Head Direction Cell Activity Monitored in a Novel Environment and During a Cue Conflict Situation

JEFFREY S. TAUBE AND IIEATHIER L. BURTON
Department of Psychology, Dartmouth College, Hanover, New Hampshire 03755

SUMMARY AND CONCLUSIONS

1. Recent conceptualizations of the neural systems used during navigation have classified two types of sensory information used by animals: landmark cues and internally based (idiothetic; e.g., vestibular, kinesthetic) sensory cues. Previous studies have identified neurons in the postsubiculum and the anterior thalamic nuclei that discharge as a function of the animal's head direction in the horizontal plane. The present study was designed to determine how animals use head direction (HD) cells for spatial orientation and the types of sensory cues involved.

2. HD cell activity was monitored in the postsubiculum and anterior thalamic nuclei of rats in a dual-chamber apparatus in an experiment that consisted of two phases. In the first phase, HD cell activity was monitored as an animal moved from a familiar environment to a novel environment. It was hypothesized that if HD cells were capable of using idiothetic sensory information, then the direction of maximal discharge should remain relatively unchanged as the animal moved into an environment where it was unfamiliar with the landmark cues. In the second phase, HD cells were monitored under conditions in which a conflict situation was introduced between the established landmark cues and the animal's internally generated sensory cues.

3. HD cells were initially recorded in a cylinder containing a single orientation cue (familiar environment). A door was then opened, and the rat entered a U-shaped passageway leading to a rectangular chamber containing a different prominent cue (novel environment). For most HD cells, the preferred direction remained relatively constant between the cylinder and passageway/rectangle, although many cells showed a small (~90°) shift in their preferred direction in the novel environment. This directional shift was maintained across different episodes in the passageway/rectangle.

4. Before the next session, the orientation cue in the cylinder was rotated 90°, and the animal returned to the cylinder. The cell's preferred direction usually shifted between 45 and 90° in the same direction.

5. The rat was then permitted to walk back through the passageway into the now-familiar rectangle. Immediately upon entering the passageway, the preferred direction returned to its original (prerotation) orientation and remained at this value while the rat was in the rectangle. When the rat was allowed to walk back into the cylinder, one of three outcomes occurred: 1) the cell's preferred direction shifted, such that it remained linked to the cylinder's rotated cue card; 2) the cell's preferred direction remained unchanged from its orientation in the rectangle; or 3) the cell's preferred direction shifted to a new value that lay between the preferred directions for the rotated cylinder condition and rectangle.

6. There was little change in the HD cell's background firing rate, peak firing rate, or directional firing range for both the novel and cue-conflict situations.

7. Simultaneous recordings from multiple cells in different sessions showed that the preferred directions remained "in register" with one another. Thus, when one HD cell shifted its preferred direction a specific amount, the other HD cell also shifted its preferred direction the same amount.

8. Results across different series within the same animal showed that the amount the preferred direction shifted in the first Novel series was about the same amount as the shifts observed in subsequent Novel series. In contrast, as the animal experienced more Conflict series, HD cells tended to use the cylinder's cue card less as an orientation cue when the animal returned to the rotated cylinder condition from the rectangle.

9. These results suggest that HD cells in the postsubiculum and anterior thalamic nuclei receive information from both landmark and idiothetic sensory cues, and when both types of cues are available, HD cells preferentially use the landmark cues as long as they are perceived as stable.

INTRODUCTION

Animals employ various strategies for orienting and navigating within their environments. Recent conceptualizations have divided these strategies into two major classes: landmark (taking-a-positional fix) and path integration (dead-reckoning) (Gallistel 1990; McNaughton et al. 1991). Landmark navigation occurs whenever an animal obtains its current position and orientation in the environment relative to surrounding landmarks. The sensory information that the animal uses may be obtained from any of the primary sensory modalities: e.g., visual, auditory, or olfactory. In contrast, for path integration, the animal knows its starting location and orientation but thereafter estimates its current position and direction by integration of internally generated information (idiothetic cues), such as vestibular, proprioceptive, or motor efference copy. Thus path integration occurs independently from visual and auditory cues. The process of path integration requires the animal to maintain an internal "model," or cognitive map, of its current location and orientation with respect to the environment, and then update its location within this map on the basis of its movements through the environment. Continual monitoring of these idiothetic cues is essential for the system to maintain accuracy; otherwise, errors would accumulate over time. The cognitive map is normally capable of integrating signals from idiothetic and landmark systems. However, when external landmark cues are unfamiliar or are not available, such as when an animal enters a new environment, the animal must rely

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1 Optic flow, which does require vision, is another process whereby animals may acquire information about their spatial movements through an environment. Although optic flow is usually not considered an idiothetic cue, it can be used in a similar way as the other idiothetic cues to keep track of the animal's position in the environment. At present, the extent to which males use optic flow for spatial orientation is unclear.
on path integration processes to maintain cognizance of its directional heading. Once an animal has become familiar with the new surroundings, it can then use the landmark features unique to that environment for knowing its spatial orientation during subsequent exposures to the same surroundings. Several behavioral studies have demonstrated the importance of idiothetic cues for accurate navigation in spatial tasks (Matthews et al. 1988; Miller et al. 1983; Mittelstaedt and Mittelstaedt 1980; Scenio and Bures 1989). For example, the Mittelstaedt study showed that the desert mouse was capable of compensating for passive angular rotation of its environment and successfully returned to its nest in the dark.

One brain region important for the processing of spatial information is the hippocampus and areas connected with it (for review, O’Keefe and Nadel 1978). Neurons within the hippocampal formation have been identified, which discharge according to some spatial aspect of the animal’s relationship to its environment. One type of neuron discharges as a function of the animal’s location within the environment (hippocampal place cells) (Jung and McNaughton 1993; Muller et al. 1987; O’Keefe 1976). Several studies have shown that place cells receive highly processed information from both idiothetic and landmark-based sensory cues (O’Keefe and Conway 1978; O’Mara et al. 1994; Wiener et al. 1995). A second type of ‘allocentric’ spatial cell identified in the rat brain is the head direction (HD) cell. These neurons discharge as a function of the animal’s head direction in the horizontal plane, independent of the animal’s location and behavior within the environment. The direction at which the cell discharges maximally is referred to as the preferred (firing) direction, and vectors drawn to represent the preferred direction at different locations indicate that all the vectors are parallel. HD cells were initially identified in the rat postsubiculum (PoS, dorsal presubiculum) (Runck 1985; Taube et al. 1990a) but have recently been reported in several other brain areas including the anterior thalamic nuclei (ATN) (Taube 1995), lateral dorsal thalamus (LDN) (Mizumori and Williams 1993), striatum (Wiener 1993), and retrosplenial cortex (Chen et al. 1994a). The findings that lesions of the PoS (Taube et al. 1992), ATN (Sutherland and Rodriguez 1989), or inactivation of the LDN (Mizumori and Williams 1993) impair the performance of animals on spatial tasks is consistent with the hypothesis that these brain areas serve crucial roles in processing spatial information. Experiments showing that rotation of a prominent visual cue in a cylindrical environment led to a near-equal shift in the cell’s preferred direction demonstrated that visual landmark cues can exert control over HD cell firing (Taube 1995; Taube et al. 1990b). Previous studies also showed that when the cylinder was replaced with a rectangular enclosure containing a cue card in the same position relative to the recording room, the cell’s preferred direction shifted by at least 48° in 8 of 10 experiments (Taube et al. 1990b). These results suggested that the HD cells treated the rectangle as a different environment than the cylinder, and this finding was utilized in the design of the present study.

The cue rotation experiments show that HD cells receive information from the landmark based navigational system, but little is known about whether they receive inputs from idiothetic sensory cues. Taube et al. (1990b) demonstrated that cell discharge was not solely dependent on a single, salient visual cue because cell discharge was maintained when the cue was removed from the apparatus. Other studies in the PoS (Taube et al. 1988; unpublished observations) and LDN (Mizumori and Williams 1993) have shown that directional discharge can be maintained in the dark over an 8-to 10-min recording session. However, it is difficult to determine from these experiments whether directional discharge was being maintained by idiothetic sensory cues or secondary landmark cues within the recording room (e.g., olfactory markings on the floor, tactile cues within the chamber, and surrounding auditory cues from recording equipment). In addition, very little is known about how HD cells respond when the animal is confronted with a situation where the spatial information from different sensory cues are in conflict with one another. In these situations, how do HD cells select from different cue types? For example, a cue conflict could arise from a situation where the spatial information concerning two landmark cues are contradictory, or from a situation when the spatial information established from landmark cues contradicts information established through idiothetic cues.

The present experiments were designed to determine the effects of a freely moving rat navigating into a novel environment and during a cue conflict situation on HD cell activity in the PoS and ATN. A two-chamber apparatus was built containing separate cylinder and rectangle arenas, with a U-shaped passageway connecting them (Fig. 1). HD cell activity was monitored daily in the cylinder chamber (familiar environment). A door was then opened, which allowed the animal to move into the passageway and led to the rectangle chamber. Because the passageway/rectangle served as a novel environment, where the original orienting cue was no longer visible, we were interested in determining whether
HD cell activity was maintained as the animal moved into the new chamber and, if so, whether the preferred direction remained the same. We hypothesized that for cell discharge to continue in the same preferred direction in a novel environment, that HD cells must be receiving idiothetic sensory information, because there are no familiar landmark cues available for orientation.

The second phase of the experiment monitored HD cell activity as the animal entered one of the environments in which a conflict situation was set up in relation to the established orientation cues. Once the animal had been exposed to the passageway/rectangle, it could learn and integrate the spatial relationships of the new landmarks, such that these surroundings now became a familiar environment. In the next session, with the animal out of view, the orientation cue in the cylinder was rotated 90°. If, as expected from previous studies, the cell’s preferred direction shifted with the cue card when the animal was returned to the cylinder, then the final phase of the experiment was conducted. The door to the passageway was opened, and the animal was permitted to walk back via the passageway into the now-familiar rectangle. Now, however, the spatial information concerning the landmark cues in the passageway/rectangle were in conflict with the spatial cues in the rotated cylinder condition. We were interested in examining what effect this conflict situation would have on HD cell discharge. In particular, we wanted to determine which landmark cues the cells would use and whether information from landmark cues would predominate over idiothetic cues. If the cell’s preferred direction returned to its originally established direction in the rectangle, then this finding would indicate that the rectangle/passageway’s landmark cues exerted more control over HD cell discharge than inputs from idiothetic cues. Alternatively, if the cell maintained the same preferred direction as the animal moved from the rotated cylinder condition to the rectangle, this finding would indicate that the spatial information concerning the rectangle’s landmark cues were weak, or did not have time to consolidate, and that idiothetic cues exerted the primary influence over cell discharge. We will show that in this conflict situation, the cell’s preferred direction shifted back to its originally established relationship in the rectangle.

In the final phase of the experiment, we monitored cell activity when the animal returned from the rectangle to the cylinder containing the rotated cue. This phase provided a second opportunity to monitor HD cell activity in a cue conflict situation. If the cell’s preferred direction shifted back to its original relationship with the rotated cue card, this finding would indicate that the cylinder’s cue card exerted more control over cell discharge than idiothetic cues. Alternatively, if the preferred direction did not shift back, then this result would indicate that the animal now perceived the cue card as an unstable cue and that idiothetic cues (or possibly other landmark cues) were exerting more control over cell discharge than the rotated cue card.

For some experiments, more than one HD cell was recorded simultaneously, and we were interested in determining whether the changes that occurred in one cell also occurred in the second or third cells. Finally, for some animals, more than one series of manipulations was conducted. Because the passageway/rectangle chamber can only be considered a novel environment once for the animal, each series was analyzed on the basis of whether it was the animal’s first exposure to the apparatus or a subsequent exposure. It is possible that as a result of experiencing multiple conflict situations in the cylinder, the animal may begin to perceive the cylinder’s cue card as unstable and consequently become less likely to use it as an orientation cue. Thus we also examined the effects that these manipulations had over time on HD cell firing. A preliminary report concerning some of these findings has been presented previously (Burton and Taube 1992).

**METHODS**

Many of the methods used in this study were similar to those employed by Taube and colleagues to record from PoS and ATN HD cells (Taube 1995; Taube et al. 1990a,b). Accordingly, only the details unique to the current set of experiments are described in detail below. Other details and procedures that have been described in the above studies are summarized briefly. In general, all animals underwent training and testing in two different apparatus.

Animals were first trained and screened for cells in one apparatus (a cylinder). When a HD cell was identified, the animal was recorded in a second apparatus, referred to as the dual-chamber apparatus.

**Screening apparatus and behavioral training**

Long-Evans female rats (n = 21) were placed on a food-restricted diet and trained to retrieve food pellets thrown randomly into a cylindrical apparatus (76 cm diam, 51 cm high). A black curtain (2.5 m diam) surrounded the apparatus from floor to ceiling, and four overhead lights arranged uniformly at the ceiling provided a low level of illumination. The cylinder was placed on a sheet of photographic backdrop paper. A vertically oriented color video camera with a 8.5-mm lens (Sony XC-711) was centered over the cylinder 206 cm above the floor. A sheet of white cardboard occupying 110° of arc, was taped to the inside wall of the cylinder and provided the major visual cue for orientation. The “cue card” was centered at 3 o’clock as viewed from the overhead video camera for all training and cell-screening sessions. This position was defined as 0° and angles increased in sequence in a counterclockwise (CCW) manner.

**Electrode and surgical techniques**

The electrodes consisted of a bundle of 10.25-μm-diam nichrome wires that were insulated except at the tips. The wires were threaded through a stainless steel cannula and attached to a modified 11-pin Augat connector, which in turn was embedded in dental acrylic and made moveable through the use of three screws (for details of electrode construction, see Kubie 1984). Once the animals were trained on the food-pellet retrieval task, they were anesthetized with pentobarbital sodium (Nembutal; 45 mg/kg ip) and injected with 0.1 ml of atropine sulfate (25 mg/ml) to reduce respiratory problems. With the use of stereotaxic techniques and Bregma coordinates, the electrode array was implanted just dorsal to either 1) the ATN: anterior/posterior (AP), 1.35 mm posterior; medial/lateral (ML), 1.40 mm right: dorsal/ventral (DV), 4.0 mm from the cortical surface or 2) the PoS: AP, 6.6 mm posterior; ML, 2.90 mm right; DV, 1.8 mm from the cortical surface (Paxinos and Watson 1986). All surgery was conducted under sterile conditions, and animals were allowed to recover for 7 days before cell screening commenced.
Screening and recording procedures

For single-unit screening, the animal was attached to a 12-wire recording cable that was connected on one end to an overhead commutator (Biela Idea Development) and to the animal’s headstage on the other end. Electrical signals were passed through a field-effect transistor (FET) in a source-follower configuration, amplified (Grass Instruments P511), band-passed filtered (300–10,000 Hz; 3 dB/octave; Peavey Electronics PME8), and sent through a series of window discriminators (Bak Electronics DD151) before being displayed on an oscilloscope (Tektronix 5113). Electrical activity on the 10 wires was monitored several days each week for several months while the electrodes were slowly advanced through the brain. When a HD cell’s waveform was adequately isolated from background electrical noise, the animal was returned to its home cage and the room prepared for testing the animal in the dual-chamber apparatus. All PoS and ATN HD cells used in the experiments had discharge properties (described below) within the range of parameters previously reported for HD cells in these brain areas (Taube 1995; Taube et al. 1990a). In addition, the preferred directions from all the recorded HD cells in each brain area were equally distributed around 360°.

Behavioral testing in the dual-chamber apparatus

The screening cylinder was removed from the room and replaced by a dual-chamber apparatus shown in an overhead view in Fig. 1. The diameter of the cylinder chamber (76 cm) was the same size as the cylinder used during cell screening, except the height was 7.5 cm lower in order to reduce the amount of obscured area viewed by the overhead video camera. The smaller height of this cylinder had no effect on HD cell discharge between the screening cylinder and the dual chamber cylinder. The dimensions of the rectangle floor were 51 by 68.5 cm, and the width of the passageway was 15 cm. A removable door separated the cylinder from the passageway. The center axis of the long passageway section was 40.5 cm from the cylinder door. The sides of the passageway and rectangle (bold lines in Fig. 1) were slanted in toward the apparatus floor by 10–30°. This design enabled the video camera to view all portions of the apparatus. The entire apparatus was painted gray, and the cylinder’s door was made to blend in with the cylinder’s wall as much as possible.

The cylinder chamber contained a white card attached to the wall that served as the primary orientation cue for the animal when it was in the cylinder. For most experiments, the cylinder’s cue card was initially placed at the 3 o’clock position, which was similar to the conditions in the screening cylinder. For five experiments, the cylinder’s cue card was initially positioned at 12 o’clock. The rectangle also contained a white cue card attached to one end of the enclosure (12 o’clock position). The entire apparatus was surrounded by the same curtain as in the cell-screening conditions. Animals were brought into the recording room in an enclosed opaque box, which was rotated briskly as the experimenter entered the room and walked around the apparatus. This procedure was conducted in order to disrupt any idiothetic cues the animal may have used while being transported from its home cage to the recording room. The animal was then attached to the recording cable and placed in the center of the dual chamber’s cylinder usually facing the direction of the cue card. The experimenter left the curtained area by different paths before each recording session. During each of the recording sessions described below, animals retrieved food pellets thrown randomly over the curtain into the apparatus. The location where the experimenter stood when delivering the food pellets was varied in order to avoid providing an extraneous orientation cue to the animal.

The behavioral testing consisted of four recording sessions, referred in order as Standard Cylinder, Novel, Rotation Cylinder, and Conflict sessions (Fig. 2). However, the Novel and Conflict sessions were later subdivided (off-line) into smaller episodes, based on which portion of the dual-chamber apparatus the animal was in (cylinder or passageway/rectangle). All the episodes in a particular chamber were summed into a composite segment. Thus the Novel session consisted of a Novel-Rectangle session and a Return-Cylinder session; the Conflict session consisted of a Conflict-Rectangle session and a Conflict-Cylinder session.

The first session monitored the cell’s activity in the dual-chamber’s cylinder for 8 min with the door closed (Standard Cylinder session). In the second session, the cylinder’s door was opened, and the animal was allowed to walk into the rectangle via the passageway (Novel session). Once in the passageway, the door was sometimes closed for a period of time (4–8 min), and the animal was confined to the new environment. During this period the animal usually explored the new environment while continuing to retrieve food pellets tossed randomly into it. The door was then reopened, and the animal could move freely back-and-forth between the two chambers. Novel sessions were generally 16 min in length, but some were longer (20–32 min). Cell activity was monitored continuously throughout the session. Later off-line analysis sorted this session into two segments based on whether the animal was in the cylinder (Return-Cylinder episodes) or in the
passageway/rectangle (Novel-Rectangle episodes). At the completion of the Novel session, the animal was removed from the apparatus and returned to its home cage.

Some animals were tested more than once in the dual-chamber apparatus when subsequent HD cells were obtained during screening sessions. To distinguish these subsequent series from the first cases when the animal was exposed to the apparatus, these sessions are referred to as Subsequent Novel-Rectangle and Subsequent Return-Cylinder sessions.

Once the animal was exposed to the passageway/rectangle, it could learn and integrate the spatial relationships of the new landmarks, such that these surroundings now became a familiar environment. In the next manipulation, a situation was set up in which the spatial information concerning the landmark orientation cues and the animal’s idiothetic cues were placed in conflict with one another. This situation was set up by rotating the cue card in the cylinder and then returning the animal to the cylinder. Under these conditions, if the cell’s preferred direction shifted with the cue card, then when the door was opened, a conflict would arise between the spatial information conveyed by the cylinder’s cue card and the spatial information conveyed by the unchanged landmark cues in the passageway/rectangle. Furthermore, if the cell were to switch its preferred direction in the rectangle to realign itself with the rectangle’s cues, it would necessitate “overriding” sensory information received through idiothetic cues. Similarly, once in the rectangle, a cue conflict would occur again when the animal returned to the cylinder with the rotated cue card. Note, however, that for a cue conflict situation to arise, the cell’s preferred direction must shift substantially in the initial session when the cue card is rotated in the cylinder.

Before the third recording session (Rotation Cylinder session), the floor paper was changed and the cylinder’s cue card rotated 90° CCW to the 12 o’clock position. For the five experiments where the cylinder’s cue card was initially positioned at 12 o’clock, the card was rotated 90° clockwise (CW). The animal was then returned to the recording room in the opaque box using the same disorientation procedures as used before the Standard Cylinder session. The animal was attached to the recording cable and placed in the cylinder containing the rotated cue card (the cylinder door was closed). HD cell activity was then monitored for 8 min. If the cell’s preferred direction shifted by at least 42° in the Rotation Cylinder session, the final phase of the experiment was conducted (Conflict session). If it did not shift by at least 42°, the animal was returned to its home cage and the series of manipulations terminated, because under these conditions it was not possible to monitor cell discharge with the situation cues in conflict.

For the Conflict session, the cylinder’s door was opened and the animal permitted to return to the now-familiar passageway/rectangle environment as HD cell activity was monitored continuously. As with the Novel session, once the animal entered the passageway/rectangle, the door was sometimes closed for several min. This procedure ensured that there was enough sampling time in the passageway/rectangle to obtain an accurate characterization of the cell’s discharge parameters. The door was then reopened, and cell activity was monitored as the animal returned to the cylinder containing the rotated cue. This phase provided a second opportunity to monitor HD cell activity in a cue conflict situation. The door remained open, and the animal could move freely back and forth between the two chambers. Cell activity was monitored continuously throughout the Conflict session. Conflict sessions were usually 16 min in length, although a few sessions were longer (20–24 min). Later off-line analysis sorted this session into two segments based on whether the animal was in the passageway/rectangle (Conflict-Rectangle episodes) or in the cylinder (Conflict-Cylinder episodes).

In sum, each experimental series consisted of four recording sessions: 1) Standard Cylinder, 2) Novel, 3) Rotation Cylinder, and 4) Conflict. The Novel and Conflict sessions were subdivided into two separate segments depending on whether the animal was in the cylinder or passageway/rectangle (each of these off-line determined segments are denoted by using a hyphen in the session name). If the series was not the animal’s first exposure to the apparatus, the sessions were labeled as Subsequent Novel-Rectangle and Subsequent Return-Cylinder sessions. The experimental series was discontinued if 1) the cell’s waveform was not sufficiently isolated from background electrical noise, 2) there was evidence to indicate that the cell recorded during the Rotation Cylinder session was not the same cell as that recorded previously during the Standard Cylinder and Novel sessions, or 3) the cell’s preferred direction shifted by <42° in the Rotation Cylinder session.

**Data acquisition**

An automated video-computer tracking system (Eberle Electronics) monitored neuronal discharge while simultaneously tracking the positions of two light-emitting diodes (LEDs; 1 red, 1 green) secured to the animal’s head. The red and green LEDs were spaced 10 cm apart along the midline of the animal’s body axis and positioned over the rat’s snout and back, respectively. The X and Y coordinates of each LED were determined to 1 part in 256, and each rectangular subregion (pixel) of the video frame was 6.9 × 6.9 mm. Recording sessions were usually 8 or 16 min in length during which time the LEDs coordinates and spike discharge were sampled at a rate of 60 Hz and the data read into a computer (National Instruments DIO-32, Macintosh IIfx). Data analysis was performed off-line at a later time with the use of a software program (LabView 2.2).

**Data analysis**

The animal’s horizontal head direction was calculated from the relative positions of the two LEDs and then correlated to cell firing. The animal’s location in the environment was defined as the point 3 cm from the red LED along the line between the two LEDs. This point corresponded approximately to the center of the animal’s head. Given the size of each pixel and the distance between the two LEDs, the maximum resolution of head direction when the animal’s head axis was in the horizontal plane was calculated to be ~3.6°. Tilting of the head backward or forward reduced the resolvability of head direction. The total time and the number of spikes discharged at each head direction for a particular session were summed from the collected samples. The cell’s firing rate was determined by taking the total number of spikes in each head direction bin and dividing it by the time spent in that head direction. Graphs of the cell’s firing rate as a function of head direction in 6° bins were then constructed. A cell’s firing characteristics for the Novel and Conflict sessions were determined by summing the individual episodes in each chamber and creating a composite firing rate/head direction graph. Because the Novel and Conflict sessions were divided according to whether the animal was in the cylinder or the passageway/rectangle, there were six types of graphs that could be compared: Standard Cylinder, Novel-Rectangle, Return-Cylinder, Rotation Cylinder, Conflict-Rectangle, Conflict-Cylinder. From the firing rate/head direction functions, four parameters were computed that characterized the properties for each HD cell. With the use of terminology and procedures adopted in previous work (Taube 1995; Taube et al. 1990a), these four parameters are 1) the background firing rate and signal-to-noise ratio, 2) the preferred direction (the head direction associated with maximal discharge), 3) the peak firing rate (the firing rate at the preferred direction), and 4) the directional firing range (the range of head directions in which the neuronal firing rate was greater than background level).

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To determine the amount a cell’s preferred direction shifted between two different sessions, or between two different environments (e.g., cylinder vs. rectangle), a cross-correlation method was used. The firing-rate/head direction function for one experimental session was shifted in 6° steps and cross-correlated with the function from the other experimental session. The amount the function needed to be shifted to yield the maximal cross-correlation (Pearson’s r) was defined as the shift in the preferred direction. Positive and negative shift values indicate CCW and CW shifts, respectively. As with previous studies (Taube 1995; Taube et al. 1999b), the maximal correlation between the two functions tested was usually >0.90 and indicates the strong similarity of shapes between the functions. For some series, more than one HD cell was recorded simultaneously. In these circumstances, the shift in the preferred direction was calculated for each cell and the values averaged across both cells to obtain a composite shift for that session. This procedure was used to avoid unfairly weighting the statistical analysis from sessions where more than one cell was monitored. Except where noted, the mean shifts in the preferred direction reported for different sessions are described as the absolute value of the shift; however, trends for CW or CCW shifts are also summarized. Differences between directional shifts for different sessions was tested with the use of unpaired t-tests. All mean values are reported with the standard error of the mean (SE).

To determine whether other discharge properties, such as peak firing rate, directional firing range, or background firing rate, changed across sessions/episodes, each parameter for the Return-Cylinder and Novel-Rectangle sessions was expressed as a percentage of its value for the Standard Cylinder session. Values for the Rotation Cylinder session were expressed as a percentage of the Return-Cylinder sessions (because these episodes were the animal’s last experience in the cylinder before the cue card was rotated). Finally, each parameter for the Conflict-Cylinder and Conflict-Rectangle sessions was expressed as a percentage of its value for the Rotation Cylinder session. Data were then tested with the use of an analysis of variance (ANOVA), and probabilities <0.05 with the use of a Scheffe test were considered statistically significant.

**Histology**

Electrodes were advanced 2–3 mm before terminating cell screening. At the completion of the experiment, animals were anesthetized, and a small anodal current (10–20 μA for 10 s) was passed through one of the recording wires in order to conduct a Prussian blue reaction. The animals were perfused with 10% Formalin (in saline), and the brains were removed and placed in 10% Formalin for at least 48 h. The brains were then placed in a 10% Formalin solution containing 2% potassium ferrocyanide for 24 h and then reimmersed in 10% Formalin (24 h) before being placed in 20% sucrose for 24 h. They were then sectioned (40 μm), stained with cresyl violet, and examined microscopically for localization of the recording sites.

**RESULTS**

A total of 27 HD cells were recorded from the PoS in 13 animals, and 20 HD cells were recorded from the ATN in 8 animals. Histological analysis after completion of the experiments verified each of the recording sites. For PoS-recorded HD cells, two series contained recordings from two HD cells monitored simultaneously. For HD cells recorded in the ATN, nine series monitored one HD cell, four series monitored two HD cells recorded simultaneously, and one series monitored three HD cells recorded simultaneously. Thus a total of 25 series were conducted in the PoS, and 14 series were conducted in the ATN. Results from the two recording sites were not different and were therefore combined for the purpose of brevity.

**Novel environment**

When the rat moved into the novel environment (passageway/rectangle), HD cells continued to discharge as a function of the animal’s head direction in the horizontal plane. The cell’s preferred direction remained nearly constant between the cylinder and rectangle, and there appeared to be little qualitative change in the cell’s firing rate at the preferred direction. Observations also showed that HD cells maintained their directional specificity during the animal’s first pass through the preferred direction when it entered the passageway/rectangle.

Although the preferred direction remained nearly constant between the Standard Cylinder and Novel-Rectangle episodes, small shifts (6°–30°) were frequently observed. Because the animal could move freely back-and-forth between the cylinder and rectangle during the Novel session, each episode in the two environments was monitored and analyzed to determine whether changes in the preferred direction occurred over time. To be considered a trip, animals had to spend at least 5 s in one apparatus before entering the other chamber. Animals made a mean number of 5.14 ± 0.45 (range: 1–12) trips back-and-forth between the two environments. Because the door between the cylinder and passageway was often closed to increase the sampling time in the rectangle environment, this value actually underestimates the true number of trips the animals might have made between the two environments if they were not forced to remain in one chamber. The range of total time the animals spent in the novel environment (both rectangle and passageway) varied between 2.12 and 17.72 min, with a mean of 10.41 ± 0.59 min. In general, there was little difference in the HD cell’s preferred direction between different episodes in the rectangle (see analysis below). Therefore each of the rectangle episodes was summed to create a mean firing rate/head direction graph for the Novel-Rectangle session. Similarly, there was no difference in the cell’s preferred direction for each episode in the cylinder after a trip to the rectangle, and episodes in the cylinder after a trip to the rectangle were summed to create a session referred to as the Return-Cylinder session.

A total of 39 series were performed in 21 animals. Because more than 1 series was conducted in several animals, only 21 experiments can be considered the animal’s first true exposure to a novel environment. These 21 series (13 PoS, 8 ATN) are considered separately from subsequent series conducted on different cells within the same animal. Figures 3, A and B, and 4, A and B, show the responses from representative PoS and ATN HD cells during the Novel-Rectangle and Return-Cylinder sessions.

**FIRST EXPOSURE SESSIONS.** Of the 21 1st exposure series, 18 series had shifts in the preferred direction that were ≤30°. Statistical analyses were conducted for 20 series, whereas the results from 1 series in an ATN HD cell are discussed separately below (see Aberrant cell responses). The mean shift in the preferred direction between the Standard Cylinder and Novel-Rectangle session was 18.00 ± 2.68 (range: 0–42°; n = 20). Interestingly, there was a significant trend for
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FIG. 3. Recordings from a postsubiculum (PoS) head direction (HD) cell during one series of manipulations. Each graph shows the cell's firing rate as a function of the animal's head direction. A: in comparison with the Standard Cylinder session, the cell's preferred direction shifted very little when the animal entered the novel environment (Novel-Rectangle session). B: the exposure to the new environment had no effect on cell activity in the original environment (Return-Cylinder session). When the cylinder's cue card was rotated 90° CCW, the cell's preferred direction shifted 60° (Rotation Cylinder session) when compared with the Return-Cylinder session (D). C: when the animal entered the passageway/rectangle during the Conflict-Rectangle session, the cell's preferred direction shifted immediately to its originally established orientation in the rectangle. D: the cell's preferred direction maintained its relationship to the cylinder's rotated cue card during the Conflict-Cylinder session. For this figure and subsequent figures, the cell's activity during the Novel-Rectangle and Return-Cylinder sessions are redrawn in C and D for comparison with the Rotation Cylinder and Conflict sessions.

shifts to occur in a CW direction ($\chi^2$ test: $\chi^2 = 8.90$, df = 1, $P < 0.005$; 16 shifts were in a CW direction, 3 shifts were in a CCW direction, and 1 session had no change in the cell's preferred direction. In contrast, there was little difference in the cell's preferred direction between the Standard Cylinder and Return-Cylinder sessions; all cells shifted their preferred direction by $\leq 12^\circ$. Eight series had CW shifts, 6 series had CCW shifts, and 6 series had no change in the cell's preferred direction. The reason for these directional biases in the Novel-Rectangle sessions is unclear, but it may be attributed to the fact that the animal's directional heading is turning in a CW direction as it initially enters both the passageway and rectangle.

After initial exposure to the rectangle, subsequent episodes in the cylinder did not lead to changes in cells preferred directions in either the cylinder or rectangle environments. Thus, if a cell's preferred direction shifted 18° during the first trip to the rectangle, subsequent episodes in the rectangle also had 18° shifts. To verify this judgment, we analyzed the differences in preferred direction across different episodes in the rectangle. The first episode in the rectangle that was at least 1 min in length was selected as the "control episode." With the use of the cross-correlation method described in METHODS, this control episode was then compared with every episode in the rectangle that satisfied the following criteria: 1) the episode was at least 30 s long, 2) every 6° bin of the episode was sampled, and 3) the best-fit cross-correlation with the control episode was at least 0.50. Of the episodes that satisfied these criteria, there was no significant difference between shifts in the preferred direction for PoS ($n = 19$) and ATN ($n = 23$) HD cells, and the two groups were therefore combined ($t = 0.308$, df = 40; $P > 0.05$). The mean difference in the preferred directions between the control and subsequent episodes in the rectangle was $-1.57 \pm 1.10^\circ$ (range: $-24^\circ$ to $12^\circ$, $n = 42$). With the use of zero as the expected value for the population mean, a $t$-test indicated that there was no significant difference between the preferred directions in the control and subsequent episodes in the rectangle ($t = 1.43$, df = 41, $P > 0.05$). The absolute mean difference in the preferred directions between the control and subsequent episodes in the rectangle was $4.71 \pm 0.86^\circ$. This difference is similar to the variability observed
between two recording sessions in the Standard Cylinder condition reported in previous experiments: PoS mean shift = 6.6 ± 1.3° (Taube et al. 1990b); ATN mean shift = 4.71 ± 1.80° (Taube 1995). These results indicate that the preferred directions in the rectangle were remarkably consistent across different trips into the chamber. An example of this consistency for one ATN HD cell is shown in Fig. 5.

The mean shift in the preferred direction between the Standard Cylinder and Return-Cylinder sessions was 4.65 ± 0.77° (range: 0–12°). This mean shift is also similar to the difference observed between the preferred directions of two Standard Cylinder sessions reported in previous studies [PoS mean shift, 6.6 ± 1.3° (Taube et al. 1990b); ATN mean shift, 4.71 ± 1.80° (Taube 1995)]. A t-test showed that there was a significant difference between the mean shifts observed in the Return-Cylinder and Novel-Rectangle sessions (t = 4.78, df = 38, P < 0.0001). Thus the small change in the cell’s preferred direction in the Novel-Rectangle sessions is unlikely to be attributed to variability in the cell’s directionality between different recording episodes. The distribution of preferred directional shifts in the Novel-Rectangle and Return-Cylinder sessions are shown in the histograms of Fig. 6. Comparison of these two histograms shows the wider distribution of preferred directional shifts in the Novel-Rectangle sessions and indicates that, although most shifts in the Novel-Rectangle sessions were relatively small, larger shifts occurred more frequently in these sessions compared with Return-Cylinder sessions.

Although small shifts in the preferred direction were sometimes present during the Novel-Rectangle sessions, the peak firing rate, directional firing range, and background firing rate remained stable in the novel environment, as well as during the animal’s return episodes in the cylinder. The mean percent change in these discharge parameters for both the Return-Cylinder and Novel-Rectangle sessions were computed, and an ANOVA showed that there were no significant differences compared with the Standard Cylinder session (Table 1).

**FIG. 4.** Series of simultaneous recordings from 2 HD cells in the anterior thalamic nuclei (ATN). These 2 cells were recorded on the same electrode wire, although they had different waveforms. For clarity, cells 1 and 2 are labeled only in A. However, throughout the recording series the 2 cells could be distinguished on the basis of their different peak firing rates. Cell 1 consistently had peak firing rates between 60 and 80 spikes/s, and cell 2 consistently had peak firing rates between 20 and 35 spikes/s. Note that the difference in the preferred directions of the 2 cells remained the same throughout the series of manipulations. A: Novel-Rectangle session. B: Return-Cylinder session. C: Conflict-Rectangle session. D: Conflict-Cylinder session. For this series the preferred directions of both cells did not shift when the animal returned to the cylinder containing the rotated cue card.
Return-Cylinder sessions is also substantially different from (Taube 1995; Taube et al. 1990b). Thus it is unlikely that corded in the same environment reported in previous studies the variability (4-6°) observed between two sessions re-

than and significantly different from the shift reported above (range: O-66°), respectively. In contrast to the first exposure to the novel environment (cf. 22.17° vs. 18.00°; t = 0.748, df = 36, P > 0.05), the mean shift in the Subsequent Return-Cylinder sessions is larger than and significantly different from the shift reported above for first exposure sessions (cf. 12.17° vs. 4.65°; t = 2.06, df = 36, P < 0.05). The larger mean shift in the Subsequent Return-Cylinder sessions is also substantially different from the variability (4-6°) observed between two sessions re-

corded in the same environment reported in previous studies (Taube 1995; Taube et al. 1990b). Thus it is unlikely that the Subsequent Return-Cylinder shift can be attributed to variability across sessions. However, most of the discrepancy can be accounted for by the results from three Subsequent Return-Cylinder sessions in the ATN that showed shifts of -24, -30, and -66°. In contrast, there were no shifts exceeding 12° in all the Return-Cylinder sessions in the first series from each animal (cf. Fig. 6B). It appears that the HD cells during these three sessions established a new relationship with the cylinder/cue card environment after exposure to the passageway/rectangle. Furthermore, this new relationship remained stable across different episodes in the two environments and across subsequent manipulations in the Rotation Cylinder and Conflict sessions. The reason for the presence of these larger shifts is unclear, although it is possible that the intervening exposures of the conflict situations in previous series led to these changes. Figure 7 shows the results from one of these series. In particular, note that the cell’s preferred direction shifted by 24° in the Return-Cylinder session compared with the Standard Cylinder session (Fig. 7B).

rectangle. HD cells maintained their discharge characteristics throughout the episodes in the rectangle, and there was no change in peak firing rate, directional firing range, and background firing rate in either the Novel-Rectangle or Return-Cylinder sessions. Small shifts in a cell’s preferred direction were also observed in the Novel-Rectangle sessions and were about the same magnitude as the shifts reported above for the animal’s first exposure to the novel environment. For the Novel-Rectangle session, only 3 of 18 sessions showed a shift in the preferred direction =24°. However, there was an uneven distribution in the direction of the shifts: 14 CW, 2 CCW, and 2 unchanged. A χ² test showed that this trend for a preferred directional shift in the CW direction was statistically significant (χ² = 9.00, df = 1, P < 0.005).

In contrast, the distribution of preferred directional shifts for the Return-Cylinder session was 7 CW, 1 CCW, and 4 no change. Thus the trend for CW directional shifts in the Novel-Rectangle sessions that was observed during 1st exposure sessions was repeated in subsequent series.

The mean shifts of the preferred directions in the Subse-
quent Novel-Rectangle and Subsequent Return-Cylinder sessions were 22.17 ± 5.07 (range: 0-81°) and 12.17 ± 3.76 (range: 0-66°), respectively. In contrast to the first exposure conditions, however, a t-test showed that the difference in the preferred directions between these two sessions was not statistically significant (t = 1.59, df = 34, P = 0.12). Although the mean shift value for the Subsequent Novel-Rectangle sessions is similar to the value reported above for the animal’s first exposure to the novel environment (cf. 22.17° vs. 18.00°; t = 0.748, df = 36, P > 0.05), the mean shift value for the Subsequent Return-Cylinder sessions is larger than and significantly different from the shift reported above for first exposure sessions (cf. 12.17° vs. 4.65°; t = 2.06, df = 36, P < 0.05). The larger mean shift in the Subsequent Return-Cylinder sessions is also substantially different from the variability (4-6°) observed between two sessions re-

corded in the same environment reported in previous studies (Taube 1995; Taube et al. 1990b). Thus it is unlikely that

![Figure 5](image-url)  
**FIG. 5.** Recordings from different episodes in the Novel Rectangle session from an ATN HD cell. This figure shows the consistency in the preferred direction across different episodes in the rectangle during the Novel session. Note that the slopes for each of the functions in the rectangular environment were also similar and were consistently shifted clockwise compared with the Return-Cylinder session. The larger variability observed in each of the episodes at head directions around the preferred direction (indicated by the jaggedness in the line plots) is attributed to short sampling times. Sampling times for episodes 1-5 were (in mins): 6:30, 0:42, 0:58, 0:43, and 0:37, respectively. The length of the Return-Cylinder session was 4:14.

![Figure 6](image-url)  
**FIG. 6.** Novel-Rectangle and Return-Cylinder histograms. Histograms showing the amount of shift in the cell’s preferred direction for the Novel-Rectangle (A) and Return Cylinder (B) sessions compared with the Standard Cylinder session. Note the larger variability in the shifts for the Novel-Rectangle sessions. There was a significant trend for cells to shift their preferred direction in a clockwise direction for the Novel-Rectangle sessions, as indicated by the numerous negative shifts in A.
TABLE 1. Mean percent changes in directional firing parameters for Novel, Rotation, and Conflict sessions

<table>
<thead>
<tr>
<th>Session Type Comparison</th>
<th>n</th>
<th>Preferred Firing Direction, deg</th>
<th>Peak Firing Rate, %</th>
<th>Directional Firing Range, %</th>
<th>Background Firing Rate, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard/Return-Cylinder</td>
<td>20</td>
<td>4.65 ± 0.77</td>
<td>96.52 ± 7.99</td>
<td>101.91 ± 4.10</td>
<td>116.25 ± 14.39</td>
</tr>
<tr>
<td>Standard/Novel-Rectangle</td>
<td>20</td>
<td>18.00 ± 2.68</td>
<td>90.05 ± 6.64</td>
<td>105.78 ± 5.55</td>
<td>137.98 ± 18.71</td>
</tr>
<tr>
<td>Standard/Subsequent Return-Cylinder</td>
<td>18</td>
<td>12.17 ± 3.76</td>
<td>100.51 ± 7.55</td>
<td>96.62 ± 2.98</td>
<td>102.05 ± 9.65</td>
</tr>
<tr>
<td>Standard/Subsequent Novel-Rectangle</td>
<td>18</td>
<td>22.17 ± 5.07</td>
<td>102.03 ± 7.26</td>
<td>100.90 ± 4.58</td>
<td>105.30 ± 8.49</td>
</tr>
<tr>
<td>Return-Cylinder/Rotation*</td>
<td>24</td>
<td>68.04 ± 4.03</td>
<td>87.47 ± 6.24</td>
<td>101.48 ± 4.03</td>
<td>92.90 ± 10.73</td>
</tr>
<tr>
<td>Rotation/Conflict-Cylinder</td>
<td>24</td>
<td>37.92 ± 5.17</td>
<td>115.01 ± 10.43</td>
<td>99.99 ± 3.19</td>
<td>126.95 ± 14.95</td>
</tr>
<tr>
<td>Rotation/Conflict-Rectangle</td>
<td>24</td>
<td>68.50 ± 3.75</td>
<td>117.50 ± 7.79</td>
<td>95.02 ± 3.40</td>
<td>137.17 ± 14.85</td>
</tr>
<tr>
<td>Novel-Rectangle Control episode/Subsequent Rectangle episodes‡</td>
<td>42</td>
<td>4.71 ± 0.86</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

The mean change in degrees of the preferred firing direction is expressed as mean ± SE. Mean percent changes for the other discharge parameters are expressed as percent of Standard session values ± SE for Return-Cylinder and Novel-Rectangle sessions, as percent of Return-Cylinder session values ± SE for Rotation sessions, and as percent of Rotations session values ± SE for Conflict-Cylinder and Conflict-Rectangle sessions. n is number of sessions. NA, not available. * Only those sessions where the shift in the cell’s preferred direction was ≥42° are reported. This value would be equal to 90° if the cell’s preferred direction shifted the same amount as the cue card was rotated. † The percent change in peak firing rate, directional firing range, and background firing rate were not determined for these episodes because there was insufficient sampling time in some episodes to obtain accurate values for these parameters.

The results from these unusual sessions mask the finding that there was actually a small difference between the cells’ preferred directions in the Novel-Rectangle and Return-Cylinder sessions. Indeed, the mean shift between Subsequent Return-Cylinder and Subsequent Novel-Rectangle sessions was 16.17 ± 2.69° (range: 0°–48°). For comparison, this value is not significantly different from the directional shifts between Return-Cylinder and Novel-Rectangle sessions for first exposures (16.80 ± 2.84°; t = 0.161, df = 36, P > 0.05). Importantly, these results indicate that even when

![Fig. 7](image-url)

FIG. 7. Subsequent exposure ATN series. These sessions recorded from an ATN HD cell were the 5th series of manipulations conducted on this animal. A: Novel-Rectangle session. B: Return-Cylinder session. C: Conflict-Rectangle session. D: Conflict-Cylinder session. For this series, unlike most other manipulations, exposure to the passageway/rectangle environment led to a 24° clockwise shift in the cell’s preferred direction in the cylinder (B). During the Conflict-Cylinder session, the cell’s preferred direction shifted to a value in between the cell’s preferred direction for the Return-Cylinder and Rotation Cylinder sessions.
there is a change in the cell’s preferred direction in the
original environment after exposure to a novel environment,
the preferred directions in two contiguous environments re-
main similar to one another.

SUMMARY OF NOVEL SESSIONS. Table 1 shows the mean
shifts in the preferred direction across different sessions for
both brain areas. In sum, the findings indicate that both
PoS and ATN HD cells maintained their directional firing
properties as the animal moved into an unfamiliar environ-
ment, although there was often a small shift in the cell’s
preferred direction. Because the animal has few, if any, land-
mark cues available for maintaining its directional orienta-
tion in the new environment, the results suggest that these
HD cells are receiving information regarding idiothetic sen-
sory cues.

Rotation cylinder sessions

Previous studies in both the PoS and the ATN have shown
that rotation of the cylinder’s cue card leads to a near-equal
shift in the preferred direction for ~90% of the recorded
HD cells (Taube 1995; Taube et al. 1990b). However, in
the present experiment, lower percentages of HD cells were
found to shift their preferred directions during the Rotation
Cylinder sessions. To determine the amount the preferred
direction shifted in the Rotation Cylinder session, the pre-
ferred directions in the Return-Cylinder and Rotation Cylin-
der sessions were compared. The Return Cylinder session
was chosen as the “control” session instead of the Standard
Cylinder session, because the Return-Cylinder session was
the animal’s last experience in the cylinder. Of the 39 Rota-
tion Cylinder sessions conducted, the cell’s preferred direc-
tion shifted by at least 42° in 25 sessions (64.1%; e.g., Figs.
3D and 4D, dotted lines). Of these 25 cases, all HD cells, except 2, showed a preferred directional shift that was less
than the 90° cue card rotation (underrotation). The mean
shift in the preferred direction for these 25 sessions was
68.04 ± 4.03° (range: 42–120°).

For comparison, in previous studies the mean shifts in the
preferred directions reported for PoS and ATN HD cells
during Rotation Cylinder sessions were 72.9 ± 3.0° and
76.74 ± 2.45°, respectively (Taube 1995; Taube et al.
1990b). The lower percentage of cells exhibiting a near-
equal shift could be attributed to the presence of the cylinder
door. Although the door was a similar shade of gray as the
cylinder wall and blended in well with the cylinder, the
door nonetheless contained two vertical edges that could be
distinguished from the cylinder wall. It is therefore probable
that the animal used these edges as distinguishing cues. In-
deed, the failure of some cells to shift their preferred direc-
tion in the Rotation Cylinder session suggests that the animal
sometimes perceived the edges of the door as a more salient
and stable orientation cue than the white cue card.

Cue conflict situation

PASSAGEWAY/RECTANGLE. The next phase of the exper-
imental sequence was conducted only for those HD cells that
rotated at least 42° in the Rotation Cylinder session, because
a shift in the cell’s preferred direction was required in order
to set up the conflict situation. If the HD cell did not shift
this minimum amount, the series was terminated and the
animal returned to its home cage. A total of 24 sessions, 13
in the PoS and 11 in the ATN, was monitored in the conflict
situation. One additional Conflict session was recorded, but
not included in the analysis because it belonged to the aber-
rant cell mentioned above; the results from this cell are
described separately below.

Immediately upon entering the passageway after the cylin-
der door was opened, all HD cells shifted their preferred
direction back to the orientation that they had originally estab-
lished in the rectangle. Each cell then maintained this shifted
preferred direction as the animal moved into the now-familiar
rectangle. Although the amount of time it took the animal to
table all directions varied across cells, the shift in the cell’s
preferred direction occurred immediately during the animal’s
first pass through the preferred direction that it had previously
established in the rectangle. For cells that had preferred direc-
tions oriented at 270° in the rectangle (i.e., preferred directions
that pointed toward the passageway entrance when the animal
was in the cylinder), the shift in the cell’s preferred direction
occurred within 1–2 s from when the animal entered the
passageway after the door was opened.

The animals were allowed to move back-and-forth be-
tween the two chambers during the conflict condition. Each
cell’s preferred direction remained stable during each epi-
sode in the rectangle (data not shown); therefore the rectan-
gle episodes were summed to determine the mean changes
in the various discharge properties. This series was then
referred to as the Conflict-Rectangle session. Figures 3C,
4C, and 6C show the responses from three different HD
cells during the Conflict-Rectangle session.

Analyses showed that there was little change in the cell’s
peak firing rate, directional firing range, and background
firing rate during the Conflict-Rectangle session (Table 1).
The mean shift in the preferred direction between the Rota-
tion Cylinder and the Conflict-Rectangle sessions was
68.50 ± 3.75° (range: 30–108°) and is similar to the mean
directional shift in the Rotation Cylinder sessions reported
above (i.e., 68.04°; Table 1). This result indicates that the
cells preferred directions returned to their originally estab-
lished preferred directions in the rectangle. In addition, the
cell’s preferred direction in the Conflict Rectangle session
was similar to the cell’s preferred direction during the Novel-
Rectangle session. Of the 24 series, 20 cells had preferred
directions in the Conflict-Rectangle session that were within
±6° of the cell’s preferred direction in the Novel-Rectangle
session. The mean difference in the preferred direction be-
 tween the Novel-Rectangle and Conflict-Rectangle sessions
was 4.13 ± 1.15° (range: 0–18°) and is similar to the mean
shift observed between the Standard Cylinder and Return-
Cylinder sessions reported above during the first exposure
sessions (i.e., 4.65°). The finding that the cell’s preferred
direction shifts back to its originally established relationship
in the passageway/rectangle indicates that when spatial in-
formation based on stable landmark cues conflicts with infor-
mation from idiothetic cues, landmark cues exert the major
influence on cell discharge.

CYLINDER. When the animal returned to the cylinder from
the rectangle, a second opportunity was present to examine
the response properties of HD cells in a cue conflict situation.
This situation occurred because the preferred direction of all HD cells shifted when the animal moved from the cylinder chamber containing the rotated cue card to the rectangle. Thus, when the animal returned to the cylinder, the cue card remained in the rotated position, and a conflict was now present between the cell’s preferred direction in the rectangle and the cell’s original relationship with the rotated cue card in the cylinder. Under these conditions, HD cells in both the PoS and the ATN did not respond as consistently as the first conflict situation where the animals moved from the “rotated cylinder” condition to the rectangle. However, individual analyses of each episode in the cylinder showed that, in general, whatever outcome occurred during the first return trip to the cylinder, that outcome also occurred on each subsequent episode in the cylinder (data not shown). Therefore all episodes in the cylinder after a trip to the rectangle were summed to create a session referred to as the Conflict-Cylinder session.

When the animal returned to the cylinder, one of three outcomes usually occurred: 1) the cell’s preferred direction shifted, such that it remained linked to the cylinder’s rotated cue card, 2) the cell’s preferred direction remained unchanged from its orientation in the rectangle; or 3) the cell’s preferred direction shifted to a new value that lay between the values for the Rotation Cylinder and Conflict-Rectangle sessions. All three outcomes were observed in both PoS and ATN HD cell populations. Upon entering the cylinder from the passageway, 6 cells shifted their preferred direction to within 12° of its established relationship with the rotated cue card (Outcome 1 above; Fig. 3D), 4 cells shifted their preferred direction by <12° (Outcome 2 above; Fig. 4D), and 14 cells shifted their preferred direction in between these values (i.e., >12° from its preferred direction in the Rotation Cylinder session and >12° from its preferred direction in the Conflict-Rectangle session, Outcome 3 above; Figs. 7D and 9D). There were no cells that shifted their preferred directions ≥66° when comparing the preferred directions between the Conflict-Rectangle and Conflict-Cylinder sessions. Furthermore, even when a cell’s preferred direction shifted by only a small amount in the Rotation Cylinder session (e.g., 42–48°), the cell’s preferred direction consistently underrotated when the animal returned to the conflict situation in the cylinder. This observation was confirmed by an analysis that computed the absolute value of the ratio

\[
\text{Shift Ratio} = \frac{\text{Amount of shift between the Rotation Cylinder versus Conflict-Cylinder sessions}}{\text{Amount of shift between the Return-Cylinder versus Rotation Cylinder sessions}}
\]

A small ratio would indicate that the cell’s preferred direction shifted back to correspond with the rotated cue card, whereas a large ratio approaching 1.0, or greater, would reflect that the cell’s preferred direction did not shift back during the Conflict-Cylinder session. An intermediate value would indicate that there was a partial shift in the cell’s preferred direction. Results showed that all PoS and ATN HD cells had shift ratios ≤1.0. The mean shift ratio from all cells was 0.530 ± 0.055 (range: 0.083–1.000). Figure 8 shows the distribution of shift ratios for both cell populations. The large variability in these shift ratios reflects the three types of outcomes described above.

The mean shift between the Rotation Cylinder and Conflict-Cylinder sessions was 37.92 ± 5.17° and was significantly different from the shifts found between either the Standard Cylinder versus Return-Cylinder first exposure sessions (mean: 4.65°; \(t = 5.82, df = 42, P < 0.0001\)) or the Return-Cylinder versus Rotation Cylinder sessions (mean: 68.04°; \(t = 5.40, df = 46, P < 0.0001\); Table 1). These findings suggest that other factors, possibly idiothetic sensory cues, continue to contribute some control over directional cell firing. Alternatively, landmark features concerning the cylinder’s doorway may also be exerting some influence on directional firing. Finally, although the preferred directional shift in the Conflict-Cylinder session varied across different cells, there was no change in the other discharge parameters (Table 1).

For two PoS series, the amount of shift in the preferred direction during the Conflict-Cylinder session varied across different episodes in the cylinder. Figure 9 shows the cell’s responses during two episodes in the cylinder from one of these series. The preferred directions between these two episodes in the cylinder differed by 24°.

**Simultaneously recorded HD cells**

Simultaneous recordings of multiple HD cells occurred in two series for PoS recordings and in five series for ATN recordings. Figure 4 shows the responses from one series of manipulations when two ATN HD cells were recorded simultaneously on the same electrode wire. In each session the HD cells shifted their preferred direction about the same amount. Similar results were observed for all pairs of recorded cells. To analyze the extent to which HD cells remained “in register” across sessions, the difference between
the preferred directions for each pair of HD cells was examined for every session. With the use of the difference in preferred directions obtained in the Standard Cylinder session as a baseline value, the amount that this difference deviated from the baseline value in the Novel, Rotation Cylinder, and Conflict sessions was determined for each pair of cells. The deviations were then averaged across series by session type. A positive deviation value would indicate that the difference between the two cells’ preferred directions was smaller than in the Standard Cylinder session; a negative deviation value would reflect a larger difference in the preferred directions. If the cells preferred directions remained exactly in register, then this value would be zero. The mean deviation values for each session type were Novel-Rectangle, 5.25 ± 3.96° (n = 8); Return-Cylinder, 5.50 ± 2.75° (n = 8); Rotation-Cylinder, −3.33 ± 9.87° (n = 6); Conflict-Rectangle, 1.60 ± 7.11° (n = 5); and Conflict-Cylinder, 1.40 ± 4.01° (n = 5). (First exposure and subsequent Novel sessions were grouped together for this analysis.) A t-test for each session type showed that these mean deviations were not significantly different from the expected population mean of zero (P > 0.05) and indicates that the preferred directions from pairs of recorded HD cells remained in register with one another throughout the series of manipulations. Furthermore, it suggests that the entire population of HD cells within one brain area are organized as a cohesive unit and that the neural inputs into these areas activates this network as an assemblage.

Multiple cells recorded within the same animal

Another important issue is whether multiple exposures to the dual-chamber apparatus had any affect on cell discharge across different Novel or Conflict sessions. To address this issue, an analysis was conducted in the seven animals (5 PoS, 2 ATN) where HD cells were monitored in more than one series within the same animal. Each of these series contained a different HD cell (i.e., none of the HD cells were monitored in >1 series). Day 1 was defined as the first day the animal was tested in the dual-chamber apparatus, and the number of days between the first series and each subsequently recorded series was determined. For the Novel-Rectangle sessions, there was no trend for cells to shift their preferred direction less over time (Table 2); this finding was true for series spanning short periods (e.g., 7 and 12 days) or series spanning longer intervals (e.g., 53 and 223 days). These results indicate that the HD cell’s “accuracy” (defined as the cell’s propensity to maintain the same preferred direction in the rectangle as in the cylinder) did not improve over time as a result of increased exposure to the novel chamber, at least under the short-term conditions of the present experiments. In contrast, for the Conflict sessions, there was a progressive decrease in the shift ratio from the first to the last series in the three of four animals in Table 2. Amount of shift in the preferred direction during the Novel-Rectangle and Return-Cylinder sessions for multiple series recorded within one animal

<table>
<thead>
<tr>
<th>Animal 1: Postsubiculum</th>
<th>Testing Day</th>
<th>Novel Rectangle, deg</th>
<th>Return Cylinder, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell 1</td>
<td>1</td>
<td>−12</td>
<td>−12</td>
</tr>
<tr>
<td>Cell 2</td>
<td>15</td>
<td>−6</td>
<td>−12</td>
</tr>
<tr>
<td>Cell 3</td>
<td>25</td>
<td>−6</td>
<td>6</td>
</tr>
<tr>
<td>Cell 4</td>
<td>35</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Cell 5</td>
<td>41</td>
<td>−12</td>
<td>6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Animal 2: Postsubiculum</th>
<th>Testing Day</th>
<th>Novel Rectangle, deg</th>
<th>Return Cylinder, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell 1a</td>
<td>1</td>
<td>−36</td>
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which sufficient data were available (from Table 2: animal 1: 0.50, 0.64, 0.50, 0.64; animal 2: 0.71, 0.50; animal 3: 0.71, 0.33, 0.29; animal 6: 1.0, 0.67, 0.54). It is possible that animals 2, 3, and 6 were learning that the cylinder's cue card was not a reliable landmark. Thus each subsequent Conflict series led to a smaller shift in the cell's preferred direction when the animal returned from the passageway/rectangle to the rotated cylinder condition.

Aberrant cell responses

The pattern of results from one ATN-recorded HD cell was different from the sessions discussed above. This “aberrant cell” was the only HD cell recorded in this animal, and the results are shown in Figure 10. When the animal was in the passageway after leaving the cylinder, there was only a 6° CW shift in the cell’s preferred direction. However, upon entering the rectangle the preferred direction shifted 78° CCW with respect to the Standard Cylinder session. It is important to note that the cue card in the rectangle is positioned 90° CCW compared with the cylinder’s cue card. Thus this cell appeared to be maintaining a similar relationship to the rectangle’s cue card as it did to the cylinder’s cue card. When the animal entered the passageway again upon its return to the cylinder, the cell’s preferred direction remained shifted 78° CCW. However, when the animal entered the cylinder again, the preferred direction shifted back to its originally established preferred direction in the cylinder (0° shift in the preferred direction between the Standard Cylinder and Return-Cylinder sessions). This pattern of shifts in the preferred direction continued for seven trips, as the animal moved back-and-forth between the two chambers. Thus this cell’s response appeared dependent on the position of the cue card in each environment, and when the animal was in the passageway (where no cue card was present), the cell’s preferred direction remained similar to the response in the chamber it just left.
This cell shifted its preferred direction $72^\circ$ in the Rotation Cylinder session. Because the cue card was rotated $90^\circ$ CCW, it was now in the same directional orientation with respect to the recording room as was the rectangle’s cue card. Thus, when the cylinder door was opened and the animal moved into the passageway and continued into the rectangle, there was little change in the cell’s preferred direction. The preferred directional shift between the Rotation Cylinder and Conflict-Rectangle sessions was $6^\circ$. Similarly there was little change in the preferred direction when the animal returned to the cylinder containing the rotated cue card. The shift in the preferred direction between the Rotation Cylinder and Conflict-Cylinder sessions was $0^\circ$. As with the other series described above, there was no change in the cell’s peak firing rate, directional firing range, or background firing rate throughout all the recording sessions for this cell.

**DISCUSSION**

The major findings of the present study were 1) the discharge properties and directional selectivity of HD cells in the PoS and ATN remained relatively stable as an animal moved into a novel, unfamiliar environment, and 2) when presented with a situation where the landmark cues in one environment conflicted with the landmark cues in a second environment, cell discharge parameters remained stable, but the HD cell’s preferred direction showed varied responses that were dependent on the type of conflict situation present. The implications of each of these findings are discussed in detail below.

**Use of sensory cues in a novel environment**

The results showed that cell discharge was maintained with the same peak firing rate, directional firing range, and background firing rate when the animal entered the new environment. In addition, there were only small shifts (6–30°) in the preferred direction in the novel environment (passageway/rectangle). What factors or inputs maintain this cell discharge? There are two possibilities. First, although there are no familiar landmark cues within the animal’s immediate vicinity, it could be using secondary cues in the recording room (e.g., the video camera). Even though we took precautions to minimize the use of secondary room cues, it is nearly impossible to eliminate them entirely. Second, the animal could be monitoring sensory information from idiothetic sources and then using this information to update its current directional heading.

We argue that the potential secondary landmark cues in the recording room contribute minimally to the observed findings for three reasons. First, if the animals were relying on secondary landmark cues for orientation, then the mean error associated with the preferred directional shift in the rectangle ($18.0^\circ$) should have been similar to the mean error between two Standard Cylinder sessions ($4.65^\circ$), because the secondary room cues are the same for both environments. However, the error associated with the rectangle was greater and shows that either the animals were not relying on secondary cues for orientation, or that they could not detect their orientation with respect to them very well. Second, previous experiments have shown that when an animal is placed in a rectangular enclosure similar to the one used in the present study, there was no trend for cells to show similar preferred directions as in the cylinder (Taube et al. 1990b). Indeed, in this previous study $80\%$ of the cells shifted their preferred direction by at least $48^\circ$. Furthermore, these cells shifted their preferred direction even though the rectangle’s cue card was positioned in the same relationship to the recording room as the cue card in the cylinder. These results suggested that the animals treated the rectangle as a different environment, because if they were using secondary room cues, one would have expected only a small, if any, shift in the cell’s preferred direction. The rectangle in the present study was a similar size and color as in the previous study. In addition, the room dimensions, curtain surroundings, and the types of electrical equipment in the room were also similar. Thus it is probable that our animals also treated the rectangle as a novel environment, and one would expect to observe preferred directional shifts of $\geq 48^\circ$ in the rectangle. However, in contrast to the experiments where the animals were placed directly in the rectangle, our results in the dual-chamber apparatus showed that almost all the cells shifted their preferred directions by $< 48^\circ$. Therefore the smaller shifts observed in the present experiments need to be accounted for by factors other than secondary room cues.

Third, previous experiments in which an animal has been introduced into the cylinder without the cue card showed that the mean change in the cell’s preferred direction was $43.8$ and $75.2^\circ$ for HD cells in the PoS and ATN, respectively (Goodridge and Taube 1995). Although the directional shifts reported in their study were not randomly distributed over $360^\circ$, if animals were using secondary room cues consistently and accurately, then these mean shifts should be closer to $0^\circ$. Both of these mean shifts are significantly larger than the mean shifts found for the Novel-Rectangle sessions ($18.0^\circ$). Thus the directional shifts in the Novel-Rectangle sessions were smaller than the shifts during the No Cue Card experiments, but larger than the shifts observed for the Return-Cylinder sessions or reported between two Standard Cylinder sessions (PoS: $6.6^\circ$, Taube et al. 1990b; ATN: $4.7^\circ$, Taube 1995). We suggest that these differences are attributed to the notion that the cells used idiothetic sensory cues to maintain their directional orientation during the Novel-Rectangle sessions, but the nature of the experimental conditions in the No Cue Card sessions (the animals were brought into the recording room in an opaque box that was rotated several times and moved translationally before the animal was placed in the cylinder) precluded the cells from using idiothetic information to maintain their preferred directions without the cue card.

Taken together, we conclude that HD cell activity was maintained in the passageway/rectangle with a similar preferred direction as in the cylinder because the cells were receiving information from idiothetic sensory cues. Unfortunately, our experiments do not distinguish which types of idiothetic sensory cues the animals were using to maintain their sense of orientation. The cells may have been monitoring vestibular, proprioceptive, motor efferent copy, or optic flow cues, or all four cue types simultaneously. This interpretation of the results does not imply that the animals were inattentive to secondary room cues, but rather, they did not rely on them for orientation under the present experimental conditions.
Conditions. Clearly, an animal must synthesize information from many different sources to form a representation of its spatial orientation. Our results, however, indicate that the salience and use of secondary room cues in determining the animal's directional orientation were minimal and that the cells relied on idiothetic cues.

Our findings also have implications on the nature of the HD cell correlate. In particular, they provide further support for the notion that HD cells discharge in relation to the animal's perceived directional heading. On the basis of previous studies (Taube 1995; Taube et al. 1990a, b), it could be argued that HD cells discharge in relation to something in the animal's view that is associated with a particular head direction. Although previous studies have shown that HD cell discharge is maintained when the cue is removed (Taube et al. 1990b) or in the dark (Chen et al. 1994b; Mizumori and Williams 1993; Taube et al. 1988), it might be argued that cell discharge persisted because of the animal's memory of the cue. However, the present findings argue against these notions because they show that HD cells continued to discharge in a similar direction when the animal moved into an environment where the landmark cues and views were completely different.

Consequences of relying on idiothetic cues for spatial orientation

Although the shifts in the preferred directions were small when the animal moved to the novel environment, the shifts were significantly different from the shifts observed between either the Standard Cylinder versus Return-Cylinder session or the Novel-Rectangle versus Conflict-Rectangle sessions. Thus it is unlikely that these shifts are attributable to variability between different recording sessions. These small shifts are probably due to the nature of processing idiothetic sensory information. Whereas information about an organism's spatial orientation using landmark cues remains stable and reliable over time, idiothetic information is constructed in an iterative manner and is thus subject to the accumulation of errors. Therefore one would expect a larger variability or shift in the preferred direction when an animal is relying entirely on idiothetic cues for updating its directional orientation. Indeed, larger errors are observed in behavioral experiments conducted on humans when they must rely entirely on idiothetic cues for orientation (Lee and Thompson 1982). Because the path length was short and the complexity of the passageway was relatively mild, the animals were only required to monitor internal cues over a short time span in order to accurately maintain its sense of orientation. We would predict, however, that if the demands of monitoring idiothetic cues were to increase, by increasing the length and complexity of the pathway between the cylinder and rectangle, larger shifts in the cell's preferred direction would be observed in the rectangle environment.

Once the animal was exposed to the passageway/rectangle, it had the opportunity to identify new landmarks in its surroundings and establish its spatial orientation with respect to them. Consequently, subsequent trips to the rectangle chamber did not lead to any further shifts in the cell's preferred direction. Indeed, if the cell shifted by a particular amount during the animal's first trip to the rectangle, it shifted by a similar amount in subsequent trips to the rectangle.

Hippocampal place cells and a novel environment

Our results are similar to a study by Hill (1978) reporting that place cells showed location-specific discharge during the first few moments in a novel environment, but they differ somewhat from findings of Wilson and McNaughton (1993). The latter study showed that some place cells (25%) required the animal to be in the apparatus for a period of time before location-specific discharge became apparent. However, our results are similar to other aspects of the Wilson and McNaughton study. They reported that the hippocampal encoding of a familiar environment by place cells was not altered by the animal's experience in the novel environment. Similarly, because the HD cell's preferred direction did not change between the Standard Cylinder and Return-Cylinder sessions, the encoding of directional heading in the familiar environment was not affected by the animal's exposure to new surroundings. This conclusion must be regarded as tentative, however, when considered with the results from the three series in the ATN Subsequent-Novel segments that showed significant changes in the cell's preferred direction after the animal's experience in the passageway/rectangle.

Cue conflict situation

The present study examined HD cell responses in two different situations where the sensory cues regarding the animal's spatial orientation were in conflict. The conditions of the cue conflicts in these two situations have some similarities and differences. In both situations, there was a conflict between the spatial information contained in the landmarks of the two environments. In the first situation (Rotation Cylinder vs. Conflict-Rectangle), the conflict existed between the orientation information regarding the cylinder's rotated cue card and the landmarks in the passageway/rectangle (e.g., shapes of the walls, rectangle cue card, and doorway). The spatial information of these landmark cues were also in conflict in the second situation (Conflict-Rectangle vs. Conflict-Cylinder). The two situations were also similar in that the animal had idiothetic cue information available as it moved into each conflict condition. The two situations differed, however, in that when the animal returned to the rotated cue card environment, it also had available landmark information regarding the opened doorway. This landmark information about the doorway is consistent with the spatial information concerning other landmark features in the passageway/rectangle.

The results of the first conflict situation showed that the cell's preferred direction always shifted to correspond with the landmark cues of the passageway/rectangle. The shift in the cell's preferred direction occurred immediately when the animal entered the passageway, whereas the other discharge properties remained unchanged throughout the con-
Conflict session. These findings indicate that the spatial information from the landmark cues of the passageway/rectangle were sufficiently salient enough to override the animal's idiothetic sensory cues as it moved into the passageway/rectangle. In contrast, the results of the second conflict situation were more variable, and three outcomes were observed. In two of the outcomes, the cell's preferred direction remained linked to the landmarks of one of the two environments. In the third outcome the cell's preferred direction shifted to a new value that was in between the cell's preferred directions for the rectangle and rotated cylinder environments. The type of response observed may depend on the extent to which the animal perceives the landmark cues of a particular environment as stable (Knierim et al. 1995). If the cues are perceived as unstable, which most likely occurred when the animal returned to the cylinder with the rotated cue card, the animal may rely on idiothetic cues or other stable landmarks, such as the doorway, for determining its directional heading.

For instances when the animal returned to the cylinder and the cell's preferred direction shifted to remain linked to the rotated cue card, the results are similar to the Conflict-Rectangle situation and indicate that the spatial information regarding the rotated cue card could predominate over idiothetic sensory cues, as well as any landmark information concerning the cylinder's doorway. In this situation, the animal must have perceived the cylinder's cue card as a stable landmark. There were instances, however, where either the landmark information concerning the cylinder's doorway or idiothetic sensory information exerted more influence over the cell's preferred direction than the rotated cue card, because there were cases in which the cell's preferred direction remained unchanged as the animal entered the cylinder with the rotated cue card. Although the use of idiothetic cues would explain why the preferred directions did not shift back in the Conflict Cylinder sessions, we consider it more likely that the animal perceived the cue card as an unstable landmark and instead used the doorway as its reference point. First, the doorway can be a very salient orientation cue as suggested by the low percentage of cells that shifted their preferred direction during the Rotation Cylinder session. Second, the doorway would be even more efficacious as a cue when it was opened than when it was closed during the Rotation Cylinder session. Third, the doorway could be considered a more stable and reliable cue than the cylinder's cue card because it always maintained a consistent relationship with other spatial features of the chamber. Taken together, when the cell's preferred direction did not remain linked to the cue card in the Conflict Cylinder sessions, its not possible to distinguish whether idiothetic cues or the doorway were exerting more control over the cell's preferred direction.

Although the cell's preferred direction usually remained linked to the salient visual cues in one of the two environments, there were many occasions (Figs. 7D and 9D) in which the cell's preferred direction shifted to a value in between the preferred directions of the two environments (Outcome 3). On these occasions, it appears that neither the rotated cue card, the cylinder's doorway, nor idiothetic sensory cues were efficacious enough to drive the cell's preferred direction to a particular value. In this situation it appeared that multiple cues were affecting cell discharge. These results are different from behavioral studies in gerbils (Collett et al. 1986) and primates (Salzman and Newsome 1994), in which a 'winner-take-all' process appears to be more operative. For example, Collett and colleagues monitored where gerbils searched for buried food after the landmark array, which initially denoted the buried food, had been expanded by a scaling factor of two. They reported that the gerbils confined their search to two locations, with each location corresponding to the correct position and direction relative to one of the landmarks. A location in between the two landmarks, representing the average of the two positions, was never searched and suggests that the decision on where to search was a winner-take-all process.

Taken together, the results in both conflict situations suggest that, although animals have information regarding idiothetic cues available to them, information from stable landmark cues, particularly visual ones, predominates over sensory information obtained from idiothetic cues. Thus it would appear that PoS and ATN HD cells initially use idiothetic cues to monitor their spatial orientation in a novel environment, but once they become familiar with the new environment, the use of landmark cues becomes the dominant input in exerting control over the cell's preferred direction as long as the animal perceives particular landmarks as stable cues. These conclusions are similar to those recently reported by Goodridge and Taube (1995) in a series of experiments that monitored HD cell responses when the salient landmark cue was reintroduced into the environment after its initial absence. In addition, even though different cells responded differently in the Conflict-Cylinder sessions, our results do not support the notion that there are different types of HD cells within a particular brain area. When pairs of HD cells were recorded simultaneously, both cells always shifted similar amounts in the Conflict-Cylinder sessions. If there were different classes of HD cells within one brain area, then one would expect to find differences in the preferred directional shifts in the Conflict-Cylinder session. Finally, the finding that the preferred direction shifts abruptly, rather than in steps, as the animal moves from one chamber to the next is consistent with models proposed for navigation showing that landmark cues can abruptly shift (or reset) the animal's perceived directional heading during transition states (McNaughton et al. 1991; Touretzky et al. 1994).

Comparisons with other behavioral and recording studies

Evidence that rodents preferentially use landmark cues compared with idiothetic cues was demonstrated in a study by Fruenne et al. (1985) that examined the effects of cue conflicts on a golden hamster's behavior while it performed a spatial task. When hoarding food under dark conditions, hamsters returned to their nest through path integration by monitoring idiothetic cues during their outbound journey. If, however, familiar landmark cues were available to the hamster, they tended to use them when returning to the nest, even under conditions where the landmark cues were moved to a different position and the hamsters returned to the wrong place. Although this study does not distinguish which idiothetic sensory cues the hamsters were monitoring during their outbound journey, it nonetheless shows that hamsters
prefer to use landmark information, rather than idiothetic sensory information, when both are available. This finding is similar to our results for HD cells in the Cue Conflict situation. Preferential use of landmark information is adaptive from an evolutionary standpoint because navigation through the use of idiothetic cues is subject to cumulative errors, whereas landmark navigation does not have this drawback.

The results from our studies are comparable with other manipulations with HD cells in the PoS and other brain areas. McNaughton et al. (1991) reported in a preliminary study that the preferred direction of PoS HD cells did not shift when the box they were in was rotated quickly. The preferred direction did shift, however, when the box was rotated slowly below the vestibular threshold. This result suggests that HD cells can use vestibular input to determine their preferred direction. In related studies in the ATN (Taube 1995) and retrosplenial cortex (Chen et al. 1994a), some HD cells were shown to require active movement in order for directional firing to be present. For example, the majority of ATN HD cells ceased discharging when the animal was restrained in the experimenter’s hands and passively rotated. Similarly, many directionally tuned cells in the retrosplenial cortical areas lost their directional firing characteristics when the animal was placed on a turntable and then rotated. Taken together, these studies indicate the importance of vestibular and motor inputs in enabling HD cell discharge. In another study, Mizumori and Williams (1993) reported that LDN HD cells were not directional when the animal was initially placed in a darkened room, but required ~60 s of exposure to the lit room before directional activity became apparent. This finding is not in agreement with our results showing that the cell’s preferred direction shifted abruptly during the Novel and Conflict sessions and did not require time to establish its preferred orientation. The reasons for this difference are unclear, although it is possible that the involvement of different brain areas may underlie these differences.

Conclusions

In summary, our results show that HD cells in the PoS and ATN receive information from both landmark and idiothetic sensory cues. It will be important to determine where in the brain these different sensory signals first converge and how this integration is accomplished at a neuronal level. Although it is probable that landmark information enters the hippocampal formation through cortical pathways via the entorhinal cortex, it is unclear how idiothetic information reaches the limbic system. Given the presence of reciprocal connections between the PoS and ATN (Shibata 1993; van Groen and Wyss 1990, 1992) and polysynaptic pathways from subcortical areas to the ATN (Allen and Hopkins 1989; Seki and Zyo 1984), it is unclear whether idiothetic information reaches the limbic system through subcortical or cortical pathways. Interestingly, recent lesion studies have shown the absence of HD cell activity in the PoS following lesions of the ATN (Goodridge and Taube 1993) and suggests that the HD signal in the PoS is dependent on intact cells in the ATN. Nonetheless, whatever route these sensory cues use to project onto limbic system structures, our results show that when both cue types are available, HD cells appear to be preferentially driven by the landmark cues.

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