ELSEVIER

Behavioural Brain Research 127 (2001) 49–69

BEHAVIOURAL BRAIN RESEARCH

www.elsevier.com/locate/bbr

Dead reckoning (path integration) requires the hippocampal formation: evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) tests

Ian Q. Whishaw *, Dustin J. Hines, Douglas G. Wallace

Canadian Center for Behavioral Neuroscience, University of Lethbridge, 4401 University Drive, Lethbridge Alta., Canada T1K 3M4

Received 2 February 2001; received in revised form 5 June 2001; accepted 25 July 2001

Abstract

Animals navigate using cues generated by their own movements (self-movement cues or idiothetic cues), as well as the cues they encounter in their environment (distal cues or allothetic cues). Animals use these cues to navigate in two different ways. When dead reckoning (deduced reckoning or path integration), they integrate self-movement cues over time to locate a present position or to return to a starting location. When piloting, they use allothetic cues as beacons, or they use the relational properties of allothetic cues to locate places in space. The neural structures involved in cue use and navigational strategies are still poorly understood, although considerable attention is directed toward the contributions of the hippocampal formation (hippocampus and associated pathways and structures, including the fimbria-fornix and the retrosplenial cortex). In the present study, using tests in allothetic and idiothetic paradigms, we present four lines of evidence to support the hypothesis that the hippocampal formation plays a central role in dead reckoning. (1) Control but not fimbria-fornix lesion rats can return to a novel refuge location in both light and dark (infrared) food carrying tasks. (2). Control but not fimbria-fornix lesion rats make periodic direct high velocity returns to a starting location in both light and dark exploratory tests. Control but not fimbria-fornix rats trained in the light to carry food from a fixed location to a refuge are able to maintain accurate outward and homebound trajectories when tested in the dark. (3). Control but not fimbria-fornix rats are able to correct an outward trajectory to a food source when the food source is moved when allothetic cues are present. These, tests of spontaneous exploration and foraging suggest a role for the hippocampal formation in dead reckoning. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Deductive reckoning; Hippocampus; Hippocampal formation; Path integration; Spatial navigation

---

1. Introduction

Among the many functions proposed for the hippocampal formation (the hippocampus, its afferent and efferent pathways and other associated structures) is a role in spatial navigation. There are a number of competing hypotheses of what that role might be. These hypotheses include the idea that the hippocampus might mediate dead reckoning or, also known as deduced reckoning or path integration [24,43,46], function as an associative network for learning about places in space [33], or serve as a cognitive map that stores memories of places [29].

The objective of the present paper is to present further evidence from new spontaneous exploratory tasks and from new formal spatial tasks to show that the hippocampus plays a role in dead reckoning [52]. We will first provide some background on the kinds of cues and strategies that animals can use to navigate. A more comprehensive description of navigation strategies can be found in Gallistel [14]. We then describe some natural behavioral test procedures that we use to study the spatial behavior of rats in the laboratory. We then present some recent evidence from our laboratory using new analyses of exploratory behavior and foraging to implicate the hippocampal formation in dead reckoning. In the course of this description, we will also provide evidence that the hippocampus is not the only neural structure that supports spatial behavior. Thus,

---

* Corresponding author. Tel.: + 1-403-329-2402; fax: + 1-403-329-2555.

E-mail address: whishaw@uleth.ca (I.Q. Whishaw).

PII: S0166-4328(01)00359-X

we will present evidence to show that neural structures that are external to the hippocampus support forms of spatial behavior other than dead reckoning.

1.1. Allothetic and idiothetic cues

In principle, a navigating animal has two sources of information with which it can locate its starting location, points of interest in its environment, or its current location. These aspects of an animal's spatial world are crucial for foraging, social behavior, and self-preservation.

The first way that an animal can locate itself is to use ambient cues (including the sights, sounds, and smells, etc.) that it encounters as it moves or that it leaves as a trail as it moves. Allothetic cues are relatively stable stimuli that can be counted upon as references over quite long periods of time. Visual and auditory cues must be some distance away from an animal so that they remain relatively fixed in relation to the animal as it moves, thus, allowing the animal to locate itself or places in relation to those cues.

The second way that an animal can locate itself is by using information acquired from its own movement. There are several kinds of cues that are available to an animal that allow it to keep track of self-motion. The animal can use information from the vestibular system or from muscle and joint receptors. It may also make use of flows of stimulus configurations (i.e. optic flow) that occur as a consequence of movement. For example, the animal may be able to compute its speed by monitoring perceived changes in stimuli caused by the movement. It may also use efference copies of the commands that it uses to generate movement.

Cues that are external to an animal and that are independent of its own movements can be referred to as allothetic cues or distal cues, whereas cues that are generated by self-movement can be referred to collectively as idiothetic cues or self-movement cues. Thus, stimuli from the environment may serve as either allothetic cues (when the cues are stable relative to an animal's movement, e.g., a beacon) or idiothetic cues (when they are generated by the animal's movement, e.g., optic flow). Of course, a navigating animal may use any combination of allothetic and idiothetic cues. Formal experimentation is required to determine which cues an animal is using in any situation.

1.2. Piloting and deductive reckoning

There are two general strategies that an animal can use to move from one location to another, piloting and dead reckoning (also called deduced reckoning or path integration). In piloting, an animal uses one or more allothetic cues to reach a target. A target could be a place from which it obtains food or it could be its home. There are different levels of complexity in navigation when piloting. At one level, an animal navigates to a salient cue. Such a cue could be a visual beacon, an auditory cue, or an odor trail. At another other level, an animal reaches a target in space using the relational properties of two or more ambient cues. The target itself need not be visible. If a set of available stimuli is sufficiently rich whereby each place in the environment can be associated with a unique stimuli configuration, then an animal can compute a location using such an external reference set. In addition, by creating a central representation of external cues, an animal can potentially pilot using a spatial map of its environment that it has created [29]. When piloting, an animal requires no record of its own movements to assist it in reaching a goal, but it does need to learn about the allothetic cues that will be used for guidance.

When dead reckoning, an animal updates a record of its movements in order to calculate its distance from its starting point and the direction from its present location to the starting point [3]. The process of adding linear displacement and angular deviation as a function of time by an animal as it moves is referred to as path integration. In principle, an animal can dead reckon using only the idiothetic cues generated by its movements. Nevertheless, using one or more salient cues in its environment, an animal may be able to correct or update, maintain a heading direction, or even initiate dead reckoning. Thus, dead reckoning can be completely self-sufficient using idiothetic cues or it can be assisted by allothetic cues.

Although allothetic cues are more likely to be used for piloting while idiothetic cues are more likely to be used for dead reckoning, either set of cues may assist both types of navigation. In order to know which navigation strategy an animal is using and which cues it employs in a given situation requires experimentation.

2. Methods for assessing allothetic and idiothetic navigation

In studying how animals navigate we have found it useful to use a behavioral testing situation that approximates the animal's natural 'world'. In our task, the animal has a home base located in a territory over which it can move reasonably freely. Also in this territory is food, which the rat can collect and return to the home cage with. In the following section we describe the foraging task, an experimental method that we devised and have found to be ideal in that it mirrors the aforementioned salient features of a rat's natural world. Somewhat different tasks are used by other researchers [8,26].

2.1. The foraging and exploration tasks

The foraging apparatus [53] is a large white table with eight holes placed equidistant around its edge (Fig. 1). The exploration apparatus was a similar circular table, but without holes. It was painted green. The rats are placed in a cage that is located beneath one of the eight holes. A rat can climb up onto the table through a hole. Once the animal is on the table, its home cage is no longer visible and the hole leading to the home is not distinguishable from the other seven holes located on the perimeter of the table. In order to return the home cage, a rat has to identify the correct hole using either the unique set of allothetic cues that mark that location or it has to integrate the idiothetic cues that it generated on its outward journey from that location.

The refuge could also be made visible by placing one or more black Plexiglas boxes (20 × 25 × 19 cm containing a 8 × 11 cm doorway) on the surface of the table [53].

2.2. Subjects

Animals used in the experiments were female Long–Evans rats (University of Lethbridge vivarium) aged about 90 days when the experiments were initiated.

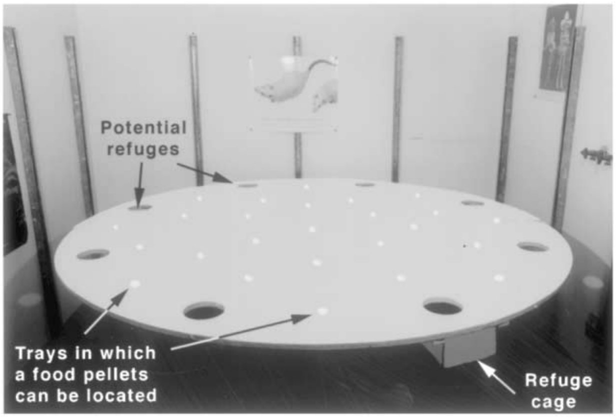

Fig. 1. The test apparatus consisted of a large circular table (204-cm diameter) that was painted white and was elevated 75 cm above the floor (Whishaw and Tomie, 1997). Eight 11.5-cm diameter holes, centered 13.5 cm from the table's edge, were located at equal distances around the perimeter of the table. A wire mesh cage (20 × 25 × 19 cm), similar to the rats' home cage, could be fixed to runners beneath one hole. This cage formed the rats' 'burrow' or refuge. Translucent white food cups (2.4-cm diameter and 1 cm high plastic weigh boats) were located at various positions on the table. The apparatus was located in a test room in which many cues including windows covered by blinds, counters, a refrigerator, cupboards, a desk with computers, etc., were present. A camera was located above the center of the table so that behavior could be video recorded.

2.3. Food

In some experiments, a large 750 mg food pellet is located on the table. Rats typically do not eat large food pellets where they find them, but rather they carry the pellets back to the home cage in order to consume them [47]. This behavior presumably lessens the amount of time that the animal is exposed to assault from predators or conspecifics while it is eating [55]. Depending upon the experimental paradigm, the rat must either search for food that is placed in a different location on every trial, or it must learn that the food is found in the same place on every trial.

2.4. Procedures

The home cage can be placed beneath any hole, therefore, an animal can be started in different locations relative to the room. The table is mounted on a bearing such that the table can be rotated relative to the room. A smaller circular table can be mounted in the center of the large table in such a way that it remains stable when the large table is rotated. These features of the apparatus allow the home cage location to be either fixed or variable in relation to the table surface itself or to the room. Furthermore, if a food pellet is placed on the smaller central table, the larger table can be rotated while the rat is retrieving food on the smaller table [50]. The rotation displaces any odor cues left by the rat on its outward trip.

Once animals have learned to forage for food on the foraging table, the experimental conditions can be changed in any number of ways. The starting location for a foraging trip, location of the food, and the location of the table can all be changed. In addition, the apparatus can be moved from one room to another. In the present studies, we have placed a fiberglass table (155-cm diameter) onto the foraging table in order to provide the rats with a homogeneous novel environment (no escape holes) to explore.

2.5. Lighting

The behavioral tests are conducted in either light or dark conditions. The light condition consists of having the room lights on allowing the animal to use the allothetic cues in the room to locate the refuge or assist it in finding food. In the dark condition, all room lights are off, and the room is sealed to block all visible light. The behavior of the animal is video recorded using a video camera mounted above the apparatus. In the dark, a Sony infrared camcorder is used to record behavior, and the experimenter wears a head-mounted infrared spotter to observe the animal [48]. Infrared is a light wave in which a rat is unable to see [27].

2.6. Video recording

The video record obtained from the camcorder is copied onto VHS format tape, which is then replayed in order to obtain behavioral measures. Time measures are obtained from a time base on the videotape. Movement patterns are reconstructed by digitizing a rat's movements using a Peak Performance system [46]. A point located directly between the shoulder blades was digitized. The digitized record also provides measures of velocity, acceleration, and cumulative travel distance. In tests of exploratory behavior, the distinction between the outward and homeward trip was delineated by the last stop made by the rat before reaching the home.

2.7. Hippocampal lesions

To evaluate the contribution of the hippocampal formation to navigation, we damage the hippocampus by making selective cell-specific lesions in the hippocampus or by making lesions to its major pathways or allied structures [44–55]. In the present, studies we damaged the hippocampus by making cathodal electrolytic lesions in the fimbria-fornix, a main input pathway into the hippocampus (Fig. 2). Cathodal current (1.5 mA for 40 s) is passed through 00 stainless steel insect pins, insulated with epoxylite except at the surface of their tips. Lesions are made at two sites in each hemisphere using co-ordinates in reference to bregma and the surface of the dura: 1.3 mm posterior, 1.5 mm lateral, and 3.6 mm ventral and 1.5 mm posterior, 0.5 mm lateral, and 3.3 mm ventral. The lesion produces a relatively selective section of the afferent fibers and efferent fibers between subcortical and rostral cortical brain regions and the hippocampus and its associated structures. Available evidence suggests that the spatial impairments produced by fimbria-fornix lesions are very similar to, if not more severe than, the spatial impairments that follow selective ablation of the cells of the hippocampus proper, including the cells of Ammon's horn and the dentate gyrus [49].

2.8. Statistical analysis

In the experiments in which interval data and repeated trials were administered, analysis of variance with repeated measures was used. In experiments in which head directions were estimated, tests of circular statistics were used [4]. Ordinal data were analyzed with parametric statistics [12,13].

3. Determining cue use and navigation strategy

Since it is necessary to conduct formal experiments in order to establish which spatial cues and which spatial strategies rats use to solve spatial problems, we will describe some simple procedures that we have used previously and the results that we have obtained. We will then describe the results of some new tests using exploratory behavior and others using simple spatial learning.

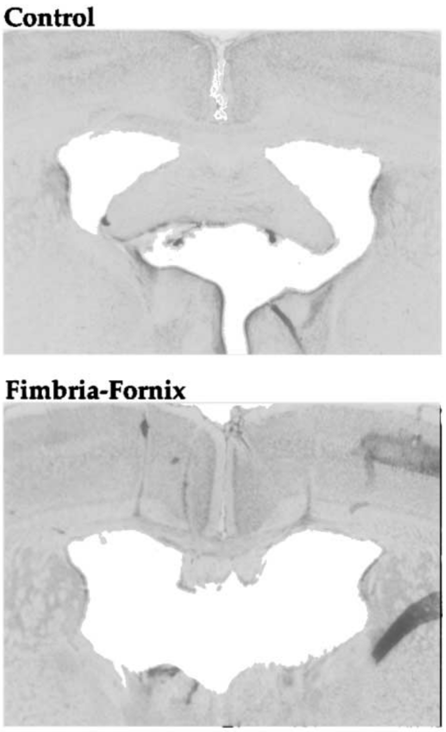

Fig. 2. An example of an intact fimbria-fornix in a control rat (top) and an absent fimbria-fornix in a rat that had received cathodal lesions of the fimbria-fornix (bottom). Electrode tracts left by the lesion electrodes are visible in the neocortex. Note that the lesion does not damage the corpus callosum or the cingulum bundle or cingulate cortex.

3.1. Piloting using allothetic cues

In principle, an animal can navigate using allothetic cues, idiothetic cues, a combination of both types of cues, or it can easily switch between cues. Therefore, to determine which cues an animal uses and the navigation strategy employed, it is necessary to design navigation tests in which cue use is controlled and for which probes can be administered to determine navigation strategies.

Navigation using allothetic cues and piloting is relatively easy to demonstrate in the foraging task [53]. A food-deprived rat is placed in its cage beneath one of the holes, and it is allowed to exit and forage for a food pellet that is located somewhere on the table. To prevent the animal from directly viewing the food, 20 or more small white weigh boats are placed on the table and the food pellet is placed in one of the weigh boats. The rat climbs out of the cage onto the table and walks around on the table until if finds the food pellet. Once it locates the food pellet, it grasps the pellet in its mouth and runs directly back to its home cage with the food pellet (Fig. 3A).

To determine what cues and strategy a rat uses to return to the home location, after it has been trained to go to that location, the animal is given a probe trial in which it and the refuge is moved from the old location to a new location. An alternate home cage left at the old location. Control rats typically leave the new location and go either directly to the old location or they first find the food and then take it to the old location (Fig. 3B). Their return to the old location suggests that they are using piloting and allothetic cues. Had they been using idiothetic cues and dead reckoning, they would return with the food to the new location. This probe also indicates that the rats are using visual cues to guide their return. Were they using olfactory cues (e.g., the odor of the cage that they have just left) or their own odor trail, they would return to the new location and not the old location. Thus, in an illuminated familiar environment, rats preferentially use visual allothetic cues and piloting to return to familiar locations [22].

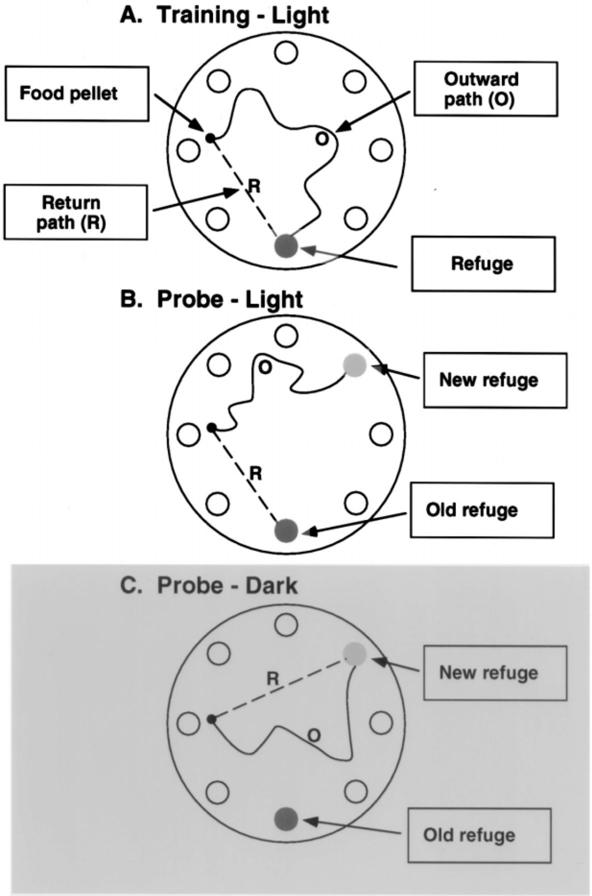

Fig. 3. (A) Typical performance of a rat on the foraging task in the light. The rat leaves the refuge and searches the tabletop (o) until it finds a food pellet. It then returns (r) directly back to the refuge with the food pellet. (B) To determine whether a rat is using a piloting or dead-reckoning strategy in the light, the refuge cage is moved to a new location for a probe trial. The rat exits the cage and searches the table until it locates a food pellet. It then returns to familiar training location, indicating that it is piloting (i.e. using allothetic cues to reach the location at which the refuge had been located during training). (C) To determine whether a rat is using a piloting or dead-reckoning strategy in the dark, the refuge is moved to a new location. The rat exits the cage and searches the table until it finds a food pellet. It then returns to the new location, indicating that it using a dead-reckoning strategy.

3.2. Dead reckoning using idiothetic cues

A demonstration of rat dead reckoning and idiothetic cue use is more difficult because this requires the removal of all allothetic cues. Visual cues, auditory cues, and even the olfactory cues left by the animal on its outward route in search of food must be removed, even though a rat could potentially use some of these cues in dead reckoning.

We test rats in a completely dark room and film their movements using infrared light. The rats are started from different locations within the room on different test days in order to prevent them from using sounds within the room. In addition, a radio is moved around the room each day to prevent the use of directional auditory cues. Typically, rats tested under infrared light return to a location that they have just left, whether it is a familiar or novel location, as is illustrated in Fig. 3C. The rat's return to a starting location on such probe trials is an indication of idiothetic cue based navigation.

Another way of controlling the cues used by an animal is to make specific cues salient. For example, we have trained rats to leave a home cage and follow an odor trail, a vanilla scented string that leads to a large food pellet (Fig. 4A). Thus, the scented string is a salient allothetic cue that provides reliable information to the animal about the location of the food. We have found that rats will follow scented strings containing the odor of vanilla, the odor of another rat, or even their own odor [40,48]. If the path of the scented string forms a polygon, the rat can use a number of cues to return back to the home base. In the light it can use the allothetic cues that mark the location of the refuge, it can use the odor trail provided by the string, or it can use idiothetic cues. Typically, control rats close the polygon by taking the more direct route home in both the light and the dark (Fig. 4B). When the same tasks are given to rats with fimbria-fornix lesions, they close the polygon and take a direct route home in the light, but they follow the odor train home in the dark (Fig. 4C). Thus, the experiment suggests that control and fimbria-fornix rats are able to pilot, but only control rats are able to use dead reckoning [48].

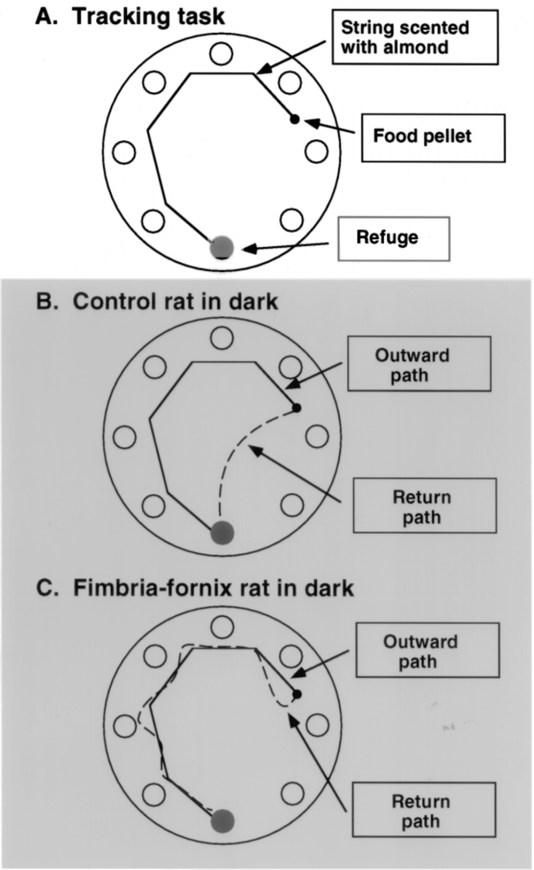

Fig. 4. Returns to a refuge by a control and a fimbria-fornix lesion rat that has been trained to follow a scented string that leads to a food pellet. (A) The task showing the pattern made by the string leading from the refuge to the food pellet. (B) The outward and return paths taken by a control rat following the scented string in the dark. Once the rat reaches the food pellet by following the scented string, it takes a relatively direct route back to the starting location. (C) The outward and return paths taken by a fimbria-fornix rat following the scented string in the dark. Once the rat reaches the food pellet by following the scented string, it turns and follows the scented string back to the starting location.

3.3. Switching cues and strategies

There is behavioral evidence that rats do not simply use one type of cue and one behavioral strategy at a time. Rats use both piloting and idiothetic strategies concurrently.

If rats are trained to carry food to a familiar home base and then are moved to a new location for a single trial, they return with the food to the familiar location, demonstrating that they are using allothetic cues and a piloting strategy. Upon not finding the home cage at its familiar location, they return directly to the new location [53], which requires the use of idiothetic cues and a dead reckoning strategy. As they have never previously returned to that location or viewed the cues marking that location, it is unlikely that they are making use of a local view. Additionally, animals with hippocampal damage, although able to pilot to the old location, are unable to return to the new location. This behavioral evidence and the dissociation produced by a hippocampal lesion supports the idea that control animals monitor both allothetic and idiothetic cues concurrently and can easily switch between piloting and dead reckoning strategies.

4. New tasks to identify dead reckoning during exploratory behavior

In the experiments that we have described to this point, rats carry food home to the refuge to eat, therefore, their food hoarding returns provide the measure of their use of piloting or dead reckoning [45]. We have found that homing also forms a central part of spontaneous exploratory behavior. We will describe findings using this new paradigm in the following sections.

4.1. Homing in the light by control rats

In an initial study, six rats that had been well handled and had participated in previous food carrying studies were given a number of tests during which they were allowed to engage in exploratory behavior (similar results are obtained with naïve rats and rats tested in completely novel environments, but well-handled rats are much more likely to engage in exploratory behavior.) First, the rats were placed in a dark box (12 cm long, 8 cm wide and 10 cm high), and the box was placed on the edge of a 155-cm diameter circular table. This table was mounted on the foraging table, such that the table, but not the room, was novel. The rats were allowed to emerge from the box and explore the table. Typically, the rats emerged from the box and then explored the outer surface of the refuge box. After this initial exploratory behavior, they began to make exploratory excursions out onto the table. A typical excursion consisted of a number of bouts of walking interspersed with pauses followed by the rat's return to the start box. Each rat was video recorded as it made five excursions (an excursion is defined as a trip away from and back to the refuge box). We examined the pattern of the rats' movements, the acceleration associated with each bout of walking, the velocity associated with each bout of walking, and the cumulative distance traveled on an exploratory trip. We directed particular attention to the portions of the excursions in which the rats returned to the refuge.

Drawings of all of the outward and homeward trips in both the light and in the dark conditions are shown in Fig. 5. This summary shows that the outward trips were circuitous and covered a considerable distance around the table. The homeward trips, although beginning from different distances and in different directions away from the home, were aimed directly to the refuge under both the light and dark conditions.

The heading accuracy of homeward trips was calculated in relation to a point at the center of the refuge cage. In addition, the time taken to make outward and homeward trips was calculated for each rat. The average heading accuracy for each rat on the five exploratory trials was calculated using circular statistics, and this average was used to calculate heading direction and the strength of the heading direction [4,32]. The results are illustrated in Fig. 6, top. The heading vector and its strength were highly significant ($r > 0.99$, $P < 0.001$). In addition, an analysis of travel time (Fig. 6, bottom) indicated that although travel times in the light and dark were not significantly different, homeward travel time was significantly shorter than outward travel time ($F(1,5) = 74$, $P < 0.001$).

A typical result from one rat is illustrated in Fig. 7. After leaving the refuge cage, the rat engaged in an exploratory excursion that consisted of three bouts of walking associated with a pause at the end of each walking bout. Then, the rat turned and went directly back to the refuge cage. The acceleration, velocity, and cumulative distance during the return to the home cage was far greater than the same measures that were recorded during the preceding bouts of movement associated with exploration. The outward route was circuitous, associated with sniffing, head movement, and other exploratory acts, whereas the return trip was rapid and direct. In fact, simple observation of the rat's movement during the exploratory session clearly indicated that the outward behavior of the animals was different from their homeward behavior. In short, the homeward portion of the trip was rapid and led directly to the home cage.

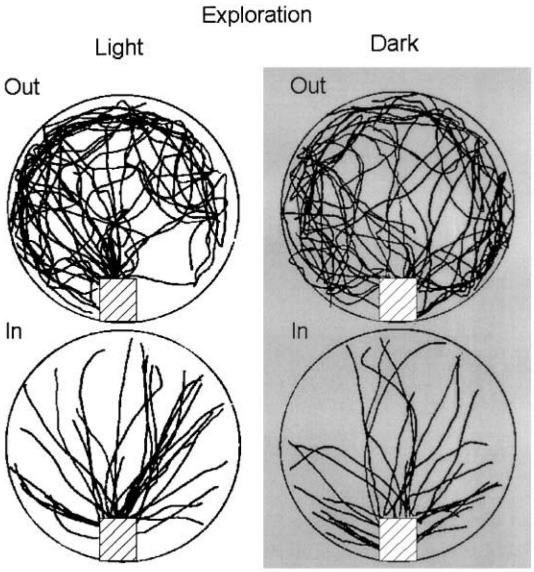

Fig. 5. The pattern of outward (out) and homeward (in) trips in the light (left) and in the dark (right). Each panel shows five trips by each of the six rats. Note that the outward trips were circuitous, whereas homeward trips were direct.

4.2. Homing in infrared light by control rats

This same test was repeated under infrared light with similar results (Fig. 8). Again the rat initially emerged from the refuge cage and explored the cage's outer surface before making a number of exploratory excursions over the rest of the table. The exploratory trips progressed relatively slowly and were associated with pauses and sniffing. The exploratory trip ended with a sudden turn and accelerated walk that returned the rat to the home base. As with testing under light conditions, the homeward route was direct, had higher velocity, and was associated with much less exploratory sniffing behavior relative to the outward portion of the exploratory trip.

The only way that the rats could generate a direct homeward trip in the dark was via dead reckoning navigation using of idiothetic cues. The similarity of the rats' behavior under dark and the light conditions suggests that perhaps the animals use dead reckoning in both conditions.

4.3. Homing after home box cue removal

In order to examine whether the rats were using dead reckoning in the light as well as in the dark, the rats were given an additional test. The refuge box was removed from the table after the rat had left the box to initiate an exploratory bout. Again the outward and homeward behavior of the rats was examined. The results of the experiment were similar under both light and dark conditions. The rats' homeward vectors were directed to the place on the table at which the refuge had been located (Fig. 9). The consistent direction of the homeward vector in the absence of the refuge cage under light and dark conditions suggests that rats were not using the refuge cage as a beacon to guide the homeward trips. Testing under dark conditions limited the set of cues available for navigation to idiothetic cues. The high level of homing accuracy to the 'absent' refuge box under dark conditions suggest that rats were using a dead reckoning strategy. Three lines of evidence suggest the possibility that the rats making spontaneous homeward trips in the light are using dead reckoning. First, the homeward trips in both the light and dark occur spontaneously and immediately, even though the testing situation was unfamiliar to the animals. Second, the character of the homeward trips in the light are similar to those made in the dark in so far as they were initiated which high velocity. Third, removing a salient cue, the highly visible home, in the light did not disrupt the rat's homeward trajectories in the light or dark.

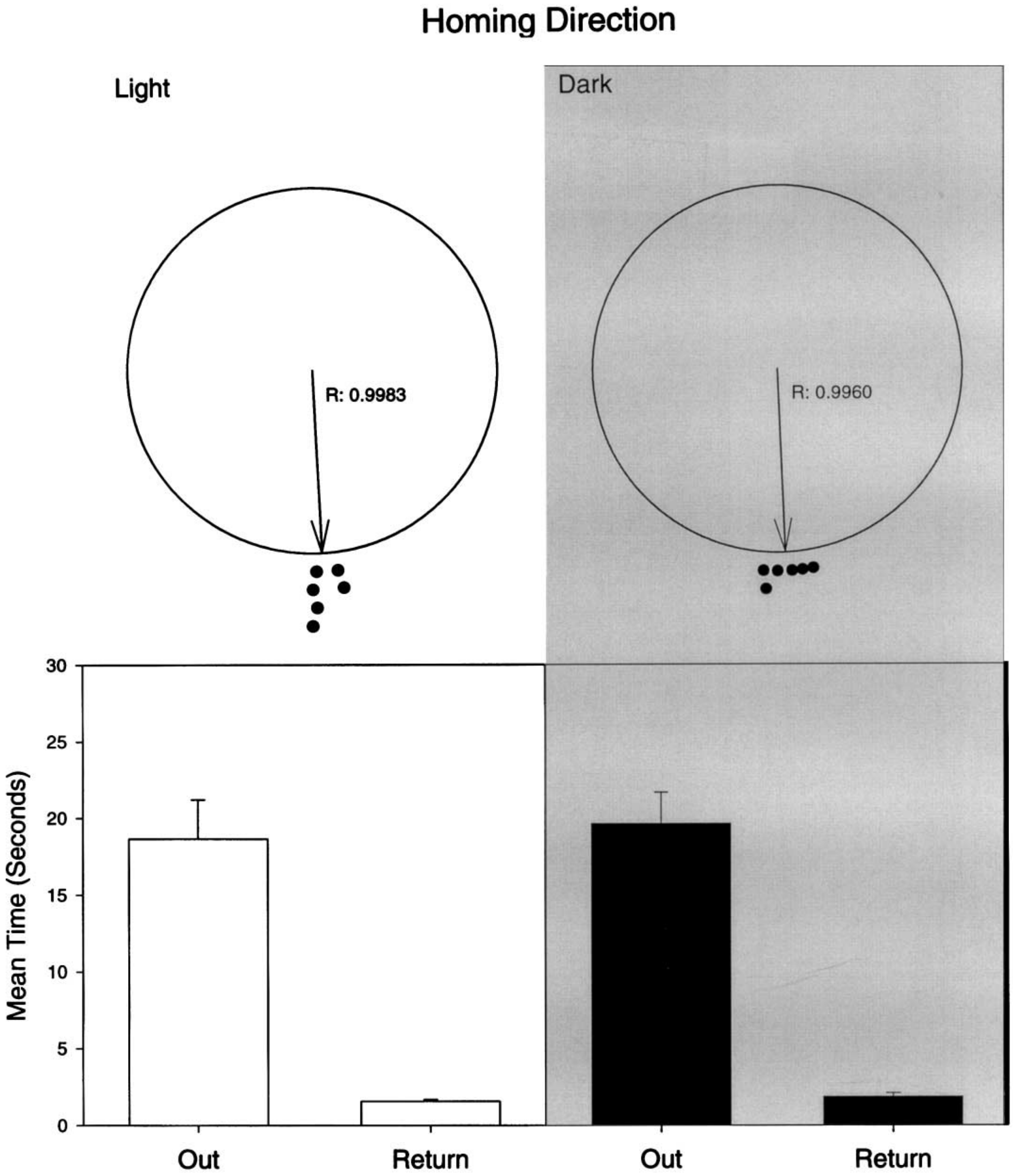

Fig. 6. Top: homing direction of rats returning to the home base location after an exploratory bout in the light (left) and in the dark (right). Each point represents the mean homing direction of one rat on five returns. The vector represents homing strength. Bottom: mean and standard error of time spent exploring and time taken to return home in the light and dark. Note that excursion and return accuracy and times were similar in both test conditions, except in the lighted conditions the refuge box was visible whereas in the dark (infrared) condition, the refuge box was not visible. Mean homing vectors for each rat were determined using circular statistics and mean contrast between conditions indicated no significant effect of condition (analyses based [4,32]).

An additional interesting feature of the behavior of the rats in this test occurred when they found that the refuge was missing. They made a number of short excursions away and then back to the refuge's previous location. This behavior suggests they were attempting to confirm that the refuge was indeed no longer there and/or attempting to confirm that the dead reckoning calculation of where the home base should be was correct.

In sum, this pattern of outward and homeward movement appears fundamental to rat exploratory behavior. The results obtained here using an actual home cage from which the rats began their exploratory trips is similar to results obtained in previous studies in which exploring rats returned to a virtual home [36,37].

4.4. Absence of homing in fimbria-fornix rats

The homing tests, described above, were administered to rats with fimbria-fornix lesions ($n = 6$). The rats were first administered the homing test in the light where they were allowed to make five excursions. They were then administered the homing test under dark conditions. Finally, a test in which the home box was removed and three excursions were recorded was also administered in light and dark conditions.

The paths of outward and homeward excursion by the fimbria-fornix rats in the light and in the dark are illustrated in Fig. 10. The fimbria-fornix rats were like the control rats, in that on their initial exits from the refuge box, they explored the surface of the box. Then on subsequent exits, they moved away from the home to explore the surface of the test field. Unlike the control rats, however, their exploratory behavior was heavily biased toward the periphery of the open field on their homeward portions of their trips. On the homeward trips in particular, they made few returns that crossed the open surface of the table. In addition, it was not possible to distinguish outward from homeward portions of an excursion, as many trips simply consisted of walking around the perimeter of the table until the refuge was re-encountered. Thus, a simple comparison of homebound trips that crossed the middle portions of the open field gave a significant difference

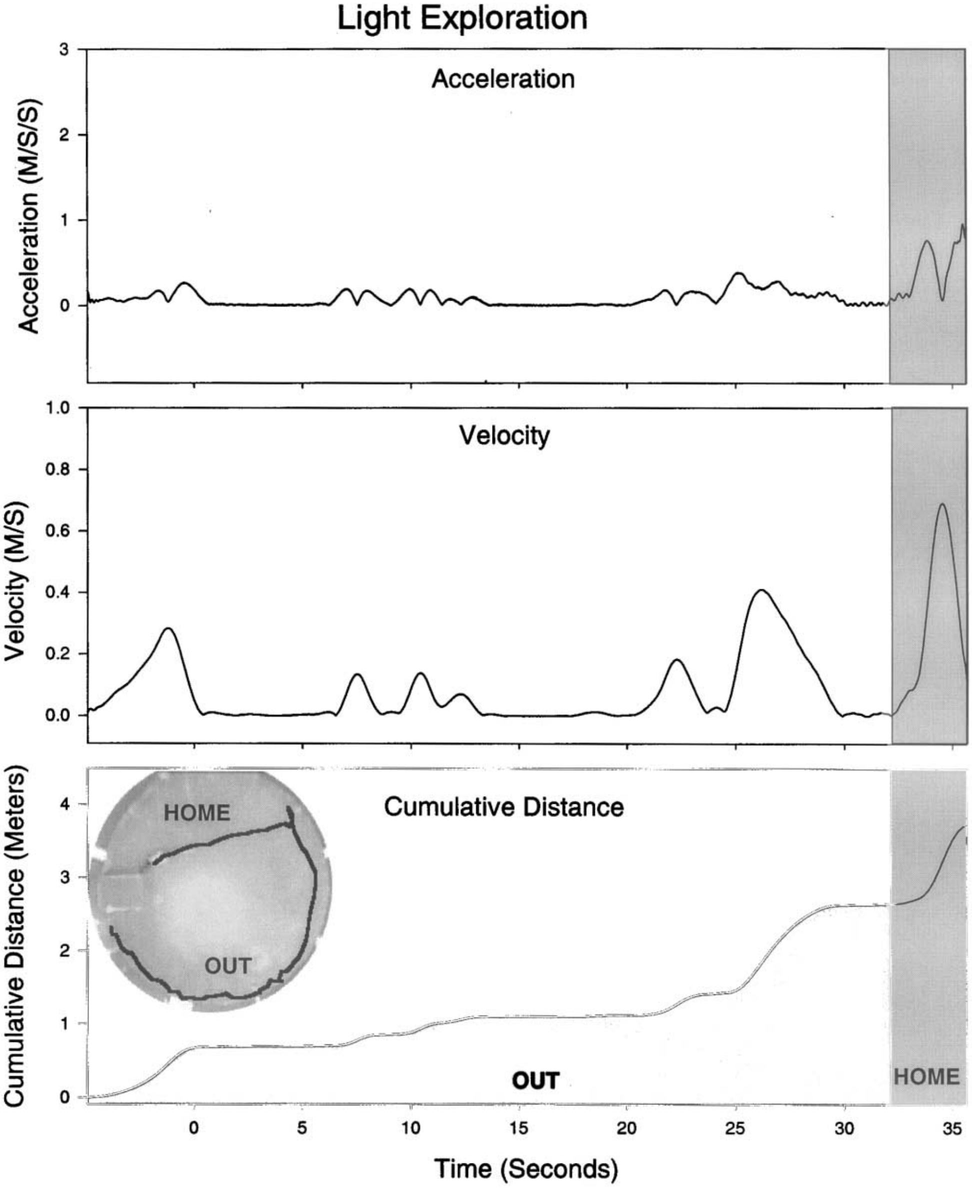

Fig. 7. Elements of movement displayed by a rat exploring a novel circular table in the light. The first long excursion away from the dark refuge cage consists of a 35 s walk around the edge of the table that was associated by a number of pauses and sniffing. Then the rat ended the exploratory bout (out) by abruptly returning to the refuge (lower left). Measures of the rat's acceleration (top), velocity (middle) and cumulative distance (bottom) show variations in movement speed during exploration and also indicate that peak acceleration, velocity, and cumulative distance occurred in the last few seconds as the rat returned to the home base (kinematic measures made with a Peak Performance System, with digitizing made at the center of the rat's shoulders).

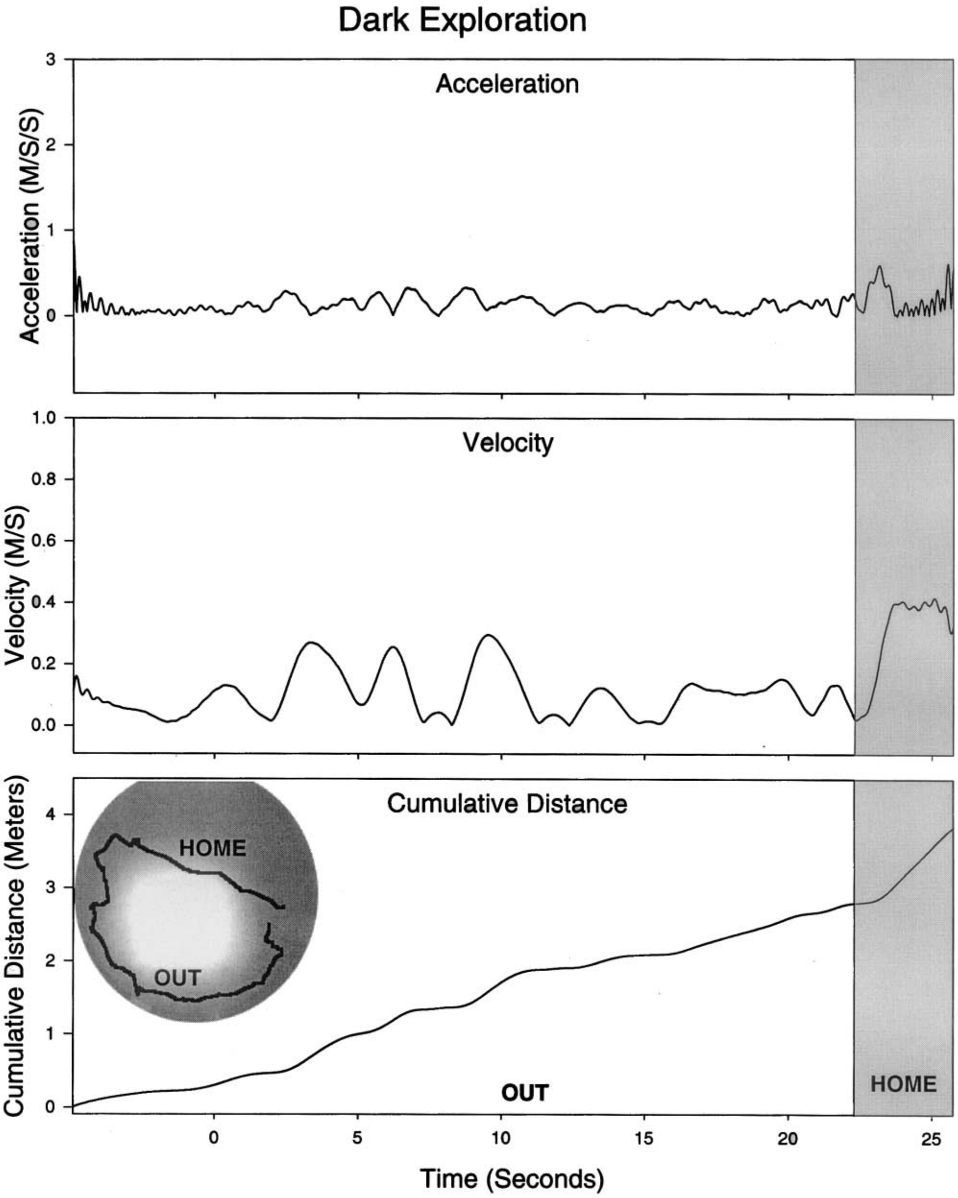

Fig. 8. Elements of movement displayed by a rat exploring a novel circular table in the dark. The first long excursion away from the dark refuge cage consists of a 22 s walk around the edge of the table that was associated by a number of pauses and sniffing. Then the rat ended the exploratory bout (out) by abruptly returning to the refuge (lower left). Measures of the rat's acceleration (top), velocity (middle) and cumulative distance (bottom) show variations in movement speed during exploration and also indicate that peak acceleration, velocity, and cumulative distance occurred in the last few seconds as the rat returned to the home base (kinematic measures made with a Peak Performance System, with digitizing made at the center of the rat's shoulders).

between the control and fimbria-fornix groups (control = 4.6 vs. fimbria-fornix 0.9, Mann–Whitney $U = 0$, $P < 0.05$). In the absence of the abrupt turns associated with increased velocity of movement of the control rats, we were forced to define homebound trips as the portion of the excursion that occurred between the last stop on the exploratory excursion and the arrival at the home base. A tendency to travel along the perimeter of the open field was similarly pronounced in the dark. Again, very few homeward trips were made across the center of the open field (control = 3.9 vs. fimbria-fornix = 0.5, $U = 0$, $P < 0.05$). An analysis of travel time for both control and fimbria-fornix rats during the five exploratory trials under both light and dark conditions indicated that outward trips were significantly slower than homeward trips ($F(1,10) = 111.83$, $P < 0.001$), all other main effects and interactions were not significant.

From visual inspection of the behavior of the animals, it was not possible to determine when the animals initiated a homeward trip. In order to estimate movement velocity, we designated the last stop made by an

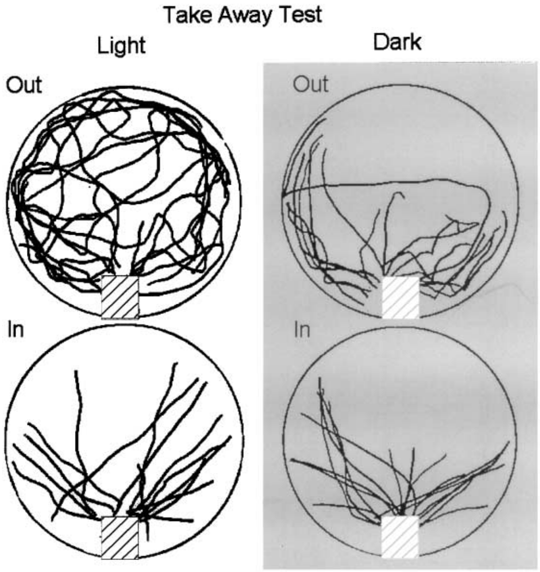

Fig. 9. Travel paths of rats on outward and return trips after a refuge was removed. The refuge was removed once the rat made its first exit from the home and reach rat was recorded as it made three outward and return trips to that location. Top: results show the first exit and the next two trips away from the previous location of the home. Bottom: results show three trips by each of the six rats back to the previous location of the home.

animal before it reached the home, and the start of the homeward portion of the excursion (Fig. 10). We then examined acceleration, velocity, and cumulative distance on the outward and homeward portions of the excursions. There was little evidence of a change in acceleration, velocity or the rate of cumulative distance to distinguished the homeward portion of an excursion from the outward portion of the excursion (Fig. 11). In some animals, under light conditions there was a slight tendency as the animals approached the home cage to orient to the home cage and walk toward it with a slight increase in acceleration and velocity. This behavior was not observed in the dark test.

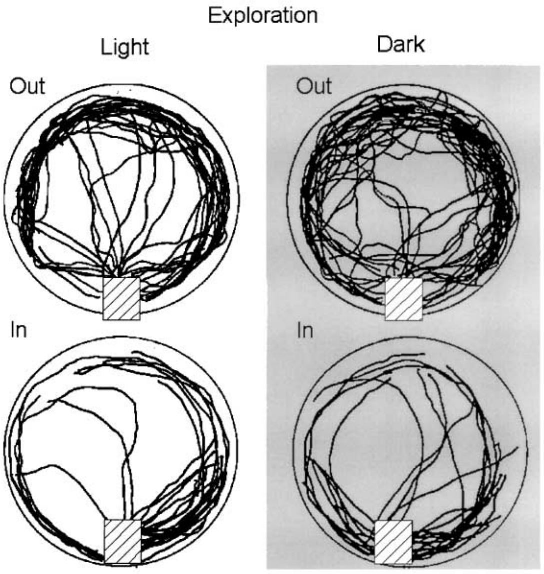

Fig. 10. The pattern of outward (out) and homeward (in) trips in the light (left) and in the dark (right) by rats with fimbria-fornix lesions. Each panel shows five trips by each of the six rats. Note that the outward trips although circuitous, were clustered toward the periphery of the table. Note also that homeward trips were also clustered along the perimeter of the table.

We also repeated the test in which we removed the home box as the rats began their excursion. The results were again similar to those obtained when the home was present, except that the homeward trajectories were even more obviously continuations of movements around the table (Fig. 12). When the home was present in the light, the animals sometimes oriented and approached it as they came close to it, but such behavior was completely absent when the home cage was not present.

We have considered the possibility that the behavior of the fimbria-fornix rats was due to a strong tendency to display thigmotaxic behavior [19]. This interpretation has two weaknesses. First, on the outward trips from the home, the fimbria-fornix rats frequently walked directly across the center of the open field, suggesting that their behavior was not simply governed by thigmotaxis. Second, it is possible to suggest that in the absence of dead-reckoning, the behavior of the fimbria-fornix rats was simplified, thus making any tendency toward thigmotaxis a result rather than a cause of their behavioral change. Finally, as the table had no walls, thigmotaxis was not likely to determine the animal behavior.

5. Dissociating dead reckoning from piloting by changing lighting conditions

In the experiments described to this point, we have argued that rats use dead reckoning to return home from a foraging or exploratory excursion and we have argued that the ability to do so is impaired following hippocampal formation damage. Nevertheless, even though rats lose the ability to used dead reckoning following hippocampal formation damage, the results of a number of studies suggest that they can still pilot [22,48]. That is, with training, they learn to travel directly to a point, such as a place where food is located, and they are able to return to a familiar starting position. In the following experiments, rats were trained to pilot and then given two types of tests. The first test involved removing allothetic cues thus examining behavior on the same task under dark conditions. In the second test, allothetic cues were not changed, but the animals had to learn to go to a new location in order to find food while the home base

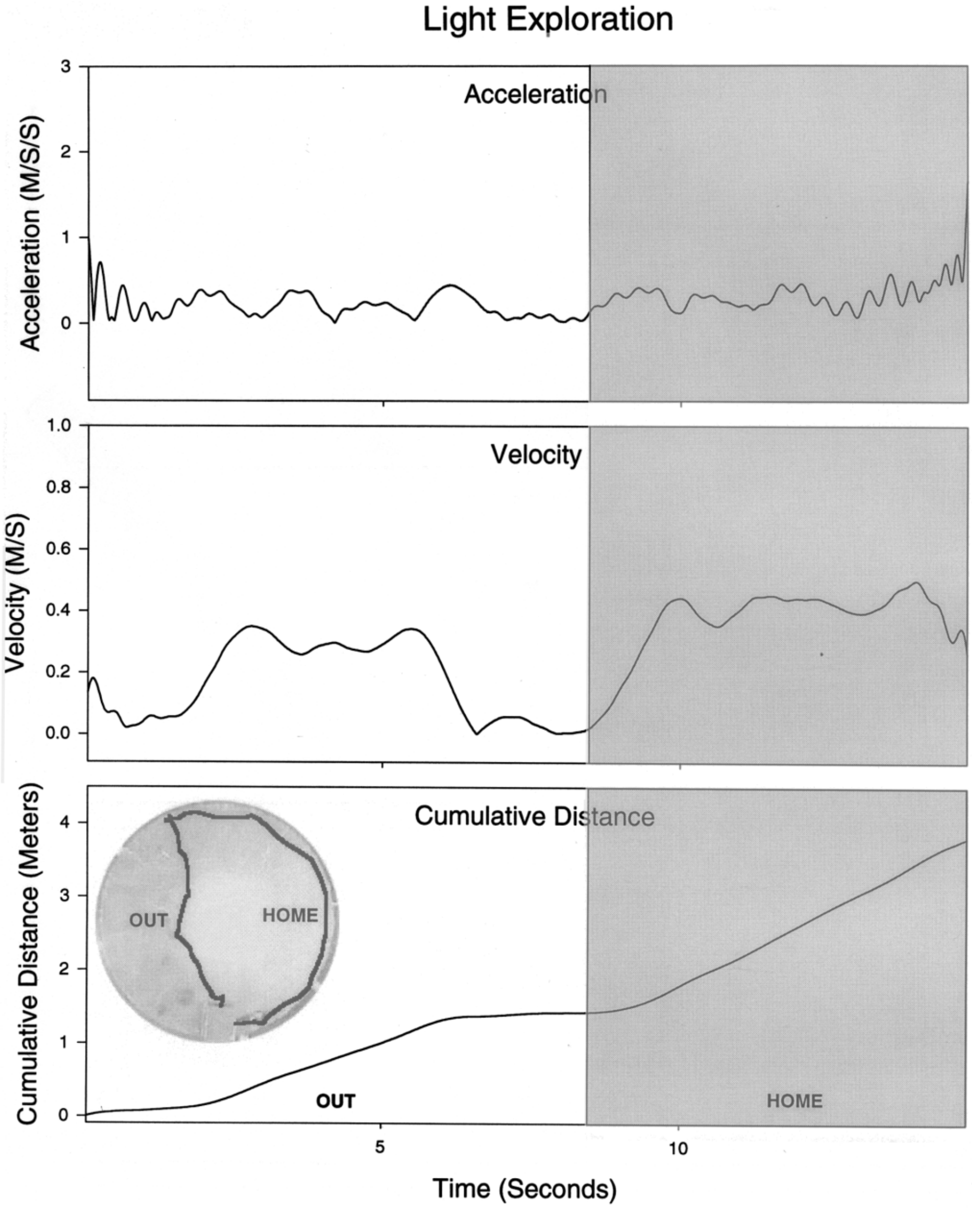

Fig. 11. Elements of movement displayed by a fimbria-fornix rat exploring a novel circular table in the light. The first excursion away from the dark refuge cage consists of an 8 s walk across the middle of the table. Then the rat then encountered the edge of the table and followed the edge back to the home base. Measures of the rat's acceleration (top), velocity (middle) and cumulative distance (bottom) show little variations in movement speed during the outward portion of the trip and the homeward portion of the trip (kinematic measures made with a Peak Performance).

remained in the same location. Thus, in the second test behavior had to be changed while allothetic cues remained constant.

5.1. *Effect of allothetic cue removal on control and fimbria-fornix rats*

The rats ($n = 8$ fimbria-fornix lesions; eight control) were trained to retrieve a food pellet from a fixed location at the far end of the foraging table from their starting position. The rats in both groups learned to climb out of the refuge hole, travel straight across the table to retrieve the food, and return back along the outward path with the food. Once the rats were traveling directly between the two points, they received three trials of testing each day for 3 days in the light followed by three trials of testing each day for 4 days in the dark. Performance was assessed using mean time, distance traveled (measure from the digitized video record), and deviation score from the direct route on the three daily trials. Rats in both groups learned the task equally quickly.

The scoring system for measuring deviations on outward and return trips is illustrated in Fig. 13. Briefly, if a rat took a direct route between the refuge and the food, it received a score of ‘0’. If the rat deviated from a direct route, the score that it received increased in proportion to the deviation by incrementing as each sector was entered.

The results of the test indicated that in the light there were no significant differences between the control and the fimbria-fornix groups (Fig. 14), because the animals in both groups took direct routes between the refuge and the food source. In the dark tests, the fimbria-fornix group was significantly impaired relative to the control group on all measures, with the exception of the time taken to reach the food pellet. On the outward trip, the distance that they traveled ($F(1,14) = 47$, $P < 0.001$), and their mean deviation score ($F(1,14) = 17$, $P < 0.001$), were higher than that produced by the control group. On the return trip time, distance, and deviation scores were all higher for the fimbria-fornix group than for the control group ($F(1,14) > 20$, $P < 0.001$).

An example of the performance of a control rat (#9) and a fimbria-fornix rat (#8) under light and dark conditions is shown in Fig. 15. Here it can be seen in both light and dark conditions that the control rat is relatively accurate in reaching the food pellet and in returning directly to the refuge with the food pellet. The fimbria-fornix rat is accurate in the light but is inaccurate in traveling in both directions in the dark. It is noteworthy that on at least some trials the fimbria-fornix rats did make some direct foraging excursions and some direct returns, but these may have been guided by surface cues. The repeated testing procedure precluded removal of olfactory cues left by the rats on their excursions, although the table was rotated between rats and days to minimize use of such cues.

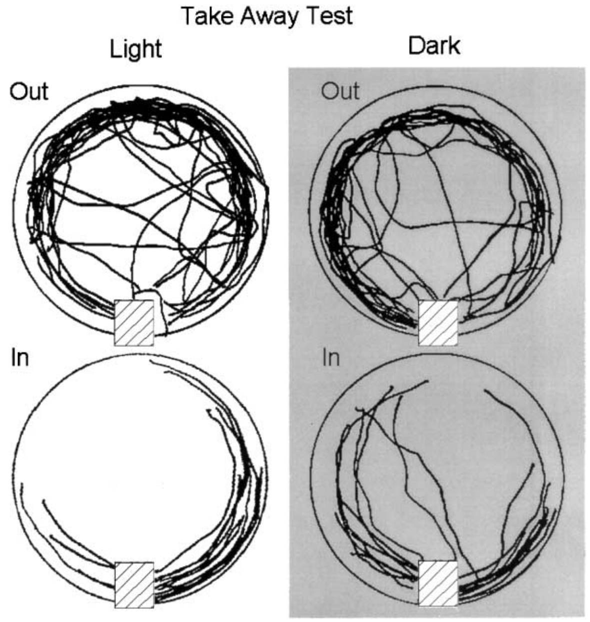

Fig. 12. The pattern of outward (out) and homeward (in) trips in the light (left) and in the dark (right) by rats with fimbria-fornix lesions. Each panel shows three trips by each of six rats. Note that the outward trips and homeward trips tended to cluster on the edge of the table. Note also that there were few direct homeward trips across the center of the table.

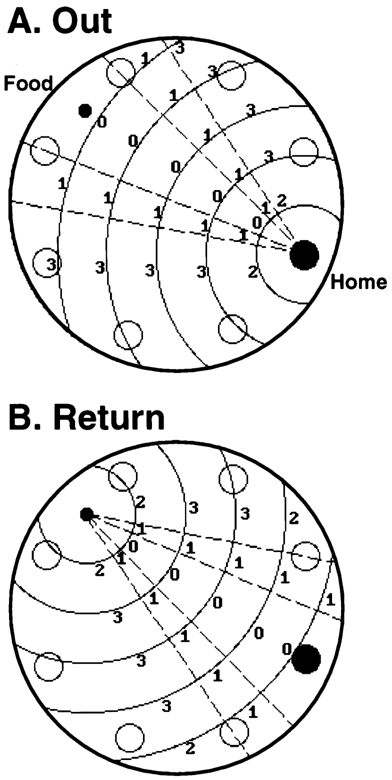

Fig. 13. Scoring system for travel accuracy to a food pellet (A) and from the food pellet to the refuge (B). If a rat remained within zone indicated by ‘0’ it received a deviation score of ‘0’. If it crossed into zones ‘1, 2, or 3’ it received that score for each line crossed in that zone.

The poor performance of the rats with fimbria-fornix lesions in the dark suggested that they were not able to use a dead reckoning strategy to navigate between the home and the food pellet. The accurate performance of the control rats in the dark suggests that they were using a dead reckoning strategy. Thus, the accurate performance of the rats with fimbria-fornix lesions in the light relative to the dark suggests that they were using a piloting strategy in the light.

5.2. Effect of changing target location under constant allothetic cues

In a second test, given to examine cue use in the light, the performance of the rats was assessed in response to changing the location of the food pellet. The rats were first over trained so that they were accurately retrieving food from a fixed location (as described above) and traveling directly to the food source and returning to the refuge with the food. Then the food was moved to a new location, and the rats were given a further 9 days of training with five trials given each day.

A summary of performance of the control and fimbria-fornix rats over 9 days of training (five trials per day) is illustrated in Fig. 16. The fimbria-fornix group was impaired relative to the control group in time out ($F(1,14) = 28$, $P < 0.001$), distance traveled ($F(1,14) = 39$, $P < 0.001$), and accuracy score ($F(1,14) = 49$, $P < 0.001$). There was also a group by direction effect across all of the measures ($F(8,112) > 14$), $Ps < 0.001$). The group differences were obtained on outward portion of the foraging excursion and persisted throughout training. There was no group difference on any measure on the homeward portion of the excursion.

The performance of a typical control rat (#9) and fimbria-fornix rat (#8) is illustrated in Fig. 17. The 45 trials, of five trials a day for 9 days, are collapsed into nine blocks of five trials. When the control rat did not find the food at the familiar location, it walked around and eventually found the food at the new location on its first trial. It then returned directly to the refuge. All subsequent trials on the first day were directed to the new location. The first trial on the second day was directed to the old location, and again all subsequent trials were directed to the new location. Thereafter, all trips were directed to the new location.

The fimbria-fornix rat on not finding food at the old location made a number of trips between the old location and the start location, before finding food at the new location. Even after finding food at the new location, it continued to travel to the old location before going to the new location. By the second day, the fimbria-fornix rat was running in a circular path to the new location that took the rat to, or nearly to, the old location. This circular pattern was characteristic throughout the rest of training. Nevertheless, its returns from the new location to the refuge were direct from the onset of training. This pattern of behavior was characteristic of all of the fimbria-fornix rats.

To examine whether the pattern of outward runs by the fimbria-fornix rats were simply the result of a learned and stereotyped motor response, we started the rats from a novel location. The control rats either retrieved the food from the new location ($n = 6$) and then returned to the old refuge location, or returned to the old refuge location before retrieving the food ($n = 2$). None of the fimbria-fornix rats ran in a circular pattern from the new location. Five of the rats went to the new food location and retrieved the food before returning to the previous starting position and three of the rats returned directly to the previous starting position. Thus, the retrieval behavior of the control and fimbria-fornix rats was not different from the new starting location. Once the rats returned to the old location with the food, however, there was a group difference. All of the control rats then went directly to the new starting location. All of the fimbria-fornix rats then began to repeatedly run the circular path from the old refuge location, past the old food location to the new food location, and then back to the old refuge location. Thus, the circular outward trajectory was locked to moving away from the old refuge location.

Our interpretation of the behavior of the control rats in this task is that they are guided both by allothetic

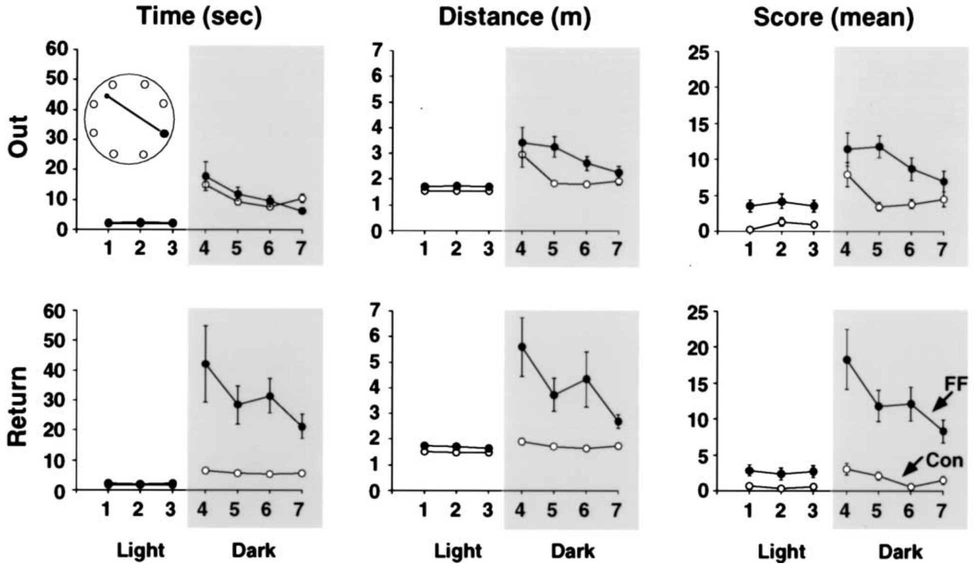

Fig. 14. The mean and standard error (S.E.) of performance on blocks of three trials by control rats and fimbria-fornix rats in a task requiring the retrieval of a food pellet that was always found at the same location. There were no significant differences in the performance of the control and fimbria-fornix rats in the light, but the fimbria-fornix group was impaired relative to the control group on both outward and return trips.

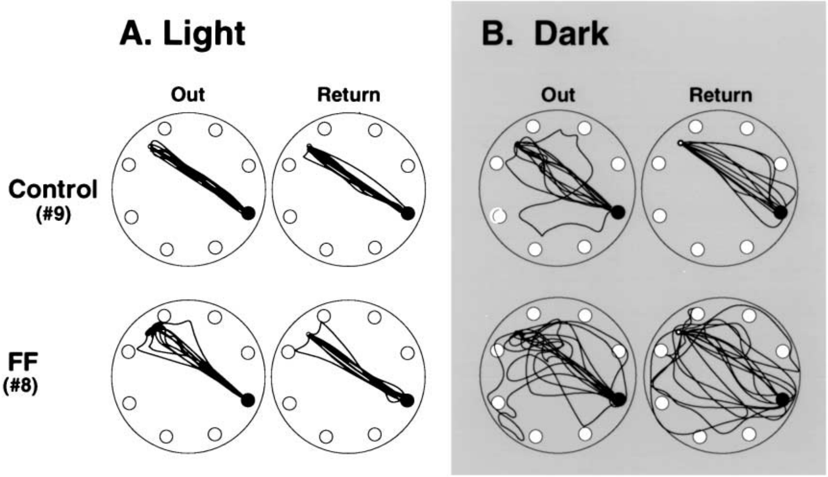

Fig. 15. Examples of excursions and returns by a control and fimbria-fornix rat to retrieve a food pellet located at a fixed location. Traces are for three trials each day for 3 days in the light condition and three trials each day for 4 days in the dark condition. Note that both rats are accurate in the light, but only the control rat is accurate in the dark.

cues and idiothetic cues. When either the food or the refuge are moved, they initially respond using allothetic cues, but then switch to the use of idiothetic cues when they find that the use of allothetic cues is not reinforced. After this correction, it is likely that they revert to the use of allothetic cues in traveling between the new food location and the refuge. By contrast, the peculiar behavior of the fimbria-fornix rats suggests that they are guided exclusively by allothetic cues. In the absence of an ability to correct their outward responses by appealing to idiothetic cues, they persist in incorporating the old food location in their outward trajectory. Their return trajectory to the old refuge is accurate from the outset in that its location continues to be found at the location marked by a familiar set of allothetic cues.

6. Discussion

In this paper, we present a series of studies that suggests that dead reckoning is an important component of spontaneous exploratory behavior and the learned spatial behavior of rats. We also present evidence to show that animals with hippocampal formation damage are impaired in using dead reckoning. Animals with hippocampal formation damage were not devoid of spatial abilities, however. They could learn to navigate to places were food was always located and they could navigate back to a fixed starting location. We suggest that in navigating to fixed targets, they used a piloting strategy and not dead reckoning. Thus, we conclude that the hippocampal formation plays a role in dead reckoning, whereas other neural structures can mediate piloting.

6.1. Dead reckoning impaired in hippocampal rats

A novel finding in the present study is that if rats are allowed to explore in either a familiar or novel environment, they make rapid direct returns to their home base after each exploratory bout. In addition, when the same measures of exploration were taken under infrared light, a very similar pattern of rapid homing was observed. The results obtained under dark conditions demonstrate that the homing behavior of the animals must be mediated using idiothetic cues, therefore, this must be accomplished using dead reckoning. Inferentially, this result suggests that the homing displayed by the animals in the light is most likely also based on dead reckoning. A test in which a visible home base, from which the rats had exited, was removed in both light and dark conditions provided experimental support for this suggestion. In both light and dark conditions the control rats returned accurately to the place from which the home base had been removed. A more definitive demonstration that the rats were using dead reckoning and not a piloting strategy in the light would involve suddenly changing or moving allothetic cues just as the rats initiated a homeward response. At present, we have not developed procedures for such a test.

Golani and coworkers in previous work report that rats returning to a virtual home base display faster homeward trips than outward trips [36,37]. Thus, the present results are consistent with these reports and much earlier studies indicating differences faster homeward trips by foraging rats [47]. Nevertheless, the studies by Golani and coworkers [36,37] do not describe the angular component of the homeward trajectories of the rats. Indeed, the only drawings of homeward trajectories that are given are not direct. Thus, the novel contributions of the present study are that homeward trajectories are direct, they have little angular variance, they are initiated with high velocity, and they are similar in both light and dark. In addition, their directness was confirmed by high *r*-values in the circular statistical tests. Nevertheless, it is important to note that there are many other differences between the exploratory tests used here and that described by Golani and coworkers [36,37]. For example, our methodology restricted the rats to one home base, whereas in the virtual exploratory task of Golani and co-workers each rat created a number of home bases. In future work, it would be interesting to explicitly compare the behavior of rats in these two exploratory tasks.

An important result that we obtained by studying homing embedded in the natural exploratory behavior of rats, is that accurate homing requires an intact hippocampal formation. This, in turn, suggests that the hippocampus is required for dead reckoning. In previous studies, we have also found that dead reckoning is impaired following hippocampal formation lesions, including fimbria-fornix [48,50], hippocampal [21], and retrosplenial cingulate cortex lesions [51]. In the present study, we found that when our exploratory tests were given to rats with fimbria-fornix lesions, the rats gave no indication in their behavior that they were using dead reckoning to return to the home base, as did the control rats. The fimbria-fornix rats did leave the home base and they did explore the open field surface, but their returns to the home base appeared to be simply a continuation of their exploratory excursion. They did not make returns from different locations on the table, returns were not sudden, and there was no obvious increase in movement velocity. In fact, most returns by the fimbria-fornix rats seemed to accidentally occur as they walked around the table. It is also important to note that the failure of the fimbria-fornix rats to make direct returns in the light occurred under conditions in which they were not trained (see below).

We obtained evidence in two further tests that rats with fimbria-fornix lesions were unable to dead reckon. We trained control and fimbria-fornix rats to retrieve food pellets at a fixed location on the table. They were then tested under dark conditions. The routs of the fimbria-fornix rats to the food and back to the refuge with the food were less accurate under dark conditions

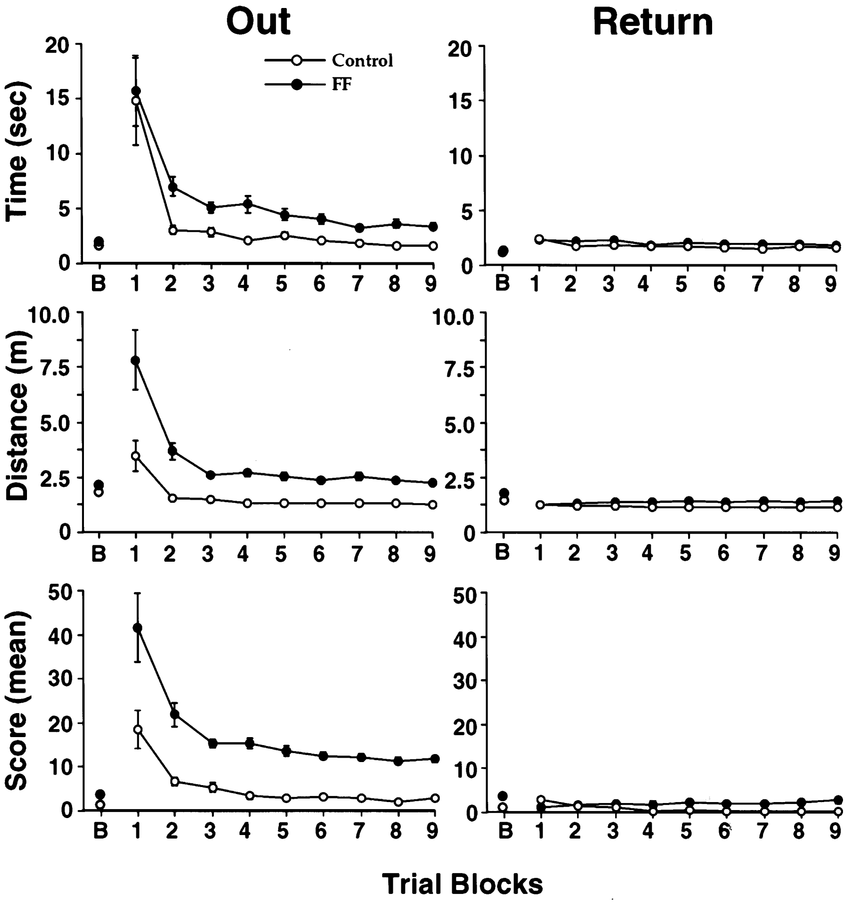

Fig. 16. Measures of accuracy (mean and S.E.) of rats travelling to the location of a food pellet that had been moved and returning to the refuge with the food pellet. (Top, time; middle, distance; bottom, deviation score). Not the inaccuracy of the fimbria-fornix (FF) group relative to the control group on the outward, but not on the return, portion of the trip.

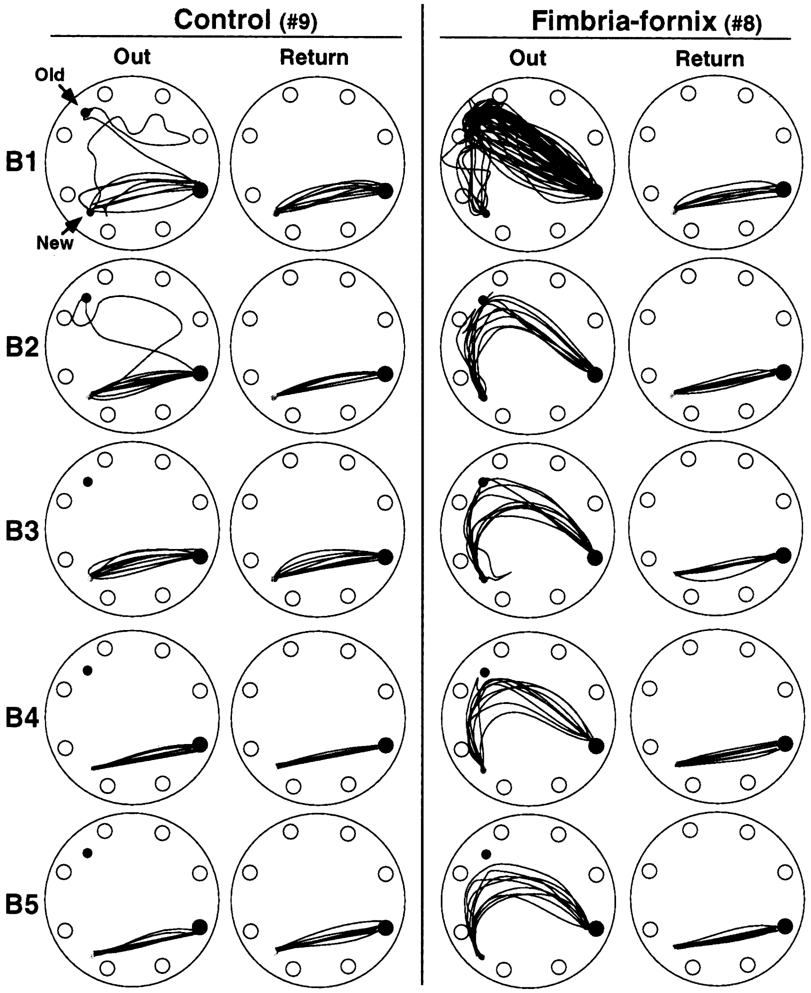

Fig. 17. Example of the outward and homeward paths made by a control rat (# 9) and a fimbria-fornix rat (# 8) in retrieving a food pellet that had been removed from its previous position (P) to a new location (N). Although both the control and the fimbria-fornix rat learned to locate the food at the new location equally quickly, the fimbria-fornix rat did not learn to run directly to the food, but incorporated a portion of its old route into the new route. Homeward trips were very accurate in both animals.

than were the routes taken by the control rats. In the second test, under light conditions, the food was moved to a new location. Now allothetic cues were constant but the rats had to change their response in relation to these cues. The control rats quickly learned to run directly to the new location, whereas the fimbria-fornix rats developed and maintained a circuitous path in which they circled by the old location. Both groups of rats returned directly to the refuge from the old location. The deficit in the outward behavior of the fimbria-fornix rats did not seem to be due to a simple learning impairment. The rats learned the new food location as quickly as did the control rats. Their deficit was due to an inability to generate a direct vector to the new food location. We interpret this finding to mean that the rats are unable to use self-movement cues and so are unable to give up an old trajectory in order to generate a new trajectory. In other words, the fimbria-fornix rats were displaying preservative behavior in response to previously learned allothetic cues.

6.2. Piloting present in hippocampal rats

In previous work, we have demonstrated that rats with fimbria-fornix lesions [43,49] hippocampal lesions [49], and retrosplenial cortex lesions [21] are able to pilot. For example, when the animals with lesions were provided with a visible cue in a swimming pool, they were able to learn to swim accurately to the cue. This response was not simply a response to a visible beacon, because when the cue was removed, the rats continued to swim to that location and search there for the platform. Thus, they had also learned the location of the platform. Substantial other new evidence also demonstrates that rats with various types of hippocampal damage are able to use allothetic cues to locate places, as well as to solve other spatial problems [1,7,11,17].

We have also observed that rats with fimbria-fornix lesions are able to learn problems using allothetic cues in the foraging task. When trained to retrieve food from a fixed location in the light, the rats are able to navigate directly to that location and return directly to the refuge. Their performance deteriorated in the dark and also deteriorated when they were faced with learning a new food location. These results suggest that animals with hippocampal lesions are able to use allothetic cues to locate the food source and the refuge, but being unable to switch to a dead reckoning strategy, were thus more dependent than control rats upon those allothetic cues.

6.3. Obtaining accuracy using idiothetic cues

One argument against the value of dead reckoning as a useful spatial strategy is that the accumulation of error as a result of successive integration will eventually mislead the animal. The argument is that the further an animal travels on an outward excursion, the more error it accumulates. The accumulation of error makes the animal less able to generate an accurate return to the starting location. Although the accumulation of error could make idiothetic navigation unreliable for any but the shortest excursions, our observation of behavior of control rats suggests, however, that not only are they accurate, they use a number of behaviors to compensate for potential error accumulation.

In a task in which we have had rats follow a circular olfactory tract to a food target, we have observed that many of the rat's return trajectories were not perfectly straight (Fig. 18). Of a total of 156 observations from six rats, we found some that were straight (23.3%), but of those that were not straight, 63.3% were concave, with the remainder being either convex (5.6%) or irregular (7.8%). The high number of concave return patterns suggests that the rats' return trip is influenced by the pattern of the outward trip. Possibly the concave error allows the rat to intersect its outward path, and thus correct its homeward path by following its outward odor trail back to the refuge. It is interesting that a very similar 'concave' error is reported by Séquinot et al. [32] in homing hamsters.

We have observed a second behavior that may be useful in correcting errors. In experiments in which we have moved the refuge location, we have frequently observed that rats will circle, sniffing around the location where the refuge had previous been located. This behavior often occurs even when the previous location has been displaced by table rotation. Sniffing may be a useful behavioral strategy in that it can assist the rat in finding the refuge even though the animal has made a slight error in its heading direction. Similarly, when a rat fails to locate a refuge that has been moved, it also makes short outward and return excursions. The use of such 'checking' behavior would likely increase the probability that a rat will reach its goal despite small navigation errors. It is interesting that Wehner and Srinivasan [41] observe similar search behavior in ants.

An additional way in which animals may maintain accuracy in dead reckoning is by making a periodic updating response during an outward excursion. We have observed that during an exploratory bout, animals will frequently initiate a homeward trip only to abort the return after a few steps in order to resume exploration. It is possible that such intention movements of returning may be useful for updating and correcting integration errors.

6.4. Evidence for a role for the hippocampus in movement

Our results suggest a role for the hippocampal formation in dead reckoning. A variety of other evidence can be seen as being consistent with the notion that hippocampus is involved in the control of movement, and thus potentially in the control of dead reckoning. The amplitude and frequency of hippocampal slow wave activity (RSA or theta rhythm) is closely related to movement [28,39,44]. In addition, stimulation of many structures within the brainstem not only produces movement but at the same time also activate hippocampal RSA [5] while blocking projections to the

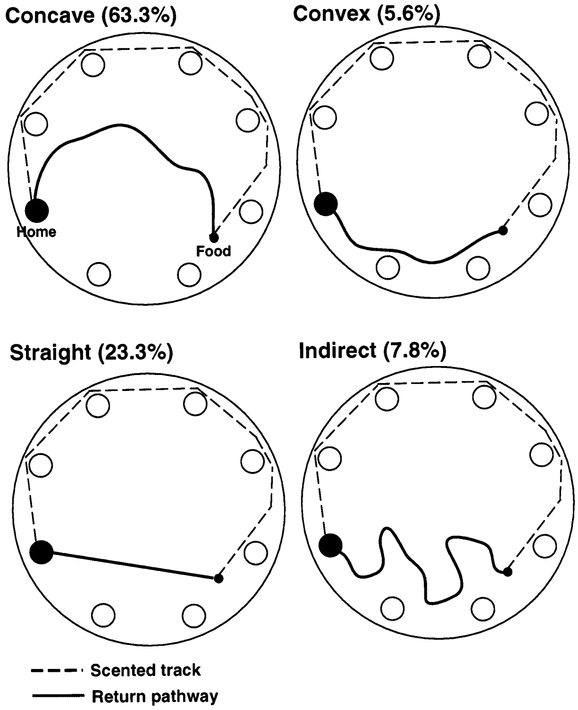

Fig. 18. Homeward trajectories by control rats that have tracked an odor trail to food under dark (infrared) conditions. The majority of homeward trajectories were concave, leading a rat to encounter its outward path and so use that path to complete a homeward trip. Many paths were also direct, but very few paths were convex or indirect.

hippocampus not only blocks RSA but also blocks movement [6]. Therefore, it would appear that through the circuitry that produces hippocampal RSA, the hippocampus is in a position to receive an efferent copy of instructions that generate movement and respond to this information with movement-related commands.

Single cell recording in the hippocampal formation also suggest its cellular activity could be related to movement, and thus to dead reckoning. Some cells, head-direction cells, are tuned to the direction that an animal's head is oriented. Others, place and movement cells, are responsive when an animal is moving in a particular direction an in a particular location in its environment. Still other cells are tuned to the location to which a rat is heading [9,25,30,35]. In addition, in studies in which rats have the choice of using trajectories in task solutions, subsets of cells are found that are tuned selectively to various trajectories [10,16,23,56]. A number of experimental and theoretical papers [15,24,34,35] have suggested ways in which such 'movement-related and direction-related' cells may contribute to path integration.

6.5. Sensory input to the hippocampus

The hippocampus is also the target of all of the major sensory systems. Thus, the hippocampus is positioned to receive information concerning sensory flow generated by movement. In addition, not only do some hippocampal cells respond to optic flow [34], the projection of the accessory optic pathway into the hippocampal formation carries information concerning optic flow [57]. Optic flow will be especially useful to an animal in maintaining straightforward movement and in gauging the extent of a turn. It is well known that there are cells in the hippocampus that are sensitive to allothetic cues [31]. Such cues might be especially useful to path integrating animals in performing running fixes, and global determinations of position and heading (see [14] for a description of these navigational processes). Finally, it is interesting that certain olfactory stimuli, especially the scent of predators, initiates distinctive bursts of fast waves in the hippocampus [18,38,58]. Perhaps such predator warnings could serve to trigger homeward escape responses that requires dead reckoning.

6.6. Two systems for spatial behavior

The most parsimonious interpretation of the results that we have obtained in our studies is that there are two parallel brain systems for spatial navigation [42]. Our studies suggest that because deficits in idiothetic navigation occur following damage to the fimbria-fornix [42], the hippocampus [43,49], and retrosplenial cortex [21] these neural structures are part of a system that hosts dead reckoning. Elsewhere a number of modeling studies have proposed how such a dedicated dead reckoning system might work using hippocampal circuitry (for a review see [31]). We propose that a second, parallel system is involved in navigating to allothetic cues. Such a system would mediate behaviors referred to as taxon and locale by O'Keefe and Nadel [29], or behaviors such as local view learning proposed by others [20].

We make this suggestion with some cautions, however. It is possible to consider that dead reckoning is mediated by fibers passing through the fimbria-fornix that do not involve the hippocampus. This seems unlikely given our previous work showing that selective lesions of the hippocampus also impair dead reckoning [21]. There is also a controversy concerning whether some dead reckoning tasks can be performed by rats with hippocampal damage [see [22] vs. [2] for a discussion]. More explicit studies using alternate tasks may be required to resolve this problem.

One deficit that reliably follows damage to the hippocampal formation is impaired performance on matching-to-place learning tasks [42,46,49]. Matching to place learning is essentially one trial learning of new spatial locations. We suggest that matching-to-place learning is impaired in rats with hippocampal damage not because animals are unable to perform place learning, but because their learning is based entirely on the function of the piloting spatial system. Therefore, they are unable to generate new responses based on the detection of errors in self-movement that would normally be detected and corrected by the dead reckoning system [54]. We must note in conclusion, however, that there are many tasks seeming impaired by hippocampal lesions that may not require dead reckoning. Future work will be required to determine whether dead reckoning makes a contribution to the performance of these tasks [44,47].

Acknowledgements

This research was supported by grants from the Canadian Institute of Health Research.

References

[1] Alyan SH, Jander R, Best PJ. Hippocampectomized rats can use a constellation of landmarks to recognize a place. Brain Res 2000;876:225–37.

[2] Alyan SH, McNaughton BL. Hippocampectomized rats are capable of homing by path integration. Behav Neurosci 1999;113:19–31.

[3] Barlow JS. Inertial navigation as a basis for animal navigation. J Theor Biol 1964;6:76–117.

[4] Batschelet E. Circular Statistics in Biology. London: Academic Press, 1981.

[5] Bland BH, Vanderwolf CH. Diencephalic and hippocampal mechanisms of motor activity in the rat: effects of posterior hypothalamic stimulation on behavior and hippocampal slow wave activity. Brain Res 1972;43:67–88.

[6] Bland BH, Vanderwolf CH. Electrical stimulation of the hippocampal formation. Brain Res 1972;43:251–6.

[7] Day LB, Weisand M, Sutherland RJ, Schallert T. The hippocampus is not necessary for a place response but may be necessary for pliancy. Behav Neurosci 1999;113:914–24.

[8] Etienne AS, Maurer R, Georgakopoulos J, Griffin A. Dead reckoning (path integration), landmarks and representation of space in a comparative perspective. In: Golledge RG, editor. Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes. Baltimore and London: Johns Hopkins University Press, 1999:197–228.

[9] Foster TC, Castra CA, McNaughton BL. Spatial selectivity of rat hippocampal neurons: dependence on preparedness for movement. Science 1989;244:1580–2.

[10] Frank LM, Brown EN, Wilson M. Trajectory encoding in the hippocampus and entorhinal cortex. Neuron 2000;27:169–78.

[11] Gaffan EA, Bannerman DM, Healey AN. Rats with hippocampal lesions learn about allocentric place cues in a non-navigational task. Behav Neurosci 2000;114:895–906.

[12] Gaito J. Measurement scales and statistics: resurgence of an old misconception. Psychol Bull 1980;87:564–7.

[13] Gaito J, Yokubynas R. An empirical basis for the statement that measurement scale properties (and meaning) are irrelevant in statistical analyses. Bull Psychol Soc 1986;24:449–50.

[14] Gallistel DR. The Organization of Learning. Cambridge: The MIT Press, 1990.

[15] Golob EJ, Taube JS. Head direction cells in rats with hippocampal or overlying neocortical lesions: evidence for impaired angular path integration. J Neurosci 1999;15:7198–211.

[16] Gothard KM, Skaggs WE, Moore KM, McNaughton BL. Binding of hippocampal CA1 neural activity to multiple reference frames in a landmark-based navigation task. J Neurosci 1996;16:823–35.

[17] Hannesson DK, Skelton RW. Recovery of spatial performance in the Morris water maze following bilateral transection of the fimbria-fornix in rats. Behav Brain Res 1998;90:35–56.

[18] Heale VR, Vanderwolf CH, Kavaliers M. Components of weasel and fox odors elicit fast wave bursts in the dentate gyrus or rats. Behav Brain Res 1994;63:159–65.

[19] Hostetter G, Thomas GJ. Evaluation of enhanced thigmotaxis as a condition of impaired maze learning by rats with hippocampal lesion. J Comp Physiol Psychol 1967;63:105–10.

[20] Leonard B, McNaughton BL. Spatial representation in the rat: conceptual, behavioral, and neurophysiological perspectives. In: Kesner RP, Olton DS, editors. Neurobiology of Comparative Cognition. Hillsdale: Erlbaum, 1990:363–422.

[21] Maaswinkel H, Jarrard LE, Whishaw IQ. Hippocampectomized rats are impaired in homing by path integration. Hippocampus 1999;9:553–61.

[22] Maaswinkel H, Whishaw IQ. Homing with locale, taxon, and dead reckoning strategies by foraging rats: sensory hierarchy in spatial navigation. Behav Brain Res 1999;99:143–52.

[23] Markus EJ, Qin YL, Leonard B, Skaggs WE, McNaughton BL, Barnes CA. J Neurosci 1995;15:7079–94.

[24] McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung JJ, Knierim JJ, Kudrimoti H, Quin Y, Skaggs WE, Suster M, Weaver KL. Deciphering the hippocampal polyglot: the hippocampus as a path integration system. J Exp Biol 1996;1999:173–85.

[25] McNaughton BL, Barnes CA, O'Keefe J. The contributions of position, direction, and velocity to single unit activity in the hippocampus of freely-moving rats. Exp Brain Res 1983;52:41–9.

[26] Mittelstaedt ML, Mittelstaedt H. Homing by path integration in a mammal. Naturwissenschaften 1980;67:566–7.

[27] Neitz J, Jacobs GH. Reexamination of spectral mechanisms in the rat (*Rattus norvegicus*). J Comp Psychol 1986;100:21–9.

[28] Oddie SD, Stefanek W, Kirk IJ, Bland BH. Intraseptal procaine abolishes hypothalamic stimulation-induced wheel-running and hippocampal theta field activity in rats. J Neurosci 1996;16:1948–56.

[29] O'Keefe J, Nadel L. The Hippocampus as a Cognitive Map. Oxford: Oxford University Press, 1978.

[30] Ranck JB Jr. Head direction cells in the deep cell layer of dorsal presubiculum in freely moving rats. Soc Neurosci Abst 1984;10:599.

[31] Redish DA. Beyond the Cognitive Map: from Place Cells to Episodic Memory. Cambridge: The MIT Press, 1999.

[32] Séquinot V, Maurer R, Etienne AS. Dead reckoning in a small mammal: the evaluation of distance. J Comp Physiol 1993;173:103–13.

[33] Shapiro ML, Eichenbaum H. Hippocampus as a memory map: synaptic plasticity and memory encoding by hippocampal neurons. Hippocampus 1999;9:365–84.

[34] Sharp PE, Blair HT, Etkin D, Tzanetos DB. Influences of vestibular and visual motion information on the spatial firing patterns of hippocampal place cells. J Neurosci 1995;15:173–89.

[35] Taube JS. Head direction cells and the neurophysiological basis for a sense of direction. Prog Neurobiol 1998;55:225–56.

[36] Tchernichovski O, Benjamini Y, Golani I. The dynamics of long-term exploration in the rat. Part I. A phase-plane analysis of the relationship between location and velocity. Biol Cybern 1998;78:423–32.

[37] Tchernichovski O, Golani I. A phase plane representation of rat exploratory behavior. J Neurosci Methods 1995;62:21–7.

[38] Vanderwolf CH. Hippocampal activity, olfaction, and sniffing: an olfactory input to the dentate gyrus. Brain Res 1992;593:197–208.

[39] Vanderwolf CH. The electrocorticogram in relation to physiology and behavior: a new analysis. Electroencephalogr Clin Neurophysiol 1992;82:165–75 Review.

[40] Wallace D, Whishaw IQ. Rats can track odors, other rats, and themselves: implications for the study of spatial behavior. Behav Brain Res 2001.

[41] Wehner R, Srinivasan MV. Searching behavior of desert ants, genus *Cataglyphis* (*Formicidae*, Hymenoptera). J Comp Physiol 1981;142:315–38.

[42] Whishaw IQ. Evidence for two types of place navigation in the rat. In: Buzsaki G, Vanderwolf CH, editors. Electrical Activity of the Archicortex. Budapest: Akademia Kiado, 1985:233–54.

[43] Whishaw IQ. Place learning in hippocampal rats and the path integration hypothesis. Neurosci Biobehav Res 1998;22:209–20.

[44] Whishaw IQ, Bland BH, Vanderwolf CH. Diencephalic hippocampal and neocortical mechanisms in voluntary movement. In: Maser JD, editor. Efferent Organization and the Integration of Behavior. New York: Academic Press, 1993:229–63.

[45] Whishaw IQ, Brooks BL. Calibrating space: exploration is important for allothetic and idiothetic navigation. Hippocampus 1999;9:659–67.

[46] Whishaw IQ, Cassel J-C, Jarrard LE. Rats with fimbria-fornix lesions display a place response in a swimming pool: a dissociation between getting there and knowing where. J Neurosci 1995;15:5779–88.

[47] Whishaw IQ, Coles BLK, Bellerive CHM. Food carrying a new method for naturalistic studies of spontaneous and forced alternation. J Neurosci Methods 1995;61:139–43.

[48] Whishaw IQ, Gorny B. Path integration absent in scent-tracking fimbria-fornix rats: evidence for hippocampal involvement in 'sense of direction' and 'sense of distance' using self-movement cues. J Neurosci 1999;19:4662–73.

[49] Whishaw IQ, Jarrard LE. Similarities vs. differences in place learning and circadian activity in rats after fimbria-fornix section or ibotenate removal of hippocampal cells. Hippocampus 1995;5:595–604.

[50] Whishaw IQ, Maaswinkel H. Rats with fimbria-fornix lesions are impaired in path integration: a role of the hippocampus in 'sense of direction'. J Neurosci 1998;18:3050–8.

[51] Whishaw IQ, Maaswinkel H, Gonzalez CLR, Kolb B. Deficits in allothetic and idiothetic spatial behavior in rats with posterior cingulate cortex lesions. Behav Brain Res 2001;118:67–76.

[52] Whishaw IQ, McKenna JE, Maaswinkel H. Hippocampal lesions and path integration. Curr Opin Neurobiol 1997;7:228–34.

[53] Whishaw IQ, Tomie J. Piloting and dead reckoning dissociated by fimbria-fornix lesions in a rat food carrying task. Behav Brain Res 1997;89:87–97.

[54] Whishaw IQ, Tomie J. Preservation of place reversals in spatial swimming pool tasks: further evidence for place learning in hippocampal rats. Hippocampus 1997;7:361–70.

[55] Whishaw IQ, Whishaw GE. Conspecific aggression influences food carrying: studies on a wild population of *Rattus norvegicus*. Aggress Behav 1996;22:47–66.

[56] Wood ER, Dudchenko PA, Robitsek RJ, Eichenbaum H. Hippocampal neurons encode information about different types of memory episodes occurring in the same location. Neuron 2000;27:623–33.

[57] Wylie DR, Glover RG, Aitchison JD. Optic flow input to the hippocampal formation from the accessory optic system. J Neurosci 1999;19:5514–27.

[58] Zibrowski EM, Vanderwolf CH. Oscillatory fast wave activity in the rat pyriform cortex: relations to olfaction and behavior. Brain Res 1997;766:39–49.