Maintenance of Rat Head Direction Cell Firing During Locomotion in the Vertical Plane

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Stackman, Robert W., Matthew L. Tullman, and Jeffrey S. Taube. Maintenance of rat head direction cell firing during locomotion in the vertical plane. J. Neurophysiol. 83: 393–405, 2000. Previous studies have identified a subset of neurons in the rat anterodorsal thalamus (ADN) that encode head direction (HD) in absolute space and may be involved in navigation. These HD cells discharge selectively when the rat points its head in a specific direction (the preferred firing direction) in the horizontal plane. HD cells are typically recorded during free movement about a single horizontal surface. The current experiment examined how HD cell firing was influenced by locomotion in the vertical plane and 2) locomotion on two different horizontal surfaces separated in height. Rats were trained in a cylindrical enclosure containing a single polarizing cue card attached to the cylinder wall, covering ~100° of arc. The enclosure contained two horizontal surfaces: the cylinder floor and an annulus around the cylinder top 76 cm above the floor. A 90° vertical mesh ladder that could be affixed at any angular position on the cylinder wall allowed the rats to locomote back and forth between the two horizontal surfaces. Rats were trained to retrieve food pellets on the cylinder floor as well as climb the mesh ladder to retrieve food pellets on the annulus. HD cell activity was monitored as the rat traversed the horizontal and vertical surfaces of the apparatus. When the angular position of the mesh corresponded to the cell’s preferred firing direction, the HD cells maintained their peak discharge rate as the rat climbed up or down the mesh. When the mesh was positioned 90° or 270° from the preferred firing direction, HD cells exhibited background firing rates during climbing up or down the mesh. While preferred firing directions were maintained on the annulus as compared with the annulus, HD cell activity was monitored as the rat traversed the horizontal and vertical surfaces of the apparatus. When the angular position of the mesh corresponded to the cell’s preferred firing direction, the HD cells maintained their peak discharge rate as the rat climbed up the mesh, but did not fire when the rat climbed down the mesh. In contrast, when the mesh was positioned 180° opposite the preferred firing direction, HD cells did not fire when the rat climbed up the mesh, but exhibited maximal firing when the rat climbed down the mesh. When the mesh was placed 90 or 270° from the preferred firing direction, HD cells exhibited background firing rates during climbing up or down the mesh. While preferred firing directions were maintained between the two horizontal surfaces, peak firing rate increased significantly (~30%) on the annulus as compared with the cylinder floor. These data demonstrate that HD cells continue to discharge in the vertical plane if the vertical locomotion began with the rat’s orientation corresponding to the preferred firing direction. One model consistent with these data are that HD cells define the horizontal reference frame as the animal’s plane of locomotion. Further, we propose that HD cell firing, as viewed within a three-dimensional coordinate system, can be characterized as the surface of a hemitorus.

INTRODUCTION

Accurate spatial orientation and navigation require the organism to estimate its current location and directional heading in three-dimensional space. This function is likely influenced by at least two distinct neural systems. Navigation is thought to involve the continual monitoring of internal, or idiothetic, cues (e.g., consequences of the animal’s movements: vestibular, proprioceptive, motor efference copy or motor corollary discharge, and optic/auditory flow), together with occasional reference to familiar external sensory cues or landmarks to correct for error accumulation over time. For example, path integration (or movement through a novel environment) involves an initial referral to a landmark, to define one’s initial orientation, and then navigating solely by internal cues (Barlow 1964; Berthoz et al. 1995; Gallistel 1990). Accurate path integration is thought to require the monitoring of vestibular signals (i.e., angular and linear acceleration cues) (Etienne et al. 1988; Mittelstaedt and Glasauer 1991; Mittelstaedt and Mittelstaedt 1980), as lesions of the vestibular system impair spatial navigation (Matthews et al. 1989; Miller et al. 1983; Össenkopf and Hargreaves 1993; Potegal et al. 1977).

Allocentric representations of spatial location and direction are thought to be processed by an integrated multimodal neural circuit within the limbic system (McNaughton et al. 1995). This notion is supported by evidence of two neurophysiologically correlates of allocentric space found in limbic brain regions of the freely moving rat. Principal neurons of hippocampus discharge in accordance with the spatial location of the rat independent of directional heading (Muller et al. 1987; O’Keefe and Dostrovsky 1971), while head direction (HD) cells discharge as a function of the rat’s head direction in the horizontal plane, independent of current location (Taube et al. 1990a; for a review see Taube 1998). The head orientation at which a HD cell exhibits maximal firing is called the preferred firing direction. The activity of the entire HD cell population is believed to represent the moment-to-moment directional heading of the animal. HD cells have been recorded in several regions of the rat brain including postsubiculum (PoS) (Taube et al. 1990a), anterodorsal thalamic nuclei (ADN) (Taube 1995), lateral dorsal thalamic nuclei (Mizumori and Williams 1993), retrosplenial and medial prestripate cortex (Chen et al. 1994), striatum (Mizumori and Cooper 1995; Wiener 1993), and lateral mammillary nuclei (Stackman and Taube 1998).

Converging evidence indicates that manipulation of environmental or idiothetic cues influences the preferred firing directions of HD cells (Blair and Sharp 1996; Goodridge and Taube 1995; Knierim et al. 1995; Taube and Burton 1995; Taube et al. 1990b; for a review see Taube et al. 1996). These studies indicate that familiar landmark cues exert preferential control over HD cell activity. Taube and Burton (1995) demonstrated that the preferred firing directions of HD cells remain stable when the rat self-locomotes into a novel environment, suggesting that idiothetic cues maintain the preferred firing directions.
in the absence of familiar external cues. The integration of angular velocity information from the vestibular system may be necessary for maintaining central representations of directional heading (Blair and Sharp 1996; McNaughton et al. 1995), under circumstances in which familiar external landmark cues are not available. However, lesions of the vestibular apparatus disrupt HD cell firing in the ADN (Stackman and Taube 1997), regardless of the presence of the familiar landmark cue. Empirical data also suggest that motor efference copy signals influence place cell and HD cell activity (Foster et al. 1989; Taube 1995; Taube et al. 1996). Together, these data suggest that internal cues play an essential role in the generation and maintenance of central representations of spatial orientation.

Currently, all empirical studies of HD cells have been conducted while the rat freely moved about the horizontal surface of enclosures and mazes. However, in the natural setting, efficient rodent navigation within the rat burrow requires the integration of movements in both the horizontal and vertical planes (Calhoun 1963). Therefore the neural mechanisms responsible for processing representations of allocentric spatial orientation must be able to maintain accuracy whether the organism is moving in the horizontal or vertical planes. Interestingly, Moghaddam and colleagues (1996) demonstrated that rats in a featureless, enclosed arena could accurately navigate to a goal location on the arena floor using the inclination of the floor surface as a primary cue. Although qualitative assessments have determined that moderate head pitch (head motion along the anterior-posterior axis) do not disrupt HD cell firing in the horizontal plane (Stackman and Taube 1998; Taube et al. 1990a), it is important to determine how the horizontal reference frame is defined by the HD cell, and whether HD cell firing is maintained when the rat is oriented vertically.

Therefore we examined the discharge properties of HD cells during locomotion in the vertical plane and in different horizontal planes within the same environment. Rats were trained to climb a 90° vertical mesh ladder from the floor of a cylindrical apparatus to a narrow annulus above the cylinder floor. We monitored ADN and PoS HD cell activity during locomotion in the vertical plane as the rat climbed up and down the ladder and as the rats moved freely about both horizontal surfaces. Each HD cell was recorded as the rat locomoted in the vertical plane, with the mesh ladder centered at specific positions relative to the cell’s preferred firing direction. This protocol enabled an assessment of HD cell activity as the rat moved one horizontal plane oriented in accordance with the preferred firing direction of the recorded cell or at the three cardinal directions orthogonal to the preferred firing direction.

METHODS

Subjects and vertical plane locomotion training

Subjects were five female Long-Evans rats, weighing 250–300 g at the beginning of the experiment. Rats were maintained on a food-restricted diet (15–20 g/day) and housed separately in suspended wire mesh cages. Tap water was available ad libitum. All training, unit screening, and recording occurred during sessions in which the rats foraged for food pellets in a cylindrical apparatus (74 cm high, 76 cm diameter; see Fig. 1A). Mounted to the top of the cylinder was a...
12.7-cm-wide rim, or annulus with 4 food wells equally spaced apart on the annulus surface. The annulus did not contain inside or outside walls, but was wide enough to enable rats to change their direction of movement once on it. The cylinder and annulus were constructed of wood and painted gray. Access to the annulus was provided by a floor-to-annulus vertical wire mesh “ladder” (74 cm high, 29 cm wide) placed onto the inside cylinder wall. The mesh ladder was cut from galvanized steel mesh (1.27 cm by 1.27 cm grid) and formed to fit tightly against the wall, thus allowing a 90° vertical transit up the cylinder wall. The angular position of the mesh was not fixed and could be placed anywhere on the inside surface of the cylinder wall. Finally, a white sheet of cardboard attached to the inside wall of the cylinder and which extended from the floor to the top of the cylinder, served as the only polarizing, directional visual landmark. This cue card was positioned at 3 o’clock (see Fig. 1), and occupied an area of 100° of arc. Black floor-to-ceiling curtains formed a featureless circular enclosure (2 m diameter) surrounding the cylinder. Room illumination was provided by four uniformly arranged overhead DC lamps. A color video camera (Sony XC-711) was centered above the cylinder 3 m from the floor surface. The cylinder was placed on a sheet of gray photographic backdrop paper, which was replaced after each recording session. A stool was placed inside the curtain enclosure, which the experimenter used while connecting and disconnecting the rat from the recording cable. The stool was out of the rat’s view while in the cylinder, but could be viewed by the rat while moving about on the annulus. The position of the stool within the curtained enclosure varied, as an attempt was made to vary the position at which the rat was released into the cylinder during each recording session.

Initially, rats received habituation trials in the cylindrical apparatus without the mesh or annulus present. Rats were brought from the colony room into the curtained enclosure in a corrugated cardboard box (~30 X 30 cm box); no attempt was made to disorient the rats before their release into the cylinder. Rats were placed into the cylinder in pairs and received at least five habituation trials (1 trial/day) during which food pellets (20 mg, PJ Noyes, Lancaster, NH) were thrown randomly into the cylinder from outside the black curtain. By the completion of training, rats engaged in nearly continuous food pellet search behavior over the entire floor of the cylinder.

After the habituation trials, rats were trained by successive approximation to climb the mesh, from the cylinder floor to the cylinder annulus, to retrieve food pellets from the annulus cups. During training, the white cue card was always present, and its position was always fixed at the 3 o’clock position. The angular position of the mesh was changed every trial to explicitly reduce the potential association of the mesh with a spatial location and its use as an orientation cue. The mesh ladder required the rat to navigate in a vertical plane that was 90° orthogonal to the cylinder floor and annulus. During the initial training trials (1 trial/day), a circular wooden platform (64 cm high) was placed on the cylinder floor. With the platform at this height, the rats were only required to climb 10 cm to access the annulus food cups. Several food pellets were placed into the food cups of the annulus and scattered on the platform surface. The rats were placed on the platform in pairs and allowed to move about freely over the entire surface of the apparatus for 15 min. Generally, after two trials, rats habituated to the apparatus and demonstrated free movement back and forth between the platform floor and annulus. Over successive trials, the floor platform was lowered to encourage the rats to climb to greater heights to access the annulus. The platform was first lowered to 54 cm above the floor, then 25 cm above the floor, after which the platform was removed and the rats were trained to climb the full length of the mesh (76 cm) to access the annulus. During the final training trials, the annulus food cups were not rebaited until the rats returned to the cylinder floor. The criterion for training completion was that all rats readily engaged in climbing up and down the complete length of the mesh, and consumed food pellets from the annulus food cups. On completion of training, rats were implanted with driveable 10-wire microelectrode arrays directed at the ADN or PoS.

**Electrode implantation.**

Electrode construction and implantation techniques used were similar to that described previously (Taube 1995). Briefly, each electrode array consisted of a bundle of 10, 25-μm-diam nichrome wires (California Fine Wire, Grover City, CA) insulated except at the tips. The wire bundle was passed through a 26-gauge stainless steel cannula and each wire attached to a modified 11-pin Augat connector. The electrode array could be advanced in the dorsoventral plane with three screws attached to the electrode’s acrylic base (Kubie 1984). On habituation to the cylindrical apparatus and adequate foraging behavior, each rat was anesthetized with a ketamine-xylazine mixture (2 ml/kg im) and stereotaxically implanted with an electrode array directed at either the PoS or ADN. Electrode coordinates, with respect to bregma, were as follows: PoS: anterior/posterior −6.6 mm, medial/lateral +2.8 mm, ventral 1.6 mm from the cortical surface; ADN: anterior/posterior −1.4 mm, medial/lateral +1.3 mm, ventral 3.7 mm from the cortical surface (Paxinos and Watson 1998). Jewelers screws, placed in the skull plates over the cerebellar cortex, parietal cortex, and frontal cortex, and dental cement anchored the electrode assembly in place. All procedures were conducted according to an institutionally approved animal care protocol. All surgical procedures were conducted under sterile conditions, and the rats were allowed a 1-wk postoperative recovery interval before we commenced single-unit screening.

**Isolation and recording of head direction cell activity.**

After recovery from surgery, activity from each microelectrode wire was assessed during daily unit screening sessions while the rat foraged for food pellets in the cylinder. During screening sessions, the mesh and annulus were not present. The electrode wires were advanced over several weeks while screening for HD cell waveforms that were of acceptable amplitude for isolation from background electrical noise. Each rat was transported into the screening area from the animal colony room in the corrugated cardboard enclosure; again, no attempt was made to disorient the rats before their release into the cylinder. The cardboard box was placed on the floor inside the curtained enclosure next to the cylinder. A recording cable was attached to the implanted electrode while the rat was held gently in a towel. The rat was then released into the cylinder apparatus from a start position that varied daily in a pseudorandom manner. Unit activity was analyzed using procedures similar to those previously described (Taube 1995; Taube et al. 1990a). Briefly, electrical signals were passed through a field-effect transistor (FET) (1 FET/electrode) in a source-follower configuration, through an overhead commutator (Biela Idea Development, Anaheim, CA), amplified (Grass Instruments P5 Series, West Warwick, RI), band-passed filtered (300–10,000 Hz, 3 dB/octave; Peavey Electronics PME8, Meridian, MS), and passed through a series of window discriminators (Bak Electronics Model DD14-1, Germantown, MD). The resultant signal was then displayed on an oscilloscope (Tektronix Model 2214, Beaumont, OR). Electrode activity was monitored while observing the rat’s behavior on a video monitor with a camera mounted 3 m above the cylinder floor. If HD cell activity was not found, the electrodes were advanced 25–50 μm further into the ADN or PoS, and the activity was monitored again the next day. Screening for HD cells occurred over the course of several weeks.

When the waveform of a single cell could be sufficiently isolated from background electrical noise, two light-emitting diodes (LEDs) were added to the recording cable. The LED arrangement used in the present study was a modification of that used previously (Taube 1990a). For the present study, the headstage included a red LED positioned just posterior to the headstage, and a green LED was...
positioned over the rat’s back. The LEDs were spaced 5.5 cm apart along the rostral/caudal axis of the rat. The x,y-coordinates of the LEDs were determined at 60 Hz by a video-tracking system (Eburtronics, Brooklyn, NY). A wide-angle video lens (8.5 mm) was used to monitor the rat’s movements in the cylinder and on the annulus of the apparatus. During recording sessions the LED coordinates and neuronal discharges were sampled at 60 Hz and acquired by a data acquisition interface board (National Instruments DIO-96, Austin, TX) in a personal computer (Apple Macintosh Quadra 840AV, Cupertino, CA). Data were stored for subsequent off-line analyses using programs written with LabView software (National Instruments, Austin, TX). For the present data, the rat’s head position was defined as the location of the red LED. During recording sessions, white noise was broadcast through a ceiling speaker centered above the cylinder to mask uncontrolled auditory cues.

**Vertical plane locomotion/recording protocol**

The protocol used to record each HD cell during vertical plane locomotion comprised at least five 8-min recording sessions and is illustrated in Fig. 1B. Throughout all recording sessions, the cue card remained in the cylinder at the 3 o’clock position (standard position). A second charge-coupled device (CCD) color video camera was attached to a tripod positioned inside the curtained enclosure and oriented to receive the video image of the 90° vertical mesh ladder from floor-to-annulus (i.e., orthogonal to the overhead ceiling camera). An experimenter-controlled video source switching box (Electronics Shop, Dartmouth College, Hanover, NH) enabled the video signal that was fed to the video-tracking system to be manually switched between the overhead camera and the tripod-mounted camera. Generally, horizontal movements of the rat on the cylinder floor and annulus were acquired by the overhead camera, while vertical movements on the mesh (i.e., climbing up and climbing down) were acquired by the second camera. The video output from the selected camera, along with the cell’s activity, was simultaneously recorded during each recording session. Each HD cell was recorded during an initial 8-min session as the rat foraged for food pellets thrown randomly into the cylinder. The mesh was not present during this initial recording session. On completion of the initial recording session, the rat was removed from the cylinder and placed into the cardboard enclosure. The HD cell’s preferred firing direction was determined, and the mesh was placed into the cylinder centered at the position corresponding to the cell’s preferred firing direction. This recording session will be referred to as the Mesh 0° session (i.e., the mesh ladder positioned 0° from the cell’s preferred firing direction). Several food pellets were placed into each of the four food cups on the annulus. No attempt was made to disorient the rat before its return to the cylinder. The rat was returned to the floor of the cylinder, and an 8-min recording session began. During this and following sessions, on retrieving all food pellets, the annulus food cups were not rebaited until the rat returned to the cylinder floor. This procedure facilitated the collection of HD cell activity during vertical plane locomotion, by increasing the occurrences of climbing behavior. On completion of the Mesh 0° session, the rat was removed to the cardboard enclosure. The mesh position was shifted to 180° opposite the cell’s preferred firing direction, and the tripod-mounted camera was positioned accordingly. This session was designated as Mesh 180°. The rat was returned to the cylinder, and a third recording session began. The fourth and fifth recording sessions followed, during which the mesh was positioned at 90° and −90° away from the cell’s preferred firing direction. These recording sessions are referred to as Mesh 90° and Mesh 270°, respectively. In general, the recording protocol provided at least four or five episodes of climbing up and down the mesh at each of four cardinal positions relative to the HD cell’s preferred firing direction.

**Data analysis**

Head direction of the rat was determined from the relative positions of the two LEDs using procedures defined previously (Taube 1995; Taube et al. 1990a). Head direction and unit data were sorted according to the video source (overhead vs. tripod-mounted camera) into files of movement in the vertical plane or horizontal plane. The vertical plane data were sorted further according to whether the rat was climbing up, or climbing down the mesh. The horizontal plane data were further sorted according to whether the rat was on the cylinder floor or on the annulus. Consistent with previous studies (Taube 1995; Taube et al. 1990a), each HD cell was analyzed to determine the basic firing properties: 1) preferred firing direction, 2) peak firing rate, 3) directional firing range, 4) directional information content, and 5) background firing rate. Information content per spike represents a quantitative measure of the amount of information that is conveyed by each spike generated by a cell (Skaggs et al. 1995). In this case, the directional information content can be thought of as a measure of the degree to which cell firing can predict the animal’s directional heading. The information content for HD cells was calculated using the following formula

\[
\text{Information content} = \sum p_i \log_2 \left( \frac{\lambda}{\lambda} \right)
\]

where \( p_i \) is the probability that the head pointed in the \(i\)th bin (\( p_i \) is the dwell time of the head in the \(i\)th bin divided by the total recording time); \( \lambda \) is the mean firing rate of the cell in the \(i\)th bin of HD; and \( \lambda \) is the overall mean firing rate of the cell for the entire recording session. A directional information content value of 0 reflects no correlation between directional heading and the firing of the cell; a value approaching or > 1 indicates a strong positive correlation between directional heading and firing rate.

To quantify any shift of the preferred firing direction during locomotion on the two horizontal surfaces (annulus vs. cylinder floor), we used a cross-correlation method described in detail previously (Taube et al. 1990a). The firing rate versus HD tuning function of annulus horizontal plane data were shifted in 6° increments and cross-correlated with the tuning function of the same cell recorded during the initial standard session of the cylinder floor horizontal plane data. The degree of shift necessary to maximize the correlation between the tuning functions of the two horizontal data segments was considered the rotation of the preferred firing direction. A positive shift in preferred firing direction reflects a counterclockwise shift, whereas a negative shift reflects a clockwise shift.

All means are reported along with the standard error of the mean. At the conclusion of the analyses for a given HD cell, the electrode array was advanced further over the course of several months, and unit activity was screened for directional firing properties. Unit screening was terminated when the electrode array had been advanced ~ 2 mm.

**Histology**

At the conclusion of unit screening, rats were overdosed with pentobarbital sodium (100 mg/kg ip). Weak anodal current (15 μA for 10 s) was passed through one of the electrode wires to mark the wire location by the deposition of iron (Prussian blue reaction). The rats were perfused transcardially with 0.9% saline followed by 10% Formalin, and the brains were removed and placed into 10% Formalin for at least 48 h. The brains were then transferred to a 10% Formalin solution containing 2% potassium ferrocyanide for 24 h, returned to a 10% Formalin solution for 24 h, after which the brains were placed into a 20% sucrose solution for at least 48 h. The brains were then blocked, frozen on dry ice, sectioned coronally at 25 μm on a cryostat, and mounted onto microscope slides. The sections were stained with cresyl violet and examined under light microscopy to determine the location of recording sites. Inspection of the stained sections for each subject verified that the electrodes had passed through the PoS or the ADN.
RESULTS

Thirteen HD cells were recorded from five rats (2 cells from the PoS; 11 cells from the ADN). Because the responses of PoS HD cells were markedly similar to those of ADN HD cells, the data from PoS and ADN HD cells were grouped together for analyses. Due to the short-duration of each climbing episode (1–4 s), it was necessary to combine data acquired from several episodes of climbing up and down the mesh to adequately judge the directional firing during vertical plane movement.

**HD cell activity in the vertical plane**

During the recording sessions, the rats engaged in several trips up and down the mesh. There were qualitative differences, however, in their behavior when climbing up the mesh as opposed to climbing down. During locomotion up the mesh, the rats followed a straight path and rarely stopped or turned around to abort an upward climb. Typically, the rats completed a climb from the cylinder floor to the annulus in ~2–3 s. In contrast, when climbing down the mesh, the rats appeared considerably more cautious, and their behavior was punctuated by several starts and stops. Behavioral observations revealed that all rats climbed down the mesh headfirst. However, the downward paths were frequently not straight, and usually cut a diagonal that often included a momentary stop in the first third of the mesh. In many cases, the rats began to climb down the mesh only to stop one-third of the way down, turn around, and then climb back up to the annulus. When rats went all the way to the floor, they usually climbed two-thirds of the way down the mesh and then jumped to the cylinder floor. Typically, the rats completed a climb from the annulus to the cylinder floor in ~3–5 s. In many cases, especially during the later sessions of the recording protocol, it was necessary to toss food pellets onto the cylinder floor to motivate the rats to climb down the mesh from the annulus.

The short latency of climbing episodes, and the fact that climbing behavior restricted the rat’s head direction sampling to an arc of ~90°, compromised the ability to completely evaluate the directional discharge of HD cells over a 360° range in the vertical plane (e.g., when the rat climbed up the mesh oriented at a directional heading of 180°, the rat never oriented itself at a directional heading of 0°). Even after combining several episodes of climbing, there were still some HD bins that were not sampled. Therefore to construct firing rate plots of HD cell activity for movements in the vertical plane, it was necessary to assign head direction bins with no sampling to a firing rate of 0 spikes/s. Consequently, it was difficult to assess shifts in the preferred firing direction during climbing at each of the four angular mesh positions.

In summary, all 13 HD cells exhibited maximal firing as the rat climbed up with the mesh aligned at the Mesh 0° position, and when the rat climbed down with the mesh aligned at the Mesh 180° position. Conversely, the cells displayed minimal, if any, discharge when the rat climbed down the mesh at Mesh 0° position or climbed up the mesh at Mesh 180° position. Table 1 presents the peak firing rates of all cells exhibited during the cylinder floor session, the Mesh 0° session, the Mesh 180° session, and the annulus session. In general, there was a remarkable preservation of peak firing rates across conditions. As discussed above, due to the rat’s stereotypic climbing behavior, the HD bin sampling rates were confined to within ±90° of the mesh during most climbing episodes. HD bin sampling rates during climbing episodes averaged ~30% of that observed during the standard cylinder floor session. Despite this decrease in sampling, peak firing rates during vertical locomotion (climbing up the Mesh 0°, climbing down the Mesh 180°) were not significantly different from those observed during horizontal locomotion (cylinder floor), \( F(2,24) = 0.17, \) n.s. Compared with firing rates during the cylinder floor session, the mean peak firing rates climbing up the mesh at the Mesh 0° position and down the mesh at the Mesh 180° position (expressed as a percent of the floor peak firing rate) were 104.4 ± 13.2% (mean ± SE) and 100.4 ± 10.9%, respectively. Therefore HD cell firing rates were not influenced by locomotion in the vertical plane when the rat’s head was aligned with the cell’s preferred firing direction when approaching the wall.

Figure 2 provides two examples of typical HD cell responses from two different rats during an initial standard session in the cylinder, and during the four subsequent recording sessions in which the rat climbed up and down the mesh, with the mesh at

<table>
<thead>
<tr>
<th>Cell Series</th>
<th>Cylinder Floor</th>
<th>Mesh 0°</th>
<th>Mesh 180°</th>
<th>Annulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Up</td>
<td>Down</td>
<td>Up</td>
</tr>
<tr>
<td>Cell 1 (ADN)</td>
<td>59.74</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cell 2 (ADN)</td>
<td>36.03</td>
<td>19.17</td>
<td>1.25</td>
<td>0.64</td>
</tr>
<tr>
<td>Cell 3 (ADN)</td>
<td>27.76</td>
<td>35.07</td>
<td>1.83</td>
<td>0.87</td>
</tr>
<tr>
<td>Cell 4 (ADN)</td>
<td>8.51</td>
<td>24.51</td>
<td>3.75</td>
<td>1.32</td>
</tr>
<tr>
<td>Cell 5 (ADN)</td>
<td>12.94</td>
<td>10.82</td>
<td>3.19</td>
<td>0.83</td>
</tr>
<tr>
<td>Cell 6 (ADN)</td>
<td>25.46</td>
<td>17.50</td>
<td>2.24</td>
<td>1.43</td>
</tr>
<tr>
<td>Cell 7 (ADN)</td>
<td>8.44</td>
<td>8.57</td>
<td>1.42</td>
<td>2.50</td>
</tr>
<tr>
<td>Cell 8 (ADN)</td>
<td>13.06</td>
<td>8.33</td>
<td>1.20</td>
<td>2.27</td>
</tr>
<tr>
<td>Cell 9 (ADN)</td>
<td>29.83</td>
<td>18.90</td>
<td>0.50</td>
<td>0.00</td>
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<tr>
<td>Cell 10 (ADN)</td>
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<td>24.83</td>
<td>2.86</td>
<td>1.45</td>
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<td>Cell 11 (ADN)</td>
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<td>27.27</td>
<td>1.71</td>
<td>1.33</td>
</tr>
<tr>
<td>Cell 12 (PoS)</td>
<td>19.51</td>
<td>20.83</td>
<td>3.25</td>
<td>1.07</td>
</tr>
<tr>
<td>Cell 13 (PoS)</td>
<td>8.51</td>
<td>57.85</td>
<td>1.86</td>
<td>2.73</td>
</tr>
</tbody>
</table>

All values represent the mean observed peak firing rate in spikes/s. HD, head direction; ADN, anterodorsal thalamic nuclei; PoS, postsubiculum.
FIG. 2. HD cell responses in the vertical plane. Firing rate as a function of head direction for 2 representative HD cells recorded from 2 different rats. A and F: firing rates during initial session locomotion on the cylinder floor. The mesh was not present during this session. Each of the remaining plots illustrates the activity of the 2 cells over each of the subsequent sessions, as the rat climbed up (—) and down (– – –) the mesh. The angular position of the mesh with respect to the preferred firing direction of the cells (arrow) is illustrated by the apparatus schematic inset in the top left of each plot. To construct the vertical plots, it was necessary to combine data from several episodes of climbing up and down the mesh. Even so, sampling was still restricted to a small range of directional headings (−90°) when climbing up and down the mesh, and head direction bins that contained no sampling were assigned firing rates of zero. Therefore the plots B–E and G–J represent somewhat artificial representations of the full directional tuning properties of HD cells during movement in the vertical plane.
each respective angular position. Figure 2, A and F, presents firing rate by HD tuning functions during 8-min sessions as the rats foraged for food pellets on the cylinder floor.

**MESH 0°.** Across the 13 HD cells recorded, rats made an average of 5 transits up and 4 transits down the mesh, when it was positioned at Mesh 0°. Figure 2, B and G, depicts typical responses of HD cells during vertical plane locomotion when the center of the mesh was positioned on the cylinder wall in alignment with the HD cell’s preferred firing direction (Mesh 0°). The preferred firing directions of these two cells were 270° and 200°, respectively. In both cases, directional discharge was maintained as the rat climbed up (—) the mesh, but not when it climbed down (— — —). Moreover, cell discharge was consistently present throughout the period when the rat climbed up the mesh. In the cases where the rat climbed down the mesh, the rat’s approach path from the annulus to the mesh was one in which the animal’s directional heading was 180° opposite the cell’s preferred firing direction. Therefore the cells did not fire at this directional heading and remained silent during the entire course of travel down the mesh.

**MESH 180°.** Across the 13 cells, there were an average of 3 transits up and 3 transits down the mesh when it was positioned at Mesh 180°. Figure 2, C and H, depicts the typical responses of HD cells during vertical plane locomotion when the mesh was positioned 180° opposite the cell’s preferred firing directions (Mesh 180°). The tuning curves indicate that when the rats climbed down the mesh (— — —) the HD cells continued to fire, but did not fire when the rats climbed up the mesh (—). Despite a decrease in the peak firing rate when the rat climbed down the mesh (compare Fig. 2C with Fig. 2, A and B), the two plots illustrate that the cell’s directional coding was still maintained during the downward trip. Table 1 shows that most cells did not exhibit a significant change in peak firing rate during vertical locomotion when the rat climbed down the mesh at this position (e.g., compare Fig. 2H with Fig. 2, F and G). In general, during the Mesh 180° session, as the rat approached the mesh from the annulus, the rat’s head orientation was in alignment with the cell’s preferred firing direction. Thus the cell discharged maximally and continued to fire at, or near, its peak firing rate as the rat climbed down the mesh. When the rat was on the cylinder floor and approached the mesh, the rat’s head orientation was 180° opposite the cell’s preferred firing direction. Therefore the cell did not fire at this directional heading and continued to exhibit no discharge as the rat climbed up the mesh.

**MESH 90° AND 270°.** Across the 13 cells, there were an average of 3 transits up and 3 transits down the mesh, when it was positioned at Mesh 90° or 270°. With the mesh positioned 90° or 270° from the cell’s preferred firing direction, all HD cells exhibited negligible firing when the rats climbed up or down the mesh. Figure 2, D and I, depicts the typical responses of HD cells during vertical plane locomotion in the Mesh 90° sessions; and Fig. 2, E and J, depicts HD cell activity during the Mesh 270° sessions. These tuning functions show that minimal, if any, firing was detected as the rats moved up or down the mesh at these positions. During these sessions the approach paths to the mesh, whether from the cylinder floor or the annulus, would lead the rat’s head orientation to be ±90° away from the preferred firing direction of the recorded cells.

In climbing down the mesh the rats would often stop one-third of the way down and turn to look around before continuing down. Such behavior would occasionally result in the rat’s head position becoming aligned with the preferred firing direction of the HD cell. In these instances, HD cells would exhibit an increase in firing rate. For example, Fig. 3A depicts the directional tuning properties of a HD cell as the rat foraged for food pellets on the cylinder floor. During the subsequent Mesh 90° recording session when the rat climbed down the mesh, the rat oriented its head toward the preferred firing direction. In this event, as shown in Fig. 3B (— — —), the cell discharged at its peak firing rate. In contrast, the cell exhibited negligible firing during the more stereotypic straight running path when the rat climbed up (—) the mesh. Thus regardless of body orientation (vertical or horizontal) or approach path to the mesh, the HD cell exhibited its maximal discharge whenever the animal’s head was aligned with the preferred firing direction, as defined by the initial cylinder floor discharge. Note that the rat’s head orientation during these instances of maximal discharge is similar to that achieved when the rat stood and faced in the cell’s preferred firing direction on the floor, while rolling its head either clockwise or counterclockwise.

**HD cell activity in the elevated horizontal plane**

In general, HD cells continued to exhibit direction-specific discharge when the rat moved about on the annulus and pointed
its head in the cell’s preferred firing direction, as defined by the
reference frame of the cylinder floor. In some cases, once the
rat climbed onto the annulus it was necessary to remove the
mesh, to increase the annulus sampling time. In such cases, we
found no differences in HD cell discharge properties, and data
were combined across all annulus sessions. To compare HD
cell firing rates on the floor versus the annulus, we combined
all the episodes on the annulus into one session for each cell.
Average sampling time per episode on the annulus was 15.8 s
(range: 5.0 – 29.9); the average total time spent on the annulus
for each rat over the entire recording session was 10.13 min
(range: 4.82 – 19.62).

Eleven of the 13 HD cells exhibited an increase in peak
firing rate during locomotion on the annulus compared with the
floor session. A paired two-tailed t-test indicated that there was a significant difference in HD cell peak firing rates between the cylinder floor and annulus, \( t(12) = -3.36, P < 0.001 \). Despite a 20% increase in the mean background firing rate of HD cells on the annulus, a t-test found that this difference was not significant (\( P > 0.05 \)). Similar analyses of directional firing range, directional information content, and signal-to-noise ratio indicated no significant differences in these parameters (all \( P_s > 0.05 \)). These results indicate that HD cells exhibit a significant increase (~30%) in peak discharge while the rats locomote about the annulus surface as compared with the peak discharge rates exhibited on the cylinder floor surface.

**TABLE 2. Comparison of HD cell activity between cylinder floor and annulus**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cylinder Floor</th>
<th>Annulus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak firing rate, spikes/s</td>
<td>24.28 ± 4.07</td>
<td>32.27 ± 5.89*</td>
</tr>
<tr>
<td>Directional firing range, deg</td>
<td>120.08 ± 11.88</td>
<td>111.74 ± 7.61</td>
</tr>
<tr>
<td>Information content, bits/spike</td>
<td>1.09 ± 0.12</td>
<td>1.11 ± 0.13</td>
</tr>
<tr>
<td>Background firing rate, spikes/s</td>
<td>1.69 ± 0.48</td>
<td>2.03 ± 0.49</td>
</tr>
<tr>
<td>Signal-to-noise ratio</td>
<td>35.50 ± 16.03</td>
<td>26.20 ± 7.35</td>
</tr>
</tbody>
</table>

Values are means ± SE. *\( P < 0.05 \), paired 2-tailed t-test.
To evaluate the increased firing rates on the annulus, an annulus/cylinder floor peak firing rate ratio was calculated for each HD cell. A ratio value of 1.0 would indicate equivalent peak firing rates across both surfaces, whereas a ratio <1.0 would indicate higher firing rates on the cylinder floor, and a ratio >1.0 would indicate higher firing rates on the annulus. The mean firing rate ratio for the 13 HD cells was 1.31 ± 0.08 (range: 0.69–1.76), and Fig. 4C illustrates the distribution of the firing rate ratios. A paired, two-tailed t-test showed that this value is significantly different from the expected ratio of 1.0 if there were no difference in peak firing rate between the two surfaces [t (12) = 4.04, P = 0.002]. As mentioned above and illustrated in Fig. 4C, only one HD cell exhibited a decrease in peak firing rate on the annulus as compared with the cylinder floor (i.e., annulus: floor ratio <1.0). In two cases, two HD cells were recorded simultaneously over the course of the entire recording protocol. In these cases, the annulus:floor ratios of the two simultaneously recorded cells were Case 1: cell 1 = 1.06, cell 2 = 1.59; Case 2: cell 1 = 1.46, cell 2 = 1.65. Thus in one of these cases, the two cells did not exhibit equivalent increases in peak firing rate on the annulus and suggests that the magnitude to which the peak firing rate increases while the rat is on the annulus may be cell specific.

To determine whether the difference in peak firing rate between the two horizontal surfaces was consistent across episodes, we calculated the annulus:cylinder floor peak firing rate ratio for each episode of transit between the two surfaces. This analysis was only conducted on 11 of the 13 HD cells because two cells were recorded before the use of the video switchbox. The analysis was further hampered by the fact that in some cases, the rat would climb up to the annulus surface, turn around, and immediately return to the cylinder floor. Such transit episodes were not included in the analyses because they were of too short-duration to accurately evaluate the peak firing rate. Depending on the rat’s activity, episodes as short as 1–2 min were often sufficient to determine the HD cell’s firing properties. For each of the 11 cells, we recorded at least 12 episodes of transit between the two surfaces that contained sufficient sampling times. Figure 4D depicts the mean change in peak firing rate ratio across the 12 episodes of transit. The mean annulus:cylinder floor peak firing rate ratio across all episodes was 1.30 ± 0.07. A repeated measures ANOVA, conducted to examine the per episode variability in peak firing rate ratio, found a nonsignificant repeated measures effect of episode on the ratio value, F(11, 110) = 1.12, n.s. These data confirm that the peak firing rate ratio did not significantly change across 12 transits between the 2 horizontal surfaces and indicates that the increased peak firing rate on the annulus surface was consistent across multiple episodes.

To further determine whether an increase in background firing rate contributed to the observed increase in peak firing rate on the annulus, we computed an annulus:floor background firing rate ratio for each cell. The mean background firing rate ratio for the 13 HD cells was 1.59 ± 0.09 (range: 0.58–4.99), and Fig. 4E illustrates the distribution of the ratios. Although this value is greater than the ratio observed for peak firing rate (1.31), a paired, two-tailed t-test showed that this value was not significantly different from the expected ratio of 1.0 if there were no difference in background firing rate between the two surfaces [t (12) = 1.85, n.s.]. The lack of significance can be attributed to two large individual ratio values (2.65 and 4.99);

without these two values, the overall mean background firing rate ratio is 1.18 ± 0.11. Figure 4F depicts the mean change in background firing rate ratio across the 12 episodes of transit. The mean annulus:cylinder floor peak firing rate ratio across all episodes was 1.06 ± 0.06. A repeated measures ANOVA found a nonsignificant repeated measures effect of episode on the ratio value, F(11, 110) = 0.75, n.s. These data confirm that the background firing rate ratio did not significantly change across 12 transits between the 2 horizontal surfaces and suggest that the observed increase in peak firing rate on the annulus was not simply due to an overall increase in the cell’s activity.

We also examined the variability in peak firing rates of the 11 HD cells between at least 2 standard cylinder sessions in the absence of the mesh, to determine whether peak firing rates were stable on the cylinder floor. This analysis also enabled us to determine whether the increase in peak firing rate on the annulus was attributed to random variability in peak firing rate across sessions. The mean (±SE) cylinder floor standard session:standard session peak firing rate ratio was 1.01 ± 0.02. A paired, two-tailed t-test assessed whether the ratio of peak firing rate between the floor and annulus was greater than the ratio between successive cylinder floor sessions. This analysis revealed a significant difference between the two mean peak firing rate ratios, t (10) = −3.62, P = 0.005. These data indicate that HD cell peak firing rates on the cylinder floor and on the annulus are consistent, but that there is a significant increase in annulus peak firing rate over cylinder floor peak firing rate.

Minor shifts of the preferred firing direction between the cylinder floor and annulus

The preferred firing directions of the HD cells were stable across standard recording sessions when the rat was on the cylinder floor and were not influenced by the session-to-session change in the angular position of the mesh on the cylinder wall. The preoperative training regimen involved the explicit attempt to decrease apparent stability of mesh orientation by varying its angular position across trials. Comparison of preferred firing directions between the annulus and cylinder floor revealed a mean absolute shift of 12.9 ± 3.2° (range: 0–36°). This shift is significantly different from that reported by Taube (1995) between two standard cylinder sessions (4.7 ± 1.8°) [t (25) = 2.25, P = 0.03]. The increased shift on the annulus may reflect the influence of additional cues and environmental features that are available to the rat while foraging on the annulus. Although 12.9° is >4°, this shift magnitude is substantially smaller than that observed following a change of apparatus. For example, Dudchenko and Taube (1997) observed a mean absolute shift in preferred firing direction of 40.7 ± 17.4° between a standard cylinder session and a session on an elevated radial-arm maze, and Taube et al. (1990b) reported a mean shift of 83.3 ± 15.6° between a cylinder and rectangular apparatus. The second apparatus in each case was also centered in the same recording room as the cylinder sessions. Thus the shift between the cylinder floor and the annulus, although significantly different, should be considered relatively minor.
**DISCUSSION**

**Locomotion in the vertical plane**

This experiment was designed to determine how the horizontal reference frame is reflected in the activity of HD cells. HD cell firing properties were monitored as the rat moved from a horizontal surface onto a 90° vertical surface that was positioned at discrete angular orientations with respect to the cell’s preferred firing direction. The study also enabled a determination of the differences in HD cell activity between the two distinct horizontal surfaces that were separated in height by ~1 m.

In general, HD cell discharge properties were maintained during locomotion in both vertical (up and down) and horizontal (cylinder floor and annulus) planes. The present results indicate that when the rat approached the mesh either from the cylinder floor or annulus with its head direction corresponding to the cell’s preferred firing direction, and maintained this head orientation during vertical movement (either up or down the mesh), cell discharge was sustained throughout vertical movement. Thus regardless of body position, as long as the head orientation corresponded to the cell’s preferred firing direction (within ±90° roll of the head), whether +90° vertical (as during climbing up the mesh) or −90° vertical (as during climbing down the mesh), HD cells will discharge at maximal rates. These results indicate that HD cells are capable of maintaining their discharge in planes outside earth horizontal. Furthermore, when locomoting in the vertical plane, HD cell firing is dependent on the directional orientation of the rat as it moves out of the horizontal plane. These data are consistent with the notion that the cell defines the horizontal reference frame as the rat’s plane of locomotion, but leaves open the question of which cue source(s) determine the horizontal reference frame: vestibular, somatosensory, visual, motor cues, or some combination of these sources.

Directional cells of the ADN and PoS are thought to be components of a neural circuit that supports landmark-based navigation and inertial navigation or path integration. In the absence of landmark cues, the firing properties of HD cells may be maintained by internal cue sources (Goodridge and Taube 1995; Taube and Burton 1995). Moreover, as mentioned earlier, vestibular input to the HD cell circuit is necessary for the directional discharge in the ADN, even in the presence of familiar landmark cues (Stackman and Taube 1997). This result indicates that idiographic cue sources may be essential for the generation of the HD cell signal. In light of the fact that HD cell activity is dependent on vestibular information, it is interesting to note that during movement in the vertical plane the HD cell circuitry is receiving different vestibular/kinesthetic input as compared with that during movement in the horizontal plane. Thus despite the different input from the semicircular canals and otolith organs during vertical plane transits, HD cell activity was maintained. There may be additional inputs to HD cells that provide information about head position in the vertical plane. For example, we have recently demonstrated the presence of head pitch cells in the lateral mammillary nuclei that discharges when the rat’s head was orthogonal to the horizontal plane (Stackman and Taube 1998). Via the mammillothalamic tract, information regarding head pitch may be conveyed to the ADN and integrated to enable a representation of head direction in three dimensions. Therefore it is conceivable that the maintained discharge of HD cells in the vertical plane was a consequence of monitoring angular and linear head movements through vestibular signals and motor efference copy. However, it is important to consider that the cue card was present throughout all recording sessions, and therefore the maintained HD cell discharge may have simply been a consequence of referencing this familiar landmark. Our experiment does not distinguish between these two possibilities.

**Three-dimensional model of HD cell firing**

How the horizontal reference frame is defined by HD cells is an important theoretical issue. There is considerable evidence in humans to indicate that the perception of horizontality and verticality are dependent on visual, vestibular, and proprioceptive systems (Howard and Templeton 1966). In the dark, vestibular deficient humans are impaired in aligning a visual target to the Earth-horizontal as compared with intact humans (Miller and Graybiel 1966; Friedmann 1970). In intact humans, the perception of horizontality and verticality can be altered by simply lying in a supine position (Miller and Graybiel 1966) or by tilting the body to one side (Werner et al. 1951). These findings illustrate the importance that vestibular signals from the otolith organs play in judging spatial orientation.

The present findings indicate that HD cells appear to maintain a representation of directional heading despite the vertical body positioning. However, it remains to be determined whether the shift in body position alters the animal’s sense of spatial orientation. Nonetheless, because HD cell discharge was maintained in planes outside the earth horizontal, our results indicate that the HD cell signal can be represented by a three-dimensional model (see Fig. 5). Figure 5A illustrates in polar coordinates a three-dimensional representation of a hypothetical HD cell with a preferred firing direction of 90° in the horizontal plane (defined as the x-y plane). Figure 5B illustrates the typical firing rate by HD tuning function of this cell during movement about the horizontal cylinder floor. In Fig. 5A, the activity of this HD cell on the horizontal surface is represented as the thick elliptical plot centered at an HD of 90° horizontal, 0° vertical. The firing rates of the hypothetical cell when the rat’s head is aligned with the preferred firing direction but at varying vertical orientations are depicted by the elliptical plots (a, b, c, d, and e). If one were to superimpose the polar plots for all possible vertical orientations, from +90° to −90°, the cell’s firing could be characterized as a hemitorus surface as depicted in the drawing of Fig. 5C. Such a model is consistent with the present results and the notion that the HD cell will exhibit peak discharge rates whenever the head orientation corresponds to the cell’s preferred firing direction, irrespective of body orientation. It is interesting to note that this model makes the prediction that HD cell firing will cease during movement in a vertical plane that is greater than +90°. In the extreme case the question becomes how an HD cell would respond if the rat approached a +90° vertical surface aligned with the preferred firing direction, climbed this surface to the ceiling, and then continued onto the ceiling. In this case, the rat’s path would culminate in climbing upside down on the

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1 A torus, defined in geometry, is a surface generated by rotating a circle around an axis that is in the plane of the circle, but does not intersect the circle (i.e., a doughnut). A hemitorus is the surface generated by rotating the circle 180° about the axis.
ceiling heading in the opposite direction from which it started.
We are currently examining whether an HD cell continues to
fire, or whether the activity of the cell is attenuated, in such a
situation.

It is tempting to suggest that the maintenance of directional
firing in the vertical plane indicates the preservation of the
directional sense while locomoting in the vertical plane. To
verify this notion, however, it would be necessary to test the
animal on a navigational task that requires vertical plane move-
ments. Interestingly, Grobety and Schenk (1992a) showed that
rats trained on a radial-arm maze containing arms of varying
vertical tilt (from 0° to 25°) acquired the task faster than rats
trained on a standard version with all arms horizontal. More-
over, in a three-dimensional cubic maze, where accessing the
goal location required movements in the horizontal and vertical
planes, rats appeared to acquire the vertical coordinate of the
goal location before successfully learning the horizontal coor-
dinate (Grobety and Schenk 1992b). These data demonstrate
the ability of rats to process spatial information concerning
their three-dimensional orientation. The added kinesthetic in-
fomation that results from movements in the vertical di-
mension may facilitate the acquisition of spatial learning and nav-
egation tasks by providing an additional cue source.

Locomotion in a horizontal plane at a different height

Although the preferred firing direction of HD cells were
similar between the two horizontal surfaces (±12°), peak firing

FIG. 5. Hemitorus model of HD cell firing. A: firing
rate of a hypothetical HD cell with a preferred firing
direction of 90° in the earth-horizontal plane is plotted
in 3-dimensional polar coordinates. The horizontal
plane is represented by the x-y plane and is depicted by
the large oval with cardinal points denoted at 0, 90, 180,
and 270°. The z-axis represents directional heading in
the earth-vertical dimension with 90° equivalent to
the head oriented to the zenith and 190° equivalent to
the head oriented to the nadir. The firing rate of an HD
cell is represented by the distance away from the origin.
Graph in B represents the 2-dimensional firing rate by
HD tuning properties of a cell with a preferred firing
direction of 90° when the rat moves around in the
horizontal plane. The polar coordinate model represents
the firing of this same cell in 3 dimensions. The thick-
lined ellipse illustrates the HD cell activity in polar
coordinates while the rat’s head is oriented at 90° horizontal, 0° vertical. (Note: because the hypothetical cell
has a nonzero background firing rate, the ellipse does
not pass through the origin). The ellipse labeled a de-
picts the cell’s activity when the rat climbs up the mesh
aligned with the preferred firing direction (Mesh 0°). In
this case, as illustrated in E, the rat’s head orientation
Corresponds to the preferred firing direction, but is tilted
to 190° vertical with its limbs generally pointed toward
90° in the horizontal plane, as indicated by the arrow in
E. The ellipse labeled e depicts the cell’s activity when
the rat climbs down the mesh aligned 180° opposite the
preferred firing direction (Mesh 180°). In this case, as
illustrated in D, the head and body axis is oriented at
290° vertical, and the limbs are generally pointed to-
ward 270° in the horizontal plane, as indicated by the
arrow in D. The remaining ellipses b–d illustrate the
HD cell’s activity given head orientations of 90° hori-
zontal and 45° vertical (b), 30° vertical (c), and 60° vertical (d). If all possible vertical orientations from
290° to 190° were superimposed on the figure, the
surface of the plot would assume the shape of a hemi-
torus surface as shown in C (C. M. Oman, personal
communication).
rates were increased by an average of 33% during locomotion on the annulus as compared with the cylinder floor. During movement on the annulus, there were no significant differences in other HD cell firing parameters. These results suggest that there are additional influences or environmental features available to the rat that affect HD cell directional coding while on the annulus that are not available to it while on the cylinder floor. Alternatively, the changes in firing rates may be a consequence of alterations in the motoric demand between the two surfaces.

It is tempting to speculate that the increase in peak firing rate on the annulus reflects an additional encoding of height from a horizontal surface by HD cells. During acquisition training rats received considerable exposure to the apparatus and cues within the recording room that could be seen from the annulus (i.e., the laboratory floor, stool, etc.), therefore it is unlikely that such cues were responsible for increased peak firing rate when the rat was on the annulus. It is also unlikely that the presence of the second camera influenced HD cell activity, because the preferred firing direction of each HD cell was stable despite moving the second camera from session to session. Such stability suggests that the rats did not use the second camera as a reference landmark. In addition, it is unlikely that the increased firing rate on the annulus reflects food consumption from the annulus food wells because the consumption of food pellets in the cylinder did not increase peak firing rate. Therefore the rats consumed food pellets on both horizontal surfaces, and we have not previously observed a consumption-dependent increase in HD cell firing rates.

Other factors also need to be considered when accounting for the increased firing rate on the annulus. For instance, the annulus was narrower than the cylinder floor and contained no inside or outside walls. Rats routinely moved about the annulus surface in a ballistic manner (intermittent episodes of forward locomotion followed by eating at the food cups, or peering over the inside or outside edges of the annulus). Thus locomotion on the annulus restricts the rat’s movement somewhat and may require a heightened demand for coordination and balance. Given the importance of vestibular signals for HD cell activity, it is possible that movement on the annulus influences the vestibular system in a way that is then reflected in the increased peak firing rates of HD cells. However, Dudchenko and Taube (1997) failed to observe any significant change in HD cell firing rates as rats performed a radial arm maze task on a platform that was elevated 34 cm above the floor. In summary, HD cells maintained their directional firing during traverses in the vertical plane when the animal approached and climbed into the plane facing the cells’ preferred firing direction. Cell firing was negligible for all other orientations. These results suggest that the HD cell defines the horizontal reference frame as the rat’s plane of current locomotion.

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REFERENCES


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