal cups could serve as within-maze orientation cues.

The viewing angle of the TV camera was adjusted each day to ensure that the rectangular arena was displayed the same size and in the same fixed position on the television screen for every trial. This made digitizing the movement patterns easier and reliable from trial to trial. During all trials and subsequent video digitizing, a large transparent grid with 1/2 in. squares was taped over the entire television screen to provide a constant reference for the coordinate system. The 38 in. × 72 in. arena was always displayed on the television as a 21-unit by 40-unit rectangle (10.5 in. × 20 in.), so the scale transformation from actual arena to television image was 3.6–1 along both the x- and y-axes. Following the experiment, the same experimenter digitized every videotaped trial by manually tracing the locomotion of the subject onto the transparent grid on the television, and then typing the grid coordinates for each 1/2 in. square into a personal computer using Microsoft Excel. To prevent experimenter bias, this experimenter was blind to the predictions of the route-finder model whose predicted movement pattern for each trial would later be compared to the rats' actual movement patterns. No inter-rater reliability measures were used.

2.3. Procedure

2.3.1. Habituation training

When the rats were 48 h food deprived, we transported all five rats in their home cages to the experimental room where we allowed them to become adjusted to the dim lighting and odors of the room for about 30 min. The rats were then individually placed on the starting platform and were allowed to explore for 10 min. Both goal cups were present, although no food was provided during habituation training. The board serving as a runway was not present during habituation training. Three experimenters stood motionless in the room and remained silent. At the end of habituation we stopped the video recording and placed each subject back in its respective cage.

2.3.2. Experimental procedure

The same general procedure was used for each trial. Differences between trial conditions are presented below. Subjects were 23 h food deprived and trials began at approximately the same time each day. All subjects were weighed and transported in their home cages (without food or water bottles) to the experimental room, where they became adjusted to the dim lighting and odors of the room for about 30 min. Subjects were run in the same order for every trial. We began recording each trial before the subject was placed into the open arena. Two experimenters were involved in all trials: one operated the VCR, placed the subject in the same position on the starting platform for each trial, and removed the subject when the trial was over. The other experimenter displayed a clipboard to the camera with the identifying details of the trial, then stood motionless one meter from the right side of the arena to observe the subject and time the subject with a stopwatch. Timing began with the subject being released on the starting platform and ended when all pellets had been consumed in both goals. Reinforcement at each goal consisted of three 45 mg Noyes pellets (Formula A/I). The trial ended when the subject appeared to stop looking for food, usually after returning to the vicinity of the starting location, at which point the video recording was stopped and the subject was returned to its home cage in the same room.

The conditions of each trial were manipulated in the following way. The board (runway) was present in the arena only for Trials 11–15. Both goal cups were present in the arena in all trials except Trials 16–19.

Trial 1. Both goal cups were present, but food (three food pellets) was available only in one of them. Food was available in the near goal for Rats 1 and 2, and in the far goal for Rats 3–5.

Trials 2–10. Three food pellets were provided in both goal cups for all subjects.

Trials 11–15. The board (runway) was present in the arena in the position shown in Fig. 1. After the subjects found the food in Trial 11, they were allowed to remain in the arena for several minutes to explore the board and habituate to the modified environment.

Trial 16. We removed the board and the goal cups for Trial 16. Three pellets were buried in the same two locations as the goal cups had been located previously.

Trial 17. For both goals, we buried three pellets and placed three additional pellets above them on the sur-face of the sand in the same location (for a total of six pellets at each goal location).

Trials 18–19. These trials were extinction trials in which no food, goal cups, or board were present.

2.3.3. Simulation details

The observed movement patterns of the rats were compared to the predictions of the Reid and Staddon (1998) dynamic route-finder model. The simulation was carried out on a 20×40 grid of units representing an eight-neighbor lattice. Thus, every grid location (except along the walls) was assumed to be adjacent to the eight surrounding locations represented by the eight standard directions on a compass (i.e., N, NE, E, SE, S, etc.). Movement and diffusion of reward expectation occurred only via these local connections. The diffusion rate parameter (α) was set to 0.08 in all simulations. At the beginning of the simulation of habituation to the arena, all nodes were initialized with the same low reward expectation, producing a uniform field of reward expectancy across the arena. Each movement (each "step") by the hill-climbing algorithm produced one iteration of the discrete diffusion equation, acting on every node represented in the arena. Each time the simulated organism stepped in a location (thus, with reward expectation >0) where no reward was present, the reward expectation for that location was set to zero for the next iteration. When reward was found at a location, the reward expectation at that location was incremented by 1.0 for the next iteration. Each iteration produced changes in the reward expectancy landscape, with unrewarded steps leaving tracks that slowly filled in due to diffusion flow from adjacent locations where reward expectation had been higher. The effect of finding reward at a single location (during Trial 1) was to create an impulse at that location, which (with repeated iterations) formed a hill of reward expectancy centered at that location. Repeated iterations produced a spreading flow from the center of the hill outward in each direction. Finding reward at additional locations produced multiple hills. Movement by the simulated organism acted on this dynamic landscape to produce a complex landscape changing dynamically at each step as a function of diffusion, additional reward, and discovered non-reward. All details of our simulations were the same as those in Reid and Staddon (1998), so the interested reader may examine this reference for further explanation and quantitative details.

3. Results and discussion

This procedure provided multiple opportunities to compare the movement patterns of rats in an open arena to that predicted by the Reid and Staddon (1998) route-finder model. The main purpose of this comparison was to identify behavioral processes involved in movement patterns that are not included in their parsimonious model. It also allowed us to compare the movement patterns to the foraging patterns observed by Hoffman et al. (1999) and Timberlake et al. (1999) using a radial arm maze placed on the floor of the experimental room.

3.1. Initial encounter with food

In Trial 1, food was provided in only one goal cup — in the near goal cup for some subjects and in the far goal for the other subjects. We wanted to know what role distal beacons have in the movement patterns of foraging rats, and how much experience is necessary for beacons to become predictive of food. Would finding food in one goal cup produce directed orientation toward the other (empty) food cup in the same trial, given that the cups were identical in appearance? Al-ternatively, the rats might orient naturally toward both goal cups as beacons in the otherwise uniform arena, independent of the presence of food, just as wood ants do (Graham et al., 2003). Finally, how would obtaining food at a single goal location affect movement patterns in subsequent trials? For example, would each subject return directly to that same goal location in the next trial before beginning a more general search?

Fig. 2 depicts the movement patterns of each subject during Trial 1, along with a computer simulation of the Reid and Staddon (1998) route-finder model. The trial lasted until each subject had visited both cups. The solid lines represent the movement patterns until both cups were visited, and the dotted lines show movement after both cups were visited, as they generally returned to the starting platform. A major question concerned the potential influence of olfaction (i.e., smelling the food pellets) in the movement patterns of these hungry rats. If the pellets could be detected from a distance, one would expect directed orientation to the cup that actually contained the food. We observed that when food was provided only in the near cup, one rat (Rat 2) visited this goal first, but the other rat (Rat 1) visited the far cup first. When food was provided only in the
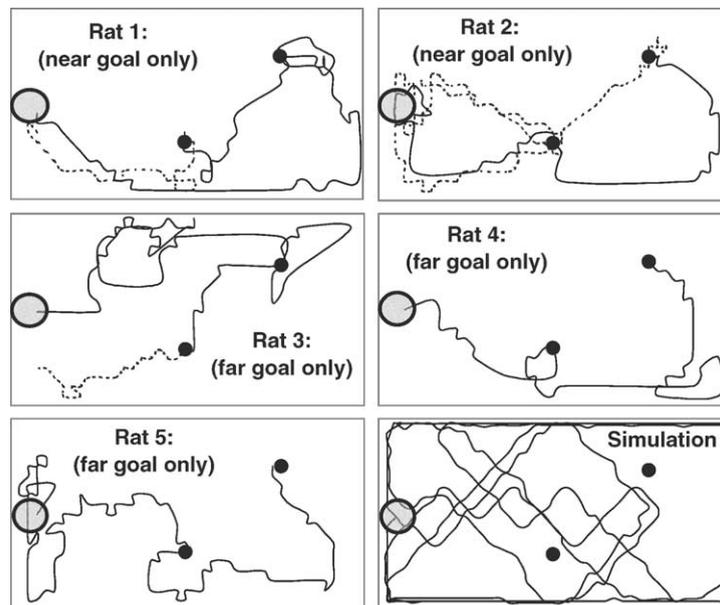

Fig. 2. Solid lines represent the movement patterns of each subject in Trial 1, following habituation training. The dashed lines represent the movement patterns after both goal cups were visited. Although food had been placed only in one cup for each subject, each subject traveled to both cups as though they served as visual beacons. The simulation of the Reid and Staddon (1998) route-finder model generally repeated the movement patterns predicted during habituation because the model does not provide for stimuli such as beacons.

far cup, only one rat (Rat 3) visited this cup first, and two rats (Rats 4 and 5) visited the (empty) near cup first. Therefore, the order of visiting the two cups did not appear to be correlated with the location of food. Movement was clearly not random, however. All subjects oriented toward both goal cups as beacons in the otherwise uniform arena, independent of the presence of food, replicating the patterns observed with wood ants and other species (Graham et al., 2003).

The computer simulation of Trial 1 is depicted in the bottom right panel of Fig. 2. Recall that subjects had been previously exposed to the open arena for a 10 min habituation session, and at the beginning of Trial 1, no food had been obtained in the arena. Therefore, the simulation needed to begin with a habituation session, followed by the depicted simulation of Trial 1. The simulated movement patterns of Trial 1 could depend upon the prior experience of habituation, so we briefly describe the habituation simulation first.

Simulation of the habituation session (not depicted) began by initializing all units with the same low value of reward expectancy (0.001) and placing the simulated organism at the coordinates representing the starting platform. Movement was oriented exclusively along the walls (thigmotaxis) until the entire arena had been circumnavigated, accurately replicating the thigmotaxis observed in the actual subjects during the habituation session. Only then did the simulated organism traverse the open areas of the arena. The movement pattern representing the simulated 10 min habituation session appeared complex and unpredictable (even though no random process was involved).

Trial 1 occurred 24 h after the habituation session. Therefore, in order to represent this time period in the computer simulation, we "removed" the simulated organism from the arena and iterated the diffusion equation for 300 steps. (*Note*: This same procedure was used in the simulations of European badger movements in Reid and Staddon, 1998.) Because diffusion is an averaging process, this procedure produced a fairly uniform field of reward expectancy across the units representing the arena, similar to the original conditions of the habituation simulation. As a result, the predicted movement patterns of Trial 1 (depicted in Fig. 2) were highly similar to those observed during the habituation simulation. Unlike the actual rats in Trial 1, the simulated organism displayed considerable thigmotaxis before venturing into the open areas of the arena. The Reid and Staddon

(1998) route-finder model does not provide the ability to detect visual stimuli such as the food cups, and even after 440 steps, the locations representing the food cups had not been visited. The food cups acted as visual beacons for the actual subjects, but the route-finder model could not replicate this influence on movement patterns.

3.2. Subsequent encounter with food

We wanted to know how obtaining food at a single goal location would affect movement patterns in the arena in subsequent trials. For example, would each subject return immediately to that same goal location before beginning a more general search? Fig. 3 depicts the movement patterns of each subject during Trial 2, along with two computer simulations (explained below) of the Reid and Staddon (1998) route-finder model. Recall that Trial 2 provided food in both goal locations. As expected, both rats that had previously received food only in the near goal (Rats 1 and 2) traveled first to the near goal, but (unexpectedly) then immediately traveled to the far goal, even though they had not found food there previously. The other three subjects (Rats 3–5), who had previously found food only in the far goal, also visited the near goal before the far goal even though they had never obtained food there. Thus, all subjects visited the near goal cup before the far goal, independent of where they received food previously.

Potentially, there are three ways of explaining this movement pattern. One potential explanation is that subjects' olfactory abilities were sufficient to detect the food from several feet away, so olfaction (not vision) determined the direction of movement. We reject this explanation because the rats' movement patterns were clearly not greatly influenced by olfaction (at a distance) in other trials. For example, olfaction clearly did not direct orientation during Trial 1. In addition, later trials led us to believe that their ability to smell the pellets was limited to several inches, not feet. In Trials 16 and 17 food pellets were presented without the goal cups, either buried in the sand or both buried and on the surface. Yet the subjects often did not find the pellets even though they traveled within 2–3 in. of the food while foraging.

A second potential explanation is that one goal-food pairing from Trial 1 was sufficient for each subject to associate both goal cups with high food probability.
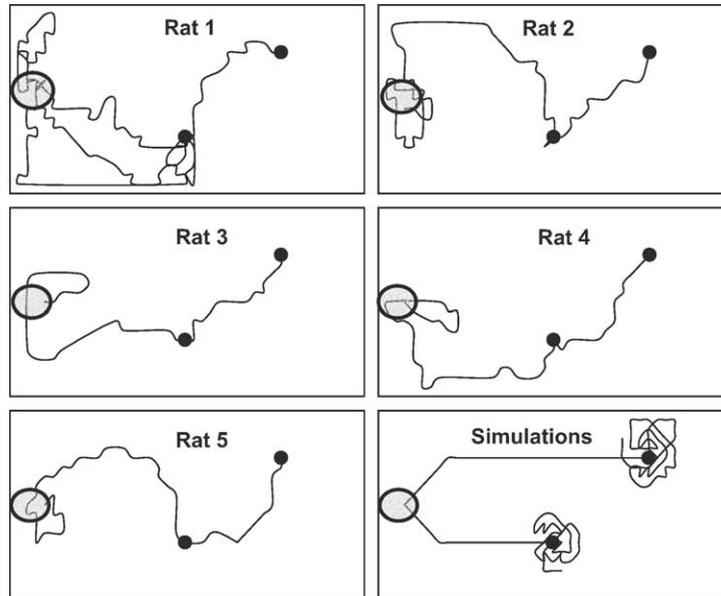
Fig. 3. Lines represent the movement patterns of each subject in Trial 2 until food was depleted in both goal cups. Two separate computer simulations of the Reid and Staddon (1998) route-finder model demonstrate area-restricted search around the single location in which food had been found in the previous trial.

This argument, based on stimulus generalization of a conditioned stimulus, assumes that subjects would generalize from the food cup where they had found food to the other food cup located at a different position in the arena. The design of this study did not allow us to test the validity of this explanation.

The third potential explanation is that foraging rats naturally orient toward visual beacons, and this tendency is enhanced when the beacon has been previously paired with food. In Trial 1, we observed that each subject did orient movement toward both food cups, even though they did not travel directly to the nearest cup. In Trial 2, they did travel more directly to the nearer cup, and this improvement in travel efficiency may have been due to associating both goal cups with high food probability. While we cannot test this explanation directly in the current study, we conclude that travel to the near goal on Trial 2 was guided more by the visual beacons than by olfaction.

The conclusion that visual beacons guide movement patterns is important because it points out a limitation of the Reid and Staddon (1998) route-finder model. This model was designed to be the most parsimonious explanation of how knowledge of space (i.e., some minimal cognitive map) and reinforcement history can produce

ostensibly goal-directed spatial behavior without providing a global overview of the arena. Thus, it provides only local connections between locations, and movement is based on a local hill-climbing rule acting on a landscape representing changing reinforcement expectations. There are no "stimuli" in the model such as goal cups (other than the unspecified landmarks presumably used by the organism to orient itself in space). Therefore, the model does not allow the organism to "see" goal cups from a distance, much less generalize from one to the other. Thus, if the organism is reinforced in one location, the diffusion process creates a peak on the reinforcement expectation landscape, and the hill-climbing algorithm moves the organism toward that peak, leaving transient footprints in its path. Two independent examples of this predicted movement pattern are provided in the two simulations in the bottom right panel of Fig. 3: if food has been obtained in the far location (the top movement pattern), movement occurs in that direction in the next trial. Once food has been depleted, movement around the goal occurs in a widening area-restricted search. A similar movement pattern is predicted if food is obtained only in the near goal, depicted by the lower pattern. After retrieving food, the model predicts area-restricted search that widens over

time, but it does not include direct travel to the second goal location (assuming food had been found only at the first goal). The model predicts direct travel between goals (shortcuts) only when multiple goals have provided food. (*Note*: Figs. 4 and 7 demonstrate the model's accurate predictions of shortcuts when food had been found at both locations.)

In Trial 2 all subjects traveled to a goal location where they had never received reinforcement, instead of traveling exclusively in the direction of higher obtained reinforcement probability. Movement patterns were influenced by the visual detection of distant goal cups, and subjects may have generalized from one goal to the other. Neither feature is provided by the current version of the Reid and Staddon (1998) route-finder model, but they seem to be general across animals (observed in all five subjects). A more comprehensive version of the model will need to incorporate both features.

3.3. Increased travel efficiency during foraging

Trials 3–10 provided food at both goals and produced similar foraging patterns across subjects. Fig. 4 depicts the movement patterns of each subject during Trial 3, as well as the predictions of the route-finder model. The solid line shows the path taken to visit both goals, and the dotted line shows the movement pattern observed after consuming all the pellets. We expected the dotted line to meander more than the solid line because all of the food in the arena had already been consumed. Fig. 5 depicts the movement patterns observed during Trial 10, showing how travel to the goals became more direct (less meandering) with repeated exposure to the same conditions. Rats 1 and 4 showed considerable thigmotaxis on the way to the goals in Trial 3, but it was eliminated by Trial 10.

In 42 of the 45 trials, subjects visited the near goal before the far goal. After depleting the food in the far goal, subjects usually revisited the near goal (e.g., the dashed line for Rat 5 in Fig. 3). In nearly all trials, to our surprise, each subject returned to the starting location after depleting the food, even though there was no requirement to return and food was never presented near that location. Returns to the starting location resulted in termination of the trial and returning the subject to its empty home cage, without food or a water bottle. Returns to the starting location were observed as early as Trial 3 for all subjects (see Fig. 4). Re-
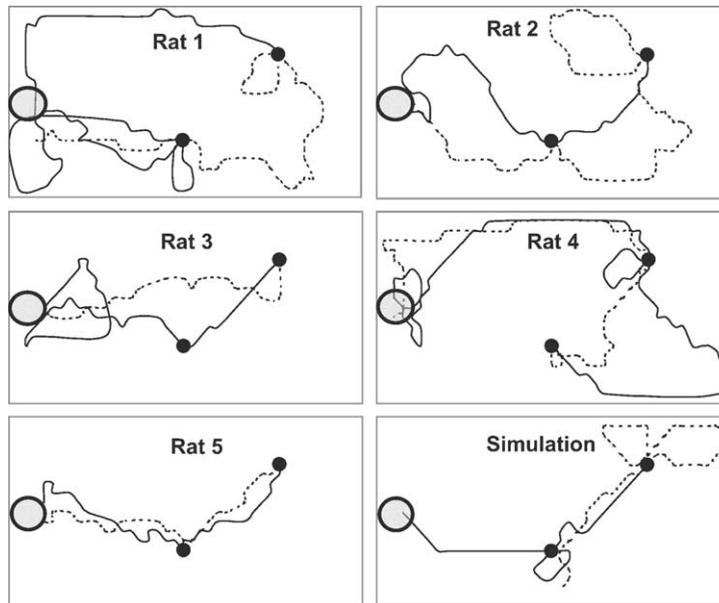

Fig. 4. Solid lines represent the movement patterns of each subject in Trial 3 until food was depleted in both goal cups. The dashed lines represent the movement patterns after all food was gone. The simulation represents the predictions of the Reid and Staddon (1998) route-finder model. The model accurately predicted direct goal-oriented movement to the near goal, and subsequent movement to the far goal, followed by a return to the near goal. It did not predict the return to the starting position observed in all subjects.
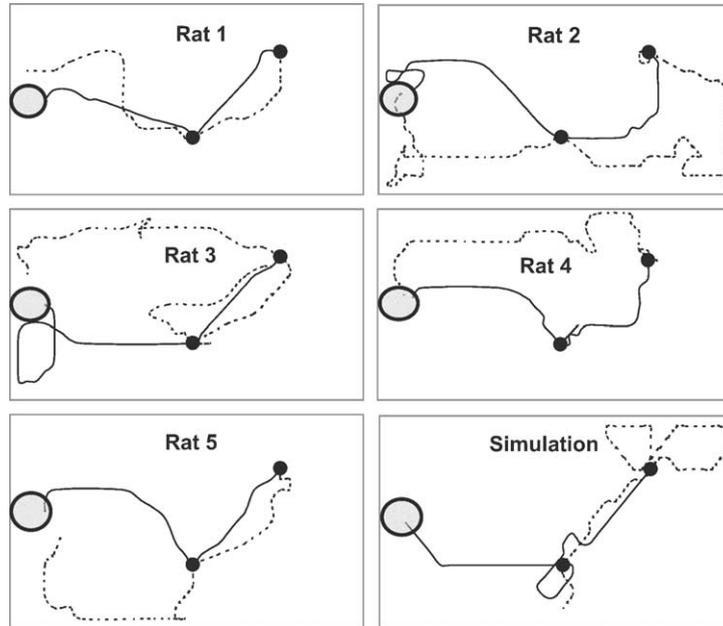
Fig. 5. Solid lines represent the movement patterns of each subject in Trial 10 until food was depleted in both goal cups. The dashed lines represent the movement patterns after all food was gone.

call that the entire arena was covered with fine sand except for the starting position, which was a circular piece of plywood (8 in. diameter, 0.5 in. thick) placed on top of the sand. At first we assumed that the rats preferred to stand on wood. However, after returning to the starting position, subjects would meander in the sand in the general vicinity of the starting position. Thus, they were not avoiding the sand. Recently, Wallace et al. (2003) have provided careful documentation of rats returning to the starting location. They argue that exploring rats set up "virtual home bases" where they rear and groom, even in impoverished environments. They argue that the outward and homeward portions of exploratory trips are distinct behaviors governed by different orientation mechanisms and serving different functions.

Fig. 4 also shows the predictions of the Reid and Staddon (1998) route-finder model. The reinforcement history at the beginning of this simulation was provided by Trial 2, in which food was obtained at both goals. The simulated organism began at the starting position and proceeded to the near goal, followed by a fairly direct route to the far goal — a clear demonstration of the model's ability to take shortcuts. After food was depleted, the organism displayed a small amount of area-restricted search in the vicinity of the far goal, before returning to the near goal and beginning more area-restricted search. Thus far, the movement pattern predicted by the model closely matches that observed in most subjects. However, the rats then returned to the starting position, whereas the simulation did not. Instead, the simulation produced a pattern of ever-widening general search (not depicted) rather than returning to the starting position (a location of presumably low reinforcement probability).

The model makes identical predictions for Trials 3 and 10 (cf. Figs. 4 and 5). The model does not include a learning rule, so it yields identical predictions when the initial starting conditions are the same.

Learning did occur between Trials 2 and 15. Fig. 6 shows the mean distance traveled across subjects from the starting location until all food had been found and consumed in both goals. The average distance decreased significantly over trials, $F(4, 13) = 24.538$, $P < 0.01$. The mean time required to deplete all food decreased significantly as well, $F(4, 13) = 2.519$, $P < 0.01$, also depicted in Fig. 6. Even though foraging behavior is likely to represent some optimal allocation of the organism's energy budget while simultaneously avoiding predation, there has been considerable disagreement
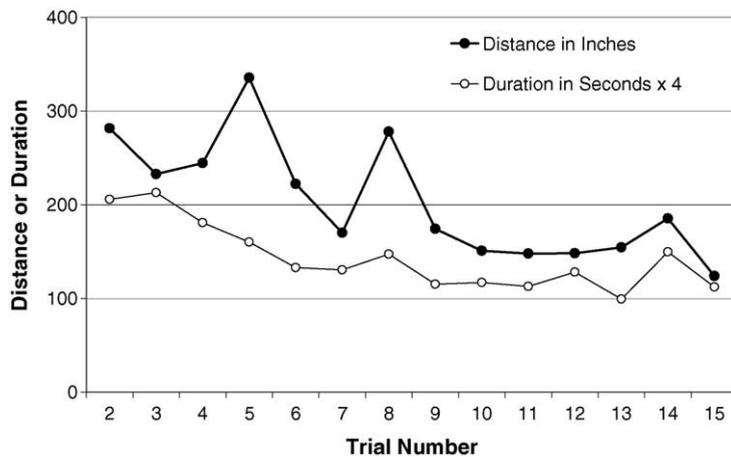
Fig. 6. Travel distance (filled circles) and travel time (open circles) decreased across trials with additional exposure to the consistent food locations in the arena.

as to whether foraging animals minimize travel distance, travel time, energy expenditure, or none of these (e.g., Krebs and McCleery, 1984; Shettleworth, 1998; Staddon, 1983; Stephens and Krebs, 1986). Travel to the goals clearly became more efficient across trials (cf. Fig. 6). Distance traveled and duration of travel both decreased from Trial 2 through Trial 15 as subjects left the starting platform and consumed all the available food in the two goal cups. Distance traveled (or time spent traveling) also strongly influenced the choice of which goal cup to visit first, as all subjects traveled first to the near goal before traveling to the far goal (in 42 of 45 trials). Movement patterns were not usually represented by straight lines (cf. Fig. 5) representing minimal distances between points, but travel to the goals generally became shorter with experience.

3.4. Evaluating trail following

Timberlake et al. (1999) presented compelling evidence that travel along the arms of a radial arm maze located on the floor (rather than elevated above the floor) and along the walls (thigmotaxis) was based on a trail-following tactic in rats. The tendency to follow the radial arms was curious because the rats could easily have taken shortcuts across arms to minimize distance to the food. Yet, they were more likely to continue along the radial arms, maintaining contact with their whiskers with the arm surface or sides of the arms. Whisker contact appeared important: trail following was reduced

when the whiskers were cut. The movement patterns in their study were interesting because the procedure pitted the tendency to follow trails against the tendency to reduce travel distance. Trail following won.

In a similar vein, in the current study we pitted trail following against the tendency to reduce travel distance by providing a board (with a surface and edges similar, but not identical, to those used by Timberlake et al., 1999) between the starting platform and the far goal. Without the board, subjects first traveled to the near goal before traveling to the far goal. Then after depleting the food in the far goal, they typically returned to the near goal (which they had already depleted) before returning to the starting location. We wanted to know if the strength of the trail-following tendency was sufficiently strong: (a) to produce a change in preference — would they visit the far goal first (adjacent to the board) rather than the near goal, (b) to produce a change after food was depleted — would they continue to revisit the near goal or return directly to the starting position? This manipulation provided a rough indication of the strength of the trail-following tactic. Changes in the route taken to the first goal would imply more strength (a more powerful tendency) than changes in the route taken after all food was depleted.

Fig. 7 shows the movement patterns during Trial 12, just after the subjects first experienced and were allowed to habituate to the board in Trial 11. In Trial 12 every subject walked either on or adjacent to the board, but only after retrieving the food from both goals. The
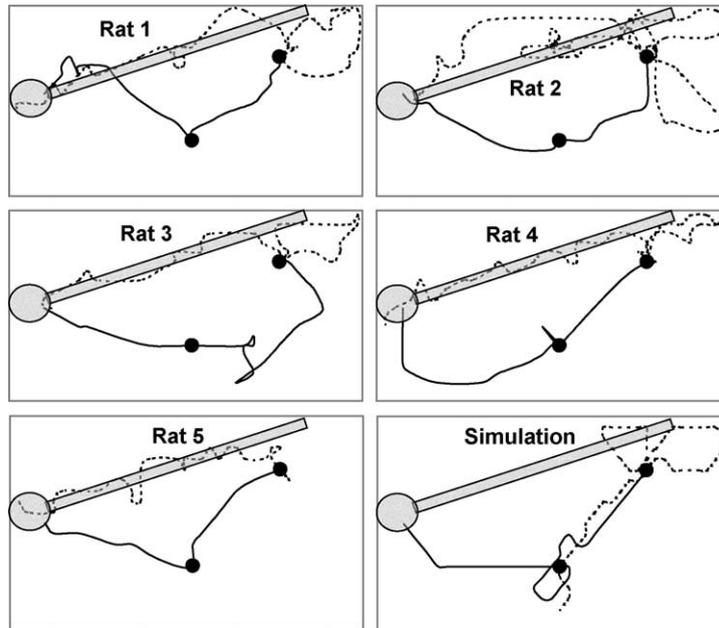
Fig. 7. Solid lines represent the movement patterns of each subject in Trial 12, just after the wooden runway was introduced, until food was depleted in both goal cups. The dashed lines represent the movement patterns after all food was gone. All subjects traveled on the runway, generally returning to the starting position, but only after all food had been depleted. The predictions of the route-finder model of Reid and Staddon (1998) were not influenced by the presence of the runway because the model does not incorporate such stimuli.

presence of the board did not reverse the order of visiting the goals. Instead, the rats generally traveled along the board as they returned to the starting location. Although the board did encourage movement in its vicinity, the "trail-following tendency" was not as strong as the tendency to reduce travel distance to the goals.

Travel along the board decreased with additional exposure to the board in Trials 12–15. Fig. 8 shows the movement patterns of Trial 15. Although every subject used the board in Trial 12, by Trial 15 all rats generally reverted to the movement pattern observed in Trial 10 (cf. Fig. 5): they revisited the near goal on return to the starting position rather than returning via the board. At this point, the board seemed to have minimal influence on movement patterns (except, perhaps, for Rat 3).

In general, the board produced a change in the route taken only after all food was depleted, and this change was transient, lasting no more than two or three consecutive trials with the board present. Thus, while we did observe evidence for a trail-following tactic, it appeared weak and transient. Clearly, different dimensions in height or width of the board could have produced different effects.

The simulation depicted in Fig. 7 is the same as that shown in Fig. 4 because the route-finder model does not include stimuli such as the texture of the sand and runway or global views such as the direction of the runway. The model does not predict travel along the board to the starting position, just as it did not predict the return to the starting position observed in Figs. 4 and 5 without the board.

3.5. Removing the beacons

Trial 16 degraded visual and olfactory cues by eliminating the goal cups and by burying the food pellets under 2 cm of sand in the same locations as before. All subjects traveled to within 5 cm of the goal locations, even though they failed to find the food in five out of 10 instances. The movement patterns on the way to both goals were similar to those observed in Trial 10 (Fig. 5), but subjects generally meandered after visiting the second goal rather than returning directly to the starting position. The frequent failure to find the three buried pellets at each goal, even though standing within 5 cm of the location, leads us to believe that
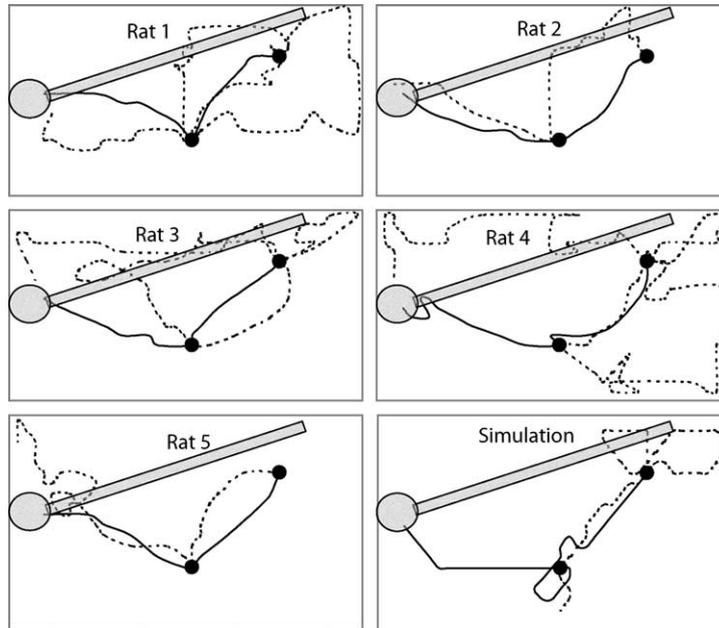
Fig. 8. Solid lines represent the movement patterns of each subject in Trial 15, several trials after the wooden runway was introduced, until food was depleted in both goal cups. The dashed lines represent the movement patterns after all food was gone. Subjects generally ignored the runway, and returned to the movement pattern observed in Trial 10 before the runway was introduced. All subjects returned to the near goal after depleting the food in the far goal. The route-finder model of Reid and Staddon (1998) replicated this movement pattern, just as in Fig. 4.

the rats probably could not smell the pellets from distances greater than several inches. The fact that each goal location was visited within 5 cm in the absence of the goal cups (often without detecting the presence of the food) is evidence that each subject had learned to locate these positions in the arena based on other cues, such as the geometry of the arena and distal landmarks.

Trial 17 confirmed our conclusion that movement patterns were not greatly influenced by olfaction. In Trial 17, three pellets of food were buried and three additional pellets were placed on the surface of the sand in the same locations as the previous positions of the goal cups. Subjects would travel directly to the near goal, but they would often fail to find and consume some of the pellets (even those on the surface) before traveling to the far goal. Only one of the five subjects found and consumed all 12 pellets before returning to the starting position. Most subjects left pellets on the surface of the sand, as well as those hidden below the sand, even though uneaten pellets were within one or 2 in. of the subjects' noses. If olfaction had been an important determinant of movement patterns in this study, one

would have expected the hungry rats to locate all the pellets since they were placed in well-known locations that the rats did visit accurately.

3.6. Extinction

Trials 18 and 19 were extinction trials in which no food, goal cups, or board were present. Movement patterns were highly variable across subjects. Fig. 9, representing Trial 19, shows that rats traveled considerably in the open area of the arena as well as occasionally along the walls. The general pattern reflected travel back and forth between the starting position and the two goal locations, rather than from one goal location to the other. This general pattern stands in contrast to the pattern predicted by the Reid and Staddon (1998) route-finder model. The simulation produced a back and forth movement pattern between the two goals in an ever-widening general search pattern. The model did not predict movement back to the starting position, which had been a prominent feature demonstrated by each subject (e.g., Wallace et al., 2003).
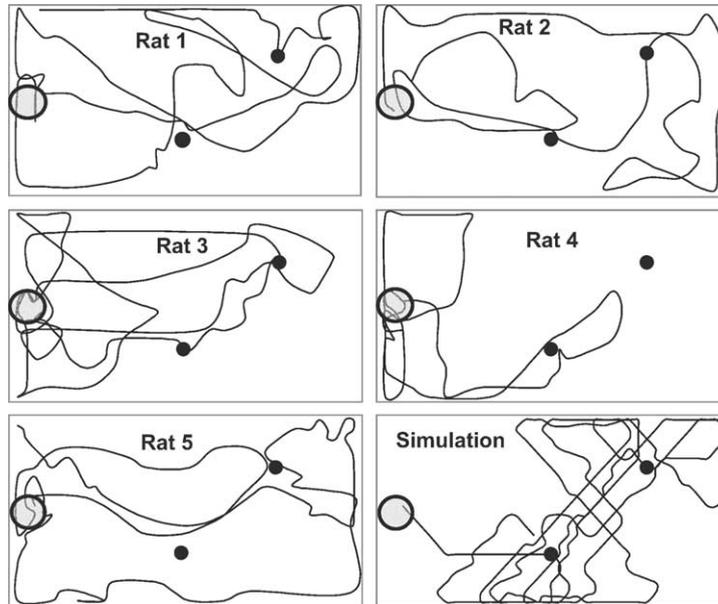
Fig. 9. Lines represent the movement patterns of each subject in Trial 19, the second extinction trial. Subjects generally moved back and forth between the starting position and the goal cups. However, the route-finder model produced alternation between the two goal cups, failing to return to the starting position.

4. Successes and limitations of the Reid and Staddon (1998) route-finder model

These results identify variables that influence movement patterns during foraging and point out successes and limitations of the Reid and Staddon (1998) route-finder model. How well did the route-finder model account for the movement patterns? The model performed surprising well for the situations in which it was designed to make predictions (i.e., those without the effects of stimuli other than food). The model successfully predicted the meandering and subsequent area-restricted search in Trial 1 when subjects found food at one goal location. It successfully predicted the shortcuts taken in Trials 3–10 and 12–15 (e.g. Figs. 4, 5 and 8) as subjects traveled directly to the near goal, from the near goal to the far goal, and back again to the near goal.

However, our results point out three limitations of the route-finder model. Some of these limitations were anticipated by Reid and Staddon (1998), and some were not. First, we observed that travel efficiency improved with practice. Reid and Staddon (1998) pointed out that their intentionally simplistic model did not con-

tain a learning rule, so it would not be able to produce improvements that relied on learning. This limitation was also pointed out by Biegler (2000), who proposed one way of incorporating learning into the route-finder model.

A second limitation was that each of the subjects traveled toward areas of low reinforcement probability in two situations: (a) they returned to the starting location after depleting the food, and (b) travel in Trial 1 was oriented toward a beacon (an empty goal cup). The route-finder model explicitly assumes that all movement is directed toward areas of higher reinforcement probability. It assumes that movement is controlled by a single behavioral system (Timberlake and Lucas, 1989) — that of foraging for food. It does not include influences of other motivational systems such as avoiding predation, grooming, or reproduction. Wallace et al. (2003) argue that the outward and homeward portions of foraging trips serve different functions. It is likely that the outward portion is governed by the feeding system, whereas the homeward portion is governed by a different system. Biegler (2003) has recently proposed ways of altering the route-finder model to include multiple

behavioral systems representing different types of goals.

Finally, the route-finder model was not successful at predicting any movement that was influenced by distal stimuli such as the beacons mentioned above. Because the local-process model does not include distal stimuli, it could not account for the routes taken in Trials 1 and 2, in which subjects traveled directly to previously unreinforced goal cups — locations in which the model predicted reinforcement probability would be low. Nor could the model account for the observed changes, albeit transient, in the routes taken when the board was first introduced. According to the model, the board would not influence movement patterns because the model does not include a mechanism of allowing environmental stimuli to influence behavior (other than blockades and the presence or absence of food). Even though the authors were well aware of this limitation, the current data provide clear evidence of the need to incorporate the influence of environmental stimuli into models that predict foraging patterns.

How should this be done? Recall that Reid and Staddon (1998) argued that spatial orientation has two logical parts, knowledge and action. Their route-finder model was designed to explain action — it is a readout process that converts spatial knowledge to action. Where do environmental stimuli exert their influence, on spatial knowledge or on action? If their influence were on spatial knowledge, then one would expect changes to the underlying representation of space (the cognitive map) that the diffusion and action rules act on, rather than changes to the readout mechanism itself. Distal stimuli such as beacons do seem to affect spatial knowledge (see Jeffrey, 2003 for a recent review). A clear example of this effect is the observation that the resolution of spatial knowledge increases with proximity to landmarks and beacons (Cheng, 1988, 1989).

Local stimuli — those that the animal encounters while moving, such as whisker contact during trail following — appear more difficult to classify because of their dynamic influence on movement. Reid and Staddon (1998) provided a way of including one type of stimulus into their model in their simulations of detours (the *umweg* problem). When their simulated organism encountered an unexpected obstacle that prevented movement in a direction, it altered the underlying representation of space by breaking the link between the current location (the active node) and the attempted location (the adjacent node). The diffusion rule and the hill-climbing rule were not affected directly, but by breaking the link between normally adjacent neighbors, neither diffusion nor movement could occur directly between the two neighbors. Thus, the underlying representation of space (spatial knowledge) would change dynamically as the simulated organism foraged.

This dynamic mechanism could be extended to trail following with slight modification. The local stimuli that are encountered while following the edges of a runway probably provide improved spatial knowledge (increased spatial resolution) of the current location. This improved resolution could be incorporated into the route-finder model by increasing the density of nodes representing the vicinity. That area of the open arena would have a denser representation in the rudimentary cognitive map than would other areas. This change may be temporary, lasting as long as the organism is in the area, as when whisker contact helps identify the edges of the runway. Or, it could be permanent, representing the enduring effects of landmarks on spatial resolution. Thus, one way of incorporating stimuli into the route-finder model is to have stimuli affect the underlying representation of space (knowledge) rather than directly affecting the mechanism that produces action (the diffusion and hill-climbing rules). An increased density of nodes may require temporary changes in the diffusion rate parameter and/or the speed of iterations, but it should not require changes in the route-finding process itself. Additional simulations will be necessary to test the adequacy of this model.

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